HarperCollins E-Books

Collins New Naturalist Library
113

Bird Migration



Ian Newton

THE NEW NATURALIST LIBRARY

BIRD MIGRATION

IAN NEWTON





Contents

Cover
Title Page
Editors' Preface
CHAPTER 1 Introduction
CHAPTER 2 Migration Studies
CHAPTER 3 Migration Around the British Isles
CHAPTER 4 Migratory Flight
CHAPTER 5 Migration and Weather
CHAPTER 6 Fuelling the Flights
CHAPTER 7 Migration Speeds
CHAPTER 8 Amazing Journeys
CHAPTER 9 Annual Schedules
CHAPTER 10 Migration Timing
CHAPTER 11 Comings and Goings
CHAPTER 12 Navigation
CHAPTER 13 Site-fidelity and Dispersal
CHAPTER 14 Vagrancy
CHAPTER 15 Evolution of Migration
CHAPTER 16 Recent Changes in Migratory Behaviour
CHAPTER 17 Glacial Legacies
CHAPTER 18 Geographical Patterns
CHAPTER 19 Irruptions
CHAPTER 20 Other Movements
CHAPTER 21 Sex and Age Differences in Migration
CHAPTER 22 Migrants in Africa

CHAPTER 23 Population Limitation
CHAPTER 24 Declining Migrants
CHAPTER 25 Postscript: British *Pioneers in Migration Studies*
References
Glossary
Index
The New Naturalist Library
EDITORS
Author's Foreword and Acknowledgements
About the author
Photographic Inserts
Copyright
About the Publisher

Editors' Preface

In the New Naturalist Series, volumes dedicated to single components of the biology of a group of species are far from the norm, but interestingly the only other, NN36, by C. B. Williams, published in 1958, also focuses on migration, but in his case of insects. While migration features in all the New Naturalists concerned with groups of birds, even including *Grouse* (NN107), this volume is a timely analysis of the fascinating phenomenon of migration itself. Dr Ian Newton's account is not only timely, but substantial in both breadth and depth, exploring every facet of bird migration across 25 engrossing chapters.

'Look, there is a Swallow' and 'There she goes, spring has come' runs the roughly-translated caption round the base of an ancient vase, depicting two youths conversing in a Greek countryside scene. Bird migration must have been a recognisable feature of their environment to even earlier human populations in western Europe: the metronomically obvious calls of the Cuckoo and Chiffchaff announcing oncoming summer warmth, the noisy arrival of the first skeins of geese or swans giving those primitive peoples the first sombre warnings that the hard times of winter were close at hand.

There, for many centuries, interest in the matter rested, with bird migration simply a seasonal fact of life, just as are blossom time or leaf-fall. Not until the advent of the enquiring naturalists of the 18th century did questions begin to be asked about the whereabouts of migrants in their 'absent' season. As recently as 1877, that meticulous and astute observer of the natural world, Gilbert White, in *The Natural History and Antiquities of Selborne,* pondered at length whether Swallows (Barn Swallows in current terminology) and House Martins flew overseas for the winter, or hibernated in the

mud at the bottom of the ponds over which he had his last autumnal sightings of them. He settled finally in favour of the hibernation theory.

The ‘where’, ‘when’, ‘why’, and above all ‘how’, of bird migration continued, and still continues to challenge naturalists and ornithological researchers. Not until the early years of the 20th century, with the invention of bird ringing, did the technology begin to become available to help solve some of the problems. Ian Newton describes and assesses the fast-moving development from a wide range of strands of research which have provided the data on which *Bird Migration* is based, acknowledging the enormous input of amateur naturalists. Appropriately, he is currently Chairman of the British Trust for Ornithology, responsible amongst other things for bird ringing in Britain and Ireland.

He reveals, among other things, that the commonly-held concept of come-in-spring, depart-in-autumn or come-in-autumn, depart-in-spring, covers only part of the migration story, though probably a very substantial part. At any time of year, but particularly in winter, periods of extreme cold weather, either near at hand on the Continent, or far away to the east, can cause mass evacuation of the affected area, usually producing a westward stream of migrants often called a weather movement. Further, studies of radar displays reveal that some birds are migrating in various directions most hours of most days and nights, most of the year.

Dr Newton is a tireless fieldworker himself, and has spent an outstanding research career in ornithological ecology, with over 250 scientific papers and several books to his credit. Most of his career has been with Governmental research bodies from the Nature Conservancy, through several metamorphoses, to the Institute of Terrestrial Ecology at its Monk’s Wood Research Station, sadly recently closed. His national and international standing in avian ecology has been recognised by his service as President of the British Ecological Society and the British Ornithologists’ Union, by an Honorary Fellowship of the American Ornithologists’ Union, and

by his election to Fellowship of the Royal Society and appointment as OBE.

Ian Newton's previous contribution to the New Naturalist library was in 1972 with *Finches* (NN55). On the cover, the (then) Editorial Board commented that his account 'seems to us a model of scientific writing for the general reader: balanced, lucid and absorbing.' Readers *of Bird Migration* will find that nothing has changed!

CHAPTER 1

Introduction

Ornithologists use the term migration to signify a regular return movement of birds each year between separate breeding and wintering areas. In the process, birds can cover hundreds or thousands of kilometres, and some can cross inhospitable areas such as seas, deserts or high mountain ranges. In contrast, non-migratory (resident or sedentary) birds tend to remain in the same localities year-round, so that their populations show no obvious large-scale seasonal shifts in distribution. In many regions, including the British Isles, some bird species are migratory, while others are resident, and yet others are classed as 'partial migrants', because some individuals remain year-round, while others from the same breeding areas leave to winter elsewhere. Migratory birds can in turn be divided into summer visitors such as the Barn Swallow and Cuckoo,[†] winter visitors such as the Fieldfare and Brent Goose, and passage migrants, which appear each autumn and spring as they travel between breeding areas to the north of the British Isles and wintering areas to the south.

Migration is shown by many kinds of animals, including butterflies and other insects, mammals, marine turtles and fish, but in none is it as extensively developed as in birds. The collective travel routes of birds span almost the entire globe, with some extreme return journeys covering more than 30,000 km. As a result of migration, bird distributions are continually changing—in regular seasonal patterns, and on local., regional or global scales. Migratory birds can thereby occupy widely separated areas at different seasons, and many individuals return repeatedly to the same

breeding places from year to year, and sometimes also to the same wintering places. Outside the tropics, their movements are most marked in spring and autumn, but can occur in every month of the year in one species or another. These facts raise questions about the ecological factors that underlie the movements and distributions of birds that simply do not arise with more sedentary organisms.

Birds are also pre-adapted for long-distance migration in ways that other animals are not. For one thing, most birds can fly. The main advantage of flight is its speed, which is much faster than running or swimming. Flight requires more energy per unit time, but because of the greater distance covered, it is the cheapest mode of travel overall. One type of flight, by still-wing soaring and gliding, is less costly than flapping flight, but is practised mainly by larger species such as albatrosses, which can travel the southern seas at little more energy cost than sitting still. Long-distance flight also allows birds to cross inhospitable areas that would otherwise act as barriers to their movements—such as seas for land birds or barren deserts for forest birds. Nevertheless, while most birds migrate by flying, penguins and some other seabirds migrate by swimming, and some land birds by walking for part or all of their journeys.

Most birds are of abody mass that enables them to become airborne. All possess feathers, whose most obvious feature is encapsulated in the expression ‘light as a feather’. Feathers come in two main types: small flexible ones which form an insulating body covering, and longer, stiffer but still flexible ones that form the major surface area of the wings and tail. In further adaptation, birds have a strong but lightweight skeleton, with hollow bones, and wing shapes that ensure efficient flight. The wings are powered by massive breast muscles, the pectoralis and supracoracoideus, which make the downward and upward strokes, respectively. The two pectoralis muscles, one on each side of the breast, are by far the largest muscles in the body of flying birds, forming more than one-third of the total body mass of some species. These muscles are well supplied with blood vessels, and consist of fast-contracting fibres,

which in many species can beat the wings continuously for hours or days on end.

Compared with other animals, birds are not only warm-blooded, but they also have exceptionally efficient respiratory, cardiovascular and metabolic systems. Together these systems ensure that the specialised wing muscles are kept well supplied with oxygen and energy-rich fuel, and that waste products are swiftly removed, preventing the muscle pain and fatigue so familiar to human athletes. Compared with mammals, birds can also breathe more effectively, with more efficient gas exchange. This is largely because of their various air sacs, which lie within the thoracic and abdominal cavities, as well as between the skin and body walls and within the bones. These air sacs are connected to the lungs, and enable birds to extract oxygen from air more effectively than could lungs alone. Respiratory movements act mainly on the air sacs, causing a continual stream of air to pass through the lungs, where oxygen is absorbed. The lungs themselves do not hold a substantial residue of used air, as in mammals, so oxygen remains readily available throughout the breathing process. These various features equip birds for long-range movements, and some species reveal extremes of ‘endurance performance’ unmatched by other animals. Compared with resident bird species, migrants exhibit these same features but in a more highly developed form as specialised modifications for long-distance travel. It is this combination of attributes that enables some species of birds to perform some of the most remarkable twice-yearly journeys in the animal world (Chapter 8).

One question which has yet to be totally resolved, however, is why birds migrate when many other animals survive through the difficult season by hibernation—a physiological shutdown involving several months of torpor. For birds, it is often argued, storage of sufficient fat to survive without food for months on end is precluded by the mechanical limitations of flight. The required amount of fat would supposedly be too heavy for birds to carry around during the lengthy period when it was being accumulated. However, migration

also requires body fat to fuel the flights, and some species may double their body weights before their journeys. Some large waterfowl can also undertake a month of incubation on the strength of body reserves. But the body reserve explanation is unsatisfactory for another reason, namely that many species of bats, which experience the same limitations of flight as birds, do hibernate. Like other mammals, they do so by entering a state of torpor in which their body temperature is much reduced, lessening their energy needs. Moreover, at least one species of bird, the North American Common Poorwill (a kind of nightjar), can hibernate in this way, while hummingbirds and others can exhibit shorter periods of torpidity, usually lasting a few hours at a time. So it seems that the need for torpor was not necessarily a total stumbling block to birds developing hibernation. We can only surmise that the supreme adaptations of birds for long-distance flight and eflicient energy use have tipped the balance in favour of migration over hibernation in the majority of species.

The phenomenon of bird migration was known to Aristotle, more than a thousand years ago, but he also maintained that some species hibernated. Both migration and hibernation were mentioned by various other knowledgeable writers in subsequent centuries, often in reference to diflerent species, and sailors frequently reported land birds settling on ships at sea. It is strange, therefore, that as late as the 18th century, a number of prominent natural historians in England were still adamant that some birds hibernated in winter. Barn Swallows were thought to bury themselves in the mud at the bottom of ponds, and some people even claimed to have found them there. It was not until the early 19th century, as the evidence became overwhelming, that the idea of migration rather than hibernation became generally accepted for birds (Birkhead, 2008).

TYPES OF BIRD MOVEMENTS

While it is now often convenient to describe birds as resident or migratory, in practice bird movements are much more varied. For

present purposes, we can divide them into six main types:

- First, there are the **routine day-to-day movements** centred on the place of residence. As part of everyday life, all birds move around from nesting or roosting sites to feeding areas, or from one feeding place to another. In most species, these movements are short and localised, in all directions, but are restricted to a circumscribed home range, extending over distances of metres or kilometres. But in other species (notably pelagic birds), regular foraging movements in the breeding season can extend up to hundreds of kilometres out from the nesting colony, which at that time forms the centre of activity.
- Second, there are one-way **dispersal movements.** The young of both sedentary and migratory bird species, after they have become independent of their parents, disperse from their natal sites. Individual young seem to have no inherent directional preferences, so within a population, post-fledging dispersal movements occur randomly in all directions. Dispersal distances can be measured in metres, kilometres or tens of kilometres, depending on species, but in a few species (again mainly pelagic ones) they sometimes extend to hundreds of kilometres. Post-fledging dispersal of this type does not usually involve a return journey (see below), and surviving young subsequently settle to breed at some distance from their hatch sites (called natal dispersal). In addition, some adults may change their nesting locations from year to year (breeding dispersal), or their non-breeding locations from year to year (here called non-breeding or wintering dispersal).
- Third, there is **dispersive migration,** so called because it involves postbreeding movements in any direction, like dispersal., but then a return movement towards the starting point in time for the next breeding season, like migration. These movements do not necessarily result in any seasonal

change in the geographical distribution of the population as a whole. They are evident in some land-bird species usually regarded as ‘resident’, and include altitudinal movements in which montane birds shift in various directions from higher to lower ground for the non-breeding season. In addition, many seabirds disperse long distances in various directions from their nesting colonies to overwinter in distant areas rich in food, returning to their colonies in the following spring.

- Fourth, there is **migration,** in which individuals make regular return movements, at about the same times each year, often to specific destinations year after year. Compared with the above movements, migration usually involves a longer journey over tens, hundreds or thousands of kilometres and in much more restricted and fixed directions. Most birds spend the nonbreeding period at lower latitudes than their breeding period, although some species migrate further to reach similar latitudes in the opposite hemisphere, moving from the northern summer to the southern summer, and thus getting the best of both worlds. Seasonal migration occurs primarily in association with seasonal changes in food availability, resulting from the alternation of warm and cold seasons at high latitudes, or of wet and dry seasons in the tropics. Overall, directional migration causes a massive movement of birds twice each year between regular breeding and wintering ranges, and a general shift of populations from higher to lower latitudes for the non-breeding season.
- Fifth, there are **irruptions (or invasions),** which are like other seasonal migrations except that the proportions of birds that leave the breeding range, and the distances they travel, vary greatly from year to year. Such movements are usually towards lower latitudes, and occur in association with annual food shortages, as well as with seasonal ones. In consequence, populations may concentrate in different parts of their non-breeding ranges in different years. Examples include some northern finches, which depend on sporadic tree-seed crops,

and some owls, which rely on peaks in fluctuating rodent populations.

- Sixth, there is **nomadism,** in which birds range from one area to another, residing for a time wherever food is temporarily plentiful, and breeding if possible. The areas successively occupied may lie in various directions from one another. No one area is necessarily used every year, and some areas may be used only at intervals of several years, but for months or years at a time, whenever conditions permit. Along with irruptive migration, this kind of movement occurs among some seed-eating finches and rodent-eating owls of northern regions, as they seek out localities with temporarily abundant food. It also occurs among birds that live in desert regions, especially in Australia, where infrequent and sporadic rainfall leads to local changes in habitats and food supplies.

These different kinds of bird movements intergrade with one another, and all have variants, but in any bird population, one or two kinds usually prevail. Almost all bird species show post-fledging dispersal movements, in addition to any other types of movement shown at other times of year, and as indicated above, some species show both nomadic and irruptive movements. Through migration, irruption and nomadism, birds exploit the resources of different regions at different times. We can assume that they thereby achieve greater survival and reproductive success (and hence greater numbers) than if they remained permanently in the same place and adopted a more sedentary lifestyle. Many species also occupy a larger geographical range than otherwise possible, though not all of it at the same time.

The main variables in these different types of bird movements include: (1) the directions or spread of directions; (2) the distances or spread of distances; (3) the calendar dates or spread of dates; and (4) whether or not they involve a return journey. They also differ in whether they occur in direct response to prevailing conditions, or in

an ‘anticipatory’ manner, in adaptation to conditions that can be expected in the coming weeks, and leading birds to leave areas before their local survival would be compromised or arrive in other areas in time to breed when conditions there become suitable. These various aspects of large-scale bird movements can all be independently influenced by natural selection (Chapter 15), resulting overall in the great diversity of movement patterns found among birds, related to the different conditions and circumstances in which the different populations live.

This book is concerned with all these types of bird movements, but the emphasis is on the seasonal return movements of migration and irruption, which are by far the most spectacular and extreme. Migration itself varies greatly between species, as well as between populations, sex and age groups, in respect of distances travelled, routes taken, timing of journeys and behaviour en route. It is often useful to distinguish between ‘short-distance’ migrants that make mostly overland journeys within continents, and ‘long-distance’ migrants that make longer journeys between continents, often involving substantial sea-crossings. There is, of course, no clear division between these two categories, but a continuum of variation in the distances travelled and the terrain that is crossed. Similarly, in terms of timing, some birds can complete their migrations in less than a day each way, while others may take more than three months each way, and may therefore be on the move for more than half of each year—most of the time they are not breeding (Chapter 7).

In theory, some birds might benefit from remaining on the move at all times of year, for they could then take advantage of rich food supplies wherever and whenever they occurred. It is mainly the requirements of breeding that tie birds to fixed localities for part of the year, because individuals need to remain at their nests, or visit them frequently, in order to feed their young. However, in some species, notably some pelagic seabirds, one parent can be away for several days at a time, while the other remains at the nest. This enables parents to collect food hundreds or even thousands of kilometres away from their nesting places. As their single chick

grows, it can survive on its own for long periods, enabling both parents to be away in search of food at the same time. Some of the foraging flights of albatrosses undertaken while breeding can cover circuitous routes up to 15,000 km, a distance far greater than the total annual migrations of the vast majority of land birds.

In many bird species, individuals breed in their first year of life. In others, individuals do not breed until they are two or more years old. The immature, non-breeders of such species are not locality-tied in the same way as breeders, and are free to feed away from nesting areas throughout the year. It is not unusual in these species for adults and immatures to concentrate in different regions in the breeding season, and in some such species the young remain in 'winter quarters' year-round, returning to nesting areas only when they are approaching breeding age. This holds for many kinds of seabirds, waders, large raptors and others (Chapters 9 and 21).

THE UBIQUITY OF MIGRATION

Migration occurs to some degree in most bird species that live in strongly seasonal environments, from Arctic tundra and boreal forest, through temperate and Mediterranean woodlands, to tropical savannahs and grasslands. It is in such seasonal environments that food supplies vary most markedly through the year, fluctuating between abundance and scarcity in each 12-month period. Generally speaking, birds time their migrations so as to be present in breeding areas during the periods of abundance and absent during the periods of scarcity. Only in the relatively stable conditions of tropical lowland rainforest, where food supplies remain fairly constant year-round, do the majority of bird species that breed there remain all year, but even these forest areas receive a seasonal influx of wintering migrants from higher latitudes. Worldwide, in response to seasonal changes in conditions, up to one-half of the world's 10,000 or so bird species, totalling an estimated 50 billion individuals, are thought to migrate every year on return journeys between breeding and non-breeding areas (Berthold, 1993).

Because almost all migratory birds travel to milder climes for the non-breeding period, they move mainly on a north–south axis. However, many populations also have an easterly or westerly component in their movements, especially those that breed in the central parts of the northern landmasses and move to the warmer edges for the winter. The predominant autumn migration direction of intra-continental migrants in western Europe is southwestward, but the further east they breed within Europe, the stronger the westerly component in their autumn journeys. Western Europe is warmer in winter than equivalent latitudes anywhere else on the Eurasian landmass, so it acts as a major wintering area for Eurasian migrants, including millions of waders and waterfowl. Nevertheless, some European birds move southeast to winter in the Middle East, East Africa or India.

Some bird species move almost directly east–west on their migrations. For example, Pochards from Siberia move up to 4,000 km in autumn to winter in western Europe, in the process crossing up to 80˚ of longitude. Many seabirds, shorebirds and waterfowl of high latitudes fly east or west in spring along the northern edge of the continents before moving inland to nest on the open tundra to the south. In the autumn, they retrace their journeys along the northern coastline, until they reach the continental edges, when they veer southwards towards their wintering areas (Alerstam & Gudmundsson, 1999).

Many other seabird species disperse eastward or westward after breeding to spend the winter away from their nesting colonies, concentrating at upwellings and other areas of abundant food, but remaining within the same oceanic zones year-round. Examples include the Northern Fulmar and Black-legged Kittiwake in the northern hemisphere, and various albatrosses and petrels in the southern hemisphere. At high southern latitudes, the Southern Ocean extends continuously around the earth, uninterrupted by continents. This allows some seabird species to circle the earth in their non-breeding periods, assisted by strong eastward-blowing winds. Such circumpolar journeys have been found in several

species from ring recoveries, and in recent years have been confirmed by the tracking of individually tagged birds. One Grey-headed Albatross completed a round-the-earth flight is as little as 46 days, averaging 950 km per day over much of the route (Croxall *et al.,* 2005). Such flights by seabirds over continuously suitable habitat are not possible at equivalent latitudes in the northern hemisphere, where large continental land areas separate the oceans. Nevertheless, several species cross from one side of the Atlantic to the other, and from one side of the Pacific to the other.

A major cost of migration, not borne by resident birds, results from the risks involved in the journeys. These risks are much less for some bird species than for others. Take for example, the Northern Gannet, a large and powerful bird that has no significant predators; it migrates entirely over the sea, where it is totally at home; it sleeps on the sea surface and hunts below it, and can survive for a fortnight or more without food. Five thousand kilometres in one direction would seem little more demanding for it than the same distance covered in the 150–300 km foraging flights from its nest which it makes regularly through the breeding season. For this species, migration poses no obvious hazards.

Now take the tiny Willow Warbler, a delicate 8 g bird adapted to feeding on insects from bushes. With its apparently weak and slow flight, it undertakes some of the longest and most arduous journeys of any land bird, involving long sea- or desert-crossings where it cannot feed. Every year, from breeding areas in northern Europe, it must cross the Mediterranean Sea and the Sahara desert; while from breeding areas in Siberia and Alaska, it must cross the Asian continent, followed by the deserts of the Middle East, to reach its wintering areas south of the Sahara. These journeys involve long flights without food or water, during which the risks of starvation and dehydration are ever present, together with the hazards of predation and adverse winds. These two contrasting examples illustrate the differing levels of demand and risk that migration puts on different species, and the degree to which birds must leave the natural habitats to which they are adapted in order to make their

journeys. Little wonder that in some species, more individuals die on migration than at any other time of year (Chapter 23).

SEDENTARY POPULATIONS

EVERYDAY MOVEMENTS

The everyday movements that birds make to obtain food vary enormously between species, depending on their particular lifestyles. In species that live year-round in territories, individuals may spend almost their whole adult lives in a confined area, varying from less than 1 hectare in some small songbirds up to many square kilometres in some large eagles. In species in which nesting and feeding occur in different places, such as the Rook, everyday movements may be longer, measured in kilometres or tens of kilometres from the nesting place in summer or the roosting place in winter. This holds in sedentary populations of such species, as well as in migratory ones. Among colonial seabirds, as indicated above, individuals may forage over very much larger areas, extending over many thousands of square kilometres. For example, Manx Shearwaters nesting on Skomer Island off southwest Wales ranged over the whole Irish Sea to obtain their food, reaching up to 400 km from the colony during the incubation period, as shown by tracking studies (Guilford *et al.,* 2008).

CONCLUDING REMARKS

In this introductory chapter, we have touched on the major morphological and physiological adaptations which equip birds for long-distance flight, and enable some species to make some of the most impressive journeys in the animal world. We have also looked at the different types of movements which birds can make, from short-distance, multi-directional dispersal to long-distance unidirectional migration. At the population level, these different

types of movements vary in their timings, directions and distances, according to prevailing needs and to the particular ecological circumstances in which different species live. In subsequent chapters, most of these aspects are discussed in greater detail, but the next chapter describes the various methods that are commonly used to study the movement patterns of birds.

---

† Scientific names of all species mentioned in the text are given in the Index, both independently and alongside the English names, and some are also given in Tables and Figure captions.

CHAPTER 2

Migration Studies

Until the late 19th century, knowledge of bird migration was based primarily on the seasonal changes evident in bird distributions, including the regular appearance of summer and winter visitors. Flocks of birds could also be seen as they passed overhead, some arriving and leaving over seas, but no one knew for sure where they came from or where they went. Since then, the numbers of interested observers have grown enormously, visual aids such as binoculars and telescopes have become better and more affordable, field guides have been published as aids to species identification, and increasingly mobile bird-watchers have begun to travel the world.

The progress of migration research has also been marked by a series of methodological breakthroughs, each of which enabled previously intractable questions to be addressed. The first advance came around the start of the 20th century with the introduction of numbered metal leg rings by which birds could be individually marked and later reported, providing proof of their movements. By the middle of the century, radar was being used to detect birds migrating overhead, and later, small radio transmitters and other devices were developed that could be attached to individual birds, enabling them to be tracked day-today on their journeys (latterly from satellites). This chapter examines the pros and cons of various study techniques, illustrating how they have contributed to our understanding of bird migration.

OBSERVATIONS

Some bird species migrate primarily by day and others primarily by night. Diurnal migrants that fly low enough to be seen can be identified and counted by observers on the ground, enabling the migration seasons of particular species to be defined, and their directions determined. In contrast, nocturnal migrants are largely invisible, and can be detected only in particular conditions, and seldom identified to species. For example, low-flying birds can sometimes be seen as they cross the lit face of the moon. As a counting method, 'moon-watching' can be used effectively only on clear nights at times around full moon, and covers only a tiny part of the night sky. Nevertheless, such counts can provide information on the seasons and directions of bird movements, and also (using adventurous calculations) on the height and speed of participants (Nisbet, 1959a). Using a telescope with 40x magnification, an estimated 50 per cent of the birds flying at 1.5 km distance from the observer could be detected, reducing to zero at 3.5 km (Liechti *et al.,* 1995). In central Europe, the patterns of bird migration suggested by moon-watching, when checked against radar records, were found to be reliable from as few as three to five observation sites scattered over each 100 km square.

Other observers have used a strong spotlight directed skywards at night to count the birds passing through the beam. A good device for this purpose is a ceilometer, as used at airports for measuring cloud height. The beam typically extends only to a few hundred metres, and in warm weather, the lower parts tend fill with insects, but birds can be seen flying through the upper part, and can be recorded in the same way as for moon-watching. Infrared recording cameras have also been used to study nocturnal migration. The camera is placed with the lens facing upwards. It is extremely sensitive to temperature, and can detect birds at altitudes of 300–3,000 m, although only in a narrow sector of sky (1.45°). Observations are recorded on video tapes, which can then be viewed through a television screen, but species cannot usually be identified.

Other evidence of nocturnal migration can be obtained by listening for the calls of birds as they pass invisibly overhead. The

unaided human ear cannot pick up the normal flight calls of birds beyond about 400 m, but use of a parabolic reflector and amplifier can extend the range to 3,000 m or more. However, not all species call frequently, and some seem to migrate in silence, so the numbers of calls heard are only broadly related to the number of birds passing over (Farnsworth *et al.,* 2004). Nevertheless, the opportunity that listening affords for identifying species makes it a useful accessory to other methods.

Whether by day or by night, systematic observations can give some indication of the numbers and species composition of birds migrating within range, the seasonal timing and directions of movements, and their relationship with weather. The main drawback of visual observations is that most birds fly far too high to be seen by observers on the ground, however good the binoculars. And at night, it is practically impossible in most parts of the world to make any consistent and reliable counts of nocturnal passage. However, some types of diurnally migrating birds regularly fly low, including many seabirds over water, but then the numbers that can be seen from the coast vary greatly with weather, strong onshore winds blowing more birds than usual within visual range. In general., then, visual observations of bird migration, although thrilling to make, usually have severe limitations, and may not be representative of the whole migration at the time (for exceptions, see Chapters 4 and 5).

The fact that bird migration is most evident on sea coasts and offshore islands led to a research programme in the late 19th century based on the records of lighthouse keepers, and of trained observers based for several weeks at lighthouses and lightships around the coast (Clarke, 1912). This was the first attempt in the British Isles to use numbers of amateur observers in the systematic collection of ornithological data. It was also known that, on dark misty nights, migrants were killed at lighthouses in large numbers. Their deaths not only confirmed that many species migrated under cover of darkness, but also provided specimens for examination. Early observers gave graphic accounts of their observations at

lighthouses, including Heinrich Gätke writing from Heligoland Island in 1882: ‘The whole sky is now filled with a babel of hundreds and thousands of voices, and as we approach … under the intense glare of the light, swarms of larks, starlings and thrushes career around in ever-varying density, like showers of brilliant sparks or huge snowflakes driven onwards by a gale, and continuously replaced as they disappear by freshly arriving multitudes. Mingled with these birds are large numbers of Golden Plovers, Lapwings, Curlews and Sandpipers.’

RINGING

Formerly studied mainly by observation, migration research received a major boost from 1899, when Hans Christian Cornelius Mortensen, a Danish schoolmaster, produced the first metal bird rings, carrying a number and address, and began to attach them to birds in his home area. His method quickly spread to other places in Europe, North America and elsewhere, and became a mainstay of migration studies worldwide. In the British Isles, two ringing schemes were started independently in 1909, one by Harry Witherby in association with the journal *British Birds,* and the other by Arthur Landsborough Thomson at Aberdeen University. The Aberdeen scheme ended during World War I, but the Witherby scheme continued until 1937 when it was transferred to the recently formed British Trust for Ornithology, where it has been based ever since.

A ring is a light but tough metal band which can be placed loosely around the leg of a nestling or adult bird, with different sizes for different species. Each ring carries a unique engraved number, identifying the individual for the rest of its life, and an address to which a recovery can be reported. Ringed birds can thus provide information on longevity and movement patterns. The locations of most recovered birds are known only twice: at ringing and recovery; and reports of many individuals are needed to provide a worthwhile picture of migration routes.

During the early 20th century, many countries established their own schemes, in most of which ringing was carried out by volunteers operating in their home areas, but also involving ringing expeditions to more remote places. From 1963, various national ringing schemes in Europe were linked by an overarching body, the European Union for Bird Ringing (EURING), which coordinates the electronic handling of data, unifies standards and formats, and stimulates projects and analyses on a pan-European basis. All ringers are trained and licensed before they can operate alone. Nearly 4 million birds are now ringed annually in Europe, giving a total of some 115 million during the 20th century, with about 2 million recoveries. In the British Isles alone, more than 36 million birds have now been ringed, and more than 700,000 (2 per cent) recovered. These islands now have more ringers (around 2,100) who mark more birds per year (around 880,000) than any other similar-sized part of Europe. The scheme currently uses rings of 20 different sizes, with internal diameters of 2–26 mm, to fit any species from a 5 g Goldcrest to a 12 kg Mute Swan. A ring weighs 0.04–0.4 per cent of the bird's weight, so can be likened to a wristwatch on a person.

Initially, most birds ringed in the British Isles were nestlings. The numbers of adults that could be caught for ringing were limited by the trapping methods available, mainly baited clap-nets and walk-in funnel traps. However, at some sites, large permanent Heligoland traps were constructed, so-called because they were first built at Heligoland Island, across the North Sea off the north German coast. The Heligoland trap is essentially a large wire-netting funnel, supported on a wooden frame, which is big enough to include bushes and other vegetation (Fig. 10). At the narrow end of the funnel is a glass-fronted catching box into which the birds are driven. These traps, which are still in use, were too few in number to have much impact on the total numbers of birds ringed each year in Britain, but they increased the proportions ringed as full-grown. They can be operated in most weathers, and at sites too windy for other methods.

The numbers of full-grown birds ringed increased significantly from 1956 with the introduction of Japanese mist nets. These nets are essentially walls of fine, almost invisible netting, each up to 20 m long and up to 2 m high (Fig. 12). Each net is erected on lightweight poles, and set against a background of trees and shrubs to ensure that it does not show up against the sky. Any small bird that hits the net slides into a pocket of netting formed by one of four or five taut shelf strings, which are threaded horizontally at different levels through the length of the net. The birds can then be extracted unharmed for ringing. Luring birds into nets with the aid of a tape recording of a species' call has proved a useful way to increase catches. Mist nets are used mainly for small birds, up to Blackbird size; they are easily portable and can be erected almost anywhere within minutes, but they do not work well in wind, and have to be closed when it rains.

A different method was developed for catching waders, waterfowl and others that gather in large concentrations on the ground. A rocket- or cannon-propelled net is placed furled on the ground near where birds assemble (a roost or baited feeding area). The several rockets, or projectiles from cannons, are then fired simultaneously, pulling the large net rapidly over the unsuspecting birds, which can then be extracted and ringed (Fig. 13). Rocket nets were developed by the conservationist Sir Peter Scott for catching geese, but they were soon adapted and used to catch waders and other species. A smaller version, called a 'whoosh' net after the noise it makes, is powered by elastic cords, and can be used the catch passerines and other small birds. As these various methods spread, and more people became bird-ringers, they began to re-trap one another's birds, giving multiple live catches of the same individuals, so that reliance on the once-only recoveries of such species provided mainly by hunters has declined. While most birds recovered by non-ringers are reported as 'shot' or 'found dead', some come in unexpected ways: for example, an Osprey was recovered from the stomach of a crocodile in the Gambia, five Black-headed Gulls were reported at

different times as killed by flying golf balls, while two Mute Swans were ‘trampled by cows’.

The main drawback of ringing is that enormous numbers of birds must usually be ringed in order to provide only a small number of recoveries. The average recovery rate for birds ringed in Britain of 2 per cent belies great variation between species and regions. Most small birds have recovery rates of less than 1 per cent (excluding personal recaptures by the ringers themselves), but larger birds that are hunted can yield recovery rates as high as 20 per cent or more. More importantly, however, recovery rates can vary greatly along migration routes, according to the numbers and literacy levels of local people, and it is often difficult to get recoveries from tropical wintering areas. To pick an extreme example, in the 20th century, nearly 300,000 House Martins had been ringed in the British Isles, with just over 1,000 recovered. Yet more than 90 per cent of these reports were from within Britain and Ireland, and so were of little help in revealing migration routes, while only one came from Africa (Nigeria), within the presumed wintering range (I. A. Hill, in Wernham *et al.,* 2002). Nevertheless, largely as a result of ringing, we now have some knowledge of the migration routes of almost all the bird species that breed or winter in the British Isles, or regularly pass through on migration. These data have been summarised in the British Trust for Ornithology’s *Migration Atlas* (Wernham *et al.,* 2002), one of many such atlases produced in various countries since the start of bird-ringing.

The behaviour and movements of birds influence the ease with which they can be caught and ringed. Returning to the House Martin, one of the reasons we have so little information from the wintering range is that they are practically impossible to catch there. While in breeding areas they sometimes roost in reedbeds where they can be caught in mist nets (Fig. 12), in wintering areas they usually choose trees and high sites, and are sometimes thought to sleep on the wing (like Swifts). They contrast with Barn Swallows, of which 1.3 million have been ringed in Britain, and around 500 have been recovered in Africa south of the Sahara. But

in both breeding and wintering areas, Barn Swallows form large communal roosts in reeds and other rank vegetation, so can be readily caught throughout their migratory range.

Normally, a ring can be re-read only if the bird is in the hand, live or dead. Not surprisingly, therefore, researchers have sought to develop methods that enable marked birds to be recorded in the field without the need to re-trap them. More conspicuous marking has been achieved in various ways depending partly on the species, including feather dyeing, colour rings on the legs, large rings bearing numbers or letters that can be read from a distance, coloured or numbered neck collars or wing tags. Colour-marking schemes have greatly increased the information gain for some species, notably waterfowl and waders, and have often yielded multiple records of the same individuals at different places, especially where observers along the potential migration route were alerted to look out for them. For example, in the Black-tailed Godwit in the British Isles, only 2.5 per cent of ringed birds were ever recovered, but following the introduction of a colour-marking programme and additional observer input, more than 80 per cent of marked birds were subsequently re-sighted, many at several different places on the migration route.

Overall, ring recoveries still comprise our main source of information on bird movements. Taken together, they reveal a network of bird migration routes that encompass most parts of the globe, and that are travelled twice each year by millions of migrating birds.

BIRD OBSERVATORIES

Appreciation of the value of systematic observations, along with bird-ringing, led to the establishment of ‘bird observatories’ (or ringing stations) around the coasts of Britain and Ireland. The first were started on Skokholm Island (Wales, 1933) and the Isle of May (Scotland, 1934), but others followed in later years, resulting in 19 that are currently operational. They are mostly maintained by

volunteers, but some are manned by paid wardens assisted by volunteers (Fig. 17). Information from these observatories soon revealed the migration periods of the main species that passed through, their flight directions and the weather conditions in which they were seen. They also provided weights and measurements from birds trapped for ringing. One of the best-known British bird observatories is on Fair Isle, which lies between the Orkney and Shetland Islands. The value of this location in the study of bird migration was first recognised by William Eagle Clarke (1912) in his pioneering book *The Migrations of Birds.* The island is known mainly for its rare vagrants, and during the 20th century it provided the first in-country record for more than one-fifth of all the new vagrant species added to the British list. In total., more than 350 species have been recorded there.

Many reports were written from the early work at bird observatories, but the volume of data soon overwhelmed the limited capacity to analyse them. It is only in recent years that many of the archived data have been computerised and analysed, mainly to check for the changes in migration dates expected under climate change. The monitoring of bird migration at bird observatories over several decades means that the data on timing of migration are the best available for many species. Daily records have been collected of birds seen on the ground, passing overhead or caught for ringing, with a sampling effort that was more consistent over the years than for most other data sources.

Experiments with ringed birds

One of the outstanding questions about migratory birds is how they find their way. From early in the 20th century, bird-ringing led to the experimental manipulation of birds in order to learn more about their navigation. Large-scale displacement experiments, in which birds were caught in one locality and released far away, were conducted to see whether they could find their home areas again, or how translocation affected their migrations. Ring recoveries

provided the necessary information. No fewer than 24 large-scale experiments, involving a wide range of species from Barn Swallows to White Storks, were carried out in the first half of the 20th century from Vogelwarte Rossitten, the original bird observatory (established in 1901), which is situated on the Courland Spit on the southern Baltic coast. These experiments were followed by others elsewhere in Europe and North America (Chapter 12). Such experiments revealed much about the orientation and navigational abilities of birds, and about differences in behaviour between young and older individuals.

The same bird observatory where such work was pioneered still exists, but it is now in Russian rather than German hands, and is known as Rybachy rather than Rossitten. It is an amazing place for watching and catching birds. At migration times, a continual stream of birds pours through, and where the Spit narrows to sand dunes, more than half a million birds can be counted in a day. Giant Heligoland-style funnel traps, built by Russian researchers, extend up to 20 m high over pine forest, up to 50 m across and up to 140 m long. They are made of soft netting supported by poles and, aligned in the direction of migration, they can catch more than 2,500 birds per day.

RADAR-BASED STUDIES

The use of radar for recording bird migration began in the 1950s. Radar was first developed and deployed in Britain to detect enemy aircraft during World War II. Birds were also detected, but initially their echoes remained a mystery, and became known to the radar operators as ‘angels’. A radar emits short pulses of radio waves and records their echoes from targets, whether birds or aeroplanes. As radio waves travel at the constant speed of light, the distance between the radar and the target can be calculated from the time lapse between pulse emission and echo reception. The use of radar revolutionised the study of bird migration, because it made observations almost independent of flight altitudes and weather,

totally independent of light conditions, and hence fully comparable by day and night. It has taught us much about unseen migration and about the influence of weather on bird movements (Chapter 5). It has provided reliable information on the seasonal and diurnal timing of migration, and on the speed, direction and altitude of flight (for reviews, see Eastwood, 1967; Bruderer, 1997a, 1997b; Gauthreaux *et al.,* 2003). However, care is needed to separate birds from large insects, and to estimate reliably the density of individual birds in the radar beam (for discussion of procedures, see Schmaljohann *et al.,* 2008).

The most obvious disadvantage of radar work is the cost: the equipment itself is expensive, and trained personnel are needed to maintain and operate it. For the most part, it is available only at a limited number of fixed installations (although mobile units are also available). The main operational drawback is that the identities of the bird species usually remain unknown, apart from broad categories distinguished by body size, flight speed or wingbeat patterns. The radar echoes often show rhythmic fluctuations that can be recorded and used to estimate the wingbeat frequency. This procedure enables waders and waterfowl (continuous wingbeats) to be distinguished from passerines (rapid wingbeats broken by pauses), and perhaps two size classes in each group. Other problems are that birds flying below the radar horizon are usually missed, and backscatter from the ground can sometimes blur the image.

Surveillance radars, like those used for traffic control at airports, have a rotating antenna, enabling a wide swathe of sky to be scanned repeatedly for echoes. They are therefore good for studies of migration intensity, speed and general direction. On some modern radar sets, small songbirds can be detected out to beyond 100 km, and larger birds to more than 500 km, providing they are high enough (Bruderer, 1999). A useful way of recording the slow-moving echoes of birds is with time-lapse photography. By setting up a cine camera to photograph the radar screen at regular intervals, say once every 1–2 minutes, the resulting film can be

played back at normal speed, enabling a whole night's migration to be viewed in a matter of minutes.

In contrast to surveillance radar, a tracking radar emits a narrow 'pencil beam' by which individual birds or flocks can be tracked. When operated in automatic tracking mode, the radar locks onto a particular target bird (or flock) and records repeat measurements of its position, from which the speed and direction of the bird can be calculated, and its flight trajectory plotted in three-dimensional space (Bruderer *et al.,* 1995). Wind profiles can be obtained by using the radar to track ascending weather balloons carrying aluminium foil for maximum reflectance. The heading and airspeed of the birds can then be calculated from analysing the tracking data against the wind data. Another radar technique involves using a vertical beam designed to quantify the amount and height of migration overhead. This gives similar results to those obtained using a ceilometer, except that the radar can penetrate clouds and detect birds at all heights.

The main pioneers of radar-based ornithology in Britain were David Lack, who had worked with radar during the World War II, and Eric Eastwood, who worked for the Marconi Company which manufactured the sets. They and their colleagues used radar to document migration at several sites around Britain, assessing the seasonal and diurnal patterns, flight altitudes, and also how the densities and behaviour of migrants varied with weather. They quickly confirmed that most bird migration occurred too high to be seen by ground-based observers equipped only with binoculars, and that much more migration occurred by night than by day. They also changed prevailing ideas about the effects of weather on bird migration (Chapter 5).

RADIO TRANSMITTERS AND OTHER SENSORS

Another major breakthrough in the study of bird migration was the development of small radio transmitters which could be harnessed to birds, enabling them to be followed on their journeys. The bird

wears the transmitter like a small rucksack with a short protruding aerial., and the harness is biodegradable so that after a time it falls off. In the earliest studies, in the United States, birds of several species were tracked over part of their journeys from small aircraft (Cochran *et al.,* 1967; Kuyt, 1992). But from the mid-1980s, satellite-based reception became available. The transmitters, called platform transmitter terminals (PTTs), can now be followed individually and automatically by the Argos satellite system. This is a joint French–American system, originally designed to locate objects on earth such as floating weather stations and buoys. It is based on satellites which continually circle the globe over the poles, detecting signals from anywhere on earth. The satellites then transmit the information to a ground station in France, from where it can be sent to the researcher. The accuracy of each reading is known, so the less reliable ones can be discarded if necessary. The method is expensive, but it has provided some of the best available data on the movements of individual birds. PTTs are now available down to 5 g, and it is expected that further miniaturisation will follow in the years ahead.

The use of this technique enables large birds to be monitored day by day on their journeys, and to be followed all the way from their breeding grounds to their winter quarters, and back again, regardless of where in the world they move. With this method, fieldwork on bird migration has advanced in new directions, providing information on migration routes and progress, stopover locations and durations, flight speeds, wind and weather effects, and orientation abilities. For some species, previously unknown breeding or wintering areas have also been detected.

Individual battery-powered PTTs lasted for only a few weeks or months, until either the transmitter or the battery failed. But from 1995, solar-powered transmitters became available which could in theory last for many years, enabling individual birds to be followed on successive journeys. The current record holder is a White Stork, so far tracked (with periodic transmitter changes) over a ten-year period on six outward and six return journeys between its nesting

place in Germany and its wintering places in different parts of Africa (Berthold *et al.,* 2004).

Other kinds of sensors and data-storage tags were subsequently developed (from 2004) which could be attached to birds and used to track their migrations. Geolocation systems (GLS) are based on continual measurements by photosensors of the ambient light intensity, which can then be used to calculate the geographical position of the bird at different dates (latitude from daylength and date, and longitude from absolute times of dawn and dusk). In contrast, global positioning systems (GPS) receive data for calculating the position of the bird at pre-set intervals (say every hour) through a network of satellites launched by the United States Department of Defense. When first introduced, both GLS and GPS systems required the recapture of the birds to recover the tags (usually attached to leg rings) and the accumulated data. This was not difficult with seabirds, for example, returning annually to the same nest sites. However, subsequent developments to link GLS and GPS to satellite receivers now allow the stored data to be downloaded directly from the bird without its recapture, and relayed to ground-based Argos processing centres at pre-set intervals. Some current solar-powered models can operate over periods of years, providing that light levels are sufficient to generate the necessary power. As the locations determined by GPS are accurate to within 20 m, the method can be used to gain precise assessments of a bird's home range at different seasons, as well as its migration routes and stopping sites. Used in conjunction with high-powered satellite images or aerial photographs of the ground (such as those available from 'Google Earth'), a bird can be placed accurately within a landscape situated hundreds or thousands of kilometres from the observer, who is seated comfortably at home in front of a PC. Additional sensors can be added to a PTT in order to measure other variables, such as altitude of flight or ambient temperature, or the heart rate (reflecting energy use) of the bird, but these increase the weight the bird has to carry. They can also indicate if a bird dies, which in time could provide measures of

mortality rates at different times of year and the areas where deaths most often occur.

The main drawbacks of such methods are the high costs of the units and their subsequent servicing. Their weights mean that they have so far been used chiefly on larger bird species, such as raptors, waterfowl, cranes and seabirds. Ideally, such units should weigh no more than 3–4 per cent as much as the bird. At this weight, they amount to less than a meal., and seem to have no significant effect on the migratory behaviour of the wearer, providing they are appropriately attached. Technology is advancing all the time, however, and devices are now appearing that are suitable for use on small passerines.

Another recent development involves the use of passive integrated transponders (PIT tags) similar to the microchips fitted to domestic pets. They can be used to record the presence of tagged birds at particular places, such as nest sites. Such microchips can be implanted under the skin or attached as a ring to the leg. Each has a unique code, and can be read automatically at subsequent dates by a battery-powered receiver and antenna placed near the nest or other regularly visited site. This method has been used to record the return dates of individual Common Terns to their nesting colony (Dittman & Becker, 2003), for example, and to identify individual Peregrines at nest sites, thus providing information on survival and site-fidelity (Smith & McGrady, 2009).

ISOTOPES AND OTHER INTERNAL MARKERS

Biochemical markers present naturally within the tissues of migratory birds can also provide information on broad-scale movement patterns. They offer an alternative approach for studies of movements in species that yield few or no useful ring recoveries, or are too small to carry PTTs or other sensors. Stable isotopes have proved especially useful in studies of this type. Isotopes of the same element differ in the number of neutrons in each atom, and hence in their atomic mass, which can be measured in a mass spectrometer.

Stable isotopes of several abundant elements, including hydrogen (H), carbon (C), nitrogen (N), strontium (Sr) and others, vary consistently across broad geographical regions or between bird habitats and food types (Hobson, 1999). For example, the ratio of hydrogen to its isotope deuterium (delta D) in rain varies across Europe, from deuterium-enriched in the west to deuterium-depleted in the east. Similarly, nitrogen and carbon isotope ratios differ between marine and terrestrial ecosystems. Birds absorb isotopes from their food and deposit them in body tissues, giving isotope signatures which reflect either the region where the food was eaten, the habitat where the food occurred or the type of food, depending on the element analysed. Birds that move between regions or food webs can retain information of previous feeding locations for periods that depend on the turnover rates of particular isotopes in different body tissues. On a short timescale, blood plasma is changing continuously, so isotope ratios reflect the food eaten in the previous few days. On a longer timescale, keratinous tissues, such as feathers, are metabolically inert following synthesis, and maintain until the next moult an isotopic signature reflecting the food eaten at the time and place of their formation.

In practical terms, by catching a bird and plucking a single feather, analysing by mass spectrometry its isotope signature, and comparing this with known geographical patterns in isotope ratios, it is possible to tell (in very broad terms) where the bird grew the feather. Even without a baseline geographical reference, feathers can reveal whether different breeding populations have their own distinct wintering areas (if they moult in winter quarters), or whether different wintering populations have their own distinct breeding areas (if they moult in summer quarters). In such cases, it is not necessary to recapture birds, and the method is equally applicable to museum specimens as to live-trapped ones.

In recent years, study of isotope ratios has been used to assess: (1) the different breeding areas of a given wintering population; (2) the different wintering areas of a given breeding population; (3) whether populations breeding in different areas also winter in

different areas; (3) the approximate broad-scale location of previously unknown breeding or wintering areas; (4) the position of a migratory divide in which populations on either side migrate to different wintering areas; (5) the passage times of different populations migrating through the same location; and (6) the latitudinal distribution in winter of birds from different breeding latitudes. Isotope studies have also been used to assess (7) whether the quality of wintering habitat used by individuals matches the quality of their subsequent breeding habitat and breeding success; and (8) whether individual migrants produce eggs from food eaten on breeding areas or from food stored as body reserves from migration and wintering areas. These and other aspects of migration ecology studied by isotope analyses are illustrated in later chapters of this book.

Trace elements in feathers have also been used to indicate the broad geographical origins of birds. This is possible because the proportions of these trace elements in feathers vary from region to region, according to geological substrate, which again influences the composition of food. For example, Sand Martins breeding in different parts of Europe differed markedly in the elemental composition of their winter-grown tail feathers, indicating that the birds from different breeding areas had moulted in different parts of Africa (Szép *et al.,* 2003). Moreover, tail feathers from the same individuals in different years were similar in elemental composition, implying that individuals were consistent in their moulting areas from year to year.

Other researchers have attempted to use DNA to distinguish different populations of a species from among the mixture of populations often found at migration and wintering sites. However, in only relatively few species can individuals from different populations be convincingly separated in this way (for examples, see Wennerberg, 2001; Smith *et al.,* 2005). Within most species, the DNA differences between regional populations are too small to be of use in this respect, at least for the methods in current use.

DISTRIBUTION STUDIES

For many years, museum collections formed our main source of information on the wider distributions of birds, and especially of the wintering areas of species that migrate to the tropics for the non-breeding season. The aim of skin collectors, operating mainly in the 19th century, was to preserve representative samples of all the species occurring in different areas. These specimens still provide valuable information on the tropical wintering areas of many migrants which have yielded few ring recoveries or observational records. Among European breeding birds, for example, the winter distribution of the Common Cuckoo *Cuculus canorus* in Africa is still better known from museum skins than from ring recoveries.

Over much of the world, however, increasing information is becoming available on the breeding and non-breeding distributions of birds through the collective efforts of bird-watchers (Chapter 18). For some parts of the world, including the British Isles, these distributions have been depicted at relatively fine scale in recent 'atlas' projects (Lack, 1986b; Gibbons *et al.,* 1993). However, in most tropical regions, where many high-latitude breeding species spend the non-breeding season, bird distributions are still poorly mapped, despite greater travel by bird-watchers. Such distributional data show where the same species occur at different times of year, revealing their broad-scale breeding and non-breeding ranges, as well as their migration routes.

RESEARCH ON CAGED BIRDS

Laboratory research on bird migration began in the mid-1920s and rapidly gained ground. Since that time, hundreds of experiments on migratory physiology, orientation and other aspects have now revealed most of the relevant physiological processes and controlling mechanisms, at least in broad terms for a limited range of species (Chapters 9 and 10). In particular, the role of daylength in influencing migration timing has been examined by manipulating

the artificial daylengths (photoperiods) to which captive birds are exposed, and then recording their condition and behaviour. The pioneer in this field was William Rowan, who was raised and educated in England but did his most important work in Canada. He discovered that, if captive birds were kept on artificial daylengths longer than they would normally experience in late winter–spring, they became migratory and reproductively active earlier than control birds exposed to natural daylengths (Rowan, 1926). This confirmed the role of daylength as a triggering mechanism in the timing of spring migration. Later researchers repeated and extended Rowan's findings in a wider range of species, and some also measured metabolic rates, food consumption, body weights and migratory activity at the same time.

Another important discovery was that, at migration times, migratory birds in captivity developed migratory restlessness *(Zugunruhe* in German), in which they hop and flutter round their cages, and may also exhibit long periods of wing-whirring (fluttering the wings while perched). This behaviour can now be registered automatically by the use of electronic trips under perches (Chapter 10). Migratory restlessness in captive birds occurs either by day (in diurnal migrants) or at night (in nocturnal ones), and has been regarded as the laboratory equivalent of migration itself. It appears chiefly in birds from migratory populations and much less so, or not at all, in birds from resident populations. Moreover, the number of days on which migratory restlessness is shown by young birds was found to correlate with the natural duration of migration (and hence distance travelled) in the population concerned (Berthold, 1973). Short-distance migrants typically showed migratory restlessness over fewer days each autumn than did long-distance migrants. Migratory restlessness therefore provided a useful means of comparing the migration seasons of captive birds from different populations, and of testing the influence of various factors on migration timing (Chapter 15).

Another discovery was that captive birds at migration times developed strong directional preferences, which corresponded to the

directions they would normally take on migration. Such preferences could be measured in individuals using circular 'orientation cages', which typically have solid sides and wire tops affording a view of the sky. In one early type, the cage was shaped like a vertical funnel, with an ink-pad on the floor. The pattern of footprints up the sides of the funnel (usually lined with white paper) indicated the directional preferences of the occupant (Emlen & Emlen, 1966). Automatic registration was achieved in circular cages equipped with radially arranged perches fitted with micro-switches or other devices to record directional activity (Wiltschko, 1968). Such apparatus has been used to study the orientation and navigation behaviour of laboratory birds, or of wild ones trapped and tested in field conditions during the migration season (Busse, 2000; Fig. 20). Using only two cages, up to six birds trapped on migration can be tested each hour by a single observer.

Another type of laboratory study, started in the 1960s, involves the analysis of bird carcasses to assess the proportions of water, fat and lean dry material (mostly protein and bone). Such studies helped to document the changes in body composition that occur in many birds at migration seasons, and to quantify the amount of fat laid down as fuel for the journeys. They showed that land birds making long non-stop flights over seas or deserts, where they could not feed, accumulated large reserves of body fat beforehand, in some species enough to more than double their normal weights (Chapter 6). Most of the birds analysed in this way were not deliberately killed for the purpose, but had fallen victim on dark misty nights to tall radio masts or lighthouses. In addition, rough indications of the fat levels of live birds can be gained from their body weights, or by judging the amount of subcutaneous yellow fat visible under the skin when the feathers are blown aside. Although less useful than full carcass analyses, such studies are non-destructive, and can be easily conducted on large numbers of birds trapped in the field for ringing, sometimes with repeated measurements from the same individuals.

From the 1970s, large-scale breeding programmes of captive migratory birds revealed much about the genetic control and inheritance of different aspects of migration behaviour (Berthold, 1996). The most convincing results came from cross-breeding individuals of the same species drawn from geographically separated populations with different migratory behaviour. In general., the resulting offspring showed migratory behaviour that was intermediate in timing, direction and duration between their two parents. By selecting and breeding only from the most migratory individuals in a population, migratory behaviour could be enhanced over several generations; and similarly, by selecting and breeding from the least migratory individuals, successive cohorts became increasingly non-migratory. These experiments, conducted mainly on Blackcaps, confirmed that all major aspects of migratory behaviour were genetically controlled, and could be altered by selection (Chapter 15).

CONCLUDING REMARKS

Application of these various methods over the years, together with others used on a smaller scale, has taught us most of what we now know about bird migration. Looking back over the past 120 years, two features of migration research stand out. The first is the enormous contribution to its study made by amateur ornithologists, who have greatly increased the available manpower and the geographical spread of field-based studies. Their collective efforts have been especially evident in studies that depend on large-scale observation, ringing and recovery. Second, professional biologists have continually added new methods of study to the arsenal., often dependent on technological advances from other fields. Throughout the history of migration research, amateurs and professionals have worked together, and unlike some other branches of science, none of the old methods has been abandoned: observation and ringing are still contributing to the growth in understanding. These traditional

methods are cheap enough to be used effectively by anyone with an interest in bird migration.

CHAPTER 3

Migration Around the British Isles

By the end of 2008, some 583 bird species had been officially recorded in the British Isles or in the seas around our coasts (not counting species known only from fossils). About 256 of these species occur here regularly, as year-round residents, partial migrants, summer visitors, winter visitors or passage migrants (Appendix I at the end of this chapter). Many fall into more than one category, being, for example, both resident and winter visitor (such as the Common Starling), winter visitor and passage migrant (such as the Brambling), or summer visitor and passage migrant (such as the Northern Wheatear). Moreover, some species behave differently in different parts of the British Isles, being more migratory in northern than southern areas or at higher than lower altitudes (such as the Song Thrush).

To these major categories can be added the various rare visitors and vagrants that now make up more than half of all the species recorded in the British Isles (and are excluded from Appendix I). They include some species that turn up in small numbers every year and others that have been found reliably no more than once or twice in the last 200 years. Also excluded from Appendix I are about ten introduced (or escaped) species, such as the Ring-necked Parakeet, Golden Pheasant and Mandarin Duck, which have established local breeding populations and are now resident in some areas. Otherwise, different bird species are categorised in Appendix I according to their usual behaviour, and in any species we can expect to find occasional individuals that behave differently from the rest.

The main wintering areas abroad for the migratory land birds that breed in the British Isles include the southern parts of Europe, mainly France and Iberia, and Africa both north and south of the Sahara desert. Many partial migrants from Britain also winter partly in Ireland. It is mainly the partial migrants that winter in Europe, while the summer visitors winter in Africa south of the Sahara. Among the latter, several species migrate beyond the equator, and some, such as the Barn Swallow, reach as far as the southern tip of Africa.

The various seabirds that breed in the British Isles winter in the surrounding seas, or further south off western Europe and western Africa, both north and south of the equator. Only some of the gulls appear inland in large numbers. However, some seabird species migrate to more distant areas: Arctic Terns as far as the seas off the Antarctic continent, and Manx Shearwaters to the seas off eastern South America. Yet other species, such as the Fulmar and Black-legged Kittiwake, disperse widely over the North Atlantic in the non-breeding season, some individuals being found at the edge of the pack ice, well to the north of their British and Irish breeding areas, and west to the seas off North America and Greenland.

RESIDENTS AND PARTIAL MIGRANTS

Some 58 indigenous species seem to be wholly resident within the British Isles, in that no evidence has yet emerged to suggest regular migration (although most are migratory in some other parts of their wider range). Such year-round residents include a wide variety of land-bird species, from the Wren and Magpie to the Red Grouse and Golden Eagle (Appendix I). Another 87 species can be classed as partial migrants, in that some individuals remain here year-round, while others migrate to winter elsewhere. Examples include the Goldfinch, Common Kestrel and Black-headed Gull. In some partial migratory species, most individuals are resident (such as the Wood Pigeon), whereas in others the majority are migratory (such as the Chiffchaff and Common Sandpiper). In most of these partial

migrants, the migratory individuals winter further south in the British Isles or in continental Europe, as mentioned above, but in some (such as the Marsh Harrier, Common Sandpiper and Stone Curlew), part of the population reaches the northern tropics of Africa. For convenience, species which breed in inland areas of the British Isles and move offshore for winter, such as the Black-throated Diver and Common Scoter, are also classed here as partial migrants. However, for some of these species, ring recoveries are so few that it is hard to be sure whether they move mainly to local coasts or further afield.

Among seabirds, the Shag and Black Guillemot could be classed on present evidence as year-round residents, although some Shags may disperse to neighbouring continental coasts in winter. About eight species can be classed as partial migrants, including six species of gulls, Gannet and Cormorant, in which mainly the younger age groups travel long distances to continental and (in some species) West African waters for the winter. Other species disperse widely in winter, with some individuals remaining around the British Isles and others spreading out over the northwest Atlantic (Guillemot, Puffin) or the whole North Atlantic across to eastern North America (Fulmar, Black-legged Kittiwake), as mentioned above. The use of tracking devices may in the future reveal more pattern to these movements than current ring recoveries suggest.

The majority of birds breeding in the British Isles each year are of resident or partial migratory species. Those of terrestrial and freshwater habitats, all species together, have been estimated at around 60 million pairs (or around 120 million individuals), while seabirds (including gulls) total nearly 3 million pairs (or 6 million individuals). To these must be added an unknown number of non-breeders.

SUMMER VISITORS

About 54 species are entirely summer visitors to the British Isles, having wintered in warmer regions further south. They include such

familiar breeding birds as the Barn Swallow and Cuckoo, long regarded as harbingers of spring, and less common ones, such as the Corncrake and Hobby. Adding together the population estimates for different summer-visiting species, their overall numbers in spring can be estimated at around 16 million individuals for Britain and Ireland together.

Almost all these summer-visiting species winter in Africa south of the Sahara. In autumn most travel through Iberia to western Africa, but several (including the Red-backed Shrike, Marsh Warbler and Lesser Whitethroat) move eastwards to enter Africa near the far end of the Mediterranean. Only three summer visitors winter primarily in Africa north of the Sahara, namely the Dotterel, Ring Ouzel and Blackcap (the latter two also in southern Europe). However, one potential colonist of Britain is the Common Rosefinch, which has bred in small numbers in some recent years. It is the only British breeding species which normally winters in India and other parts of Southeast Asia, although specific information on the wintering areas of British breeding birds is lacking.

Among seabirds, summer breeding visitors include the Manx Shearwater, Storm and Leach's Petrels, Arctic and Great Skuas, and five kinds of terns. In most of these species, the British and Irish breeding birds winter off the west coasts of Africa in the eastern Atlantic, but Manx Shearwaters cross the Atlantic to winter off eastern South America, while Arctic Terns extend south to Antarctic waters, as mentioned above.

WINTER VISITORS

Lying in mid-latitudes off the edge of a continental landmass, and warmed by the Gulf Stream, the British Isles offer a milder winter climate than anywhere else of equivalent latitude on the Eurasian landmass. Perhaps not surprisingly, therefore, they draw birds for the winter from a wide swathe of northern land, extending over more than 200° of longitude, from northeast Canada in the west to central northern Siberia in the east. Although not all species

breeding in these areas winter in the British Isles, no other equivalent-sized area on earth draws its wintering birds from such a wide longitudinal span, extending more than halfway round the world in arctic regions (Fig. 22).

About 72 species occur in the British Isles as winter visitors (including 20 only as winter visitors), while another 68 occur as both winter visitors and passage migrants, making 140 winter-visiting species altogether (Appendix I). They include mainly waterfowl, waders, gulls and passerines. These populations can be divided according to whether they breed to the northwest of the British Isles: in northeast Canada–Iceland–Greenland, or to the northeast and east, in Svalbard and Eurasia. Some species arrive in the British Isles in autumn from both these regions, including the Whooper Swan, Barnacle, Brent and White-fronted Geese, various ducks and waders, the Merlin, Redwing, Northern Wheatear, Meadow Pipit, Common Redpoll, Lapland Bunting and Snow Bunting. In most of these species, as shown by ring recoveries, birds from Canada–Greenland–Iceland winter mainly in Ireland and the west of Britain, while those from Eurasia winter mainly in the east. Among Barnacle, Brent and White-fronted Geese, which concentrate in specific localities, the separation between western and eastern types is effectively complete, with no appreciable overlap between the two populations. The same holds for the Icelandic and Eurasian populations of Whooper Swans.

From the total of various land-bird species which come to the British Isles for the winter, at least 77 (including land-feeding gulls) come from northern Europe, at least 36 from Iceland, at least 10 from Greenland and at least 4 from northeast Canada, but there is wide overlap between the species composition from different areas. They include most of the migratory land-bird species that breed in Iceland, apart from the few (such as the Northern Wheatear) that pass through en route to Africa. The British Isles also hold in winter more than half the entire northwest European populations of many other species, notably waterfowl, waders and small gulls. These facts

again emphasise the importance of the British Isles as a wintering area for migratory birds.

Some of the most conspicuous winter visitors include the waterfowl, which mostly assemble in large concentrations at wetlands and coastal areas, from which many spread to surrounding land to feed. More than 1.6 million individuals of these migratory species winter in the British Isles, including some 20,000 swans, around 515,000 geese, more than one million freshwater ducks and over 100,000 sea ducks, in many species adding to resident populations (Stone *et al.,* 1997). To these can be added more than 20,000 migratory Coots, plus at least 25,000 divers (mainly Red-throated) and grebes on the seas around our coasts. For many waterfowl species, the British Isles represent the end point in long migrations. Among those from Eurasia, the numbers reaching the British Isles each year tend to peak between January and February, with the greatest numbers appearing in the years of severe weather on the continent.

In winter, the British Isles also host more than 4 million waders from abroad, again adding to some local populations (Stone *et al.,* 1997; Rehfisch *et al.,* 2003; Austin *et al.,* 2008). The most numerous species are Lapwing (nearly 2 million), Golden Plover (at least 380,000), Red Knot (more than 307,000), Dunlin (more than 585,000), Curlew (more than 140,000) and Redshank (more than 130,000). These figures are the most complete available, but some are now more than 15 years out of date, so may need revising, mainly downward. The Common Snipe, Jack Snipe and Woodcock are the most difficult waders to count in winter because of their wide distributions and cryptic behaviour, but they also total hundreds of thousands of individuals. Woodcock come in far greater numbers than casual observations might suggest. In fact, some 740,000 individuals from northern and eastern Europe are estimated to winter in the British Isles each year (information from the Game & Wildlife Conservation Trust), and spectacular ‘falls’ are sometimes apparent, with more than 1,000 counted on one occasion on Fair Isle alone.

With some of the greatest tidal ranges in the world, extending in some places to over 12 m, the British Isles have extensive coastal mud flats, offering plentiful foraging for wintering shorebirds. The greatest area of intertidal habitat found around the British Isles is the Wash in eastern England, which covers more than 100 sq km at low water, including 50 sq km of saltmarsh and 30 sq km of mud, with a tidal range extending over 5 km. This area alone supports up to about one million shorebirds during autumn migration and up to 400,000 in mid-winter. Other particularly important sites in winter include the North Norfolk coast (245,000 birds), the Ribble Estuary (240,000) and Morecambe Bay (220,000), all of which host internationally important numbers of eight or more species (Austin *et al.,* 2008).

The eastern side of Britain forms a major wintering area for Black-headed and Common Gulls, which arrive from late summer, and reach peak numbers in mid-winter. Including local birds, the total wintering populations of the two species in the British Isles have been estimated at around 3 million Black-headed Gulls, of which more than two-thirds are probably winter immigrants, and around 702,000 Common Gulls, of which less than one-half are probably immigrants. The British Isles provide the main wintering area for the European populations of these species, both being found commonly across farmland, as well as at sea coasts. Compared to these species, the numbers of larger gulls entering the British Isles from Europe each year are relatively small, with most Herring and Lesser Black-backed Gulls seen here in winter being of local origin. Nevertheless, the North Sea area in general holds the bulk of the European population of Great Black-backed Gulls, many foraging over the open sea far from land. Small numbers of more northerly breeding gulls are seen in the British Isles in winter, including a few hundred each of Glaucous, Iceland and Little Gulls, and occasional individuals of other species. Although Kittiwakes breed commonly here, most are too far from land to be seen in winter, except when gales blow them close to shore.

Despite the impressive numbers of waterfowl, waders and gulls, the most abundant and familiar winter visitors to the British Isles include the passerines, which collectively may number more than 20 million in mid-winter, mostly adding to resident populations. The most widespread and obvious are Fieldfares and Redwings, which are found commonly on farmland. They are at peak numbers in Britain in the autumn, after which many move on to Ireland or to southern Europe, but there is a marked return passage in spring. It has been estimated that up to a million of both of these species maybe present in Britain and Ireland in mid-winter (Lack, 1986b). Even larger numbers of Common Starlings and Chaffinches from the continent also winter in the British Isles, as do smaller numbers of Blackbirds, Song Thrushes and Robins, along with Rooks and Jackdaws, but because all these species add to the resident populations, away from the coast their comings and goings tend to be less obvious than those of Fieldfares and Redwings. Various other seed-eating or fruit-eating irruptive species, such as the Common Redpoll, Siskin, Brambling and Waxwing, arrive in the British Isles each autumn, but in numbers that vary greatly from year to year (Chapter 19).

Unlike neighbouring parts of Europe, hardly any continental raptors winter here on a regular basis, but some Kestrels from northern Europe winter mainly in the eastern parts of the British Isles, as do Merlins from Iceland mainly in the western parts. We have no basis from which to estimate their numbers, because the local populations are likely to greatly outnumber them. Another significant non-passerine winter visitor is the Grey Heron, which probably comes in thousands, but again the numbers are hard to estimate reliably. Many other species come in small numbers (Appendix I), including Peregrines, Rough-legged Buzzards, Long-eared and Short-eared Owls and Great Grey Shrikes, and in some years occasional Gyr Falcons and Snowy Owls. In the latter two species, some individuals probably derive from Greenland or North America, and others from the Eurasian Arctic.

The shallow seas around Britain support abundant seabirds in winter. Some derive from British and Irish colonies, while others come from further north, including Little Auks, together with large numbers of sea ducks, divers and grebes. Some of these species remain far offshore, except in unusual weather, but have occasionally been counted from the air.

PASSAGE MIGRANTS

In addition to the breeding and wintering birds, about 20 bird species occur in the British Isles almost exclusively as passage migrants, being seen here in late summer or spring as they travel between breeding areas to the north and wintering areas to the south. Land-bird species in this category include the Curlew Sandpiper, Little Stint, Grey Phalarope, Black Tern (formerly bred), Wryneck (formerly bred), Richard's Pipit, Bluethroat and Aquatic Warbler. Seabird species that occur here primarily on passage include Sabine's Gull, Pomarine and Long-tailed Skuas, which breed in the Arctic and winter mainly south of the equator. All three species are seen commonly on the east and west sides of the British Isles during autumn, but on their return journey in spring, they mostly travel up the west side. Another 102 or so species which breed or winter in the British Isles also occur as passage migrants from elsewhere (Appendix I).

Passage migrants include at least four species of seabirds that breed to the south of Britain and Ireland. The Great Shearwater and Sooty Shearwater breed in the southern hemisphere and pass the austral winter (northern summer) in the North Atlantic; they travel northward mainly up the west side of the Atlantic and southward mainly down the east side, so they pass through British and Irish waters chiefly between August and October en route back to their breeding areas. However, both species usually remain well offshore, the Great further out than the Sooty, but both come within view of the coast in onshore winds. The Cory's and Balearic Shearwaters breed in Mediterranean latitudes, and move north into British and

Irish waters between July and October (mainly August to September). Both species depend largely on the northward flow of warm waters from Mediterranean latitudes, which bring their particular foods, and the numbers of both vary greatly from year to year. Both have been seen more often in recent years, mainly off the south coasts of England and Ireland, but the Balearic Shearwater has extended all around the British Isles. The Yellow-legged Gull breeds in Europe mainly south of Britain, and also occurs around southern English coasts chiefly in late summer.

Although overall bird numbers are greater in autumn after a breeding season than in spring, passage migrants are not always seen in greatest numbers in autumn. This is because some species take different routes or stop for different periods at the two seasons. Examples of species which seem more prevalent in Britain in spring than in autumn include the Whimbrel and Black Tern, while other species, such as the Aquatic and Barred Warblers, are seen almost entirely in autumn and are virtually unrecorded in spring. Other migratory species seem to occur mainly as spring visitors, but these are mostly rarities from further east in Europe such as the Red-footed Falcon and Black Tern.

While in winter some species may be present in the British Isles as two or even three different populations (drawn from different breeding areas), this holds for even more species at migration times, each population behaving differently from the others. For example, at least three populations of Dunlins are present here during the autumn migration season: birds of the race *arctica* from northeast Greenland occur briefly on passage to wintering areas in West Africa; birds of the race *schinzii* from the British Isles (as well as Greenland–Iceland–south Norway) also migrate through to West Africa; while those from northern Eurasia *(alpina)* winter in the British Isles and other parts of western Europe. Similarly, Knots from eastern Canada–Greenland (race *islandica)* arrive in autumn and spend the winter here, while Knots from Eurasia (race *canutus)* occur in small numbers in eastern England in autumn en route to wintering areas in West Africa.

Other birds that are conspicuous on passage migration through the east side of Britain include many passerines which migrate between northern Europe and Iberia or Africa. These birds normally travel down the western seaboard of continental Europe, but in easterly winds many are blown over the North Sea to reach the eastern side of Britain. Bird-watchers are well aware of the conditions that lead to falls of continental migrants on the east coast, and on some days thousands of Northern Wheatears, Bluethroats, Redstarts, Pied Flycatchers and others can be seen in coastal localities (Chapter 5). Such events provide an opportunity for British bird-watchers to see species otherwise now rare here, such as the Red-backed Shrike and Wryneck, or even rarer species from further east, such as the Rustic and Ortolan Buntings. Other regular passage migrants include Sparrowhawks and Kestrels as they travel between northern and southern Europe, and in some years also Honey Buzzards.

VAGRANTS

The British Isles are well placed geographically to receive rare visitors from remote regions and, as mentioned above, such vagrants form more than half the total bird species recorded here. Some species reach the British Isles from as far away as Siberia to the east and others from Alaska to the west. Many of these species are seen on coasts and offshore islands, and several sites are famous for the rarities they attract. The best-known island site is Fair Isle, situated between the Orkney and Shetland Islands, but others include North Ronaldsay (Orkney), Foula (Shetland), Barra (Outer Hebrides), St Kilda, the Isle of May (Fife), Bardsey (north Wales), the Scilly Isles (Cornwall) and Cape Clear (southern Ireland). Favoured coastal sites include Cley and other parts of the Norfolk coast, Dungeness in Kent, Portland Bill in Dorset, Flamborough Head in Yorkshire, Holy Island in Northumberland, and headlands such as St Abbs Head (Borders), Fife Ness (Fife), Girdle Ness and Rattray Head (both Aberdeenshire), Tarbert Ness (Ross and Cromarty) and Noss Head

(Caithness). Growth in the popularity of bird-watching has continued to add increasing numbers of vagrants to the British and Irish lists, and no doubt these lists will continue to grow for many years to come.

Most species classed as rare visitors or vagrants have regular seasons of occurrence, some in the autumn or spring migration periods, and others in summer or winter. They also tend to be seen mainly in particular parts of the country, some in the south, others in the north, east or west, depending largely on their region of origin. They are discussed in Chapter 14.

ANNUAL CALENDAR OF MIGRATION

Some idea of the overall migration seasons of birds in the British Isles can be gained from Figure 40, which shows the numbers of species whose average arrival and departure dates fall at different times of year. It is based on daily counts of migrants over a number of years at Dungeness Bird Observatory situated near the southeast tip of England. With occasional exceptions, the mean spring arrival and passage periods of different species at this site are spread over a three-month period from mid-February to beyond mid-May (overall mean 9 April), while the mean autumn arrival and passage periods of different species are spread over a three-month period from early August to mid-November (overall mean 3 October). Some species show more than two weeks of spread on either side of their mean dates.

In general., short-distance (mostly partial) migrants, wintering within Europe, tend to arrive at Dungeness earlier in spring and to depart later in autumn than long-distance migrants that winter in Africa south of the Sahara, although there is overlap between the two groups (as shown for passerines in Figure 41). All species that have mean arrival dates before mid-April winter entirely or partly north of the Sahara (mainly in Iberia and North Africa), while those with mean arrival dates after mid-April winter south of the Sahara in Africa (mainly in the tropics). Among the summer visitors, the

earliest passerine species to arrive at Dungeness, with mean dates around mid-March, include the Chiffchaff, Black Redstart and Ring Ouzel, all wintering largely or entirely north of the Sahara; while the latest, with mean dates around 20 May, include the Reed Warbler and Hobby, wintering south of the Sahara. The main arrival period for most familiar summer visitors, such as Barn Swallows, House Martins, Cuckoos, flycatchers and warblers, spans the period mid-April to late May in southern parts of the British Isles and somewhat later further north.

Different species generally arrive, leave or pass through Dungeness (as elsewhere) in consistent sequence from year to year (Chapter 11). In general., summer-visiting species tend to leave the British Isles in late summer and autumn in reverse order to that in which they arrive in spring: that is, the latest to arrive are first to depart, although exceptions occur (Fig. 43). The earliest species to leave include the Cuckoo, in late July, followed by the Reed Warbler and Common Sandpiper, with mean dates around 10 August. These are followed by other warblers, swallows and martins, which leave through August and September into October. The latest summer visitors to leave, with mean dates around early October, include the Blackcap, Chiffchaff and Ring Ouzel. Among the partial migrants, the finches, pipits, wagtails and larks which winter within Europe depart mainly in September and October extending into November, leaving behind the resident individuals of their species.

As the same time as summer visitors arrive in the British Isles each spring, other species that have spent the winter here leave for their breeding areas elsewhere. This return movement may begin in late February, but increases through March and April, and in some species continues into May. It is then not long before some of these passage and winter visitors begin to return. The postbreeding movement into the British Isles begins in late June, with the arrival of waders from breeding areas lying to the north and east. Some of these species, such as the Green Sandpiper and Ruff, may be seen at almost any shallow wetland which offers damp feeding areas at this time of year, but many soon pass on further south. However, the

most conspicuous migration in late June–July is the massive influx of Lapwings that occurs from the east into Britain, although their numbers have declined greatly in the last few decades. As summer proceeds, more and more shorebirds begin to arrive, and numbers build up in coastal districts into October. Gulls also start to arrive in July and continue into autumn, with Black-headed and Common Gulls predominating.

From late September through to November, northern finches, such as Siskins and Bramblings, and thrushes, such as Blackbirds, Song Thrushes, Fieldfares, Redwings and Robins, arrive from the north and east, along with large numbers of Starlings and others. Many waterfowl arrive in these months to overwinter here, and some of the ducks continue to come into December. The autumn arrival of passage and wintering birds in the British Isles thus spans more than five months each year, from late June to early December.

Although in mild winters there is little movement beyond November, in hard winters snow and ice can drive many species westward from the continent into Britain, or from Britain west to Ireland or southwest toward Iberia. Such hard-weather movements are less frequent than in the past, but include mainly species whose food is rendered inaccessible by snow or ice, including ground-feeding plovers, gulls, starlings, thrushes and larks, and nocturnally migrating ducks, coots and inland waders (Chapter 14). Otherwise, January and February are the slackest months for migration around the British Isles.

Overall then, despite the peaks in April–May and September–October, migration around the British Isles can be seen in every month of the year, but movements in mid-winter depend largely on prevailing weather, which affects the distribution across Europe of ice-free areas where birds can feed.

AXES OF MIGRATION

As a result of the geographical spread of breeding and wintering areas, several major axes of migration occur across the British Isles, each apparent in mainly different regions and wind conditions. In autumn, the following movement patterns are evident:

- Birds migrating south-to-southeast, consisting of summer visitors, partial and passage migrants as they leave the British Isles and head towards southern Europe or Africa. These movements are especially evident on the south and east coasts.
- Birds migrating southwest-to-west, consisting of partial migrants, passage migrants and winter visitors as they head towards Ireland or southwest England. These movements are most evident in southwest Scotland, and the west coasts of England and Wales.
- Birds arriving from northern and eastern Europe, consisting of winter visitors and passage migrants, heading southwest or west into the British Isles. These movements are most evident on the Northern Isles, and on the east coasts of Scotland and England.
- Birds arriving from northeast Canada–Greenland–Iceland, consisting of winter visitors and passage migrants, heading southeast into the British Isles. These movements are most evident on the Northern Isles, the Hebrides, and the west coasts of Scotland and Ireland.

In spring these directions are reversed, as the same populations return to their specific breeding areas. In southeast England, different species can be seen migrating in opposite directions at the same times of year, as winter visitors leave for the continent and summer visitors arrive. However, two-way movements are not entirely due to different populations taking opposing directions, for many species also show ‘reverse migration’, occasionally backtracking for part of their routes (Chapter 4).

The British Isles lie within the prevailing southwesterly wind-belt associated with mid-latitude depression tracks. These continual depressions are responsible for our ever-changing weather patterns, with their marked influence on bird migration. Westerly wet and windy weather alternates for short periods with more settled weather and northerly or easterly winds. The weather at migration times can thus change from day to day and season to season, giving the great variety of migrant falls which are so familiar to British and Irish bird-watchers. Weather clearly has a major influence on the day-to-day movement patterns of birds (Chapter 5), and, in the case of rarities, whether they turn up at all.

Migration can be seen almost anywhere around the British Isles, but diurnal observations seldom do justice to the scale of the movements. This is because most migration occurs at night or at altitudes too high to be easily seen by ground-based observers. For the most part, migration is marked by the sudden appearance of species previously absent, or by the disappearance of others previously present. However, in coastal areas, diurnal migration is often spectacular, as large numbers of birds come in off the sea or fly along the coast. In contrast to land birds, most seabirds generally fly low over the waves. They can be seen on migration at the coast in almost any weather conditions, but are most obvious when onshore winds blow them within sight of land-based observers. Headlands provide some of the most productive watch points.

CONCLUDING REMARKS

The allocation of species to the different movement categories of resident, partial migrant, summer visitor, winter visitor and passage migrant (as in Appendix I) is based on knowledge accumulated mainly during the 20th century from observation and ringing. Most bird species found commonly in the British Isles lie in more than one movement category, as different populations reside, visit or pass through. Thus, although at least 140 species occur in the British Isles as winter visitors, only about 20 of these occur solely as winter

visitors, and not also as regular breeders or passage migrants. Some of the recorded movements affect only a small proportion of individuals. Detecting these movements therefore depends partly on population size, a fact that has two implications. First, some of the species listed may have other movement patterns through the British Isles as yet unrecorded; and second, species whose numbers have changed greatly over the past 100 years may appear now to have more or fewer movement patterns than previously, even though the proportions of individuals involved may not have changed. In the early 20th century, Tree Sparrows may have been common winter visitors to Britain from the continent, for they were frequently recorded in autumn on the Kentish Knock lightship in the English Channel, or seen arriving on some eastern coasts. The fact that no firm evidence for cross-channel movements has emerged in recent decades may be due to change in migratory habits or to population declines which make such movements harder to detect. On the other hand, in the early 20th century, Hooded Crows arrived over the sea into eastern counties of England in their thousands, but despite no obvious population decline in their region of origin, this immigration has now become almost non-existent, so probably reflects a genuine change in migratory habits. Clearly, care is needed in distinguishing real changes in migration patterns expected under climate and other environmental change from apparent shifts resulting from alterations in population size (Chapter 16).

Although the migratory habits of many species that occur in the British Isles are now well known from both observations and ring recoveries, this is not true of all. Some species are so difficult to catch that they are hardly ever ringed or recovered. They include mainly aquatic species, such as some northern ducks, grebes and divers, which breed on inland freshwaters and winter on the seas around our coasts. There are several relatively common species for which no useful ring recoveries have yet been obtained. However, knowledge of their movements could improve rapidly if such species were studied with radio tags or other location-recording devices

(Chapter 2). The occurrence of some species as rare winter visitors to the British Isles is known only because continental races differ in plumage colour from British ones, the Dipper and Barn Owl providing examples.

The movements of seabirds are obviously more difficult to study than those of land birds, especially in the open ocean. Ring recoveries of some species relate mainly to birds caught up in fishing gear, and maybe more representative of favoured fishing areas than of bird distributions. Other seabirds are recovered when their bodies are washed ashore, some perhaps having drifted long distances from the place of death. Again, in future years the greater use of location-recording devices is likely to yield more representative information on seabird movement patterns.

Nonetheless, without ring recoveries or other information, it is sometimes hard to know what is going on. For example, Blackcaps are found here year-round, but are much more abundant in summer than in winter. It would seem reasonable to assume that the birds found here in winter were local breeders that had stayed on: in other words, that the species was a partial migrant. In fact, ring recoveries have revealed that the summer and winter birds are drawn from different populations, the former being summer-breeding visitors mainly from Iberia and northern Africa, and the latter winter visitors from central Europe (Chapter 11). Similarly, Shovelers occur here year-round, but the summer birds mostly leave for the winter, and are largely replaced by wintering birds from elsewhere. The same seems true for Dunlin, as the local *schinzii* race leaves after breeding to winter in West Africa, while the *alpina* race moves in to winter here from further north. Similar so-called ‘chain migrations’ occur in many other species, including the Black-tailed Godwit, Redshank, Curlew, Ringed Plover and Woodcock, but do not always result in the total seasonal replacement of one population by another. Clearly, in species that are present year-round, we cannot always assume that the same individuals are involved without confirmation from ringing or other evidence.

This brief review gives some idea of the complexity and variety of bird movements evident in the relatively small area covered by the British Isles. They represent the situation in the late 20th century, and we can expect that many movement patterns will alter in the years ahead under the influence of climate change and other human impact. In addition, further improvements in understanding may emerge from new information for species as yet little studied. For obvious reasons, our knowledge is still sketchy on the species that winter in the seas around the British Isles, but this will change as more birdwatchers take to boats in search of birds, and as more species are studied using satellite tags or other location-recording devices.

APPENDIX I

Bird species occurring in the British Isles as regular year-round residents, partial migrants, summer visitors, winter visitors or passage migrants. Partial migrants refer to populations in which some breeding individuals remain year-round while others leave for the winter. The term passage migrant is used only for species that pass through the British Isles (or nearby sea areas) on their migrations, and not merely for species that pass through one part of the British Isles to reach another. Some passage migrants appear abundantly in both autumn and spring, and others in only one or other season. Categorisation is supported by ring recoveries, except for those numbered [1], for which no instructive ring recoveries are currently available, and migratory status is based on other evidence. Recently introduced alien species, all of which remain in Britain year-round, are excluded, as are scarce visitors and vagrants, and rare and irregular breeders. Brackets indicate uncertainty or small numbers.

Key: B/R = Breeding population resident year-round; B/PR-PM = Breeding population partially resident, partially migratory;

B/SV = Breeding summer visitor; NB/WV = Non-breeding winter visitor; NB/PM = Non-breeding passage migrant

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Red-throated Diver *Gavia stellata*		+		+	+
Black-throated Diver *Gavia arctica* [1]		+		+	+
Great Northern Diver *Gavia immer* [1]				+	+
Little Grebe *Tachybaptus ruficollis*		+		+	
Great-crested Grebe *Podiceps cristatus*		+			+
Red-necked Grebe *Podiceps grisegena* [1]				+	
Slavonian Grebe *Podiceps auritus* [1]		+		+	+
Black-necked Grebe *Podiceps nigricollis* [1]		+		+	+
Northern Fulmar *Fulmarus glacialis*		+		+	(+)
Cory's Shearwater *Calonectris diomedea* [1]					+
Great Shearwater *Puffinus gravis* [1]					+
Sooty Shearwater *Puffinus griseus*					+
Balearic Shearwater *Puffinus mauretanicus* [1]					+
Manx Shearwater *Puffinus puffinus*			+		
European Storm Petrel *Hydrobates pelagicus*		+			+
Leach's Storm Petrel *Oceanodroma leucorhoa*		+			+
Northern Gannet *Morus bassanus*		+		+	+
Great Cormorant *Phalacrocorax carbo*		+		+	+
European Shag *Phalacrocorax aristotelis*	+				
Great Bittern *Botaurus stellaris*	+			+	
Little Egret *Egretta garzetta* [1]		+		+	
Grey Heron *Ardea cinerea*		+		+	
Eurasian Spoonbill *Platalea leucorodia* [1]					(+)
Mute Swan *Cygnus olor*	+			+[2]	
Tundra Swan *Cygnus columbianus*				+	
Whooper Swan *Cygnus cygnus*				+	
Bean Goose *Anser fabalis*				+	

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Pink-footed Goose *Anser brachyrhynchus*				+	
Greater White-fronted Goose *Anser albifrons*				+	
Greylag Goose *Anser anser*	+			+	
Barnacle Goose *Branta leucopsis*				+	
Brent Goose *Branta bernicla*				+	
Common Shelduck *Tadorna tadorna*		+		+	
Eurasian Wigeon *Anas penelope*		+		+	
Gadwall *Anas strepera*		+		+	
Common Teal *Anas crecca*		+		+	(+)
Mallard *Anas platyrhynchos*		+		+	
Northern Pintail *Anas acuta*		+		+	(+)
Garganey *Anas querquedula*			+		
Northern Shoveler *Anas clypeata*		+		+	+
Common Pochard *Aythya ferina*		+		+	
Tufted Duck *Aythya fuligula*		+		+	+
Greater Scaup *Aythya marila*				+	
Common Eider *Somateria mollissima*	+			+	
Long-tailed Duck *Clangula hyemalis* [1]				+	
Black Scoter *Melanitta nigra* [1]		+		+	+
Velvet Scoter *Melanitta fusca* [1]				+	
Common Goldeneye *Bucephala clangula*		+		+	
Smew *Mergus albellus* [1]				+	
Red-breasted Merganser *Mergus serrator*		+		+	
Goosander *Mergus merganser*		+		+	
Red Kite *Milvus milvus*	+				
White-tailed Eagle *Haliaeetus albicilla*	+				
Eurasian Marsh Harrier *Circus aeruginosus*		+			
Hen Harrier *Circus cyaneus*		+		+	
Montagu's Harrier *Circus pygargus*			+		
Northern Goshawk *Accipiter gentilis*	+				
Eurasian Sparrowhawk *Accipiter nisus*	+			+	+
Honey Buzzard *Pernis apivorus*			+		+
Common Buzzard *Buteo buteo*	+				
Rough-legged Buzzard *Buteo lagopus*				+	
Golden Eagle *Aquila chrysaetos*	+				
Osprey *Pandion haliaetus*			+		
Common Kestrel *Falco tinnunculus*		+		+	+
Merlin *Falco columbarius*		+		+	(+)
Eurasian Hobby *Falco subbuteo*			+		
Peregrine Falcon *Falco peregrinus*	+			+	
Red Grouse *Lagopus lagopus*	+				
Rock Ptarmigan *Lagopus muta* [1]	+				
Black Grouse *Tetrao tetrix*	+				
Western Capercaillie *Tetrao urogallus*	+				
Grey Partridge *Perdix perdix*	+				
Common Quail *Coturnix coturnix*			+		
Water Rail *Rallus aquaticus*		+		+	
Spotted Crake *Porzana porzana* [1]			+		
Corncrake *Crex crex*			+		
Common Moorhen *Gallinula chloropus*	+			+	
Common Coot *Fulica atra*		+		+	
Common Crane *Grus grus* [1]	+				(+)
Great Bustard *Otis tarda*	+				
Eurasian Oystercatcher *Haematopus ostralegus*		+		+	+
Pied Avocet *Recurvirostra avosetta*		+		+	

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Stone Curlew *Burhinus oedicnemus*			+		
Little Ringed Plover *Charadrius dubius*			+		
Ringed Plover *Charadrius hiaticula*		+		+	+
Eurasian Dotterel *Charadrius morinellus*			+		+
European Golden Plover *Pluvialis apricaria*		+		+	+
Grey Plover *Pluvialis squatarola*				+	+
Northern Lapwing *Vanellus vanellus*		+		+	+
Red Knot *Calidris canutus* [3]				+	+
Sanderling *Calidris alba* [3]				+	+
Little Stint *Calidris minuta* [1]					+
Temminck's Stint *Calidris temminckii*		(+)			+
Curlew Sandpiper *Calidris ferruginea*				+	+
Purple Sandpiper *Calidris maritima*		(+)		+	+
Dunlin *Calidris alpina*			+	+	+
Ruff *Philomachus pugnax*				+	+
Jack Snipe *Lymnocryptes minimus*				+	+
Common Snipe *Gallinago gallinago*		+		+	+
Eurasian Woodcock *Scolopax rusticola*		+		+	(+)
Black-tailed Godwit *Limosa limosa*		+		+	
Bar-tailed Godwit *Limosa lapponica* [3]				+	+
Whimbrel *Numenius phaeopus*			+		+
Eurasian Curlew *Numenius arquata*		+		+	
Spotted Redshank *Tringa erythropus*				+	+
Common Redshank *Tringa totanus*		+		+	+
Common Greenshank *Tringa nebularia*		+		+	+
Green Sandpiper *Tringa ochropus*				+	+
Wood Sandpiper *Tringa glareola* [3]			+		+
Common Sandpiper *Actitis hypoleucos*		+			+
Ruddy Turnstone *Arenaria interpres* [3]				+	+
Red-necked Phalarope *Phalaropus lobatus* [1]			+		+
Grey Phalarope *Phalaropus fulicaria* [1]					+
Pomarine Skua *Stercorarius pomarinus* [1]					+
Arctic Skua *Stercorarius parasiticus*			+		+
Long-tailed Skua *Stercorarius longicaudus* [1]					+
Great Skua *Stercorarius skua*			+		
Mediterranean Gull *Larus melanocephalus*		+		+	
Little Gull *Larus minutus* [1]				+	+
Sabine's Gull *Larus sabini* [1]					+
Black-headed Gull *Larus ridibundus*		+		+	
Common (Mew) Gull *Larus canus*		+		+	
Lesser Black-backed Gull *Larus fuscus*		+		+	+
Herring Gull *Larus argentatus*		+		+	+
Yellow-legged Gull *Larus michahellis*				+	
Iceland Gull *Larus glaucoides*				+	
Glaucous Gull *Larus hyperboreus*				+	
Great Black-backed Gull *Larus marinus*		+		+	+
Black-legged Kittiwake *Rissa tridactyla*		+		+	
Sandwich Tern *Sterna sandvicensis*			+		
Roseate Tern *Sterna dougallii*			+		
Common Tern *Sterna hirundo*			+		
Arctic Tern *Sterna paradisaea*			+		
Little Tern *Sterna albifrons*			+		
Black Tern *Chlidonias niger* [1]					+
Common Guillemot *Uria aalge*		+		+	
Razorbill *Alca torda*		+		+	

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Black Guillemot *Cepphus grylle*	+				
Little Auk *Alle alle* [1]				+	
Atlantic Puffin *Fratercula arctica*		+		+	
Rock Dove/Pigeon *Columba livia*	+				
Stock Dove/Pigeon *Columba oenas*		+		+	+
Common Wood Pigeon *Columba palumbus*		+		+	+
Eurasian Collared Dove *Streptopelia decaocto*	+				
European Turtle Dove *Streptopelia turtur*			+		
Common Cuckoo *Cuculus canorus*			+		
Barn Owl *Tyto alba*	+			(+)	
Little Owl *Athene noctua*	+				
Tawny Owl *Strix aluco*	+				
Long-eared Owl *Asio otus*		+		+	
Short-eared Owl *Asio flammeus*		+		+	
European Nightjar *Caprimulgus europaeus*			+		
Common Swift *Apus apus*			+		
Common Kingfisher *Alcedo atthis*	+				
Eurasian Hoopoe *Upupa epops* [1]					+
Eurasian Wryneck *Jynx torquilla*			(+)		+
Eurasian Green Woodpecker *Picus viridis*	+				
Great Spotted Woodpecker *Dendrocopos major*	+			+	
Lesser Spotted Woodpecker *Dendrocopos minor*	+				
Wood Lark *Lullula arborea*		+		(+)	+
Skylark *Alauda arvensis*		+		+	+
Horned Lark *Eremophila alpestris* [1]				+	
Sand Martin *Riparia riparia*			+		(+)
Barn Swallow *Hirundo rustica*			+		(+)
Northern House Martin *Delichon urbica*			+		(+)
Richard's Pipit *Anthus novaeseelandiae* [1]					+
Tree Pipit *Anthus trivialis*			+		+
Meadow Pipit *Anthus pratensis*		+		+	+
Rock Pipit *Anthus petrosus*		+		+	+
Water Pipit *Anthus spinoletta* [1]				+	
Yellow Wagtail *Motacilla flava*			+		
Grey Wagtail *Motacilla cinerea*		+			
Pied/White Wagtail *Motacilla alba*		+		+	+
Bohemian Waxwing *Bombycilla garrulus*				+	
White-throated Dipper *Cinclus cinclus*	+			+	
Winter Wren *Troglodytes troglodytes*	+			+	
Hedge Accentor *Prunella modularis*		+		+	+
European Robin *Erithacus rubecula*		+		+	+
Common Nightingale *Luscinia megarhynchos*			+		
Bluethroat *Luscinia svecica*					+
Black Redstart *Phoenicurus ochruros*		+			+
Common Redstart *Phoenicurus phoenicurus*			+		+
Whinchat *Saxicola rubetra*			+		+
Common Stonechat *Saxicola torquata*		+		(+)	
Northern Wheatear *Oenanthe oenanthe*			+		+
Ring Ouzel *Turdus torquatus*			+		+
Common Blackbird *Turdus merula*		+		+	+
Fieldfare *Turdus pilaris*		(+)		+	+
Song Thrush *Turdus philomelos*		+		+	+
Redwing *Turdus iliacus*		(+)		+	+
Mistle Thrush *Turdus viscivorus*		+		+	+
Cetti's Warbler *Cettia cetti*	(+)				

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Common Grasshopper Warbler *Locustella naevia*			+		
Aquatic Warbler *Acrocephalus paludicola* [1]					+
Sedge Warbler *Acrocephalus schoenobaenus*			+		+
Marsh Warbler *Acrocephalus palustris* [1]			+		+[4]
Eurasian Reed Warbler *Acrocephalus scirpaceus*			+		(+)
Icterine Warbler *Hippolais icterina* [1]					+[4]
Dartford Warbler *Sylvia undata* [1]		+			
Barred Warbler *Sylvia nisoria* [1]					+[4]
Lesser Whitethroat *Sylvia curruca*			+		+
Common Whitethroat *Sylvia communis*			+		+
Garden Warbler *Sylvia borin*			+		+
Blackcap *Sylvia atricapilla*			+	+	+
Yellow-browed Warbler *Phylloscopus inornatus* [1]				(+)	(+)
Wood Warbler *Phylloscopus sibilatrix*			+		+
Common Chiffchaff *Phylloscopus collybita*		+			+
Willow Warbler *Phylloscopus trochilus*			+		+
Goldcrest *Regulus regulus*		+		+	+
Firecrest *Regulus ignicapillus*		+		+	+
Spotted Flycatcher *Muscicapa striata*			+		+
Pied Flycatcher *Ficedula hypoleuca*			+		+
Red-breasted Flycatcher *Ficedula parva*					+[4]
Bearded Tit *Panurus biarmicus*		+			
Long-tailed Tit *Aegithalos caudatus*	+			(+)	
Marsh Tit *Parus palustris*	+				
Willow Tit *Parus montanus*	+				
Crested Tit *Parus cristatus* [1]	+				
Coal Tit *Parus ater*	+			+	
Blue Tit *Parus caeruleus*	+			+	
Great Tit *Parus major*	+			+	
Wood Nuthatch *Sitta europaea*	+				
Eurasian Treecreeper *Certhia familiaris*	+			(+)	
Eurasian Golden Oriole *Oriolus oriolus* [1]			+		+
Red-backed Shrike *Lanius collurio*			+		+[4]
Great Grey Shrike *Lanius excubitor*				+	+
Eurasian Jay *Garrulus glandarius*	+			+	
Black-billed Magpie *Pica pica*	+				
Red-billed Chough *Pyrrhocorax pyrrhocorax*	+				
Eurasian Jackdaw *Corvus monedula*		+		+	
Rook *Corvus frugilegus*	+			+	
Carrion Crow *Corvus corone*	+			+	
Hooded Crow *Corvus corone cornix*	+			+	
Common Raven *Corvus corax*	+				
Common Starling *Sturnus vulgaris*	+			+	(+)
House Sparrow *Passer domesticus*	+				
Eurasian Tree Sparrow *Passer montanus*	+			+	
Chaffinch *Fringilla coelebs*	+			+	(+)
Brambling *Fringilla montifringilla*				+	+
European Greenfinch *Carduelis chloris*	+			+	
European Goldfinch *Carduelis carduelis*		+			
Eurasian Siskin *Carduelis spinus*		+		+	+
Eurasian Linnet *Carduelis cannabina*		+		+	(+)
Twite *Carduelis flavirostris*		+		(+)	
Common/Lesser Redpoll *Carduelis flammea*		+		+	
Common Crossbill *Loxia curvirostra*		+		+	+
Scottish Crossbill *Loxia scotica*	+				

Species	B/R	B/PR-PM	B/SV	NB/WV	NB/PM
Common Rosefinch *Carpodacus erythrinus* [1]					+
Common Bullfinch *Pyrrhula pyrrhula*	+			+	
Hawfinch *Coccothraustes coccothraustes*	+			+	
Snow Bunting *Plectrophenax nivalis*		+		+	+
Yellowhammer *Emberiza citrinella*	+			+	+
Lapland Bunting *Calcarius lapponicus* [1]				+	+
Cirl Bunting *Emberiza cirlus*	+				
Reed Bunting *Emberiza schoenidus*		+		+	+
Corn Bunting *Miliaria calandra*	+				

1. No useful ring recoveries.

2. Probably in hard weather only.

3. Mainly winter visitors in which some individuals (mostly first-year birds) stay through summer without breeding.

4. Species that breed to the east of Britain, on the continent, and migrate southeastward toward winter quarters, so would not be expected as strict passage migrants, but nevertheless occur at migration seasons, in spring apparently having ‘overshot’ their breeding areas.

Overall, 99 species fall within only one migratory category, 104 into two categories and 53 in three categories, because different populations of the same species occur as breeding, wintering or passage birds.

CHAPTER 4

Migratory Flight

The main advantage of flight, as a means of locomotion, is its speed, which is much faster than the alternatives of swimming, walking or running. Whether by flapping or gliding, flight facilitates rapid longdistance travel, and allows birds to accommodate migration as a twice-yearly event within their annual schedules. Nevertheless, birds vary greatly in the lengths and types of journeys that they can undertake, depending on their body size, wing shape, muscle power and other aspects. These various features influence the speed and mode of flight and the amount of fat that birds can carry as an internal body reserve to fuel their journeys.

BODY WEIGHT, SPEED AND FLIGHT MODE

The flight speeds of birds have often been measured using a car or airplane travelling alongside, or by using radar to track the movements of particular flocks or individuals. Radar measures are the most accurate, and can be applied directly to birds on migration. They can also be corrected to allow for wind effects (as measured by use of air balloons) and for flight altitude (as measured by the radar). Such correction makes different values more comparable, for both wind and altitude can affect the speed of flight. The flight speed of a bird tends to increase with rising altitude as the air density decreases and the bird then has to fly faster in order to generate the same forces required to support its weight and propel itself forward at lower altitudes. In addition to measured values, theoretical flight speeds can be calculated from aerodynamic

principles on the basis of body mass, wingspan and wing area (Pennycuick, 1969, 2008). These various sources of information, whether measured or estimated, all indicate that larger birds generally fly faster than small ones, although body and wing structure have an additional influence.

This relationship between flight speed and body weight arises because each unit of wing area has to carry more weight in a large bird, since the ratio of surface area to volume is less. Therefore, the air has to flow faster over the underwing surface to provide the necessary lift, which the bird achieves by flying faster. As a rough guide, 10 g birds cruise in flapping flight at around 32 km per hour, 20 g birds at around 40 km per hour, 100 g birds at around 43 km per hour and 1,000 g birds at around 54 km per hour (Bruderer & Boldt, 2001). In practice, however, species of similar weight vary considerably in their actual flight speeds, according to body and wing shape and other features. Wings vary between long-and-thin or short-and-broad according mainly to the needs of everyday life (Rayner, 1990). Largely for reasons of wing design, terns, harriers and owls fly slower than expected from their body weights, while pigeons, ducks and auks fly faster.

In addition, individual birds can vary their flight speed and wingbeat frequency according to prevailing conditions and intent, and some can also switch between different types of flight, such as flapping and gliding. The result is that some species can change their flight speeds in still air by more than threefold (Bruderer & Boldt, 2001), with wind effects adding yet further variation. And as birds change their speed and mode of flight, their power requirements change accordingly. The power is generated by the flight muscles, which are in turn fuelled from stored carbohydrate (glycogen) and fatty acids delivered to the muscles by the blood stream (Chapter 6).

Within species, power requirements do not increase in direct proportion to the speed of flight. All birds have a particular speed at which the power required for flapping flight is minimal, and flying either slower or faster than this speed is more costly (Pennycuick,

1969, 1975). This may explain why birds on migration do not usually fly at the maximum speed of which they are capable: full speed demands too much energy. Birds are likely to fly either at 'minimal power speed', which gives minimal rate of fuel use and hence maximum time airborne, or at the somewhat faster 'maximum range speed', which gives the longest distance on a given amount of fuel. These two speeds span the most useful range of flight speeds for migration, and measured flight speeds from birds in the field are generally fairly close to their estimated maximum range speeds (small birds often fly slightly faster than expected on theoretical grounds and large birds slightly slower; Welham, 1994). On migration, birds are likely to fly substantially faster than maximum range speed only in special circumstances, such as when countering a headwind or fleeing a pursuing falcon.

Power requirements in relation to body weight

Using aerodynamic models, relationships between power requirement and flight speed have been calculated for birds over a wide range of body weights. The power (P) required for flapping flight at maximum range speed increases with body mass (M) roughly according to the proportion $P = M^{1.17}$ (Pennycuick, 1975). However, because larger birds have relatively lower metabolic rates (in the proportion Mass $^{0.75}$), flight at maximum range speed is disproportionately more costly for larger birds. The power needed by a bird for flapping flight is often expressed as a function of its basal metabolic rate (BMR), which is the lowest rate of energy consumption that an inactive living bird can normally achieve. As expected from the above relationship, the power required to fly at minimum power speed or maximum range speed is a smaller multiple of BMR in smaller birds than in larger birds (varying in measured values for flapping flight from 8 to 30 times BMR).

The upshot is that small birds have more power available to them than do large birds, relative to that required to fly (Pennycuick,

1969). This in turn means that smaller species can carry relatively more fuel for migration (Hedenström, 1993). As body size increases, birds become progressively more restricted in the proportion of extra weight that they can carry, which, despite their greater speed, reduces their potential non-stop flight range. The proportionate weight of fuel that can be carried by a bird at maximum range speed has been estimated to decrease linearly with increasing body size, down to none at about 6 kg. Birds with even greater fat-free body weight than 6 kg, and carrying fuel reserves, would have to fly at speeds slower than their maximum range speed. Species with a fat-free body mass less than 750 g can theoretically double their weight through fuel deposition and still have sufficient power to fly at maximum range speed.

Effects of migratory fattening

The relationships between body mass and maximum range speed derived from comparisons between species should also hold within individual birds as they change weight through fuel deposition and use. The heavy fuel load carried by long-distance migrants provides the necessary energy, but it also obliges the birds to fly faster if they are to achieve maximum range. Birds doubling their lean body mass through fuel deposition (as some do) should theoretically increase their maximum range speed at the start of the flight by about 1.4 times. However, to achieve this, power output by the muscles must be increased about 2.8 times at the start of the flight, according to calculations by Pennycuick (1969). This increased power is achieved partly by muscle growth (Chapter 6).

During a long flight, in which body mass declines through fuel consumption, the bird would be expected to gradually reduce its cruising speed (and power output) so as to achieve the maximum possible range. Reduction of flight speed during migration has been confirmed in radio-tracked Brent Geese (Green & Alerstam, 2000). However, few birds are likely to manage to fly at their maximum range speed throughout a long flight, especially with a heavy fuel

load, which would require exceptionally hard work and might put big demands on the heart and lungs. To begin with, they are therefore more likely to fly at the slower minimum power speed.

Cutting the costs of flight

Another way in which some large birds cut their fuel costs is by flying in line or V-formation. This is usual among geese, swans, gulls, cranes, pelicans, cormorants and others. Each individual flies behind and to the side of the one in front, benefiting from its slipstream, gaining lift and reduced drag. This is possible because each bird sheds vortices from its wing-tips which gives lift to the one behind. Individuals flying in V-formation have been estimated to save 12–20 per cent on energy costs compared with birds flying alone. The lead bird has no such advantage in power saving, and frequently relinquishes its position, pulling out and joining the line further back. Other birds migrate in flocks of varying shapes, which may again save on energy costs.

Some large birds reduce their fuel costs by soaring and gliding on outstretched wings, making use of updrafts to climb and remain aloft, and gliding, losing height, from one place of updraft to another. Updrafts are mainly produced by thermals (columns of rising air caused by uneven heating of the ground) or by horizontal winds being deflected upwards off slopes and cliffs (‘orographic lift’). For some large bird species, soaring–gliding flight affords massive energy savings, as their flight costs are only 5–25 per cent of the requirements estimated for continuous flapping. The heavier the bird, the more difficulty it has in creating lift for flapping flight by muscle power alone, and the relatively greater is the energy saving from switching from flapping to soaring. This maybe one reason why soaring flight is seen mainly in large birds, such as eagles and pelicans (Pennycuick, 1975).

FLAPPING AND SOARING FLIGHT

Whether a bird flaps or soars influences many aspects of its migration. In steady flapping flight, a bird must generate the forces which support its weight against gravity and which provide the thrust necessary for forward propulsion against friction and other drag. The power for both the lift and forward thrust is supplied by the breast muscles, while directional control is provided by the wings and especially by the tail. Given sufficient fuel reserves, some birds that migrate by continuous flapping flight can travel for hours or days on end. They can cross water or other adverse terrain, and can fly by night as well as by day, and at high as well as at low altitudes. In moving between their breeding and wintering places, therefore, such birds often travel directly, taking the shortest routes. As populations, they migrate mostly on a broad front, but concentrate to some extent through mountain passes or along coasts or other 'leading lines' that deviate little from their main direction. As flapping flight uses a lot of fuel, however, such species must normally lay down substantial body reserves, especially for travelling over seas or other inhospitable areas where they cannot feed. Sustained flapping also produces heat, which may enable birds to fly at high latitudes and altitudes without having to burn extra fuel to keep warm. In hot conditions, however, heat production from continued flapping can result in the need for evaporative cooling (panting), which can prevent overheating, but only at the expense of increased water loss and dehydration risk.

It is because the lift in soaring birds comes largely from rising air currents and the forward motion partly from gravity that this still-wing flight mode requires much less internally generated energy than continuous flapping. Many soaring species use a mix of gliding and powered flight, with intermediate costs, but seek to maximise the contribution from gliding, and resort increasingly to flapping as thermal conditions deteriorate.

Soaring land birds also tend to concentrate in spectacular numbers along narrow land bridges (such as Panama), or at narrow sea-crossings (such as Gibraltar or the Bosphorus), and thereby avoid spending long periods over water where thermal soaring is

seldom feasible. They often take long roundabout routes between breeding and wintering areas in order to make as much of the journey as possible over land, and minimise the distance travelled by expensive flapping flight. Despite the greater distances, the total energy consumption by the birds is thereby much reduced. Moreover, because their travel routes are determined largely by geography and topography, soaring birds tend to take the same traditional narrow-front 'corridor' routes year after year, but may use different routes in autumn and spring. And because they usually travel low enough to be seen by ground-based observers armed with binoculars, they can be counted and studied in ways that other higher-flying or night-flying birds cannot. Systematic counts of migrating raptors and other soaring birds have been made annually over many years at a number of migration watch sites, including Falsterbo in Sweden (Kjellén & Roos, 2000).

Compared with small soaring species, such as sparrowhawks, large eagles (with greater wing-loading) have to start later in the day, when thermals are strong enough to lift them; they also tend to rise more slowly, mainly because their turning radius is greater so they spend more time near the edges of the thermals where air currents are weaker than in the centre. But having reached the top of a thermal, large species can then glide more rapidly across country than smaller species, their greater weight adding speed along a given glide angle (Pennycuick, 1975). The overall cross-country speed of soaring–gliding birds therefore depends partly on the strength and height of thermals, and partly on the body weight (or more strictly wing-loading) and aerodynamic design of the birds themselves. In general, smaller species rise faster within thermals, but travel more slowly between them than larger species, and being able to make use of weaker thermals, small species can travel for longer each day, starting earlier in the morning and continuing later into the evening. Observations largely support theoretical predictions that soaring species make more rapid progress on long migrations than flapping species of similar body mass (Hedenström, 1993; Hedenström & Alerstam, 1998). This is chiefly because

soaring species consume less energy (relative to body mass), so have to spend less time replenishing their body reserves during their journeys.

No sharp division separates land-bird species that travel by soaring–gliding flight from those that travel by continued flapping. Different species form a continuum of variation between the two extremes, depending on their body size and wing shape, and in all soaring species the ratio of flapping to gliding varies with air conditions at the time. Among birds of prey, vultures and eagles depend most on soaring–gliding, followed in decreasing order by buzzards *(Buteo),* kites *(Milvus),* hawks *(Accipiter)* and honey buzzards *(Pernis),* and then by harriers *(Circus)* and ospreys *(Pandion)*. Falcons are more active fliers, depending less on updrafts, but making use of them when available. This order of listing broadly follows the sequence of wing-loading, from lowest to highest, and the variation in wing shape from long-and-broad to narrow-and-pointed. It also reflects the dependence of these various species on updrafts, and hence the extents to which they form into concentrated migration streams and avoid long sea-crossings. It is chiefly the falcons that regularly make long ($>$100 km) flights over water, but other species do so in some parts of the world.

It is not only land birds that travel by soaring–gliding flight. Many seabirds make use of upcurrents formed either as the wind is deflected off waves, or as a wave of ‘swell’ displaces air upwards as it moves over the sea surface. Some seabirds also use ‘dynamic soaring’, which depends partly on wind speed being slowed by the sea surface. The bird first climbs into the wind, then turns to glide with the wind, gaining distance while losing height. After making a low turn in the trough of a wave, it starts the cycle again.

A bird can also make use of discontinuities in wind flow near the sea surface as it flies first behind a wave crest and then emerges for a time into unobstructed wind. At this moment, the bird tilts its body so that the temporary gust strikes its underside, providing lift, enabling further onward gliding flight (Pennycuick, 2002). This behaviour is often seen in shearwaters. Over most oceanic areas,

soaring seabirds usually fly low over the sea surface, where updrafts are strongest, and even flapping species (such as ducks) benefit from flying within a few metres of the water surface.

Summarising this section, migrating birds that travel by flapping flight have high fuel needs but can normally (a) migrate day or night; (b) use direct and straight routes; (c) cross large areas of inhospitable substrate without stopping; (d) use prior fat stores to migrate long distances without feeding and, if necessary, without resting; (e) migrate on a broad front rather than on a well-defined, narrow route; and (f) travel at high altitudes. In contrast, land-bird migrants that travel mainly by soaring–gliding have greatly reduced fuel needs, but normally (a) migrate chiefly in the warmest part of the day and not at night; (b) avoid large water bodies, and often take roundabout routes that offer good wind and thermal conditions, thereby increasing the total distance covered; (c) migrate along well-defined and relatively constant routes, some of which are taken year after year by birds from large areas; and (d) are usually limited in flight altitude by the height reached by thermals (seldom more than 1.5 km at noon over land). Because soaring migrants require less internal energy per distance covered, they can progress more rapidly on long migrations, and can travel with smaller fat reserves than flapping migrants.

Soaring-bird migration corridors

There are two main systems of migration corridors for soaring land birds travelling between Europe and Africa (Fig. 51). One converges on the narrow sea-crossing at the Strait of Gibraltar in southern Spain (the west European–West African flyway). At least 200,000 raptors of 22 species travel along part of this route, which at Gibraltar is dominated by Honey Buzzards (117,000) and Black Kites (39,000) (Bernis, 1975). The nearest significant site to the British Isles on this system of corridors is the Falsterbo peninsula in southern Sweden, which funnels raptors and other birds before they

make the short sea-crossing to Denmark, and southward through Europe.

THE ROLE OF BODY SIZE IN BIRD MIGRATION

It will be evident by now that body size sets constraints on migration in birds. With increasing body mass, costs of flapping flight increase, as do flight efficiency (energy cost per unit weight) and flight speed, but the amount of fuel (relative to body weight) that can be carried declines, reducing the maximum possible non-stop flight range. Wing design has additional influence on flight speed and efficiency, but it seems influenced as much by the needs of everyday life as by those of migration. Some large birds, such as albatrosses, vultures and eagles, can travel long distances by soaring–gliding. Although this flight mode requires much less fuel than flapping flight, as explained above, in land birds it can restrict the times and routes of travel.

The range that a bird can attain on a full load of fuel influences the distance it can fly over water or other inhospitable terrain. Large birds are not the best performers in this respect, because they are limited in the fuel they can carry, but nor are small birds, which fly too slowly. Some medium-sized birds, such as some shorebirds, can undertake the longest non-stop flights, because they can carry large fuel loads and at the same time fly fast. Both passerines and shorebirds can sustain flapping flight for up to a hundred hours (or more), but because shorebirds fly faster, they can cover greater distances in this time. These same features may also enable shorebirds to perform better under adverse winds than slower species. It is largely their wing design that enables them to fly so fast.

Bird species also vary greatly in the distance they can fly without needing to rest. Near one extreme, some grouse species can fly less than 1 km before having to land (Palmer, 1962). Near the other extreme is the Common Swift, which normally spends both day and night in flight outside the breeding season. Swifts ascend in the

evening and apparently sleep on the wing. Roosts are unknown from winter quarters, so after leaving the nest in August, young Swifts probably remain on the wing until they re-enter nest sites as pre-breeders in the following or a later year (C. M. Perrins, in Wernham *et al.,* 2002). Swifts are among the few groups of birds that also obtain all their food on the wing.

Non-stop flights are clearly limited by the body reserves available to fuel them, but well inside this limit, some birds may have to come down periodically in order to rest. Apart from extreme examples, such as some game birds, this is difficult to prove, because migrants come to ground for various reasons, including adverse weather, and not merely to rest or sleep. However, many birds appear tired on arrival from migration, and may break their journeys for several hours apparently without feeding. Individuals that arrive low over the sea are sometimes seen to collapse onto the beach or into the first patch of vegetation available. Those that are caught by bird-ringers are often found to have substantial body reserves, so have not run out of fuel. They just seem to be tired.

In many birds after a long flight, sleep may prevail over most other activities (Schwilch *et al.,* 2002b). Some Pink-footed Geese arriving in Scotland after a long flight from Iceland first drank a good deal, and then spent many hours sleeping, standing on one leg in shallow water. At times they also waded into deeper water, where they splashed and preened for long periods. Not until the next morning did some fly to nearby fields to feed (Newton & Campbell, 1970). Shorebirds after long flights have been seen to fall asleep within minutes after arrival on coastal mud flats, and to remain sleeping for several hours before feeding; while passerines after arrival from long over-water flights have been seen to rest under coastal bushes for much or all of the following day before moving on again apparently without having fed (Schwilch *et al.,* 2002b).

DIURNAL AND NOCTURNAL FLIGHT

Some birds migrate mainly by day and others mainly by night. Regular nocturnal birds such as owls and nightjars, or optional diurnal–nocturnal species such as waterfowl and waders, might be expected to migrate at night, but many normally diurnal species also migrate under cover of darkness. To judge from their eye structure, diurnal birds may have no better vision at night than do humans, but this would still enable them to fly safely through the open skies, and recognise star patterns and landscape features that might help them find their way.

TABLE A. Diurnal and nocturnal migrants among European birds

Mainly diurnal:
Divers, pelicans, gannets and cormorants, storks, herons and egrets, ibises, spoonbills, cranes, bustards, pratincoles, raptors, grouse, pigeons and doves, bee-eaters, woodpeckers, swifts, swallows and martins, jays and crows, titmice, creepers, accentors, larks, pipits and wagtails, waxwings, sparrows, cardueline finches, fringilline finches, buntings.
Mainly nocturnal:
Grebes, quail, rails and coots, bitterns, waders (sandpipers, snipe, woodcock), stone curlews, cuckoos, owls, nightjars, woodpeckers, wryneck, flycatchers, nuthatches, tree-creepers, wrens, wheatears, robins, chats, thrushes, goldcrests, shrikes, warblers, orioles, starlings.
Both diurnal and nocturnal:
Albatrosses, petrels and shearwaters, loons, flamingos, swans and geese, ducks, auks, skuas, gulls and terns, waders (plovers), swifts.

N.B. The same distinctions occur in the North American avifauna, even though many different species in many of the same families are involved, showing that the distinctions are phylogenetic rather than geographical.

Apart from soaring land birds, which depend on daytime thermals, it is not immediately obvious why particular species migrate at one time rather than another. Among passerines: crows, finches, pipits, larks, wagtails, tits, hirundines and others migrate primarily by day; while warblers, flycatchers, thrushes, chats and others migrate primarily by night (Table A). Among non-passerines: pigeons, raptors, cranes, herons and egrets migrate by day; while

cuckoos, grebes, rails and coots migrate mainly by night. Among seabirds, gannets and cormorants seem to migrate by day, and petrels and shearwaters by either day or night. Comparison of different taxonomic families reveals no obvious and consistent connection between migration times and any aspect of their ecology. Although most species within families seem similar in their migratory behaviour, occasional exceptions occur, with the tendency to nocturnal migration increasing with migration distance (Dorka, 1966). For example, most species of *Emberiza* buntings in western Europe migrate by day over short distances, but the Ortolan Bunting migrates by night over long distances, being the only west European *Emberiza* species to winter in Africa south of the Sahara. Similarly, most pigeons migrate by day over short distances within Europe, but the Turtle Dove migrates partly by night over long distances to Africa. In addition, Tree Pipits are more nocturnal than Meadow Pipits, Willow Warblers than Chiffchaffs, and Common Redstarts than Black Redstarts. In all these species pairs, the first mentioned species migrates further than the second. Nevertheless, there are still some puzzling exceptions: for example, European Robins and Goldcrests are short-distance migrants, yet still travel mainly at night.

Clearly, the division between diurnal and nocturnal in most birds cannot be taken as hard and fast. Of 147 species (from 16 bird orders) surveyed at British Bird Observatories, no species fell into an exclusively nocturnal or diurnal category, but 75 per cent of species had been recorded at night at some time, including such usual day migrants as the Chaffinch and Barn Swallow (Martin, 1990).

The main supposed advantages of nocturnal migration are that: (1) more time is left for feeding during the day, the only time that most birds can feed, so the entire journey could be accomplished more quickly; (2) temperatures are lower at night than in the daytime, which could help to prevent overheating and dehydration in warm regions; (3) humidities are usually higher at night and early morning, which could further reduce dehydration risk; (4) energy demands are lower, because it costs less to fly in cooler,

denser night air than in warmer daytime air; (5) wind speeds are generally lower at night, thus reducing the effects of headwinds or crosswinds, and vertical turbulence is less, so winds are less variable in direction, further reducing the total energy cost of flight; and (6) the likelihood of predation during flight is much reduced. The main threat to flying migrants is from falcons during the daytime (plus gulls and skuas over water), but a wide range of other raptors take migrants when they are on the ground. Owls do not normally fly high enough to encounter migrants and in any case seldom catch birds on the wing (although Short-eared and Long-eared Owls have been seen at night attacking birds dazed at lighthouses and oil rigs).

The advantages of nocturnal migration can thus be summarised as energy-saving, time-saving and risk-saving. In particular, the reduced turbulence at night must greatly lessen the energy costs of flight, especially in small birds (Kerlinger & Moore, 1989). Even diurnal migrants concentrate their flight into the first few hours of the daylight period, when turbulence is less than in the warmer middle part of the day. Among small birds, only swallows, which are adapted to fly throughout the day regardless of turbulence, seem to migrate at similar intensity throughout the daily light period. The various advantages of night-flying are so obvious that it is hard to understand why some birds migrate primarily by day (apart from those dependent on thermals). Excluding the soaring species, diurnal migrants mostly travel short distances overall, and restrict their flight to brief favourable periods. In flying by day, they also gain a clearer view of the terrain below, which may help in recognising familiar landmarks and in finding areas of favourable foraging habitat.

Radar studies have revealed that diurnal migration usually starts up to an hour before sunrise (when colour vision returns). It builds to a peak in the next three hours and then declines from late morning to early afternoon. Occasionally there is a slight resurgence in the late afternoon (Dorka, 1966; Bruderer, 1999). In contrast, night-migrating passerines mostly set off in the hour after sunset (when colour vision goes), and reach peak densities and altitudes

one or two hours later, well before midnight. The volume of migration remains high during the first half of the night, and then declines from around 2 am to mid-morning, as increasing numbers of birds settle. In addition, migrants that normally travel by night sometimes undertake 'morning flights', which start 1–1.5 hours after sunrise, and continue for up to 2 hours. Many do not follow the normal migration direction, so have been interpreted as attempts by newly arrived birds to find better feeding areas or to compensate for overnight drift (Alerstam, 1978b; Gauthreaux, 1978a; Åkesson & Sandberg, 1994; Sandberg *et al.,* 2002). Night-migrating shorebirds mostly set off in the two or three hours before sunset, depending to some extent on the stage of the tide, while waterfowl seem more variable in their takeoff times than most other birds, starting at any time of day or night, but mostly around sunset, providing winds are favourable.

By flying at night, birds lose sleep, but at migration times they are adapted to this, and the effects seem minimal. Even captive birds reduce their sleep during migration periods, without apparent ill-effect, although they often doze for brief periods during the day, and may have obvious rest periods in the late afternoon before they would normally depart (Berthold, 1990a; Fuchs *et al.,* 2006). Sometimes they close only one eye at a time, but rarely for more than 30 seconds, which suggested to the researchers 'uni-hemispherical sleep', in which only one side of the brain is rested at a time. How the Bar-tailed Godwits that fly non-stop for 7–9.5 days between Alaska and New Zealand cope with extreme sleep deprivation remains a mystery (Chapter 8).

SOCIAL FACTORS

Many bird species migrate in flocks. Through social interactions, including vocalisations, individuals of flocking species seem to communicate their readiness to migrate, and thereby synchronise their departures. Some species (notably shorebirds) display pre-flight intention movements, with intense calling, repeated takeoffs

and landings, before finally setting off. Individuals thus take off together and probably largely remain together during the flight, although they do not necessarily stay together for the next stage of the journey. Frequent calling, especially at night or in overcast conditions, may help to maintain flock cohesion and direction, and also induce grounded birds in appropriate condition to join the passing stream (Dolnik & Blyumental, 1967). Migrating in flocks may improve navigation through the collective efforts of individuals. It may also improve food-finding and foraging efficiency during stopovers, and give more effective predator detection and evasion than lone travel.

Another common advantage of migrating in flocks, mentioned earlier, is the energy-saving resulting from specific flight formations, such as the V-formation usual in geese, gulls and others, or the dense flocks of some passerines and shorebirds. Some usually solitary raptor species are also seen in flocks on migration. This may result partly from the sharing of narrow migration corridors, but individuals are clearly influenced by the behaviour of others in moving from one thermal to another. In effect, each bird watches and follows those ahead.

The benefits of migrating in flocks may explain why many birds do not start migration from their nesting places, which are scattered over wide areas, but first assemble at particular staging sites, often used year after year, and from which birds depart over a period of days or weeks. This behaviour is especially obvious in shorebirds and waterfowl, but occurs in many others, including swallows and martins, cranes, gulls, terns and shearwaters. Other normally solitary birds seemingly make special efforts to travel with others. For example, Bitterns have been seen to rise from reed beds around dusk and circle aound for up to half an hour, calling until they are joined by others, before departing on migration. Other normally solitarily heron species also travel in small groups, so this behaviour may occur in several species (Hall, 2008).

Some large bird species, such as swans, geese and cranes, travel in pairs or families within the flocks. Other waterfowl, including many

species of ducks, form pairs in winter quarters, and the male then accompanies the female back to her breeding area (Chapter 13). Despite these examples, reproductive pairing before arrival at breeding areas seems uncommon among birds, because in most species that have been studied, the two sexes behave independently when away from their breeding sites, the males arriving, on average, at least several days before the females (Chapter 21)

REVERSE MIGRATION

Migratory flights in directions opposite to those expected occur commonly in both autumn and spring. They have been explained as responses to adverse weather (with birds turning back when conditions ahead are bad), as orientation errors, or as attempts to correct previous orientation errors, wind drift or overshooting (with birds backtracking to a point en route). At coasts, reverse movements have been interpreted as attempts by birds with small fuel reserves to feed and fatten inland, where they can avoid the high competition, depleted food sources and predation risk caused by the build-up of birds near the coast (Alerstam, 1978b). To judge from recoveries of 20 passerine species ringed in southern Sweden in autumn, reverse movements varied between 9 and 65 km, and species with small fat reserves were more likely to perform reverse movements than species with larger reserves (Åkesson *et al.,* 1996). Moreover, among Chaffinches and Bramblings in the same area, the peak time of reverse movements occurred about 3.5 hours after the early morning departures in the normal direction; and the average weights of reverse migrants and of birds lingering at the coast were lower than those of birds of the same species that proceeded in the normal direction (Lindström & Alerstam, 1986).

In spring, if northward-migrating birds encounter snow or other bad weather en route or after arrival in breeding areas, they often retreat for some distance, providing that body reserves permit (Gätke, 1895; Williams, 1950; Svärdson, 1953). Many thousands of birds can be involved in such reverse movements. The birds can

advance again with the next warm front, and at times of alternating mild and cold periods, back-and-forth shuttle movements sometimes ensue until the birds can eventually settle in their nesting areas. The same occurs among birds that breed on high mountains, which having settled on their breeding areas in spring, move downslope during spells of bad weather, and back again when conditions improve. In the British Isles, Meadow Pipits provide one of the most conspicuous examples. For these various reasons, migration—particularly in spring—is not always a direct one-off movement in a consistent direction.

CONCLUDING REMARKS

The main message to emerge in this chapter is that migration involves different constraints and possibilities for different bird species. Overall body size and wing design have a large influence on what particular species can achieve on migration—their flight speeds, maximum possible fuel loads and non-stop flight distances—and whether they can travel by energy-saving soaring–gliding flight, as opposed to energy-demanding flapping flight. These features in turn influence the lengths and types of journeys that different types of birds can make, and the conditions in which they can travel.

While some species migrate largely by day, others migrate mainly at night, with all the apparent advantages of time-saving, energy-saving and predation reduction that this can provide. Particularly in spring, migration is not always a continual journey towards a goal, because birds may frequently be held up by adverse weather or for various reasons may backtrack along part of their route, only to try again at a later date. Many aspects of migratory flight bring costs as well as benefits, and the balance is drawn differently in different types of birds, according mainly to their size, shape and flight behaviour.

CHAPTER 5

Migration and Weather

Successful migration depends on weather conditions, which influence the times when birds can travel safely, the energy costs and risks of the journey, and the visibility of any celestial or ground-based cues that point the way. However, it is not easy to assess the effects of weather on the volume of bird migration. This is partly because migration depends less on the weather than on the intrinsic migratory state of the birds themselves (Lack, 1960). Conditions that in spring or autumn would lead to migration have no effect at other times of year. In addition, after a hold-up due to bad weather in the normal migration season, an improvement may result in unusually heavy passage; and after a long hold-up or late in the season, birds may take off in conditions that would earlier deter them. Moreover, birds in particular localities seldom all set off together, but over periods of days or weeks, as they become physiologically prepared, with adequate body reserves for departure. The underlying controlling factor is evidently the migratory state of the individual, which interacts with weather and other external conditions to influence departure dates. If the internal changes are well advanced, and the bird has abundant fat reserves, migration may sometimes occur under apparently poor conditions, but if the bird is less prepared, departure may occur only under especially good conditions or not at all.

The association between the weather and the volume of migration on particular days is therefore not constant through the season. Towards the end of the season, few birds may be left to migrate, whatever the weather. In addition, because species differ in body

size, flight mode and other aspects, they are affected by poor weather to different extents, some species being able to migrate in conditions that would ground others (Lack, 1960; Alerstam, 1978a; Elkins, 2005).

In the early days, another problem in assessing weather effects on migration was that researchers had to rely entirely on visual observations. But as we now know, the proportions of birds flying within sight, and the proportions coming to ground, tend to be greatest in unfavourable conditions (Lack, 1960). Thus, land-bird migrants tend to fly low in opposing rather than following winds, and to settle whenever they encounter strong headwinds, mist or rain over land. The observer equipped only with binoculars might conclude that these were the very conditions that favoured migration, a view once firmly held by some but counter to reality. Birds also tend to fly low along coasts in these conditions, reluctant to strike out over water. We therefore have to distinguish the influence of weather in promoting migration from its influence in making migration conspicuous to the ordinary observer (Lack, 1960; Alerstam, 1978a).

The advent of radar clarified the situation, because it detected migrants at almost all heights (missing only those below the radar horizon), day and night, and in all weathers. It appears that, within the appropriate seasons, migration is favoured by fine anticyclonic conditions with favourable tailwinds, and also by rising temperatures in spring and falling temperatures in autumn. In effect, at both seasons birds prefer to migrate under clear skies with following or light winds. Under these conditions, though, most birds fly too high to be seen with binoculars. Clear skies assist navigation, especially at night, by making celestial or ground-based cues more visible, while following winds reduce the time and energy spent on the journey, and the risk of being blown off course. In contrast, birds seldom take off to migrate in strong opposing winds, dense cloud, mist and rain. Opposing winds make progress difficult or impossible, cloud hampers navigation, while mist or rain can soak many kinds of birds and force them down.

Another difficulty in assessing weather effects is that different weather components tend to vary in parallel, with some occurring under cyclonic and others under anticyclonic conditions (Lack, 1960; Richardson, 1978, 1990). It is therefore often hard to tell which factors are causal and which are coincidental. However, the prevailing view, resulting from many detailed analyses, is that migrants almost certainly do not react to the general weather situation as such, but to one or more components of it, particularly wind and rain, which are the two variables likely to have most influence on flight.

An almost complete picture of autumn migration was recorded in one year near Nuremberg in Germany by use of a conically scanning pencil-beam radar (Erni *et al.,* 2002). At this site, bird migration increased in volume from early August, reached high levels between September and mid-October, and then declined. Allowing for this seasonal trend, about two-thirds of the variation in daily migration volume was explained by wind and rain. But because of the association between different weather factors, migration volume was also correlated with change in temperature, pressure and cloud cover. It was more closely correlated with the duration of rain than with the overall amount per night. After short heavy showers, birds continued migration, whereas on nights with continuous drizzle, migrant densities remained low.

Around the British Isles, as elsewhere, the likelihood of strong bird migration on particular days within the season can be predicted from examination of synoptic weather maps of the kind published in newspapers. The atmosphere around northern Europe is organised into high- and low-pressure systems which move approximately eastward. Winds blow clockwise around high-pressure systems and anti-clockwise around low-pressure systems. The air masses within these systems are separated by fronts: warm fronts where advancing warm air is replacing cold air, usually east or southeast of an approaching low; and cold fronts where cold air is replacing warmer air, usually south or southwest of a low. Precipitation and thick cloud occur most commonly near lows and fronts.

Migration timing can be related to these large-scale atmospheric features, even if birds react only to their local manifestations. At our latitudes, peak southward migration tends to occur with cool northerly tailwinds as a 'low' moves away to the east, or a 'high' approaches from the west, or both. Conversely, peak northward migration tends to occur with warm southerly tailwinds, as a 'high' moves away to the east, or a 'low' approaches from the west, or both. At both seasons, much migration also occurs with light winds near the centre of a high (Richardson, 1990). In the southern hemisphere, different (but related) trends are seen, because winds there blow in the opposite directions to those in the northern hemisphere around lows and highs. The proportions of days that are favourable for migration clearly vary greatly from region to region, from year to year, and from autumn to spring in the same region.

The importance of temperature to migration is uncertain. In spring, warmth occurs in association with other conditions favourable to flight, as does cold in autumn. But temperature may have direct effects through influencing the energy balance of the birds, and more importantly through influencing food supplies, because all vegetative growth, insect activity and ice melt are temperature-dependent. It is therefore of obvious advantage for migrants to adjust their migratory schedules to year-to-year variations in temperature, and they are clearly deterred in spring by extreme cold and snow. It is also uncertain to what extent (if at all) migratory birds can predict the weather before it arrives, say by a change in barometric pressure. Bird movements in autumn and spring have been correlated with changes in pressure, associated with an approaching front (Richardson, 1990; Dau, 1992). Whether the birds were reacting to pressure as such or to associated weather variables is hard to say, but other findings suggest that birds have some sort of pressure sense (Chapter 12).

Observations of birds at departure are consistent with the findings from radar studies. Takeoff occurs most often on nights with good visibility, bright stars, no overcast, no rain, and with light or following winds, these conditions being more influential in long-

distance than in short-distance migrants (Cochran & Kjos, 1985; Bolshakov & Bulyuk, 1999). In some species, individuals usually take off singly without preliminary activity (Hebrard, 1971). Passerines leaving from trees and bushes at dusk at first flutter uncertainly upwards, in ones and twos or small parties, and then, climbing all the time, proceed confidently in the direction of travel. In other species, departure can be noisy and impressive, as flock after flock takes wing and heads into the distance, climbing till out of sight.

Regardless of the weather at takeoff, migrants can encounter poor conditions en route. If they meet low cloud and unfavourable wind, birds may be forced low and, if over land, they can settle and wait for conditions to improve. When over the sea at not too great a distance, they can turn around and return to land. Further out at sea, as radar has revealed, land-bird migrants that enter cloud or mist banks usually become disorientated, milling in all directions and gradually drifting or actively flying downwind. This behaviour gives a good chance of reaching clearer weather (Williamson, 1955; Lack, 1960; Richardson, 1978). If cloud persists, migrants over the sea are sometimes attracted in large numbers to lighted ships or oil rigs (Bourne, 1979, 1983).

Although heavy overcast appears inimical for migration, some birds seem to maintain more or less straight courses with complete cloud cover. Below the cloud they can see the ground, and above it the sun or stars (although flying above the cloud seems infrequent). The survival of land-bird migrants over the sea is likely to depend largely on their abilities to cope with adverse weather and off-route displacement. Once en route, the best course of action for a bird is likely to depend on prevailing circumstances, the strength and direction of the wind, and particularly on whether the bird is fat or lean, and over favourable or unfavourable terrain.

THE IMPORTANCE OF WIND

In general, wind speeds are stronger at midday than at night or early morning; they increase with altitude from the ground, where friction slows the wind, up to several thousand metres. In addition, the air mass in which birds migrate is continually changing in speed and direction, and birds must repeatedly adjust their behaviour if they are to reach their predetermined destination in the most energy-efficient way. That birds respond to wind is evident from the findings that: (1) they tend to depart only in favourable (following) winds; (2) they often select flight altitudes where winds are favourable; and (3) they often compensate for wind drift, at least to some extent.

Migrants that are about to set off on a long sea-crossing seem to pay more regard to weather than those making short overland flights. This was apparent, for example, in the departures of two races of Northern Wheatears from Heligoland Island in spring. Birds of the Greenland race (O. *o. leucorrhoa)* had to face a longer non-stop flight than those of the smaller European race (O. *o. oenanthe)*. With an overcast sky and headwind, few *leucorrhoa* left the island, whereas many *oenanthe* departed in less than ideal conditions. Only when sky and wind were favourable were no differences between subspecies observed in the percentage of birds departing (Bairlein, 2008).

Wind assistance is like food or fat reserves: it is a resource that fuels migration. If a bird with a given flying speed in still air was blessed with a tailwind of the same speed and direction as itself, it could in theory fly up to twice as far (with respect to the ground) on the same fuel and in the same time, or the same distance on about half the fuel and in half the time. Yet a bird flying into a headwind of the same speed as itself could make little or no progress, however great its fuel reserve. In practice, it seems from radar studies that birds flying over land do not behave in quite this way, but fly slower than usual (with respect to the air mass) with a tailwind, and faster than usual against a headwind (Bellrose, 1967; Liechti, 2006; Hedenström *et al.,* 2005). It is as though they conserve energy when conditions allow, and expend more than usual when necessary, but

further study is needed. In any case, following winds reduce the energy cost of migration, which is important to many migrants. But where following winds exceed the birds own flight speed, they also bring risks, especially over inhospitable terrain. For if the wind changes direction, birds are then unable to maintain their preferred flight direction; and if their body reserves dwindle or conditions deteriorate, they cannot easily return. Small-bodied slow-flying species obviously face the greatest risks from adverse winds.

The problem of crosswinds

If a bird encounters a wind that deviates from its intended track, it can in theory correct for this by adjusting its heading so as to remain on track with respect to the ground (Fig. 60). Birds do not then progress in the direction they are heading, but at some angle to it, which is closer to the intended track. The greater the crosswind component for a given flight speed, the greater this compensating angle must be (aircraft pilots refer to the angle between heading and track as the drift angle, *alpha)*. This angle can be reduced if the bird flies faster. The point at which a bird is no longer able to compensate for lateral drift is thus a function of wind speed and direction, as well as the maximum flight speed that the bird can maintain (Evans, 1966). Two main types of drift can be distinguished in migratory birds. One type occurs when a bird flies along a fixed heading towards its destination, and is drifted from that heading by side winds (called full lateral drift). The second type occurs when the bird compensates for side winds, but only partly (called partial drift). In a third situation, the bird compensates fully, so stays on track despite the wind and does not drift off course. As radar studies have revealed, all three situations are commonly seen among migrating birds.

In addition, birds could minimise the effects of crosswinds in ways other than by immediate lateral compensation. For example, they might allow themselves to be drifted partially at high altitudes and then correct for this by overcompensation at low altitudes, as they

approach the end of their flight. By flying high at the start of the flight they gain the advantage of faster winds at those altitudes, even though their direction might not be ideal. They then make the correction later in the flight under weaker winds that prevail at lower altitudes (Fig. 61). Alternatively, if winds shifted direction predictably along a migration route, as is common at latitudes 25–35°N, birds could allow themselves to be drifted in one direction at the start of a flight and in the opposite direction towards the end. This seems to occur in some overseas flights, in which selection of appropriate wind conditions at departure could be much more important than for birds over land. Many birds fly from northeastern North America directly over the Atlantic to the West Indies or South America (Williams & Williams, 1990). In autumn, the passage of a cold front brings favourable winds blowing south-southeast that trigger departure. Once over water, as radar has shown, the birds continue flying south-southeast. When they encounter the trade winds near 25°N, their tracks are drifted to the south and south-southwest as they pass over the Caribbean. This drift is essential if birds are to reach South America, unless they redirect their heading en route. By not compensating fully for wind drift on the first part of their journey, the birds achieve a faster and more energy-efficient migration to latitudes where wind direction changes, which then allows them to compensate for their previous drift in an energy-efficient manner. They are able to follow the pattern in Figure 61, making no obvious compensation, because crosswinds change normally from one direction to the opposite direction along the route. At the time of spring migration, the winds are in the same direction as in autumn, yet the birds must fly in the opposite direction. They make their northward journey further to the west over land, a safer route, so that their entire two-way migration follows a clockwise loop, southward over the sea and northward over the land.

Despite the effects of crosswinds, some birds can maintain remarkably straight tracks on migration, at least where ground-based features are visible. During a radar study of migrating

waterfowl in Denmark, individual flight trajectories of bird flocks showed minor zigzag patterns rather than straight lines (Desholm, 2003). Analysis of these continual small changes in flight directions showed that geese and Common Eiders were flying, on average, only 0.7 per cent and 1.6 per cent longer distances than if they had flown along exact straight lines. The frequent small changes in flight direction could have resulted from birds repeatedly compensating for wind drift as they travelled towards their goal.

Weather affects soaring land birds in some of the same ways as other birds. Wind strength and direction influence the number of soaring birds that migrate on particular days, their travel routes, flight altitudes and speeds. Low dense cloud and rain suppress migration altogether. To provide ideal migration conditions, however, different wind directions and temperatures are needed at different sites, depending on local topography, and on the importance of thermals as opposed to updrafts from slopes. Compared to other birds, soaring species depend more on the interaction between wind and topography than on wind alone. In addition, thermals cannot form in strong winds which, in the absence of other updrafts, bring soaring-bird migration to a standstill, however favourable the wind direction. Hence, on some days that are ideal for most migrating birds, soaring species may be grounded. Soaring birds also show no particular tendency to migrate on cold days in autumn, as do many other birds, probably because the necessary thermals develop best on warm days (Alerstam, 1978a; Kerlinger, 1989).

The same occurs under easterly winds in spring, when species that do not breed regularly in Britain, but which are heading for Scandinavia, such as the Red-spotted Bluethroat and Icterine Warbler, maybe deflected across the North Sea. Again, large numbers of birds may sometimes be involved, including rarer species with more easterly distributions, such as the Red-throated Pipit and Rustic Bunting. At least one species, the Red-footed Falcon, is much commoner as a drift migrant in Britain in spring than in autumn, probably because it is a ‘loop migrant’ whose spring

migration route through Europe lies far to the west of the southward autumn route.

ALTITUDE OF MIGRATION

To judge from radar studies, most birds migrate within 1.5 km of the ground, with decreasing numbers at higher altitudes up to 3 km or more (Eastwood, 1967; Bruderer, 1999). When birds need to cross high mountains or find favourable airstreams, they sometimes fly much higher (Fig. 64). Radar studies in central Europe have also shown that migration occurs at generally higher elevations in spring than in autumn and by night than by day. However, these differences may depend on the particular wind conditions at the time, and may not apply everywhere.

Wind has a major influence on the height above ground at which birds fly, for it can change in direction as well as strength, affecting the choice of cruising height. This is strikingly illustrated by the trade winds, which higher up give way to the anti-trades blowing in the opposite direction. This situation allows birds to find following winds in both autumn and spring, providing they fly at an appropriate height. In southern Israel, the shift from trade to anti-trade winds fluctuates around 1.5 km. Birds studied by radar flew mainly below this level in autumn and mainly above it in spring, when some reached heights of 5–9 km above sea level. In the low-level jet streams of this region, birds also achieved ground speeds of up to 180 km per hour, far faster than they could ever fly in still air (Liechti & Shaller, 1999).

Waders leaving the West African coast for Europe in spring must climb rapidly to altitudes greater than 3 km, for it is only at these heights that tailwinds keep the flight costs within reasonable bounds, thereby enabling the birds to complete their 4,300 km non-stop flight to the Dutch Wadden Sea coast (Piersma, 1990). Similarly, radio-tagged thrushes tracked on migration in North America ascended as much as 3 km each evening until they found suitable winds (Cochran & Kjos, 1985). If they failed to find

favourable winds, they returned to the ground, and did not migrate that night. Their migration therefore seemed to involve the adoption of a constant heading, and mitigation of wind drift mainly by altitudinal adjustment rather than by lateral compensation. With weak winds, however, they flew lower and accepted some lateral drift. In regions with little altitudinal variation in wind direction, birds can only wait for favourable conditions.

In the absence of slopes to deflect wind upwards, soaring birds are limited in flight altitude by the height reached by thermals, which is greatest around noon over land, and in most conditions seldom exceeds 1.5 km. During their migrations, soaring birds are continually rising and falling, as they climb in successive thermals and lose height while gliding between them (Leshem & Yom-Tov, 1996b; Spaar & Bruderer, 1996). Unlike many other birds, therefore, they do not maintain constant altitude over long distances.

Apart from wind, the main weather factor affecting the altitude of migration is the cloud base. Most birds fly below the clouds where they can see the ground, so if the cloud descends, the migration stream is compressed downwards, reducing the average flight altitude. However, birds sometimes fly above the clouds, presumably relying entirely on celestial or magnetic cues for navigation, with no visual reference to the ground below. Migration streams can also be compressed laterally as they are funnelled through mountain passes, or concentrate along coasts, river valleys or other ‘leading lines’, when birds may fly at low levels even without cloud cover.

Consequences of high-altitude flight

As they ascend from ground level, migrating birds face progressively changing conditions. Wind speed increases, while air density, oxygen availability and temperatures decrease. Once birds break through the cloud layer, however, they can escape from mist, rain and snow. Air densities and associated oxygen levels decline by just over 10 per cent for each 1,000 m rise in altitude, which roughly

translates to a 27 per cent decline at 3 km, 41 per cent at 5 km and 65 per cent at 10 km, with minor temporal and regional variations. The decline in air density means that, in theoretical still air, birds have to work harder to keep aloft at high altitude, but meet less resistance to forward flight. The maximum range speed increases by an estimated 5 per cent for each 1,000 m rise in altitude (Alerstam, 1990a), but so does the power required to fly at this speed, which in turn entails a corresponding increase in energy and oxygen consumption. Although there may be no gain in overall flight range, it is still advantageous to fly high because stronger winds and reduced turbulence at high altitudes may reduce the energy costs and flight times. Other advantages of high-altitude flight include: (a) a wider view of the ground (which may help birds to stay on course and maintain a straighter track); (b) avoidance of obstacles and deflection by mountains; and (c) reduced predation risk as birds rise above the zone where falcons and other aerial predators normally hunt.

One cost of high-altitude flight, already mentioned, is the climb involved. This is a major effort for heavy species such as swans, although some of this cost maybe offset towards the end of the flight, as the birds gain distance while losing height. Climbing capacity becomes critical to Brent Geese during spring as they attempt to cross the 2,500 m high Greenland icecap (Gudmundsson *et al.,* 1995). These birds leave Iceland with enough fuel to reach their breeding areas in northeast Canada 2,600–3,500 km away. Five radio-marked individuals were tracked by satellites to west Greenland. Their climbing rates were extremely low, only 0.01–0.06 m per second, reflecting the severe limits to their flight power when carrying large body reserves. Their average movement up the ice slope was so slow (on average only 2.5–14.0 km per hour) that the geese must have stopped frequently on the way up. Their downward journey was of normal speed, 29.5–54.7 km per hour, indicating a more or less uninterrupted descending flight. Not all birds crossing high-altitude areas would have the option of resting en route, because suitable habitat may not be available.

Low-level flight

Species that migrate by night at high altitude often seem from their radar tracks to be little influenced by the terrain below; they usually fly on broad fronts and often cross mountains and coastlines without deviation. In such species, the need to reduce time or energy expenditure may have led them to take the shortest routes across barriers, even at the cost of increased risk (such as severe weather). In contrast, birds which migrate by day often fly fairly low (within visual range) and react to the presence of topographical features, such as mountains or coastlines. They may form into streams as they fly along shorelines or river valleys, or become funnelled through mountain passes. The compromise between time-saving or energy-saving direct routes on the one hand and longer risk-reducing detours on the other maybe drawn differently in different species, according to their flight capabilities and refuelling needs, the length of their journeys, and the habitat and weather expected en route.

Most of our understanding of weather effects on migration is based on radar studies which, as explained above, can provide less biased information on mass migration than any other method. Nevertheless, observations show that some low-level flight (below the radar horizon) occurs under headwinds and other conditions that inhibit higher-level flight. In these situations, many small birds migrate by 'bush-hopping' or 'tree hopping', in which they flit from bush to bush or from tree to tree, feeding as they go, but travelling continually in the same direction. Warblers, which normally migrate at night, sometimes pass in daytime through extensive bushy or reedy areas in this way, as do tits and other canopy-feeding passerines as they move through woods. Many small birds also fly low for short distances in the gaps between showers. They take more account than highflyers of topographical features, being more deflected by hills and lakes, and in strong winds they take advantage of shelter provided by slopes or forests. In these ways, small birds can maintain some progress on days when they might not otherwise travel because of strong headwinds or insufficient

body reserves. By their combination of flying and feeding, these small passerines resemble swifts and hirundines that forage as they go. But as headwinds increase, fewer and fewer birds take part in the migration, as species after species drops out. Some land birds also habitually fly low by day: for example, Barn Swallows which pick off insects rising from vegetation, or harriers which hunt on the wing as they go.

Clearly, the costs and benefits of flight at different altitudes vary with circumstances, as well as between species, and the physiological constraints under which they operate. Considering all the different external factors, along with the variations in body mass, shape and flight mode between species, it is not surprising that different types of birds seem to fly at mainly different altitudes: sea ducks just above the waves, songbirds mostly up to 1.5 km and shorebirds often at more than 3 km. Even on the same night, geese migrating over southern Sweden flew at 100–800 m, while shorebirds over the same site flew at up to 3.7 km above sea level (Green, 2004). The altitude of migratory flight thus differs between species, as well as varying according to wind speed and direction, cloud thickness and height, time of day or night, topography and other factors.

Descending from migration

When landing from migration, not all birds lose height steadily like an aeroplane. Instead, they drop almost vertically from high altitude into habitat below, as described long ago on Heligoland Island by Gätke (1895). Similarly, on Cyprus, small nocturnal migrants were seen to ‘drop like stones from the sky at first light and immediately dive into cover’ (Bourne, 1959); while on the Louisiana coast in spring, migrant passerines were seen to descend nearly vertically from more than 1 km, producing ‘a whizzing sound as they pulled out of the dive just above the trees’ (Gauthreaux, 1972). Such ‘fallout’ occurs in other circumstances, as when migrating birds are confronted by a sudden downpour, and literally drop from the sky

to seek refuge. Thousands of birds seem to come from nowhere, settling in trees and bushes or carpeting the ground. Geese have a particular form of flight, known as ‘whiffling’, through which they lose height rapidly when over their destination, and this behaviour is seen not only on migration but also as they return to their night roosts.

CONCLUDING REMARKS

Weather clearly has major affects on bird migration. It influences not only whether birds migrate at all on particular days, but also their behaviour during flight, and their cruising altitude. The huge day-to-day fluctuations in the volume of bird migration reflect the continual adjustment of bird behaviour to prevailing conditions. But what are the overall advantages in birds responding so much to wind? In conditions prevailing in central Europe in autumn, a bird migrating only on nights with favourable wind can, on average, increase its flight speed by 30 per cent compared with an individual that disregards wind (Liechti & Bruderer, 1998). Selecting the most profitable flight altitude may result in a further 40 per cent gain in flight speed. In other words, by reacting appropriately to wind conditions, and taking advantage of favourable tailwinds, a bird can greatly increase its flight speed and reduce its energy use during a journey through this region. The time needed for refuelling decreases accordingly, or the safety margins provided by the body reserves are extended. The bird is also at less risk of being blown far off course. Clearly, there are great benefits to a migrant in responding appropriately to wind and other weather variables, selecting whenever possible the best days on which to travel.

CHAPTER 6

Fuelling the Flights

AT TIMES OF MIGRATION, many birds put on extra body fat and other reserves for use as fuel, the amount depending on the type of journey. When birds migrate over favourable terrain, they tend to progress by short flights, each lasting up to several hours, using relatively small amounts of fuel which are replaced during the daily periods of foraging. But when birds migrate long distances over inhospitable areas, they accumulate much larger body reserves, able to sustain them for up to several days and nights without feeding. The accumulation of such large body reserves may take small birds one to three weeks of intensive feeding, and before departure over sea or desert, individuals may have more than doubled their normal weights. The patterns of energy storage shown by long-distance migratory birds reveal some remarkable adaptations.

ENERGY NEEDS AND BODY COMPOSITION

The most important migratory fuel is fat, which provides much more energy per unit weight than protein or carbohydrate, the only other potential fuels a bird can use. On breakdown, 1 g of fat will yield around 9.2 kilocalories of energy, while 1 g of protein yields 1.3 kcal and 1 g of carbohydrate about 1.0 kcal (Table B). Weight for weight, therefore, fat contains seven to nine times more energy than other potential fuels, and provides the greatest energy return for the smallest weight gain. When oxidised within the bird, fat also yields an equal weight of water, and both energy and water are

needed on long-distance flights. Moreover, fat can be stored as adipose tissue without the need for extra water or protein, and can be metabolised with less loss of heat and body glucose than is required in the breakdown of protein or carbohydrate. Fat is not the perfect fuel, however, for its metabolism requires the breakdown of small amounts of protein to provide enzymes for the chemical processes involved (the citric acid cycle). In addition, while most tissues in the bird's body can extract energy from fat (or fatty acids), some cannot and rely instead on carbohydrate or ketone bodies (a reduced form of fatty acids). Such tissues include the brain and nervous system, blood cells and kidney medulla.

Pre-migratory weight increase also involves deposition of additional body protein, but not necessarily in consistent ratio to the extra fat. Typically, as a bird gains weight, the ratio of additional fat to protein increases, although there is considerable variation between individuals of a species (Redfern *et al.,* 2000, 2004). Beyond this effect, however, species vary greatly in the relative amounts of fat and protein accumulated. In some species, the weight increase consists of roughly equal amounts of fat and protein, but in other species it can comprise up to ten times as much fat as protein. This variation may result simply from differences in diet or metabolism between species. But it may also represent an adaptation to the different types of journey birds make, or relate to the needs of the time, as the same species can differ in body reserves between seasons. For example, the 40–50 g mass gain by 200 g European Golden Plovers during stopovers consists almost entirely of fat in autumn, but mainly of protein in spring. These birds have different needs at the two seasons. They face energy deficits in autumn and winter when they eat mainly protein-rich earthworms, but they risk protein deficits in spring, for after arrival in their arctic breeding areas they eat mainly berries left from the previous year but must soon produce eggs (Piersma & Jukema, 2002).

TABLE B. Energy and water yield of the three main fuel types in birds. *Note*: One kilojoule (kJ) is equivalent to 0.24 kilocalories, and a kilocalorie is popularly called a 'calorie' in human dieting. (Modified from Jenni & Jenni-Eiermann, 1998)

	Lipids in adipose tissue	Protein in skeletal muscle or digestive organs	Glycogen
Energy density (kJ g^{-1}) in dry mass	39.6	17.8	17.5
Energy density (kJ g^{-1}) in wet mass	37.6	5.3	3.5–4.4
Water content (%)	5	70	75–80
Metabolic water production (g water per g dry matter)	1.05	0.39	0.56
Total water production (g water per g wet tissue)	1.10	0.82	0.89–0.91
Water produced (g water per kJ expended from wet mass)	0.03	0.16	0.21–0.25

The third source of energy, carbohydrate, is stored as glycogen in the liver and muscle tissue, but when some birds prepare for migration, they change from using mainly glycogen for energy to using mainly fat (Dolnik & Blyumental, 1967; Jenni-Eierman & Jenni, 1996). At migration times, therefore, carbohydrate is of relatively minor importance as an energy source. The highest glycogen values reported from birds amount to no more than about 3 per cent of liver mass and about 0.5 per cent of total body mass (Marsh, 1983; Blem, 1990). Despite being stored 'wet', glycogen in such small amounts is also of little value as a water source.

Total body reserves

An idea of the amount of fuel deposited by migratory birds can be gained from their body weights (comparing individuals at different

stages of fattening; Fig. 70), and from their ‘fat scores’ based on the yellowish fat that can be seen through the skin of a live bird when the feathers are blown aside. Most researchers record the fat in the furculum (wishbone), which appears as a V-shaped hollow at the base of the neck. Such scores do not necessarily bear a consistent relationship to the total fat in the bird’s body, but they can be recorded from live birds without harm, and can be compared within species. In geese, the shape of the belly changes as they deposit fat, so an indication of fat content can be gained by noting the ‘abdominal profile’ as the birds walk around (Madsen & Klaassen, 2006).

More detailed studies of fuel deposition have involved analyses of bird carcasses in order to assess accurately the relative proportions of fat, water and lean dry material (the latter comprising mainly body protein, feathers and skeleton). Such studies have shown how the body composition of particular species changes during the migration season, and how these changes vary between species, according to the journeys they make. In general, all species seem to accumulate body protein as well as fat at migration times, but because fat is stored in anhydrous form, the overall proportion of water in the bird’s body declines with increasing fat content. These findings are far removed from an earlier notion that the entire weight increase in migratory birds was due to fat.

Costs and benefits of body reserves

As the body mass of a bird increases, so does its flight speed and its potential flight range, but not in constant proportion, because the fuel itself requires energy to synthesise, maintain and transport. So as body reserves increase, so do the flight costs per unit distance travelled (Pennycuick, 1989; Lindström & Alerstam, 1992). In addition, extra fuel makes a small bird more cumbersome and often less able to evade predators. This is another reason why birds do not put on more extra body weight than necessary. Even the slight weight increase shown by small birds during the course of a normal

day greatly reduces their lift-off speed and manoeuvrability, and birds accumulating large amounts of migratory fat suffer much greater impediment (Witter *et al.,* 1994; Metcalfe & Ure, 1995; Lind *et al.,* 1999; Burns & Ydenberg, 2002). In one experiment, captive Blackcaps were exposed to simulated predator attacks and filmed as they attempted to flee. It was found that individuals carrying a fuel load equivalent to 60 per cent of lean body mass (the most recorded in this species) suffered a reduction of 32 per cent in angle of ascent and 17 per cent in velocity compared with lean Blackcaps (Kullberg *et al.,* 1996). This degree of effect could put fat birds at substantially greater risk. One might suppose, then, that migration should ideally consist of short flights, frequent fuelling and low fuel loads, with the alternatives of long flights, infrequent fuelling and heavy fuel loads resorted to only when necessary.

Not all birds suffer from weight increase if they have alternative means of avoiding predators, such as camouflage and 'freezing', as shown for example by Northern Wheatears in the presence of a Sparrowhawk (Chapter 23). For these species, the risk of predation presents less of a constraint on the amount of fuel the birds could safely carry. On the other hand, some species, such as flycatchers and accipiters, may depend so much on agility to catch their prey that they are limited in the amount of extra weight they can carry. They have to travel light, and adopt some sort of migratory strategy that avoids heavy fattening.

Alternative strategies

Without special reserves, small birds could not survive much more than a day without food, but they could travel in this way on short flights lasting a few hours, followed by feeding. However, large birds, such as swans, geese and eagles, can normally survive for several days without food, so in theory they could travel for longer periods without prior fuel deposition, making up at a later date. Most soaring species obtain most of the energy needed for migration from the ambient atmosphere, and generally accumulate relatively

small amounts of fuel for overland flight. In fact, no pre-migratory fattening is apparent in White Storks at either season, despite migrations of up to 10,000 km (Berthold *et al.,* 2001). These birds feed as they go, mainly in the mornings and evenings, and travel in the middle part of the day, when the thermals that permit soaring–gliding flight are best developed. But they face large stretches of the journey, notably through deserts, when they could not expect to feed for two to three days. They presumably lose weight at such times, and make up afterwards. In contrast, cranes also travel partly by soaring–gliding flight, but accumulate substantial body reserves (up to one-third of body weight) during the several weeks they spend at favoured stopover sites (Krapu *et al.,* 1985).

While most bird species must stop migrating in order to feed, species such as swallows and swifts that depend on aerial prey items can pick up food as they go. Although they do not necessarily make the entire journey without pausing to refuel, an ability to catch and eat food on the wing could enable them to migrate with smaller body reserves and make faster progress than other birds of similar size. Swifts are normally on the wing all year both day and night, except when they have nests to tend, so in this respect their migration could be little different from normal daily life. Moreover, birds that feed on aerial insects do not necessarily depend entirely on local food sources. Many insects drift passively on wind currents, while others migrate over long distances at similar altitude to birds, with regular diurnal and nocturnal species. The extent to which migrating birds use these millions of migrating insects to fuel their journeys is unknown, but swifts and nightjars would seem ideally equipped to catch high-flying butterflies and moths.

Some raptors and shrikes may also be able to get food at places offering little for other species, if only by catching and eating their fellow travellers. Bird-eating falcons and accipiters travel with their prey species, and skuas with the terns they rob for food. These are all species which depend on agility to catch their prey, so as they accumulate body fat, they may become increasingly constrained in their ability to obtain further food. It is not hard to imagine,

therefore, a continuum of variation among birds in which some populations migrate entirely on prior body reserves, others entirely on a continually replenished deficit, and yet others on both.

DURATION OF STOPOVERS

It is tricky, even with marked individuals, to estimate how long birds stop and feed at sites en route. We seldom know how long each bird has been present at a site before it is recorded or how long it stays on afterwards. Nevertheless, at some sites, arrival and departure dates can be recorded with reasonable certainty, and at others, birds can be caught at frequent enough intervals for their stopover periods and turnover rates to be estimated using statistical models (Kaiser, 1999). It emerges that many birds at many sites stay less than one day, and may not even feed at such times. They move on rapidly. Others may stay for several days building up body reserves. Examples of stopover periods recorded in trans-Saharan migrants are given in Figure 73, from studies at an oasis in the Sahara desert. While these periods may have been typical at this site in autumn, they would not necessarily be expected in the same species at other sites where birds face shorter flights through more favourable terrain, or in spring when their behaviour may differ. However, these records refer to songbirds, but for larger birds equipped with tracking tags, stopover periods can be recorded accurately and do not need to be estimated from re-trapping or re-sightng records.

The most obvious way for a bird to increase its daily energy intake is to eat more. The amount of food that can be consumed per 24 hours is influenced partly by the feeding efficiency of the bird itself, but also by external conditions such as daylength, food availability and the pressures imposed by competitors and predators. Hyperphagia (eating more than needed to maintain a stable body weight) is evident especially in captive passerines, which at migration seasons suddenly begin to eat around 25–30 per cent more per day than usual (range 10–50 per cent). This promotes

mean weight gains of up to 10 per cent per day, occasionally up to 20 per cent. On a 20–30 g bird, with a fattening rate of 1.0–1.5 g Per day, the accumulation of sufficient fat for a long flight may take between four and ten days. The bird may increase its energy intake in various ways, including feeding more rapidly or for longer than usual each day, or by selecting from potential foods the most calorific and easily digestible items. But the most obvious way in which a diurnal bird could conserve feeding time is to migrate at night. This may not increase feeding time over what is usually available, but it at least prevents potential feeding time being reduced by flight time. Some waterfowl and waders are able to feed by both day and night, and can thus achieve higher rates of food throughput than other birds, and correspondingly higher rates of fuel deposition (Zwarts *et al.,* 1990). In the wild, feeding times of coastal waders are normally limited by tidal rhythms, but at high tides when mud flats are flooded, some species feed in nearby fields or inland marshes.

Rates of energy intake in birds are often measured as multiples of basal metabolic rate (BMR), which is the amount of energy consumed by a bird of that species at rest and not digesting a recent meal. At normal daily activity, birds consume energy at a rate equivalent to around 2 x BMR, but when fattening they can consume energy at higher rates, the record for a wild species being the 5–7 x BMR recorded in spring for Red Knots (Atkinson *et al.,* 2007). However, with food available round-the-clock, various captive wader species achieved maximum daily energy intakes that were six to ten times higher than their BMRs (Kvist & Lindström, 2003). These figures give some idea of the rapid rates at which some birds are able to accumulate the energy required to fuel their journeys.

Changes in gut structure and digestive capacity

Another type of constraint is imposed by digestive efficiency which, regardless of the rate of intake, limits the amount of food that can

be processed per unit time (Diamond *et al.,* 1986; Klaassen *et al.,* 1997). Again, birds might maximise throughput in various ways, such as ensuring that food is always present in the crop, ready for passage down the gut as soon as space becomes available, or increasing the throughput rate so as to digest food less thoroughly but in greater quantity than usual, or by modifying gut structure so as to digest food more rapidly. At migration times, some birds increase the size of the digestive tract, or adjust its structure to better deal with particular types of food. Such amazing changes usually occur over a few days, and have been noted in several migratory species from songbirds to geese (McLandress & Raveling, 1983; Jordano, 1987; Bairlein, 1996; McWilliams & Karasov, 2005; Piersma, 2007). Studies on captive Blackcaps *Sylvia atricapilla* confirmed that the rate of energy assimilation under freely available food was proportional to the size of the intestinal tract and liver (Karasov & Pinshow, 2000).

Change of diet

Another way in which birds can increase their calorie intake is to concentrate on easily digestible, energy-rich food items. Many songbirds eat fruit at the time of migratory fattening. They include not only regular fruit-eaters, such as *Sylvia* warblers, but also others not normally considered as frugivores, such as the Pied Flycatcher, Yellow Wagtail and even House Martin (Brookes, 2008). This change of diet does not occur simply because fruit is more available than insects in late summer, because captive birds, given a choice of insects or fruit, also select fruit then. Most fruits contain high proportions of carbohydrate and unsaturated fatty acids that can be easily converted to body fat. The main drawback of most fruits is that they are poor in protein (mostly 1–7 per cent of dry mass), the few exceptions including Olive *Oleo europaea* (8 per cent protein) and Elder *Sambucus nigra* (12–18 per cent protein), both of which are relished by birds (Jenni-Eiermann & Jenni, 2003).

Another advantage of feeding on fruit is that it can be obtained more easily than insects and other invertebrates. It is concentrated, predictable and conspicuous, and requires little time and effort to obtain. Requiring less agility than foraging for insects, it may enable birds to carry more body fat than they otherwise could. It is also quick and easy to digest, and its high water content may reduce the need to drink. Interestingly, many songbirds that remain insectivorous at migration times prefer insects that are rich in fats (such as caterpillars) or carbohydrates (such as aphids), and these birds can at times show fattening rates as high as those of fruit-eaters. This holds, for example, in Sedge Warblers feeding on aphids (Bibby & Green, 1981). Other warblers on spring migration prefer nectar over insects, presumably for similar reasons.

It remains unclear to what extent other types of birds change their diets at migration times for reasons other than availability. Nevertheless, shorebirds, gulls and cranes have all been seen eating fruits before autumn migration, and many species of ducks change from plant material to invertebrates before spring migration, which would provide more protein (Arzel *et al.,* 2006).

Reducing expenditure

As well as increasing energy intake during migratory fuelling, birds can also lessen expenditure by reducing their daily activity. The switch from insects to fruits, for example, may lead to reduction in the energy spent on foraging movements. Birds may also lower their metabolic rates and body temperatures when sleeping at night, thereby conserving energy, and migrant hummingbirds usually become torpid at night, even when very fat for migration (Carpenter & Hixon, 1988). Barnacle Geese showed a progressive reduction in mean daily abdominal temperature (down to 44°C below usual), beginning just before departure on migration and continuing, on average, for about three weeks (Butler *et al.,* 2003).

Combined measures

Many bird species clearly employ more than one of these measures to facilitate migratory fuel deposition. For example, Garden Warblers at migration time were found to eat up to 40 per cent more per day (in terms of energy content), and switch from a mainly insect to a mainly fruit diet (often Elder *Sambucus niger* at northern latitudes and figs *Ficus* at Mediterranean latitudes). They also increased their digestive and assimilation efficiency, which accounted for another 20 per cent increase in energy intake at migration time (Bairlein, 1985b, 1991a). This increased efficiency was achieved by an increase in gut weight, and in the rate at which fatty acids were synthesised in the liver. In contrast, no such change in digestive efficiency was found in seed-eaters, the extra calories for fuel deposition being obtained entirely from longer feeding periods (King, 1961, 1972; Gifford & Odum, 1965).

DAILY RATES OF WEIGHT GAIN

Repeated trapping of migrants in the days before departure has provided information on their individual rates of weight gain (Fig. 75), from which average and maximum rates have been calculated for different populations (Alerstam & Lindström, 1990; Lindström, 2003). Average daily rates of pre-migratory weight gain in 58 bird populations ranged from less than 1 per cent to more than 7 per cent (maximum 13 per cent) of their lean body weights. Rates varied greatly among individuals, and exceptionally high individual rates were recorded on particular days, but were not sustained over longer periods.

CHANGES IN BODY COMPOSITION

In birds making long uninterrupted flights, the muscles and internal organs can undergo considerable changes in size. Before departure, exercise organs (pectoral muscle and heart) gradually enlarge, while

at a later stage nutritional organs (stomach, intestine and liver) tend to shrink. These changes make sense on long flights where feeding is impossible and weight reduction is at a premium. But while in some species the digestive tract is reduced immediately *before* the flight, in others it is apparently reduced *during* the flight, contributing to the fuel and water needs of the migrant on its journey. Changes in body structure occur not only at the start of the journey, but also at each major stopover. Evidently, a bird on long-distance migration is not like an aeroplane landing, refuelling and taking off again. Unlike the plane, a long-distance migrant partly reconstructs its body at each stopover, switching between flying to feeding and then back to flying modes (Piersma, 1998).

Body changes during migration have been studied in detail in the Garden Warbler, a trans-Saharan migrant which can increase its body mass from 18 g in summer or winter to a maximum of about 37 g shortly before setting out over the desert in autumn or spring (Bairlein, 2003). Pre-migratory weight gain typically takes 10–14 days, with mean rates of 0.7–1.0 g per day, and maximum rates at 1.5 g per day (10 per cent of lean body mass), depending on the food available. By comparing Garden Warblers caught in autumn in Turkey (just before a southward Mediterranean–Saharan flight) with others caught in spring in Sinai (just after a northward Saharan flight), it was concluded that about 70 per cent of the loss in body mass during migration comprised fat, while the rest was protein and associated water (Biebach, 1998). The protein came mostly from the digestive tract, which lost 39 per cent in weight, but partly from the breast and leg muscles, which lost 19 per cent. Overall, 5.1 g fat and 2.2 g protein were used on this trans-Saharan flight in approximate ratio of 2.3:1. Assuming a flight of 2,200 km and a mean weight loss of 7.3 g, this gave a mean weight loss of 3.3 g per 1,000 km flown—a similar estimate to the 3.6 g per 1,000 km calculated for this species at other sites (Bairlein, 1991b). After a trans-Saharan flight, it took one to two days before gut function and metabolic intake returned to pre-flight level, and two to three days for the digestive tract to recover its size (Biebach, 1998). This was consistent with a

more general finding that, after arrival at stopover sites, long-distance migrants often do not gain weight for one to three days, and may even lose weight in this period. The mean weight loss in eleven passerine species studied after arrival was 4.4 per cent, with a range of 0–13 per cent (Alerstam & Lindström, 1990). This could be regarded as the reconstruction period.

The degree of weight loss during a migratory flight is likely to vary not only with the length of journey, but also with wind and other conditions. In another study of Garden Warblers migrating north over the Sahara in spring, Biebach & Bauchinger (2003) estimated a generally lower rate of weight loss of 1.8 g per 1,000 km, but obtained more detailed information on the loss from particular organs (Fig. 76). The most pronounced weight reduction took place in the liver (57 per cent) and gut (50 per cent), followed by the flight muscles (26 per cent), heart (24 per cent) and leg muscles (14 per cent). By reducing the size of organs before or during a flight, Garden Warblers were estimated to save around one-fifth of the energy they would have needed if they had shown no organ reduction. About 34 per cent of this saving came from protein breakdown, 22 per cent from reduced tissue maintenance costs and 43 per cent from reduced flight costs (resulting from reduced weight). Savings were estimated to be roughly the same whether birds flew continuously or intermittently (flying at night and resting by day). A similar ranking of organ reductions was found in Pied Flycatchers, Willow Warblers and Barn Swallows (Schwilch *et al.,* 2002a), and may well occur in other species that cross the Sahara. Organ flexibility in birds may thus have evolved largely on the basis of energy savings, which in migrants may in turn lengthen the maximum flight range.

The fact that nutritional organs are not fully functional on arrival after a long flight may also explain why some migrants, on reaching a stopping site, do not appear to feed. Such short-time stoppers simply rest, and depart later in the day or at night (Rappole & Warner, 1976). Typically, they are less specific in their habitat use than feeding birds, and individuals of normally territorial species

make no attempt to establish a territory but sit around in groups. They are in flight mode rather than feeding mode, and it may be more energy-efficient for them to move on while reserves last rather than to reconstruct digestive machinery and start to feed again before this becomes essential.

Body reserves for survival and breeding

In most bird species that have been studied, individuals were found to arrive in breeding or wintering areas with residual body reserves not totally used on the journey (Fransson & Jakobsson, 1998; Widmer & Biebach, 2001; Morrison, 2006; Krapu *et al.,* 2006). For example, in the sub-arctic environment of Swedish Lapland, long-distance songbird migrants arrived with enough fat to fly an estimated further 242–500 km, depending on species, while short-distance migrants arrived with lesser amounts (Sandberg, 1996). These residual body reserves varied greatly between individuals, however, and from year to year in the same population.

Considering the energy cost of transporting body reserves, why do birds carry more than they need? Extra reserves might act as insurance against emergency situations, such as food shortage or bad weather en route; they might enable migrants to fly faster than the most economic flight speed (maximum range speed); or they might help to ensure survival after arrival, especially in spring when local food supplies may still be scarce. At this time, they might also enable newly arrived males to concentrate on territory acquisition, or females to produce eggs earlier than otherwise possible (Chapter 23). Or they may serve more than one of these various functions.

It is at high latitudes where the potential breeding season is short that the advantage of body reserves maybe greatest, especially if they enable birds to start nesting earlier than they otherwise could. This applies particularly to large species, which generally have long breeding cycles and are therefore most pushed for time. In some waterfowl, reserves accumulated in wintering and migration areas, and especially at the last stopover site, help the female to form eggs

and to survive through incubation (Newton, 1977; Ebbinge, 1985). Arctic-nesting geese often arrive before vegetation has begun to grow in their breeding areas, and when little food is available. In scientific jargon, they are described as ‘capital breeders’, because they reproduce largely on the strength of existing body reserves. They contrast with ‘income breeders’, which reproduce on the strength of food eaten at the time. In different goose populations, weight gains of 25–53 per cent have been recorded before the birds set off on spring migration or from staging sites en route (McLandress & Raveling, 1981). This is a lot for birds of this size. Typically, females accumulate more weight than males, in association with the needs of egg production and incubation (in which males do not participate, except in nest-guarding). Although large body reserves on arrival are necessary for successful reproduction in some populations of geese, they do not guarantee it, because other things can go wrong. Nevertheless, in the same population, females with larger body reserves generally show better reproductive success than females with smaller reserves (Chapter 23). Both fat and protein are used during egg-laying and incubation, and geese also rely largely on internal mineral reserves (in bone) for eggshell calcium.

The most detailed studies have involved North American species. Among Canada Geese wintering in Minnesota, males and females increased their body weights by 26 per cent and 36 per cent respectively in the month before spring migration. Carcass analyses revealed that the weight gain of males comprised 47 per cent lipid, 13 per cent protein and 35 per cent water, while that of females comprised 61 per cent lipid, 10 per cent protein and 21 per cent water. Initial weight gain was predominantly protein (and accompanying water), probably contributing to gut enlargement, while most of the later weight gain was due to fat. These reserves were judged sufficient to cover migration and maintenance after arrival in the breeding areas, egg-laying and incubation by females, and territorial defence by males (McLandress & Raveling, 1981).

At least some populations of high arctic geese, such as the Dark-bellied Brent Goose, Lesser Snow Goose and Ross's Goose, can start egg-laying two to five days after arriving in their breeding areas, before plant growth has begun, by relying entirely on body reserves. Their eggs begin to form during migration. In Lesser Snow Geese, the relationship between body reserves and reproductive output was studied from females shot at various stages of breeding in the Northwest Territories of Canada (Ankney & MacInnes, 1978). The potential clutch size of pre-laying females was determined by counting the number of large vascularised follicles in the ovary, and females with larger body reserves had, on average, larger potential clutches. Yet females collected after laying clutches of different sizes had residual reserves of similar size to one another. The authors concluded that clutch sizes of these geese were determined by the levels of prior nutrient reserves: females with the largest reserves laid the most eggs. Breeding females used most of their remaining fat and protein reserves during incubation (85 per cent and 24 per cent). Late in incubation when they had depleted their body reserves, some females left their nests to feed, while others were found dead on their nests, apparently having starved. Hence, like the Canada Geese mentioned above, female Lesser Snow Geese reproducing successfully in this area had to accumulate enough body reserves to support the last stage of migration, egg production and maintenance during the four weeks of incubation. Only after hatch were they able to feed intensively again, and build up body reserves for the return migration to wintering areas. Similar findings have emerged for other species (Chapter 23).

Stable isotope analyses of eggs provides additional means of telling whether eggs are produced from food eaten in breeding areas or from food eaten in migration and wintering areas. The method depends on the fact that foods eaten in different habitats or different regions have different isotope ratios, and that these differences are reflected for a time in bird body tissues and eggs (Chapter 2). Such analyses confirmed that Lesser Snow Geese were largely capital breeders, with reserves accumulated mainly south of breeding areas

(Klaassen, 2003). In contrast, Greater Snow Geese nesting on Bylot Island, Canada, seemed to obtain most of their protein and fat requirements for egg production after arrival in breeding areas (Gauthier *et al.,* 2003). Other populations of geese that depend partly on reserves and partly on current intake include the Greater White-fronted Goose *A. a. frontalis* and Dusky Canada Goose B. c. *occidentalis* in Alaska (Budeau *et al.,* 1991; Bromley & Jarvis, 1993). Hence, among different populations of arctic-nesting geese, considerable variation exists in the extent of reliance for reproduction on post-migration residual body stores.

Much of this variation may depend on the availability of suitable staging areas en route, on the distance between the last staging place and the breeding place, and on the length of the snow-free season in the nesting locality concerned. Where food becomes available through ice melt relatively early in the season, there is less need for geese to depend so heavily on imported body reserves. Otherwise, these birds gain in the long run from transporting the necessary body reserves to the breeding grounds despite the energy costs of doing so, because they can then start nesting early in the season. Geese in several populations seem to increase in body weight during the course of spring migration, putting on more weight at successive staging areas than was lost in the flights between them.

How much the strategies found in different studies represent inherent responses by the geese is uncertain, but individuals are clearly not rigidly tied to specific patterns of behaviour. Some Pink-footed Geese were seen to change their use of different spring stopover sites according to their breeding success the previous year: geese that failed in one year tended to change their use of sites the following year, which in turn had knock-on effects on fattening patterns (Madsen, 2001).

Some duck species also depend for reproduction at least partly on body reserves accumulated in wintering or migration areas, as found for example in the Mallard and Northern Shoveler (Krapu, 1981; Heitmeyer, 1988; MacCluskie & Sedinger, 2000). However, other

ducks accumulate most of the necessary reserve after arrival in breeding areas, as found for the Common Eider (Korschen, 1977). Among Northern Pintails *Anas acuta* nesting in Alaska, individuals that arrived with the largest residual body reserves started nesting earlier and produced larger clutches than individuals with smaller reserves which produced small clutches later in the season (Esler & Grand, 1994). As in geese, particular species seem to vary from region to region in the extent to which they depend on body reserves for egg production, and in the degree to which these reserves are accumulated in wintering and migration areas, as opposed to breeding areas.

Unlike geese and those ducks which feed on vegetation, waders depend largely on animal matter. Invertebrate food items from tundra and estuarine habitats differ in carbon and nitrogen isotope ratios. In several wader species nesting in arctic Canada and Greenland, carbon isotope analyses showed that egg protein was formed from terrestrial rather than marine foods, and hence was influenced by food eaten after arrival in tundra breeding areas (Klaassen *et al.,* 2001). On the other hand, in another study, eggs in the earlier clutches of Red Knots and Turnstones in the northeastern Canadian Arctic were rich in those isotopes of carbon and nitrogen expected if marine nutrients had been used in their production (Morrison & Hobson, 2004). They could only have come from residual body reserves accumulated before the birds had reached their inland nesting areas.

Capital and income breeding evidently represent opposite ends of a continuum of variation found among birds. Species and populations may vary in the contribution that body reserves make to reproduction, as may individuals within the same population. Populations also vary in where on the migration route between wintering and breeding areas they acquire the reserves for breeding. Larger species, in which clutch weight forms a small proportion of total body weight, are much more likely to rely heavily on body stores for egg formation than are small species in which the clutch weighs as much or more than the female herself. The body reserves

that small passerines and shorebirds carry to their breeding areas can provide at most a minor contribution to the total protein and fat needed for clutch formation, but they may help with initial survival and reproductive activities, as mentioned above.

These various studies highlight the ability of birds to change their body composition rapidly, according to the varying extents to which they depend on previously accumulated body reserves for breeding and the varying stages of the journey at which such reserves are accumulated. It is remarkable that some birds can lay down body reserves for both migration and breeding at the same time, and that they transport reserves hundreds or thousands of kilometres from wintering to breeding places. They do this in order to produce young early enough to exploit the seasonal peak of food at high latitudes and have their young ready to migrate before winter sets in. It is also remarkable that birds can shift protein from one body organ to another, as the muscles and digestive organs change their relative sizes before and after flights. Although less research has been done on the condition of birds when they arrive in wintering areas, studies indicate that residual body reserves are usual there too, and can influence subsequent survival (Chapter 23).

FAT DEPOSITION IN NESTLINGS

In most migratory bird species, fattening for the first journey of life does not begin until after the young are full-grown and able to feed themselves. In some species, however, the young fatten while in the nest on food provided by their parents, and then migrate on their own within a few days after fledging. They include many seabirds, notably various petrels *(Procellariiformes),* in which the single nestlings reach peak weights that greatly exceed the adult weights. Thereafter, they receive little or no additional food from their parents and lose weight until they leave the nest. The young continue to grow their feathers after their parents desert them, but are still extremely fat when they first fly. This fattening of seabird nestlings has usually been regarded as an insurance to tide the

young over difficult times until they learn to feed themselves. However, in many such species, the young set off within a few days after fledging on long journeys for which fuel reserves are almost certainly needed.

Take the Manx Shearwater as an example. At their peak body mass, at around 50 days, the young weigh around 20 per cent more than the adults, and are extremely fat, from which point they are fed at a much reduced rate. After about ten more days, the young leave for the sea and thereafter have no further contact with their parents (Harris, 1966). Some 36 hours after they were ringed on Skokholm Island off Wales, some recently fledged shearwaters were recovered several hundred kilometres to the south, in the Bay of Biscay. Within six weeks, many others were recovered in the seas off Brazil, more than 9,000 km across the Atlantic Ocean. One was found, an estimated three days after it had died, on the coast of Brazil 16 days after having been ringed at the nest. Even if it had left immediately, this bird made a 9,600 km journey at a speed of at least 740 km per day (Perrins *et al.,* 1973). Another young bird was recovered in the Canary Islands, presumably en route to Brazil, six days after it was ringed on Skokholm, having flown an average of at least 460 km per day. These flights must have required substantial fuel reserves, for they left little time for feeding by such inexperienced birds and also involved crossing warm tropical seas poor in nutrients. Judging from the estimated fat content of the young, and the likely energy costs of their migration, the young could have made the 9,000–10,000 km flight entirely on their body reserves (Perrins *et al.,* 1973). These reserves may not only support the young during their first migration, but may also allow their parents in the late nestling period to divert food to building up their own body reserves and so to migrate earlier than otherwise possible.

Like petrels, young Northern Gannets also become very obese before fledging, reaching around 30 per cent heavier than adults, and carrying around 1 kg of fat in a total body mass of 4 kg. The young leave the nest before their flight feathers are fully grown, but can glide up to 5 km from the colony (Nelson, 1978; Wanless &

Okill, 1994). Once on the sea, they seem unable to take off again, at least for several days, by which time they have lost further weight, and gained more feather growth. They swim long distances during this period; but once they become airborne, they travel further afield. Six young gannets that were caught on the sea before they could fly were recovered 10–16 days later at distances of 394–2,483 km (Wanless & Okill, 1994). They had mean rates of travel of 15.1–155.2 km per day, similar to those of many other birds on migration (Chapter 7). Again, these birds were unlikely to have covered the longer of these distances without substantial fuel reserves.

The young of some land-bird species also migrate immediately after they leave the nest, and without further parental support. An example is the Common Swift, in which the young also fly at weights that often exceed those of adults (Lack, 1956). One individual was recovered in Madrid three days after it left the nest in Oxford, having covered at least 1,300 km (C. M. Perrins, in Wernham *et al.,* 2002). Clearly, migratory fat deposition occurs not just in full-grown birds, but in some species it is an integral part of nestling growth.

CONCLUDING REMARKS

In this chapter, we have touched on some of the most remarkable adaptations found in long-distance migratory birds. One is their ability to fuel high-intensity endurance flight with fatty acids that are stored in adipose tissue and delivered continuously to the working muscles by the blood stream, a facility exceptional among vertebrates (McWilliams *et al.,* 2004). In addition, for rapid fuel deposition, birds have various ways of temporarily raising their daily energy intakes. They include an extension of feeding times (sometimes into night-time), nocturnal migration to leave the day for feeding, a switching of metabolic emphasis from carbohydrate to fat, a change of diet, and an increase in the size of the liver and digestive tract. All these temporary changes permit rapid deposition of additional body fat and protein just before migration. Fat has

several advantages as the predominant migratory fuel: it yields the highest concentration of metabolic energy per unit weight; it can be stored dry without accompanying water or protein; it can be metabolised more efficiently than protein or carbohydrate; and it can be oxidised efficiently by most body tissues, including the all-important flight muscles, which can work for long periods without tiring.

For the migratory flights themselves, adaptations include the increase in size of flight muscles and heart, reduction in size of digestive organs, and the metabolism of body protein to supply essential enzymes and other compounds. These changes in the body structure and composition of birds at migration times are some of the most rapid and striking in the animal kingdom. Along with the selection of favourable wind conditions discussed in Chapter 5, these are all ways in which birds can increase the efficiency of their migrations. They are mostly measures that birds can take for short periods only, because they also have costs, and conflict with other activities or with requirements at different stages of the annual cycle. They nevertheless enable some bird species to perform extreme journeys that would otherwise be impossible, or to carry body reserves from one region to facilitate reproduction in another far away. What remarkable creatures birds are.

CHAPTER 7

Migration Speeds

How long do birds take over their migrations and at what speeds do they travel? In most species, migration consists of periods of rest and feeding when body reserves are accumulated, interspersed with periods of flight when these reserves are used. Both activities need to be taken into account in assessing the overall speed and duration of a journey. On long migrations, it is the repeated replenishments of body reserves, rather than the flight periods themselves, that have most influence on the times taken. Except on non-stop journeys, therefore, how fast a bird can fly bears only limted relationship to the overall speed of migration.

The periods that different bird populations spend on their travels depend largely on the distances involved and the conditions encountered. At one extreme, some birds can complete their migration in less than a day (as shown by a radio-tagged Bald Eagle in North America which flew the entire 435 km journey within one day; Grubb *et al.,* 1994). At the other extreme, some land birds take more than three months to reach their distant winter quarters, and a similar period to return, so that they spend more than half of every year on migration. Some seabirds, including many shearwaters and petrels, have a fixed base only during the breeding season, and are effectively on migration for the rest of the year, pausing to feed wherever they encounter food. While some birds may benefit from migrating as quickly as possible, they are often constrained by external conditions. Food availability influences their fuelling rates, and prevailing weather can speed or slow their journeys. Adverse

winds, rain or cold can sometimes delay migrating birds for days or weeks at a time.

Information on the migration speeds of birds has come from three main sources. First, we have the records of individual birds ringed and recovered on passage. Such records are available for a wide range of species, but carry the risk of error because it is seldom known precisely when a ringed bird leaves one place or arrives in another. The temptation is therefore to use only the fastest records, as an indication of maximum possible migration speeds. Not only do such records then come from extreme individuals, they often also cover only part of a migratory journey.

Second, we have population-based records from successive places on a migration route. Such records provide more representative data on average migration speeds. They have come mainly from calculating the mean geographical positions of ring recoveries obtained from a defined breeding population at successive dates through a journey. If recoveries of birds already on migration were centred in mid-October at latitude 30°N, say, and those in mid-November due south at latitude 20°N, then an average of one month would have been needed to cover the distance spanned by 10° of latitude. Similar estimates can be made from the dates that particular populations pass through different watch sites or trapping sites along a migration route, or from the dates that museum skins were collected at different places en route. In using such records, we have to bear in mind that many species can break their autumn journeys for weeks at a time if conditions are favourable, much longer than is needed merely to replenish their body reserves.

Third, we have the details from individual birds that were fitted with radio transmitters or other location tags and tracked on their journeys. Such records probably provide the most reliable information on individual migration speeds and, with daily records of position, they enable flight periods to be separated from stopover periods (although in practice, short breaks of a few hours are easily missed). As yet, such data are available only for birds big enough to

carry tracking devices, and bear the assumption (probably in most cases justified) that migration is unaffected by the device itself.

None of these three sources of information reveal the duration of the initial fuelling period before birds leave their breeding or wintering areas. To judge from recorded rates of weight gain, small passerines take from a few days to three weeks over this process, while long-distance waterfowl can take up to two months or more, depending on the length of the subsequent flight and the body reserves required. This period could be considered as part of the migration, but it can be determined only by separate study.

MIGRATION SPEEDS FROM INDIVIDUAL RING RECOVERIES

Individual migration speeds were calculated for various passerines and waders that were ringed on autumn passage in Fennoscandia, and recovered 10–50 days later at points on their migration routes. From these and other records for individual ringed birds, the following generalisations emerge:

1. Including stops at staging areas, waders migrated more rapidly than passerines, giving a median speed of 79 km per day, based on 13 species (Alerstam & Lindström, 1990). Not only do waders fly faster than passerines, they are also more selective of days with favourable winds, and migrate at higher altitudes where winds are stronger. Waders can also feed at night in suitable tidal conditions, which could facilitate more rapid fuelling (Chapter 6). In moving between successive staging areas, waders typically fly 500–1,000 km in one to two days, interrupted by stops lasting up to several days, whereas passerines typically migrate over land almost every day, maintaining a more even speed, with shorter flights and shorter stops. Maximum speeds of 400–1,000 km per day have been recorded from waders, compared with 200–300 km per day from passerines.

2. Among passerines, species that left early in the migration season made faster progress than those that left later (Fig. 78). The early departing species were long-distance migrants that wintered in Africa south of the Sahara (median speed 75 km per day, 13 species); species that left in mid-season travelled shorter distances and wintered mainly in the temperate zone of Europe (median speed 53 km per day, 19 species); and those that left latest were partial and irruptive migrants that travelled short but varying distances within Europe (median 27 km per day, 11 species). This seasonal trend in migration speeds could result from seasonal declines in food supplies or daylengths, leading to
3. In association with the above relationships, migration speeds were correlated with the length of journey (Fig. 85). Juvenile passerines travelling 1,000 km on autumn migration covered about 80 km per day, on average, whereas those travelling 5,000–6,000 km covered about 140 km per day (Alerstam, 2003). Long-distance migrants that left early in the season seemed to migrate in longer steps, and were more selective of good weather conditions. Most migrated by night, using time for flying that would otherwise have been spent at roost, without reducing the time available for foraging. Nocturnal migrants thus travelled at a median speed of 72 km per day (17 species), compared with 53 km per day in diurnal migrants (6 species). In addition, mean flight lengths on migration were longer in nocturnal (177 km) than in diurnal migrants (111 km) (Ellegren, 1993).
4. Despite their faster migration speeds, Eurasian–Afrotropical migrants, with mean migration distances of 6,000–10,000 km, still travelled for much longer autumn periods (median 88 days, 13 species) than regular short-distance migrants (median 42 days, 10 species, distances 1,700–3,000 km), or than partial migrants (median 32 days, 11 species, distances 200–300 km).

5. Extremely rapid migrations were recorded in some individuals of long-distance passerine migrants. For example, one Willow Warbler travelled 8,000 km from Finland to Congo within 56 days, a mean speed of 145 km per day (Hildén & Saurola, 1982), while another Willow Warbler travelled from Finland to South Africa in 47 days, a mean speed of 218 km per day (Hedenström & Pettersson, 1987). A Marsh Warbler travelled 1,400 km within Africa in five days, an average of 280 km per day (Cramp, 1992); and three Barn Swallows travelled average distances of 250, 350 and 433 km per day over journeys of 8,500, 12,000 and 3,000 km respectively (Turner, 2006). However, all these records were exceptional, most individuals of their species progressing much more slowly.
6. The decline in migration speed with lateness of departure date did not apply within species. On the contrary, late migrants tended to progress more rapidly than early migrants of the same species, at least in the initial part of the autumn journey. This trend would enable birds that were delayed in their departure from breeding areas to 'catch up' to some extent during their journey. For example, Blue Tits migrating along the southern Baltic coast (from one ringing station to another) travelled an average of about 28 km per day between 15 and 24 September, increasing significantly to about 38 km per day between 15 and 24 October (Nowakowski & Chruciel, 2004). Similar seasonal trends in migration speeds have been described in various other passerines (Chapter 10).
7. In some species, adults travelled faster than juveniles. For example, adult Dunlins took an average of 4.5 days to travel 660 km, while juveniles took an average of 13 days over the same journey (Hildén & Saurola, 1982). A similar age-related difference held in various *Sylvia* warblers migrating in autumn from northern Europe (Fransson, 1995). By the time they start migrating, juvenile birds appear 'full-grown',

and in this respect as well equipped for migration as older birds. Their slower migration may be due in part to their inexperience and lower feeding efficiency.

Three main conclusions emerge: waders migrate faster than passerines; early migrating passerine species migrate faster that later ones; but within species, late-departing individuals migrate faster than early ones. This seasonal trend, together with age differences, contributes to great variation in migration speeds within species. As a rough guide, we can say that small birds which migrate within Europe take 4–6 weeks to reach their wintering areas, while those that migrate to Africa south of the Sahara take around 8–12 weeks. These generalisations are based on ringing data from autumn studies of passerines and waders, while similar records for other species await analysis.

AVERAGE MIGRATION SPEEDS FROM POPULATION-BASED RECORDS

Average estimates are more useful than those obtained from individual flights, because they derive from many individuals and not just a few extreme ones. They indicate that Barn Swallows complete the 10,000 km journey between northern Europe and southern Africa at an average speed of at least 150 km per day (as against selected recoveries of ringed individuals which indicate exceptional speeds of up to 340 km per day) (Alerstam & Lindström, 1990). Other estimates of average speeds relate to Spotted Flycatchers between southern Africa and Fennoscandia (spring) at 140 km per day (Fransson, 1986), and to Willow Warblers between Fennoscandia and Africa (autumn) at 85 km per day, both over distances exceeding 10,000 km (Hedenström & Pettersson, 1987).

Birds do not necessarily maintain the same rate of progress over their whole migration. Ring recoveries indicate that some species speed up during the course of their journey, while others slow down (Hedenström & Pettersson, 1987; Ellegren, 1990a, 1993; Fransson,

1995; Bensch & Nielsen, 1999). Migration speed increased more rapidly through the journey in long-distance migrants en route to Africa than in short-distance migrants wintering within Europe (Alerstam, 2003). The reasons are unknown, but weather-induced delays maybe fewer as birds reach lower latitudes. In any case, speeds calculated over the early parts of a journey through Europe (which often provide most ring recoveries) may not be typical of the whole route. For one thing, birds may have fattened before they left. In addition, for obvious reasons, journeys over seas or deserts are almost always more rapid than same-length journeys through more favourable terrain.

Being dependent on food and weather, migration speeds would also be expected to vary greatly from year to year over the same route. Annual variations have been little studied, but over the period 1963–98 a fourfold variation in average migration speed was recorded among Blue Tits travelling between various bird-ringing stations along the southern Baltic coast (Nowakowski & Chru ciel, 2004). In the slowest year, the birds averaged less than 10 km per day, compared with 38 km per day in the fastest year. The Blue Tit migrates relatively slowly compared with other European passerines, and often travels in short flights just above the treetops. The annual variations in speed paralleled those in Great Tits, which migrated generally faster. Coal Tits studied in the same way migrated twice as fast in invasion years (40–80 km per day) as in other years (30–40 km per day), possibly because the urge to migrate was stronger in invasion years (Rute, 1976), a difference also noted in Siskins (Payevski, 1971).

BIRDS TAGGED WITH RADIO TRANSMITTERS OR OTHER DEVICES

Studies involving the attachment of radio transmitters and geolocation devices have involved mainly large species able to carry the extra weight. The resulting data complement those derived from ringing, which refer mainly to small species. However, they allow us

to explore in more detail than by the other methods the variation in journey times achieved by individuals. Some studies have involved species that migrate by flapping flight, while others have involved species that migrate mainly by soaring–gliding flight.

Birds that migrate by flapping flight

Brent Geese migrating mainly over land between the Dutch Wadden Sea and the Siberian Taimyr peninsula covered the mean flight distance of 5,004 km in an average of 42 days (range 34–52 days), with a mean speed of 118 km per day (range 97–148) (Green *et al.,* 2002). The slowest birds thus took half as long again as the fastest. Seven males on their longest non-stop flights covered an average of 1,056 km (range 768–1,331 km). Much greater individual variation was recorded among Barnacle Geese migrating from Svalbard via Bear Island and Norway to Scotland in autumn over a total distance of 2,500–3,000 km. At one extreme, some birds completed this journey in as little as two to three days, travelling more than 1,000 km per day, with stops too short to replenish reserves (Butler *et al.,* 1998). At the other extreme, four birds held up en route by unfavourable winds took 9–36 days over the journey, giving mean migration speeds of 76–306 km per day. Overall journey times thus varied more than 12-fold between individuals. Possibly many Barnacle Geese left Svalbard with enough fuel to complete the journey to Scotland if they could do it within two to three days. But if they were held up by weather, their reserves would have been depleted, requiring additional feeding and refuelling.

Birds that migrate by soaring flight

Many seabirds travel by soaring–gliding flight, and several estimates have been made of their migration speeds mainly through use of geolocation tags. Sooty Shearwaters breed in the Southern Ocean and migrate to spend their non-breeding period (the northern

summer) in the north Atlantic and Pacific Oceans. On their figure-eight migrations, 19 birds travelled an average of 64,037 km in 198 days, giving a mean speed of 323 km per day (Shaffer *et al.,* 2006). On parts of the journey, speeds rose to an average of 910 km per day, not very different from the highest recorded from albatrosses, which achieved average speeds up to 950 km per day (e.g. Croxall *et al.,* 2005). Even faster travel was recorded from a Manx Shearwater from Skomer Island, which on autumn migration covered 7,750 km in 6.5 days, averaging 1,192 km per day (Guilford *et al.,* 2009).

These pelagic seabirds that travel by gliding flight are among the fastest of all migrating animals. They are en route most of the time between breeding seasons, but linger in areas where they encounter concentrations of food. These areas are equivalent to the stopover sites of land birds, but are not static, as they continually shift position to some extent in response to changing sea currents.

Overall, the mean migration speeds of tracked raptors varied between 12 and 294 km per day in autumn, and between 23 and 196 km per day in spring, but they were mostly in the range 50–250 km per day at both seasons (Newton, 2008). Raptors showed little tendency to migrate faster on longer journeys, any such relationship being less clear than in passerines—but more studies are needed (Fig. 82). Although Peregrines and Ospreys often progress by flapping flight when soaring is not possible, their mean migration speeds were within the range of values recorded for other soaring species. Three studies of Peregrines gave mean speeds of 126–196 km per day, and six studies of Ospreys gave mean speeds of 145–294 km per day (Newton, 2008). There was also little variation between the migration speeds of smaller and larger species, for although larger species could glide more rapidly than small ones, small ones could utilise weaker thermals, and so could migrate over a longer part of each day (Chapter 4).

A striking feature in those species with reasonable samples was again the large individual variation in the duration of migration. Among 13 Ospreys migrating from Sweden to West Africa, the total length of journey varied between 5,813 and 7,268 km (longest

journey 1.25 times longer than the shortest), but these journeys took between 14 and 55 days to complete (greatest value 3.9 times longer than smallest) (Kjellén *et al.,* 2001). Among 9 Honey Buzzards over a similar route, journeys varied between 6,299 and 7,091 km (longest journey 1.13 times longer than the shortest), and took between 34 and 70 days to complete (greatest value 2.06 times longer than the smallest) (Hâke *et al.,* 2003). In other species, some individuals took up to three times longer than others to travel similar routes. In general, within regional populations, those adults that spent the longest periods on migration spent the shortest periods in their wintering areas, while no effect was apparent on the amount of time spent in breeding areas.

To economise on battery power, the tags of most raptors studied in the early years were set to transmit signals every few days. But the later development of solar-powered GPS transmitters enabled birds to be monitored every day and night on their journeys, allowing their various roost sites, daily travel distances and stopover periods to be recorded with great precision. For example, one adult Osprey took 42 days over the 5,803 km journey from Senegal to Scotland (Fig. 84); she travelled on 26 of these days, covering 65–756 km per day (mean 298 km). She spent one 12-day period on stopover in Spain, and other shorter periods elsewhere, mainly at times of poor weather (www.ospreys.org.uk). In good conditions, other Ospreys have completed similar autumn journeys in as few as 21 days, travelling every day typically for 8–9 hours. In general, however, it seems rare for raptors to cover more than 400 km per day, despite occasional exceptions.

Not surprisingly, those raptors tracked between Europe and Africa travelled more rapidly over the Sahara (which probably offered excellent soaring conditions but no food) than over other parts of the route. This held for a Short-toed Eagle (Meyburg *et al.,* 1998), and for numbers of tracked Ospreys (Kjellén *et al.,* 2001) and Honey Buzzards (Hâke *et al.,* 2003). Elsewhere, these birds broke their autumn journeys for up to several weeks at a time, apparently when they encountered good feeding areas. Once in winter quarters,

individuals of most species remained in one place throughout their stay, and those individuals studied in successive years returned to the same breeding and wintering localities each year, as recorded for example in Ospreys. However, some Lesser Spotted Eagles wandered over a large area in southern Africa, frequently making extensive moves during the course of their stay (Meyburg *et al.,* 1995, 2004). These eagles are known from observations to move over large areas, concentrating temporarily in places with abundant food (Newton, 1979). In effect, the Lesser Spotted Eagles that were tracked from Europe remained on migration for most of the time between leaving the nesting area in one year and returning there the next, as they followed the rain-belts in southern Africa in search of emerging termites and other prey (Meyburg *et al.,* 2004).

Among various raptors, in contrast to passerines, no consistent difference was apparent between the durations of autumn and spring journeys, either from the mean values calculated for different populations or from the values for individual birds tracked on both outward and return journeys (Fig. 85). In some populations (or individuals), the autumn journey took longer, and in others the spring journey.

Turning now to non-raptorial soaring species, radio-tagged White Storks covered the first part of their autumn migration from Europe to East Africa by almost daily travelling. They took an average of 18.9 days over this part of their journey, which included only 1.4 non-travelling days (93 per cent of all days were travelling days), giving an overall speed of 243 km per day (Berthold *et al.,* 2001). This is a remarkable speed for a bird of this size, and no differences were apparent between adults and juveniles. The storks did not eat excessively before their departure, but seemed to forage opportunistically in the mornings and evenings en route, regaining any net loss in body mass at their intermediate destination in northern Africa (mostly Sudan). Some individual White Storks showed great variation in the timing, length and duration of their migratory journeys from year to year, as well as in the duration and location of stopovers. Finally, among various species of cranes,

mean speeds in the range 33–146 km per day were recorded, somewhat slower than the raptors and storks, but cranes often migrate by flapping flight and stop for longer periods to refuel. Again, individual variation was often great: Common Cranes migrating from Germany to Spain took 3–28 days over the journey, a ninefold variation over the same route (Alonso *et al.,* 2008).

Knowledge of the duration of migration and of the usual flight speed of a species enables us to calculate how much of the total journey time of that species is spent actually travelling. For example, Chaffinches usually leave northern Finland in the first half of September and reach their wintering areas in France and Iberia around mid-October, the complete journey taking around five weeks. The birds thus cover 3,000 km at an average of 86 km per day. As they could cover 86 km in 3 hours, and the whole distance (if they could fly non-stop) in 105 hours, they must have spent up to 88 per cent of their total five-week journey stationary, giving a ratio of flight-to-stopover of about 1:7. This agrees with theoretical estimates of such ratios for birds of this size, which are based on the rates at which individuals can accumulate body reserves and the rates at which they normally consume them during flight.

As the energy requirement per hour of flight is generally greater in large birds, and their refuelling rates are lower, they take longer to accumulate the fuel necessary for a standard journey than do small birds. In Brent Geese migrating mainly over land between the Wadden Sea and the Taimyr peninsula, the mean flight distance of 5,004 km is equivalent to about three days and nights (72 hours) on the wing, assuming a mean ground-speed of 70 km per hour (Green *et al.,* 2002). But it took six geese an average of 42 days to cover this distance, giving a mean speed of 118 km per day (range 97–148). So in these birds, only 7 per cent of the time spent on spring migration consisted of active travel, giving a flight-to-stopover ratio of 1:13. If the time needed for initial pre-migratory fuel deposition had also been included, the mean flight speed would fall to 62 km per day and the flight-to-fuelling ratio would become 1:25.

To take an even larger species, consider the five Tundra Swans radio-tracked on their autumn migrations between Siberia and the Baltic region (en route to northern Russia; Beekman *et al.,* 2002). These birds travelled the 2,023 km journey in 34 days, on average. With a mean flight speed of 64 km per hour, an estimated 32 hours was spent on the wing, giving a flight-to-stopover ratio of 1:25. The equivalent figures from two swans studied in spring were also 1:25. These estimates again excluded the initial fattening period, but they broadly agree with the observational finding (reported earlier) that Tundra Swans take around two months, on average, on both their autumn and spring journeys. They also give some idea of the small proportion of the overall journey time spent by large birds in flapping flight when migrating over land. Most of the time is spent on resting and refuelling at stopover sites, or on delays caused by bad weather. We should not be misled by the fact that some swans can cross 1,000 km of sea in less than two days (see later), because this makes no allowance for the period of prior fuel deposition. In practice, of course, birds often stay longer at stopovers than is needed solely to accumulate fuel, and in addition, their energy costs in flight are greatly influenced by wind conditions. On the spring journey, some birds may also be accumulating extra body reserves for breeding, all of which is additional to their daily maintenance costs (Chapter 6). Nevertheless, these and other estimates of flight-to-stopover ratios in different bird species generally support the notion that, among birds that travel by flapping flight, large species spend a greater proportion of the total journey time on stopover than smaller species (Newton, 2008).

The situation in soaring birds is somewhat different because, as we saw in Chapter 4, much of their flight is powered by atmospheric energy. They therefore need less body reserve, which reduces the time they need to spend feeding. In almost all the soaring species for which relevant data are available, the flight-to-stopover ratios in adult birds varied between 1:3 and 1:7, reflecting the much reduced time spent on stopovers, but a few studies gave much longer stopover periods (Newton, 2008). Considerable variation was

apparent within species, with mean values of 1:4–1:7 from three studies of Peregrines, and of 1:3–1:7 from five studies of Ospreys. Their stopover times are generally much shorter than equivalent figures from similar-sized birds that migrate by flapping flight, and some are lower even than those from small passerines. They reaffirm the great advantage of soaring flight for large birds: it requires much less feeding time, so gives faster overall migration speeds. However, all the values quoted above for raptors were from adult birds; and the non-breeding immatures of some species, which were under less pressure to return to breeding areas, showed more leisured spring journeys (Newton, 2008).

NON-STOP SEA-CROSSINGS

Apparent non-stop sea-crossings provide some striking examples of the flight capabilities of birds, as they often involve long distances covered rapidly. To begin with some extreme examples, the times taken for Brent Geese to cover the 5,000 km journey over the Pacific Ocean from Alaska to Baja California, in autumn were estimated at 60, 60 and 95 hours in three different years, which implied average speeds of 1,992, 1,992 and 1,344 km respectively per 24-hour day (or of 83, 83 and 56 km per hour) in the three years (Dau, 1992). Variation in mean journey times between years was associated mainly with differences in wind speed and directions. Over this period of two to four days, birds lost an estimated one-third of their pre-departure body weights. Some of the birds may have rested on the sea for a while, but journey times were so short that any such rests cannot have lasted long. Similar journeys were made by Cackling (Canada) Geese and by various waders, all under the same weather conditions, when the passage of moderate to strong pressure systems brought favourable winds.

The Bar-tailed Godwits (race L. *l. baueri)* that migrate 10,400 km from Alaska to New Zealand were estimated to cover this distance in about 175 hours (7.3 days) of non-stop flight, giving a mean speed of 1,512 km per 24-hour day (or 63 km per hour). These values

were later confirmed by radio-tracking individual birds. These godwits perform the longest and fastest over-water flights known from any land-bird species, and lose around half their initial body weights over the journey (see also Chapter 8; Gill *et al.,* 2005).

MIGRATION WITHIN THE ANNUAL CYCLE

For some species, we can calculate how much of each year, on average, is spent on migration. Ring recoveries suggest that Barn Swallows migrating between northern Europe and southern Africa spend around 16 weeks per year on migration (or 31 per cent of the entire year). Marsh Warblers can spend around twice this time migrating, at around 62 per cent of the year. Among waterfowl, radio-tracked Tundra Swans spent about 33 per cent of the year on migration; storks and cranes gave figures up to 59 per cent in different populations, and raptors up to 42 per cent in different populations (Newton, 2008). As expected, migration periods depended mainly on the length of the journey and on the nature of the underlying terrain.

Long-distance migrants can clearly spend large parts of their lives travelling, and together with other events in the annual cycle, this may have other consequences. In some large bird species, the breeding cycle takes so long that it may constrain the amount of time available for migration, thereby limiting the length of journeys possible, and perhaps also the birds' geographical range. Birds cannot occupy otherwise suitable areas if doing so would require so much time on migration as to preclude breeding. This does not apply to non-breeding immatures, however, which in some bird species winter further from the breeding areas or spend the summer further from the wintering areas than the adults.

CONCLUDING REMARKS

There is clearly great variation in migration speeds among individuals from the same population making essentially the same journey. Among the species studied, some individuals took two to three times longer than others, and occasionally up to 12 times longer. Much of this variation was associated with the weather encountered en route, as birds departing at different dates met different conditions, but some may have reflected the varying foraging and other capabilities of the individuals concerned. The inclusion of juveniles nearly always added further variation to the recorded migration speeds, for in many species juveniles travelled more slowly than adults. Rain or unfavourable winds sometimes held up birds for days or weeks at a time, long beyond the date at which they should have been physiologically prepared to depart. All these types of constraints tend to slow migration and increase the variation found within populations.

In addition to food and weather, fuelling rates may also be influenced by the prevailing daylengths, which determine the maximum daily feeding times and hence the maximum possible migration speeds (Kvist & Lindström, 2000). In many bird species, spring migration occurs closer to the summer solstice and therefore under longer days than autumn migration (Bauchinger & Klaassen, 2005). This may partly account for why many species travel more rapidly in spring than in autumn, and may also explain some of the changes in migration speed that occur during the course of a journey, as the bird moves through latitudes with different daylengths.

If a bird had no other events in its annual cycle, it would seem advantageous for daylength reasons to undertake both migrations as close to the summer solstice as possible, thereby gaining longer days for feeding and fuel deposition. This maybe one reason why, in some large bird species, the immatures in their non-breeding years migrate from wintering to breeding areas much later in spring than the breeding adults, and return much earlier in late summer or autumn. They thereby spend only a few weeks per year in breeding

areas, but perform both migrations under longer days and more favourable conditions than adults.

Findings on migration speeds also suggest that some bird populations are not under pressure to migrate in autumn as fast as they could. Perhaps at this time of year they have a certain period in which to migrate, depending mainly on other events in the annual cycle, and can adjust their travelling speed accordingly. By migrating slowly, birds can take advantage of any rich feeding areas they encounter en route, yet do not need to accumulate the large fuel reserves required by long flights, thereby avoiding the associated costs and predation risks (Chapter 6). Making the most of plentiful food supplies en route is especially important for irruptive species, which cannot be sure of finding similarly abundant supplies further along the route (Chapter 20). It is perhaps in ideal conditions in spring when birds are migrating to reach their breeding areas that the maximum speeds are most likely to be approached. But even then, most birds cannot migrate ahead of the appearance of suitable food supplies.

CHAPTER 8

Amazing Journeys

Most birds that travel by flapping flight can migrate over small areas of inhospitable habitat that they can cross in a few hours. The difficulties come mainly on longer journeys which require more than 24 hours of non-stop flight, or which present unusually harsh conditions. Many of the birds that breed in the British Isles face difficult journeys, as do birds elsewhere, and this chapter focuses on the various adaptations that enable birds to complete such journeys successfully. The fact that some land birds can traverse inhospitable areas does not imply that all could do so. Much depends on features of the birds themselves, such as their body sizes and physiology, and also on the habitats to which they are adapted.

SEA-CROSSINGS

Land birds that migrate over oceans provide some of the most extreme examples of endurance flight and precise navigation, when they travel, without the opportunity to feed, drink or rest, over tracts of open water devoid of helpful landmarks. They cannot take shelter, as birds do over land, when the weather turns against them. While some land birds on over-sea flights take whatever opportunities for rest are available, stopping on ships, oil rigs and other installations, or even on mats of flotsam, these individuals probably represent an exhausted minority, and almost certainly most land birds make water-crossings non-stop.

Some moderately long sea-crossings are made by birds that breed or winter in the British Isles (Fig. 22). Birds that cross the North Sea must fly up to a few hundred kilometres non-stop, depending on where they cross, those that cross the Irish Sea some 20–200 km, and those that migrate southwards from Britain over the English Channel cross distances of 30 km in the east increasing to 170 km in the west. Birds that pass on to Africa cross similar short distances over the west end of the Mediterranean (as little as 15 km at the Strait of Gibraltar). However, some birds may leave from Ireland and fly directly across the Atlantic to northern Spain, an over-sea journey of about 800–1,000 km. Other species migrate from Svalbard to Britain, which includes the 700 km sea-crossing to Norway, and then later in the journey the North Sea. Yet other species make the 1,100 km journey from Iceland to the British Isles, and a few, such as the Northern Wheatear, may fly more than 2,500 km directly from Greenland to the British Isles without stopping in Iceland. Some Greenland Wheatears, which more than double their body weight before takeoff (increasing from 22 to 54 g), supposedly fly directly to Iberia or North Africa, missing out Iceland and the British Isles (Thorup *et al.,* 2006). Depending on the start and end points, this flight would involve around 3,000–4,200 km of sea-crossing, which would make it the longest known over-water flight made by any songbird species worldwide.

On a wider scale, all the major seas and oceans of the world are crossed regularly by some land-bird species (Newton, 2008). Each year, millions of birds of a wide range of species cross on abroad front the Mediterranean Sea in the Old World or the Gulf of Mexico in the New World (Moreau, 1961; Gauthreaux, 1999). At their widest points, both these crossings involve flights of more than 1,000 km. Frequent storms make the trans-Gulf crossing one of the most hazardous in the world, especially in the autumn hurricane season. Smaller numbers of other birds also cross major inland waters, such as Caspian and Baikal in the Old World and the Great Lakes in the New World. Crossing these waters by direct flights

involves risks, but saves time and energy over the alternative of flying around them.

Some species regularly cross even longer stretches, such as the western Atlantic between northeastern North America and northeastern South America (2,400–3,700 km), or the northern Pacific between Alaska and Hawaii and other central Pacific Islands (5,000 km). To judge from their normal flight speeds, land birds would take more than 100 hours of non-stop flight in still air to accomplish the longer of these over-water journeys, but by taking advantage of favourable winds, they can greatly shorten their flight times. Participants include many passerines (shorter journeys only) and shorebirds, but also waterfowl, which, unlike the others, can rest on the sea if need be.

But the most impressive of all over-water migrations by a land bird is undertaken by the Bar-tailed Godwits (race L. *1. baueri)* which breed in eastern Siberia and Alaska, and each autumn accomplish an astonishing flight to New Zealand over a minimum distance of 10,400 km. This flight requires enormous fat reserves, and despite considerable shrinkage of other body organs, the birds depart at twice their normal weights (Chapter 6). Radio-tracking of individuals has confirmed that this southward flight is indeed without break and takes around seven or eight days. One female covered a distance of 11,680 km in just 8.1 days. On return passage, when the wind is less favourable, the birds follow a more circuitous route, travelling first to the Yellow Sea region in China, a distance of about 10,000 km, which radio-tagged birds also covered in about seven days (one individual took 9.5 days). The birds then refuelled for the second main stage of their journey, which took them to their breeding areas in Siberia and Alaska (Gill *et al.,* 2009). Apart from the length of the journey, the navigational precision required on a trip of this type is breathtaking. From the autumn departure point in Siberia or Alaska, the target area of New Zealand is so small in the vastness of the south Pacific that it gives little scope for off-route deviations that cannot be corrected.

In all long sea-crossings by land birds, behaviour with respect to weather is paramount. Birds often wait in coastal localities for days at a time for conditions to improve. Even then, they sometimes seem reluctant to strike out over water, flying along the coast or turning back inland. For a long sea-crossing, birds ideally need clear skies, a good tailwind and enough body fuel for any emergencies that might arise. For despite favourable conditions at takeoff, the weather may worsen en route, and a sufficient body reserve is the most obvious way a migrating bird can cope with conditions that a human pilot, benefiting from weather forecasts, could anticipate and avoid. In sea-crossings, natural selection acts harshly against any kind of mistake or mishap, and abundant evidence points to heavy mortality (Chapter 23). If birds fly high enough, they can avoid the hazards of mist and rain, and on long over-water flights birds have often been detected by radar at heights exceeding 4 km above sea level (Chapter 5).

In contrast to land birds, seabirds migrating over water would seem to have plenty of opportunity to rest and pick up food en route. But this is not always the case. Many seabirds breeding at high latitudes migrate over the equator, and some tropical seas are among the poorest on earth. In any case, foods such as fish tend to be concentrated in particular areas, which may be few and far between. Evidence is accumulating that, like some land birds, seabirds can make extremely long journeys without eating, refuelling chiefly at traditional staging areas. For example, after breeding in western Europe, Black Terns *Chlidonias niger* assemble at one major feeding area, the IJsselmeer on the Dutch coast. Here they increase in body mass by 25–30 per cent within two to three weeks, enabling a non-stop flight of more than 3,600 km to West Africa. The birds ascend in the evening to high altitudes ($>$500 m) and start migrating. Although Black Terns are seen at localities en route, no important stopover site is known between the Netherlands and West Africa (van der Winden, 2002). In spring, a similar increase in the body mass of Black Terns occurs just before spring migration from Namibia, so the whole northward journey maybe

made in two or three main stages. Other terns may also make long flights between rich feeding areas, rather than hunting as they travel. Arctic Terns *Sterna paradisea* staging in Norway and the British Isles in autumn would need to accumulate fuel equivalent to 30–40 per cent of body weight before conducting a direct flight of 3,000–5,000 km to West Africa. These and other seabirds (mentioned in Chapter 6) make their journeys so quickly that they can spend little (if any) time feeding en route.

The longest of all bird migrations are performed by seabirds, again notably by the Arctic Tern, some individuals of which migrate each year between Arctic and Antarctic waters, giving return journeys of more than 30,000 km. In the process, these terns experience more daylight per year than any other organism, as they shuttle between the continuous daylight of the northern and southern summers. However, even this distance was exceeded by at least one Common Tern *S. Hirundo,* which was ringed as a chick in Sweden and found freshly dead five months later on Stewart Island, New Zealand. If this bird had travelled an over-sea route to South Africa and then eastward to New Zealand, it might have covered 25,000 km, and if it had lived to return, it would have covered 50,000 km. In other seabirds, which can be on the move throughout the non-breeding season, even these distances are exceeded (for example, the 64,000 km covered by the Sooty Shearwaters mentioned in Chapter 7).

DESERT-CROSSINGS

Overall, one-third of the earth's land area is classed as desert, a term that covers all arid landscapes, from the sparsely vegetated regions of western North America to totally barren rock and sand typical of much of the Sahara. Providing there is some vegetation, specialist bird species can flourish in such habitats, but most other birds cannot find sufficient food or water, or remain active at such high temperatures. Outside the tropics, most deserts are at their best in spring, after sparse winter rains have promoted plant growth and

flowering. They are much less hospitable in autumn, when plants have withered under the desiccating heat of summer. The problems of desert flights result from the long distances without food or water, and the searing daytime temperatures which bring risks of overheating and dehydration.

The largest and most severe desert in the world sits across one of the main bird migration routes, between western Eurasia and the Afrotropics (Fig. 254). It is crossed twice each year by many birds that breed in the British Isles. The Sahara stretches from the Atlantic coast in the west to the Saudi Arabian peninsula in the east. It extends 1,000–1,500 km from north to south, and covers an area of 12 million km^2, about the same as the USA. Much of it is totally bereft of vegetation, lacking even the sparsest of desert scrub. Daily maximum temperatures during the autumn and spring migration periods average 25–38˚C, but sand surface temperatures during the day may reach 70˚C. Relative humidity can drop below 10 per cent. The desert varies greatly in severity in different longitudes. The Atlantic coastal strip in the west provides a continuum of scrubby vegetation running north to south. In places, this coastal strip is more than 200 km wide, beyond which the scrub becomes progressively sparser into the desert. In the east, the Nile valley provides a narrow green corridor for migrants, the only route that is abundantly supplied with both food and water. Over the rest of the desert, vegetation is mostly sparse to non-existent, apart from the few isolated oases, which are mere pinpricks in the vastness of the desert.

Yet despite its harshness, this desert is crossed and re-crossed every year at all longitudes by an estimated 5,000 million individuals of 186 land-bird species, a density equivalent to one migrant per hectare of breeding range. This figure was derived by Reg Moreau (1972), mainly on the basis of published estimates of the breeding densities of various Eurasian–African migrants. Revised estimates, made 40 years later on the basis of radar observations mainly by Bruno Bruderer at sites across the Mediterranean region, lay between 3,500 and 4,500 million birds, but these figures (unlike

the earlier one) would have excluded most birds that enter Africa via Arabia. They also follow several decades of population decline among many migratory species in Europe (Chapter 24). Taking these facts into account, the two estimates, found in different ways by different researchers, are not wholly at odds with one another. They show that crossing the Mediterranean and Sahara is a journey accomplished not only by a minority of specialists, but by a large proportion of Eurasian birds from a wide range of species.

Land birds that follow the Atlantic coast in the west, with its sparse desert scrub, or the Nile valley in the east, with its narrow border of swamps and cultivated land, could in theory migrate with short flights and frequent stops, because they could find food at various points en route. As revealed by radar, the concentrations of migrants are greater at the west and east ends of the desert than in the middle section, at least in autumn, but seem unexceptional in the Nile valley itself, apart from waterbirds (Moreau, 1961; Biebach, 1990; Bruderer & Liechti, 1999). The option of flight from oasis to oasis is possible only along a row of mountains and oases that stretches southeast from Morocco, for elsewhere, they are too few and far between. Most species apparently migrate on a broad front over the most barren parts of the desert, but the same species may behave differently in spring and autumn, or at different points in the crossing (Moreau, 1961).

The lower densities of migrants in the middle section of the desert may result largely from the funnelling effect of land areas to the north rather than from the desert conditions themselves. Most of the west European migrants cross the Mediterranean at its narrowest, around Gibraltar, from which they reach the western edge of the desert, while the east European and Asian migrants enter northeast Africa and cross the desert in its eastern sector. Yet other migrants from Asia enter Africa via Arabia and miss the Sahara altogether.

Throughout its breadth, the desert would have offered better conditions a few thousand years ago than it does today. In fact, the difficulty of this journey is increasing all the time, as the desert expands north and south under human influence, an extra 60,000

km^2 per year being added to its area. In these times of climate change, other areas on the migration route are also becoming drier, including parts of Spain, much of North Africa and the Sahel zone to the south. These various changes mean that, over the centuries, birds have had to cross ever-widening areas with little or no access to food or water, while suitable staging areas have become smaller and more widely spaced. These trends are likely to continue into the future.

The scorching daytime temperatures, combined with almost total lack of food and water, make crossing the Sahara one of the most arduous journeys undertaken by migratory birds. For some birds, it also follows (in autumn) or precedes (in spring) a crossing of the Mediterranean Sea at its widest points. The west and east parts of the North African coastal region support abundant green habitat extending hundreds of kilometres to the south, but in the central part little vegetated habitat is available between the sea and the desert, offering only limited opportunities for refuelling. This central coastal strip over most of its length is typically less than 20 km from north to south, consisting of sparse perennial scrub, with the addition in spring of ephemeral herbage dependent on winter rain. Beyond this to the south lies barren desert.

Fuelling strategies

Analyses of the weights of six species of trans-Saharan migrants caught at 34 trapping stations located in widely scattered parts of Europe and North Africa revealed four main types of fattening patterns on the southward autumn journey (Schaub & Jenni, 2000):

1. Birds accumulated large fuel stores well before they reached the northern edge of the desert, and then flew to sub-Saharan Africa without refuelling. This pattern was shown by western populations of Sedge Warblers (as just described), by western populations of Pied Flycatchers

(which fatten in western Iberia), and possibly also by some individuals of other species.

2. Birds accumulated more fuel at each stopover than was needed to fly to the next, leading to a progressive increase in body mass southwards through Europe toward the desert. This strategy was shown by Garden Warblers and more eastern populations of Pied Flycatchers.
3. Birds migrated in short stages, and accumulated only enough fuel at each stopover site to fly to the next, with especially large amounts just before the desert-crossing. This strategy depends on finding good feeding sites in the southern Mediterranean region, and is used by Eurasian Reed Warblers (as mentioned above) and possibly also by Common Whitethroats.
4. The same strategy as (3), except that birds put on only moderate reserves before the desert-crossing, relying instead on finding food at desert oases or on catching migrant insects. Various hirundines and Spotted Flycatchers seem to adopt this strategy, and the same may also be true for shrikes, which can feast upon smaller migrants.

Similar variations in fuelling patterns occur in spring. At this season, most northward-bound passerine populations fatten well to the south of the Sahara, and undertake a flight much longer than the desert alone, while others proceed in stages to the southern edge of the desert and fatten there. In West Africa, Nightingales, Wood Warblers, Common Whitethroats, Blackcaps, Garden Warblers and others usually fatten far south of the desert, in the wetter Guinea Zone (Dowsett & Fry, 1971; Hjort *et al.,* 1996; Ottosson *et al.,* 2005), while Sand Martins, Yellow Wagtails and others fatten around Lake Chad in the Sahel zone (Fry *et al.,* 1970, 1972).

Important stopover areas

The above migration strategies were inferred from fattening patterns among trapped birds, but are supported by ring recoveries (Wernham *et al.,* 2002). Some summer migrant species ringed in Britain, such as the Reed Warbler, Common Whitethroat and Sand Martin, yield recoveries in late summer widely scattered through southern France and Iberia, implying that these species can stop almost anywhere on their journeys toward Africa. However, other species have provided recoveries that are heavily concentrated in particular regions, with few or none elsewhere: Pied Flycatchers and Tree Pipits in western Iberia, Lesser Whitethroats in the Alps region of northern Italy and Wood Warblers in peninsular Italy. The inference is that these species migrate in a single long flight from their breeding areas to specific regions in the southern half of Europe, and from there they may move without other long feeding stops to sub-Sanaran Africa. Their whole journey could thus be accomplished in two long stages, separated by a single long stopover for the replenishment of body reserves. This view is generally supported by other data on the same species from Britain, such as their body weights on departure or their appearance, or lack of appearance, at coastal bird observatories.

Crossing the desert

In a number of bird species, at least some individuals seem to cross both the Mediterranean Sea and Sahara desert in a single non-stop flight. In autumn, a combined sea- and desert-crossing has been claimed for various waterfowl and waders, and for some slower-flying species, such as the Sedge Warbler and Pied Flycatcher mentioned above, together with the Yellow Wagtail and Common Cuckoo (Moreau, 1972; Wood, 1992). Circumstantial evidence stems partly from the relative scarcity of these species on the ground in North Africa in autumn, and partly from the body reserves accumulated, which are calculated to be sufficient for a journey of this length. A combined sea- and desert-crossing may also be performed by some hirundines, Swifts and Bee-eaters, which could

pick up food on the way, at least over vegetated areas. Other birds break their journeys for refuelling in North Africa, and hence separate the Mediterranean and Saharan crossings (Moreau, 1961; Casement, 1966; Bairlein, 1985a, 1992; Biebach, 1998).

While some small passerines may cross the desert in a single non-stop flight, others have been found to break their journeys in the daytime, but mostly without feeding. At least some individuals of many passerines species (notably the Garden Warbler, Lesser Whitethroat and Willow Warbler) descend to spend the day sheltering motionless near oases, or even in the open desert in the shade of rocks, continuing their journey in the cool of night (Bairlein, 1992; Biebach, 1990, 1992; Biebach *et al.,* 1986). In this way, they could cross the desert in a few nocturnal flights. The majority of trapped migrants at such sites showed high body mass and fat loading, with sufficient reserves for onward flight, so they had not been grounded through lack of fuel. In resting by day and flying by night, such birds travelled in cooler conditions, and may thus have reduced their dehydration risks, but they would have added many hours to their journey time (giving two to four nights for the total journey across the desert). Yet other individuals of these same species stopped at oases, where they fed and drank, usually remaining for two to four days, but occasionally for up to three weeks at a time, if they needed to rebuild their body reserves. However, the birds stopping at oases can only be a tiny proportion of the numbers passing over. Strictly diurnal migrants, such as broad-winged raptors dependent on daytime thermals, may stop every night (as shown by radio-tracking of several species; Chapter 7), but would normally have little or no opportunity to feed or drink en route.

Conditions for trans-Saharan migration differ greatly between autumn and spring. When the migrants move south in autumn, the Sahel zone immediately to the south is near the end of its wet season. Vegetation is green, flood pools are common and insects are plentiful. This reduces the distance that birds must fly without feeding, and favourable southward winds on most days help to

speed them on their journeys. But in spring, when the migrants move north, the Sahel zone is reaching the end of the dry season, potentially adding another 500 km to the desert-crossing. However, this is offset to some extent by the greening of about 300 km of the northern Sahara as a result of winter rains in the Mediterranean region. The net effect of these seasonal changes is therefore to increase the desert-crossing by about 200 km in spring compared with autumn. Moreover, the same southward winds that helped the autumn migration also prevail in spring, so hamper northward progress. At this season, birds crossing the Sahara must expect to meet headwinds unless they are travelling diagonally northeast at altitudes greater than 2 km (Moreau, 1961). At these high altitudes, they meet the anti-trade winds blowing in the opposite direction to those below, and it seems likely that many birds take advantage of them (radar having confirmed higher flight altitudes in spring than in autumn). Otherwise, the only way to reduce the effect of headwinds would be to fly low, say within 500 m of the ground, but temperatures are high at these low altitudes.

So while in autumn many small birds are apparently able to cross the Mediterranean and Sahara without replenishing their body reserves, they are less likely to do so in spring. This seasonal difference in conditions may explain why many more migrants are seen in North Africa and around Mediterranean coasts in spring than in autumn, even though overall population levels are lower in spring (Nelson, 1973; Shirihai, 1996). Moreover, as indicated above, winter rains ensure that conditions in the Mediterranean region are much better in spring than in autumn. It is therefore not surprising that many more birds seem to make a combined Mediterranean–Saharan crossing in autumn than in spring, and that many more stop to refuel in North Africa in spring than in autumn.

Further studies are needed to find the relative frequencies of non-stop Mediterranean–Saharan flights, two-stage flights with a stop in North Africa or multi-stage flights, stopping in North Africa and at points in the Sahara (with use of oases or of stopping points along the Nile valley). The relative frequencies of these different patterns

clearly differ between autumn and spring, linked with different winds, ground conditions and time constraints. From autumn radar studies at sites in the Egyptian Sahara, it was concluded that about 20 per cent of all migrants detected were involved in non-stop migration and 80 per cent in intermittent migration, with stopover at the coast (70 per cent) or in the desert (10 per cent) (Biebach *et al.,* 2000). Other studies have suggested that in western Mauritania, an even greater proportion of individuals descend and rest by day. These variable strategies may represent ways in which individuals adjust their desert-crossing behaviour to their own physiological state and environmental conditions at the time.

Physiological constraints

In their daily lives, birds normally need to drink every day or have some alternative source of water, and it has long been appreciated that water rather than fuel could limit the lengths of non-stop journeys. So how do small birds, flying continuously over the hot Sahara, meet their water needs? Only about 15–25 per cent of the energy expended by muscle is converted to mechanical power, and the rest to heat. The body temperatures of birds measured during flight are generally greater than 41˚C, up to 4˚C higher than normal. The metabolism of fat, carbohydrate or protein results respectively in the production of 1.10, 0.90 and 0.82 g of water per g of wet tissue expended, or 0.03, 0.23 and 0.16 g of water per kJ of energy released (Table B, Chapter 6). Up to a point, therefore, flying birds could meet their water needs as a by-product of fuel metabolism. But with a rise in ambient temperature, the bird must eventually start to pant to avoid overheating, which leads to further water loss (Chapter 4). In the absence of drinking water, the risk of dehydration could be offset by additional metabolic water production, or by flying at high altitudes where the air is cooler or at night when temperatures are lower than during the day. The need to conserve water has thus been suggested as the reason why many small passerines, in crossing the Sahara, opt to rest in the shade by

day and fly at night. The argument is that, by remaining immobile by day without food or drink, the birds actually conserve more water than if they flew in the heat of the day and accomplished their journey more quickly.

Although flying high, where temperatures are lower, can conserve water, at very high altitudes reduced humidity could actually raise water loss. This is because the thinner air at high altitudes leads to increased ventilation, and hence to a further rise in respiratory water loss (Carmi *et al.,* 1992; Carmi & Pinshow, 1995; Klaassen, 1995; Klaassen *et al.,* 1999). Overall, therefore, the best option for a small bird in the Sahara may be to fly at night at moderate altitude where winds are favourable (say 500–2,000 m) and rest by day.

Birds are unlikely to fix their flight altitudes in terms of water conservation alone, however, for they must also take into account the energy costs of flight. Precise radar measurements of the height distributions of migrants over southern Israel in autumn and spring, combined with simultaneous altitudinal recordings of weather variables, offered an opportunity to examine the presumed importance of wind conditions, energy and water constraints on flight range (Liechti *et al.,* 2000). Predictions were made of the optimal flight altitude, in the conditions prevailing, if birds took account only of energy conservation, or of both energy and water conservation, in achieving maximum flight range. These predicted flight altitudes were then compared with the actual height distributions recorded in the field. It was concluded that wind profiles—and thus energy rather than water limitations—governed the altitudinal distribution of nocturnal migrants in this region. However, this conclusion, drawn from large samples of birds spread over a wide range of altitudes, does not exclude the possibility that individuals may adjust their altitude to whatever was most limiting for them at the time, including water if they were becoming seriously dehydrated.

Further insight can be gained from studies of body composition. The proportion of water within a bird's body decreases with increase in fat content, because fat is stored in anhydrous state

(Chapter 6). However, the proportion of water within the fat-free component of a bird's body usually remains stable at around 67 per cent, but can reduce to around 55 per cent before the bird dies from dehydration (Haas & Beck, 1979). Willow Warblers experience reduction in body water over one night from 67.5 to 63 per cent, which is well within the tolerable range, and over two rest days they experience further reduction to 58 per cent, which is still above the value at which death becomes likely (Biebach, 1990). Moreover, the water contents of birds caught in the Sahara desert were in general around 67–69 per cent of the fat-free weight (equivalent to a water:lean dry mass ratio of around 2:1), which is within the usual range for healthy birds (Chapter 6). In addition, the levels of sodium (Na^+) ions and urea in the bloodstream, measured as further indicators of the state of body hydration, were normal in most of the birds examined, and high only in lean ones (Biebach, 1990, 1991; Bairlein & Totzke, 1992). Furthermore, Willow Warblers and other small passerines found dying in the Libyan desert showed normal water levels, but had run out of fat, so in these birds, fuel rather than water seemed to have been limiting (Biebach, 1991).

Most of the evidence cited for lack of water stress in migrant birds derives from the absence or scarcity of individuals found with lowered water contents, even near the end of a long migration (Biebach, 1990, 1991; Gorney & Yom-Tov, 1994; Landys *et al.,* 2000). This is not true of all samples, however, for 78 per cent of 409 birds of various species obtained on the Egyptian coast in autumn, after crossing only the Mediterranean Sea, had water:lean dry mass ratios less than 2:1 (67 per cent water), including 12 per cent with ratios less than 1.4:1 (58 per cent water) (Fogden, 1972). The latter were therefore close to the level at which death would be expected to occur. Moreover, because birds could offset increasing water loss by metabolising body protein to yield water, the finding of migrants in the Sahara desert with high fat but low protein might also signify dehydration. Migrants clearly show behaviour that could be construed as anti-dehydration, such as shade-seeking,

remaining immobile during the hottest part of the day and drinking heavily on arrival at stopover sites (Biebach, 1990; Klaassen, 2004).

To conclude, research suggests that crossing the Sahara even by non-stop flight is practicable with a balanced water budget providing the bird flies at an appropriate altitude. This is difficult during the day in autumn because of the need for tailwinds, which occur mainly below 1,000 m, where temperatures are high. This may be why in autumn many small birds, in order to conserve water, fly by night and rest by day. Of course, birds resting in the desert by day are also confronted with high temperatures and low humidity, but they can seek shade and remain inactive, so as not to generate additional body heat. Given sufficient fat, small warblers could easily endure three nights of flight and two stopover days without feeding or drinking, which would suffice to cross the desert (Biebach, 1991). It seems, therefore, that with sufficient body reserves, small migrants are able to avoid both overheating and dehydration in the hot desert mainly by suitable behaviour. Nevertheless, evidence from the body composition of birds obtained on the Mediterranean–Saharan crossing suggests that, while fuel energy could be limiting in some, water could be limiting in others.

One might imagine that many birds die while attempting to cross the Sahara, if not from shortage of food or water, then from sandstorms, which could be fatal to grounded or low-flying birds. The Sahara desert produces an estimated 400–700 tons of wind-born sand and dust per year, and dust storms increased dramatically from 20 events per year before the mid-1960s to about 100 events per year in the 1990s (Goudie & Middleton, 2006). Despite the difficulty of finding dead birds in the desert, incidents have been described, involving White Storks, Northern Wheatears, Barn Swallows and Quail: ‘In the hollows between the dunes there were a few small bushes, and under each one of them the carcasses of Quail in various stages of desiccation were huddled’ (Moreau, 1928).

The study of radio-tagged birds on migration is now giving other opportunities to assess mortality on desert-crossings. Of 80 recorded crossings by various raptors, averaging six travel days, aberrant

behaviours occurred in 37 per cent (Strandberg, 2008). They included abrupt course changes, unexpected interruptions, aborted crossings and deaths. Birds started and then retreated out of the desert on at least 6 per cent of all crossing attempts, followed by late arrival in nesting areas and in some cases breeding failure. Mortality was significantly higher among juveniles (at 34 per cent of all autumn crossing attempts) than among adults (at 4 per cent of all crossing attempts), and this desert mortality made up half the total annual mortality recorded in both groups (almost all the rest being attributed to illegal killing in Europe). Seven recorded deaths occurred near the southern edge of the desert, in a region known for severe sandstorms. There are clearly costs in crossing the Sahara, but whether they are higher in smaller than larger bird species remains to be seen.

Asian–Afrotropical migrants

Migrants travelling between eastern Asia and the Afrotropics also face a difficult and even longer journey than those migrating between Europe and the Afrotropics. Among others, they include eastern populations of the Willow Warbler, Sedge Warbler, Garden Warbler, Common Redstart and Northern Wheatear. Birds from these eastern populations have overall journeys up to 15,000 km each way, about twice as long as those of their European equivalents. They have to cross a succession of difficult areas, including the deserts and semi-deserts of western Central Asia, the almost treeless Iranian highlands and the deserts of the Arabian peninsula. A number also have to cross some of the world's highest ground in western Asia, including the Tien Shan and western Himalayas.

The deserts of central Asia are more hospitable than the Sahara, because they support more rivers and lakes and generally more vegetation, especially in spring after winter snow. From work by Russian ornithologists, the basic strategy used by passerines migrating through this region centred more on effective refuelling

during daily stopovers than on massive fuel storage beforehand (Dolnik, 1990). The birds maintained a moderate rate of travel across the desert, limited by the opportunities for refuelling, but with no net fat loss over the journey. As in the Sahara, birds found by day in shady places that offered little food tended to have high fat levels, whereas those found at potential foraging sites near water tended to have low fat levels. Evidently, lean birds were more specific in their choice of stopping sites than fat ones.

The numbers of birds seen and caught in the western Asian deserts were much higher in spring than in autumn, about 2.6 times higher according to data obtained by 'moon-watching' (Chapter 2). This was partly because birds took mainly different routes at the two seasons, but also because a high proportion of birds stopped in spring but flew over in autumn (Bolshakov, 2003). In spring, practically all nocturnal passerine migrants avoided crossing the highlands of Central Asia, which at that time were still snow-covered, and took the desert route instead, whereas in autumn, mountain-crossing was much commoner. In addition, captures at stopovers and long-distance recoveries of ringed birds suggested that, in autumn, most transit passerines from the forest zone of central and eastern Siberia made a detour round the north and northwest edges of the deserts. By heading westward towards Europe, before veering southward to Africa, they migrated through more hospitable areas but added another 2,000 km to their already long journeys. It seems, therefore, that, in spring, when the Asian deserts are at their most propitious, many migrants cross them, feeding en route; however, in autumn, birds largely avoid the deserts by migrating over the mountains to the east, or by heading far to the west, before veering south towards Africa. By taking somewhat different routes in autumn and spring, the birds again make the best of prevailing conditions at both seasons.

The Arabian peninsula offers an alternative route from Eurasia into the more genial parts of Africa (Bourne, 1959). Not only is this desert narrower than the Sahara, but the hills and mountains around its borders are green. It supports a number of oases, and is generally

better vegetated than the Sahara, because it receives more rain. Not surprisingly, therefore, the Arabian peninsula is crossed not only by the migrants from Asia heading to Africa, but also by many birds from central and eastern Europe (including the Blackcap, Lesser Whitethroat and Red-backed Shrike), which on their spring journey from Africa head mainly across Arabia, to the east of the route through eastern Africa that they take in autumn.

Despite the huge scale of movement over the African and Asian deserts, the longest trans-desert flights are actually made in Australia, where each year thousands of waders cross the central desert on migration between the southeast and northwest coasts, both of which offer important feeding areas. This involves a journey of around 4,000 km, during which there is no suitable habitat where coastal waders could stop and feed. So far as we know, waders are the only species which make this flight.

HIGH MOUNTAINS

Mountains in the British Isles are too low to present significant obstacles for migrating birds, and elsewhere birds regularly cross mountain ranges much higher than any in Britain. The highest mountain range in the world, the Himalayas, sits right across a major north–south bird migration route, as do several European ranges, such as the Pyrenees, Alps and Carpathians. Depending on their primary direction, birds may cross high mountains or fly around them. Radar studies suggest that many birds cross mountain ranges in high-altitude non-stop flights, but visual observations confirm that others are funnelled through valleys and passes, where they may stop and feed, at least in autumn when conditions are favourable. For example, at the high pass of Col de Bretolet in the Swiss Alps, about 75 species have been found regularly to rest and feed, and many more occasionally. In effect, this amounts to almost all the small species that take this route.

The main problems of mountain-crossing are the costs of climbing to high altitudes (greatest in large birds), and the extreme cold, thin

air and low oxygen levels encountered on the highest ranges. In autumn, many birds stop and feed in the high valleys, but these same areas may be snow-covered and frozen in spring, affording no source of food. Moreover, strong winds are often funnelled through the valleys, which can greatly hinder birds that have to fly against them. Not surprisingly then, many birds fly around high mountain areas rather than taking a more direct route over the tops (Bruderer, 1999). Most short-distance migrants, flying northeast–southwest through central Europe in autumn, tend to circumvent the Alps. However, longer-distance migrants en route to Africa fly more directly north–south, at higher altitude, and mostly cross the Alps. Both groups fly lower in headwinds, smaller species being more affected than larger ones, and hence being more often deflected by mountains from their most direct route.

Migrants captured in high Alpine passes often have more fat and longer wings than birds of the same species caught in nearby lowland areas, implying that the two groups derive from different populations, one breeding further north than the other. This view is supported by ring recoveries. For example, Robins occurring in the Alps during autumn migration originate from further north (Scandinavia), while those occurring in the nearby lowlands originate mainly from Germany and Czechoslovakia (Bruderer & Jenni, 1990). Such differences presumably arise because longer-distance migrants from higher latitudes migrate at higher altitude, or have been longer on the wing, giving more time to attain high altitude before they reach the Alps. Among trapped samples of Garden Warblers, the proportions of long-winged (northern) individuals increase on days with headwinds, which induce lower flight, than on other days.

Wetland and soaring species tend to avoid the higher passes. Raptors which migrate mainly by flapping flight, such as falcons, appear in the high Alpine passes much more often than those that depend on soaring, such as kites and buzzards. The few migrating Common Buzzards seen in the high Alps occur early in the autumn migration season, when soaring is most often possible. The average

climbing rate of soaring birds decreases by one-third over the autumn migration season as temperatures cool, decreasing the lift provided by thermals (Bruderer & Jenni, 1990).

Any tendency of birds to cross the Alps thus varies with the innate directions, flight capabilities and physiological state of the migrants, as well as with the source area, the date in the season and local weather at the time. These findings from the Alps may well apply also to other mountain areas at similar latitude. But by far the highest flights are undertaken by those birds that cross the Tibetan plateau and the Himalayas. The best known are the Bar-headed Geese which reach flight altitudes exceeding 8 km above sea level. Moreover, they can do so without needing to acclimatise, for they start their spring migration in some localities from near sea level in India and within hours are crossing some of the highest peaks. In the same region, Demoiselle Cranes have also been recorded at more than at 7.5 km above sea level. Such birds are evidently pre-equipped physiologically to avoid altitude sickness (hypoxia), and can achieve feats of high-altitude performance that are matched by very few other animals. Not all birds have such flexibility, however, and whatever the advantages of high-altitude flight, many species seem confined to migrate at low elevations, presumably for physiological reasons (Chapter 4). In the New World, most of the mountain ranges, including the Rockies and the Andes, run approximately north–south, so do not need to be crossed or circumvented by most lower-ground migrants travelling roughly on a north–south axis.

OTHER BARRIERS

Some birds on their migrations also cross substantial stretches of sea ice, as occur in spring between Norway and Svalbard or between Siberia and Alaska. Nevertheless, such flights would seem to offer less of a challenge than over-water flights of similar length, because the birds can at least stop and rest in emergencies. Many Arctic and Antarctic seabirds cross more than 100 km of sea ice in order to

reach their breeding areas in spring, including some penguin species, which have to walk.

During the glacial periods, birds may have faced much longer ice-crossings than they do now, as they migrated from south of the extensive ice sheets to the few ice-free refuges that persisted as tundra north of the ice. Such ice-crossings must in some cases have involved journeys exceeding 1,000 km. That birds made these journeys is supposition, based on the patterns of subspeciation seen in some waders and other arctic-nesting species today, with each subspecies centred on an area known to have remained ice-free in summer throughout the glacial periods (Newton, 2003). To form subspecies, the birds breeding in each major refuge must have remained genetically isolated from those in other refuges, which in turn implies that they must have migrated there in summer from the only possible wintering areas lying south of the ice sheets.

Continuous forest would seem to represent a barrier for open-country birds. Four Hobbies, radio-tagged in Sweden, migrated to wintering areas in the southern African savannahs (Strandberg, 2008). Their tracks were initially widely spread, but converged to cross the central African rainforest at its narrowest point at 15°E, after which they spread out again. By converging on this point, these Hobbies reduced their trans-forest flight distance to about 450–600 km, about half of what it would have been elsewhere. Only by migrating very far to the east, at 30–40°E, where the forest gives way to savannah, could they have avoided it altogether. It is unlikely that this pattern applies only to Hobbies, and many other open-country species may also take routes that minimise their forest-crossings.

CONCLUDING REMARKS

The various migrations described in this chapter reveal what some birds are capable of achieving on their annual travels. The journeys involved may be assumed to push birds to the limits of their endurance: long non-stop flights without sleep, rest, food or water,

and often in harsh conditions. Most such flights require high fuel deposition beforehand, and some also involve special adaptations for high-altitude flight, extreme heat or cold, dehydration, low air densities and oxygen levels—conditions in which few other animals could survive. Yet some birds can achieve these high-endurance feats without any apparent prior training or acclimatisation. The main gap in our understanding is how birds that make non-stop flights extending over several days and nights manage to cope with extreme sleep deprivation. How much do they depend on 'uni-hemispherical sleep', resting one side of the brain at a time? This is an obvious question for further research.

Depending on their journeys, birds need fuel and water in different proportions, and on non-stop flights when they can neither feed nor drink, birds are able to address these different needs physiologically or behaviourally. Physiologically, they may adjust the ratios of reserve fat and protein that are metabolised, yielding different ratios of energy and water. Behaviourally, birds might adjust the times of day (day or night) or the altitudes at which they fly, both of which influence rates of heat and water loss, as well as energy use. Birds can also reduce their energy needs by selecting times or altitude zones with favourable winds (Chapter 5). In fact, one of the most striking findings from studies of difficult journeys is how much birds use behavioural (as opposed to physiological) means to overcome difficulties, involving, for example, choice of wind conditions, flight altitudes and flight times, as well as stopover frequency and duration, and whether to feed or rest during stopovers. Some types of behaviour are appropriate in some circumstances but not in others. So in order to maintain a favourable energy and water balance, a bird must continually adjust its flight times, flight altitudes and other behaviour according to its own body state and external conditions at the time. It is this adaptability and flexibility which allows certain bird species to cope with some of the most difficult journeys on earth.

CHAPTER 9

Annual Schedules

EVERY NATURALIST KNOWS THAT birds breed and migrate at the same times every year. So consistent are birds in their movement patterns that in the past, people used the arrivals and departures of migratory species to mark the seasons long before any other form of calendar was available. But how do birds themselves come to time their migrations at roughly the same dates each year? In order to answer this question, we have to look at how migration relates to other events in the bird's life, specifically breeding and moult, and how all three events relate to the changing seasons. This process of adjustment turns out to be more subtle and amazing than one could ever imagine, but it requires that we look at breeding and moult in some detail, as well as migration.

Most parts of the world are seasonal, in terms of daylength, warmth or precipitation, giving regular warm and cold seasons at higher latitudes, or wet and dry seasons over much of the tropics. This annual climatic cycle produces regular fluctuations in plant growth and productivity, in insect and other invertebrate abundance, and hence in the food supplies of birds. With increasing latitude, the daylength and temperature cycles become more marked, and the annual growing season shortens, giving rise to more pronounced seasonal fluctuations in food availability.

The annual cycles of birds and other animals, in which different activities occur at different times of year, can be regarded as an adaptation to climatic seasonality. In different bird species, the three main components of the annual cycle—breeding, moult and migration—vary in their timing and duration, in the sequence in

which they occur and in the extent to which they overlap. The pattern depends on the species and on the ecological circumstances in which it lives. All three processes require additional food above that required for everyday maintenance. During breeding, extra food is needed to produce eggs and feed young, during moult to support new feather growth, and during migration to create the body reserves which fuel the flights. All these processes take time and energy, and investment in one may compromise the others, so not surprisingly the three events tend to occur at different times of year. Many birds also show a quiescent period in winter, during which they are not breeding, moulting or migrating. Outwardly, they seem to be doing little except eating and surviving, but inwardly they may be undergoing some physiological change, such as growing gonads in preparation for breeding at a later date. Not all birds exhibit this quiescent stage, however, as they pass without obvious break from one major process to another.

In terms of food needs, breeding is the most demanding event in the annual cycle, because birds have to provide particular types of food for their offspring every day throughout their growth. Broadly speaking, therefore, breeding occurs during the season when food suitable for the young is most plentiful. The other events, which are somewhat less demanding, are fitted around breeding. Most birds have only one breeding season per year, but some tropical species in regions with two distinct wet seasons can have two breeding seasons each year, between which they may moult. Within a breeding season, most species raise only one brood, but those with short breeding cycles, such as many songbirds, can often raise two or more broods in quick succession.

Moult is the time of plumage renewal. Feathers are special lightweight structures consisting of a tough inert protein called keratin. Small flexible feathers cover the body surface and provide insulation, while the bigger and Stiffer feathers of the wing and tail provide the aerofoils that permit flight. Once they are formed, feathers become attached dead structures in which damaged parts cannot be repaired. They deteriorate with time mainly through the

action of physical wear and sunlight, and must therefore be renewed periodically. During a moult, feathers are replaced sequentially, in predetermined order, so that body insulation and (in most birds) flight are maintained throughout. Many birds moult only once a year, others two or more times. Moults may be complete, involving body, wing and tail feathers, or partial, involving body feathers alone (sometimes with a few wing feathers).

Some birds show only one major period of movement each year, as a result of which they may shift from natal site to first breeding site, or from one breeding site to another. But migrants, by definition, make long return joumeys between widely separated breeding and wintering areas, the two journeys usually being separated by more sedentary periods. Typically, the spring journey starts early enough to allow the birds to reach their breeding areas in time to exploit the seasonal food peak. In fact, many species seem to arrive in their breeding areas as soon as suitable food appears sufficiently available, and their survival there becomes possible. Autumn departure occurs under a declining food supply, and seems timed so that birds leave their breeding areas before their continued survival there becomes jeopardised. Comparing species, migration can last from less than one day to more than four months, depending mainly on the distances involved.

ULTIMATE AND PROXIMATE FACTORS

In discussing the timing of annual cycle events, it helps to distinguish the ultimate from the proximate factors involved. The ultimate factors in timing are those which influence the survival and reproductive success of individuals. The most important is the seasonal change in food supply. We can say that birds breed in spring because, from a food point of view, that is the best time to do so. Any individuals that breed at other times of year are likely to get insufficient food and therefore fail. In contrast, the proximate factors are those environment features, such as change in daylength, which birds use as cues to date, enabling them to prepare for each

event in time to take advantage of the optimal season. They allow an 'anticipatory' response so that the bird is ready for each process at the right time. We can therefore say that birds breed in spring because lengthening days stimulate them to do so. In this example, both food supply and daylength are controlling factors, but food is the ultimate (evolutionary) cause and daylength a proximate timing mechanism. Daylength is of crucial importance as a timer because of its reliability: it is the most obvious environmental factor which in any one place changes in a consistent manner from year to year, and therefore gives an accurate guide to date. Other seasonal factors, such as temperature and day-to-day food supply, are more variable from year to year, but may act as modifying proximate factors, fine-tuning the bird's response to conditions at the time (see later).

ANNUAL CYCLES

Not all bird species breed, moult and migrate in the same order as one another. At least eight different sequences of events occur commonly among different European bird populations and others less commonly, depending on the particular circumstances in which each population lives (Fig. 97). In different species, moult is much more variable in timing than breeding or migration, probably because moult scheduling is less crucial. In general, residents and short-distance migrants moult in summer after breeding (residents more slowly; Fig. 97, sequence 1). Long-distance migrants moult either in late summer in the breeding area (as in sequence 1), in autumn at a migratory staging area (sequence 2) or in winter quarters (sequence 3) (Jenni & Winkler, 1994; Newton, 2008). Different populations show different patterns, but generally all the individuals in a population show the same pattern. Moulting in wintering areas is widespread among northern hemisphere species which spend their non-breeding period in the southern hemisphere, where the seasons are reversed (the southern summer coinciding with the northern winter).

In many other migratory species, the moult occurs partly in one area and partly in another, separated by migration. The moult can be split between the breeding area and wintering area (sequence 4), between the breeding area and a staging area (sequence 5), or between a staging and wintering area (sequence 6). The moult normally stops during migration, so that the bird can fly with a full set of flight feathers, some new and others old. The bird resumes the second part of moult wherever it left off in the first part. In the last two of these patterns (sequences 5 and 6), a split moult is associated with a split migration. In other (mostly large) species, split moults are associated with breeding (as moult stops temporarily during chick-feeding), or with periods of winter food shortage. It seems from these various patterns that breeding normally takes precedence over both migration and moult, and that migration takes precedence over moult, which therefore shows most variation in timing between populations.

These various generalisations apply mainly to small or medium-sized birds, in which moult occurs as a distinct event in the annual cycle (Fig. 97). In many species, all three processes each occupy short enough periods that they can all be fitted within a year without overlap, and often with a quiescent period as well. In some large birds, however, such as vultures and albatrosses, breeding cycles and moult take so long that they cannot both be fitted within a calendar year without overlapping, and in some such species moult may also overlap with migration (Stresemann & Stresemann, 1966). In most raptors, for example, moult begins during incubation (earlier in females than males) and overlaps with most of the breeding cycle, although it may stop temporarily during chick-rearing. Smaller raptor species can normally finish their moult before the post-breeding migration, but larger ones, which take longer to grow their feathers, arrest moult during migration, and continue after reaching winter quarters. In some of the largest flying birds, such as vultures, condors and albatrosses, each moult cycle lasts more than a year, but again may be interrupted during difficult periods, such as chick-rearing. Otherwise, such birds appear to

moult more or less continuously, and may have two or more moult waves in the primary and secondary flight feathers at once (so-called serial moult), even overlapping with migration.

INTERNAL TIMEKEEPING

If captive birds are kept for many months under constant artificial daylengths, such as 12 hours of light alternating with 12 hours of dark, they usually moult and reach breeding and migratory condition in the correct sequence, and at roughly appropriate intervals. This happens even though such birds are kept totally insulated from the outside world, and have no external cues as to what the date might be. It is taken to imply the existence within the birds of some underlying 'endogenous' controlling system—a self-sustaining rhythm (or 'body clock') which tends to ensure that the major processes of migration, breeding and moult occur in the correct sequence each year, and at roughly the right times. However, in conditions of constant daylength, the cycles do not stick strictly to a year, but tend to drift, getting either shorter or longer, hence the term 'circannual' cycles ('about a year'). In such captive birds, which are unable to breed and migrate naturally, breeding condition is indicated by song and other features, and migratory condition by restlessness and fattening, while moult is obvious from the shed feathers.

The importance of daylength

Under natural conditions, the endogenous rhythms of many birds are kept in phase with the seasons by daylength changes, which ensure that the different processes occur at appropriate times of year. The synchronisation of the internal rhythm to daylength has been shown most convincingly in experiments in which birds were exposed to seasonal photoperiodic cycles with periods deviating from 12 months. As a rule, the birds' biological rhythms then conformed to the altered daylength regime (Gwinner, 1986, 1990).

For example, when the normal annual cycle of daylength was shortened to six months without altering its amplitude, Garden Warblers went through four instead of two moult periods within one calendar year, two instead of one gonad cycle and four instead of two periods of migratory restlessness (Berthold, 1996). The same occurred in various other passerines given similar treatment. The implication is that the internal rhythm of the bird is kept in step with external conditions by the annual daylength cycle. This ensures that the internal rhythm of breeding, moult and migration fits the external rhythm of environmental conditions.

A second line of evidence for the role of daylength as a timekeeper involves birds from the northern hemisphere that were introduced into the southern hemisphere by people. Such birds normally adjusted to the local daylength regime within a year or two after their release. Their annual cycles remain essentially unaltered, except that they become six months out of phase with those in their original home. European birds introduced to New Zealand breed in October–January (the southern hemisphere spring–summer), compared with April–July in Europe (the northern hemisphere spring–summer). By manipulating the annual daylength cycle, this finding has been duplicated in experiments on various captive birds (Gwinner, 1986).

The importance of daylength as a timekeeper derives, as mentioned earlier, from its reliability. Its seasonal changes at particular sites are consistent between years, so that it gives a reliable cue to date at most latitudes. However, at particular dates, the weather, food supplies or other conditions vary from year to year. It is therefore advantageous for wild birds to respond not only to daylength, but also to other secondary factors, modifying their activities to suit conditions at the time. In cold springs, plant growth and invertebrate activity begin much later than in warm ones, and any bird that did not respond appropriately to this variation could be seriously disadvantaged. Hence, secondary environmental factors may act in addition to daylength to fine-tune the timing of various

events to the conditions prevailing in particular years (Lack, 1954; Wingfield *et al.,* 1993; Wingfield, 2003).

Geographical variation in response to daylength

With increasing latitude, the annual warm season becomes progressively shorter and the cold season longer. Correspondingly, most migratory bird species arrive later in spring, often breed over a shorter period, and leave earlier in autumn at higher latitudes than at lower ones (Chapter 11). Yet in the northern hemisphere, birds from the north of the breeding range do not start nesting when they pass through the southern parts, at a time when individuals that breed in those areas may already have eggs or chicks. Nor do southern birds continue migrating northwards with others of their species once they have reached their own particular breeding areas. The implication is that birds habitually nesting at different latitudes have different inherent responses to daylengths, thereby adjusting their annual schedules to the latitude at which they breed. The result is that birds that breed in the south of the breeding range arrive earlier than those that breed in the north. Similarly, in association with the earlier onset of winter at high latitudes, many species withdraw from high-latitude parts of their breeding range first, and from lower-latitude parts later (for exceptions, see Chapter 11). The assumption is that, in order to prepare for both spring and autumn migration, populations have evolved responses to different daylength regimes, appropriate to the latitude at which they breed. Again, these views are confirmed by experiments involving the manipulation of photoperiods, as shown for different captive populations of Chaffinches (Dolnik, 1963), Willow Warblers (Gwinner, 1972), flycatchers (Gwinner, 1986), Stonechats (Helm, 2003), various waterfowl (Murton & Westwood, 1977) and others. In each case, birds breeding at higher latitudes required longer daily light periods in spring to stimulate migratory fat deposition or gonad growth than birds of the same species from populations breeding at lower latitudes. The evolution of this appropriate

response is dependent on the ‘homing’ behaviour of birds, in which individuals normally return to breed in the region of their birth, rather than in some markedly different latitude, the process continuing in generation after generation.

The endogenous rhythm in migrants

While many birds live year-round in the same place, and are therefore subject to the same daylength cycle year after year, migratory birds change their place of residence over long distances within a year. They are therefore exposed to two or more different daylength regimes within a year, in breeding, migration and wintering areas, and can sometimes pass from one to another in the space of a few days. This could bring problems in the use of prevailing daylength alone as a timing mechanism, especially in long-distance migrants which winter close to or beyond the equator, as the following situations reveal.

Birds that winter near the equator can spend up to half of each year under constant daylengths. So in contrast to other species, such birds cannot rely on changes in daylength for timing those seasonal activities that occur in their wintering areas, notably the spring departure for breeding areas. Moreover, in many equatorial regions, other environmental factors vary little or unpredictably through the year, and so are also unreliable as seasonal cues. So after spending several months in constant daylengths, how do such birds time their departure from wintering areas? The problem is highlighted in Yellow Wagtails, in which several different races winter together in equatorial Africa, but set off at different dates from one another, depending on where they breed. The race that breeds in the most southern parts of Eurasia leaves first and the race that breeds furthest north leaves last, while other races are intermediate (Curry-Lindahl, 1958, 1963; Wood, 1992). These various races arrive in their breeding areas in the same sequence that they leave the equatorial wintering area, spanning the period March–June, from south to north. In explaining this pattern, Curry-Lindahl (1958)

speculated that the birds used ‘an internal clock’ (equivalent to an endogenous rhythm) which was set on the breeding areas, and then kept running for some months in order to trigger migration at an appropriate date in the following spring: different dates in different populations.

The idea of endogenous influence is further supported by the observation that the onset of spring migratory restlessness in caged warblers in Europe coincides with the spring departure of conspecifics from their equatorial wintering grounds (Gwinner, 1968). Captive migrants spontaneously resume spring migratory activity after a winter rest, even when kept under constant daylengths. Moreover, different species or different races of the same species kept under identical captive conditions reach breeding, moulting or migratory condition at different dates appropriate to the latitude at which they breed (for *Phylloscopus* warblers, see Gwinner, 1972).

It seems, then, that in long-distance migrants that winter in the tropics and beyond, endogenous time programmes may operate for the entire life of the individual, and regulate the timing of all seasonal activities, whether breeding, moult, fat deposition or migratory restlessness. Although the cycles are intrinsic to the individual, and do not require environmental cues to operate, they are normally synchronised by changes in daylength that keep the endogenous components in step with the seasons. In long-distance migrants, the ‘clock-setting’ imposed by daylength may operate during only part of the year, then enabling the internal rhythm to run for some months independently of the daylengths to which the bird is exposed on migration. A good time for clock-setting would be the summer solstice, which gives an unequivocal signal of date to any creature that can measure daylengths, but it is not known whether birds actually do use the solstice in this way.

Among populations wintering in Europe, endogenous control would seem less important than in equatorial regions, because at the same latitudes different wintering populations could respond to particular threshold daylengths, so that they left at appropriate

dates. One species or population might be stimulated to begin migrating under March daylengths, while another needed the longer days of April. However, an endogenous influence, or an ability to separate increasing from decreasing days, would still be necessary at European latitudes in order to prevent such birds from moving northward (rather than southward) in autumn under the same daylengths that stimulate northward migration in spring.

Evidence for genetic influence on circannual cycles derives partly from the fact that, on natural daylengths, first-generation hybrids exhibit patterns of migratory timing and fat deposition that are intermediate between those of their parents. This has been shown for waterfowl (Murton & Westwood, 1977), for *Sylvia* warblers (Berthold, 1993, 1996), for *Phoenicurus* redstarts (Berthold, 1990) and for Stonechat races (Helm *et al.,* 2005). Other evidence of genetic influence comes from heritability studies based on parent–offspring comparisons, and from the changes that have occurred in wild birds in response to particular selection pressures, as explained in Chapter 15.

Departure from different latitudes: the role of daylength

Many migratory species winter over a wide span of latitude. In general, northern breeding populations that winter furthest south, and have further to migrate, start their return migration earliest in spring, whereas those that winter further north start later. In other words, wintering populations withdraw in sequence from south to north, as they return to their northern breeding areas, the departure dates being latitude-specific. Again, the assumption has been that each population evolves a specific response to the daylengths prevailing in its own wintering area (possibly in association with an endogenous rhythm), so as to start migration at an appropriate date.

The difficulty arises in populations which winter over a wide latitudinal span, or winter at different latitudes in different years, yet still depart earliest from furthest south. Even individual birds show different starting dates in different years according to the

latitude at which they are wintering at the time. Take, for example, a radio-tagged White Stork satellite-tracked on its round trip to Africa in six different years (Berthold *et al.,* 2004). In two years, this bird wintered around the equator, about 7,000 km from its nest, and in four other years wintered in the Cape Province of South Africa, 11,000 km from its nest (it used the same nest each year). When wintering in the south, it set off nearly a month earlier than when it wintered near the equator, but it arrived at its nest on about the same dates each year. Clearly, in this situation an internal clock is not enough, because birds must also have adjusted their departure dates in some way to the conditions (presumably daylength) where they wintered. So far as I am aware, these complicated issues of the timing of spring migration from different latitudes have not been studied by experiment. They illustrate some of the remarkable things that birds can do, and some of the gaps in our understanding.

DEFERRED RETURN TO BREEDING AREAS

In some long-lived bird species, individuals migrate from the breeding range in their first autumn, and do not return in the next spring, but only in a later one, when they are two or more years old. These young birds either remain in their 'wintering' areas year-round over one or more years, or they may return only part way towards the breeding areas. Alternatively, they may visit the breeding areas for only a small part of the season, migrating later in spring and earlier in autumn than older birds. Unconstrained by the needs of breeding, they perform both migrations less hurriedly than the breeding adults, and at a more favourable time. Such patterns are shown by various raptors, seabirds, waders and others in which individuals do not breed until they are several years old (Chapter 21).

The tendencies of immature birds to spend their first summer in 'winter' quarters or to travel shorter distances or later than adults might result from an inability to obtain enough food and accumulate fat at an adequate rate (Chapter 21). Alternatively, it

might result from an inherent endogenous response that matures with age, leading birds of some species not to return to nesting areas in their earlier years or to visit nesting areas only to prospect for suitable sites but not to breed. Resolving these questions must await more research, but whatever the answers, endogenous factors are presumably involved in initiating moults and movements at appropriate dates, at least in birds that winter in equatorial or opposite-hemisphere regions.

CONCLUDING REMARKS

In comparing the different annual cycles of birds, one of the most striking findings is the great variation in the sequence and duration of breeding, moult and migration among species, or even among different populations of the same species. This variation shows how the cycles are constrained by features of the birds themselves and adapted to the areas and circumstances in which different populations live. In each population, the cycle is adjusted primarily to the seasonal changes in climate and food to which the birds are exposed on their travels, migration timing apparently having evolved in concert with the other events that make up the yearly schedule.

The annual cycles of birds usually involve substantial changes in morphology, internal body structure and composition, as well as in physiology and behaviour. Only some of these aspects are visible from the outside, yet they accompany each of the major processes of breeding, moult and migration. Some changes are obvious to the casual observer, as birds replace their drab winter colours with brighter breeding plumage. Behavioural changes are also obvious, as many species which flock in winter switch to conspicuous territoriality in breeding areas, later becoming quiet and elusive during moult. Increases in body weight and gonad size are associated with the production of sperm or eggs, and high weight also with incubation. Migration is likewise associated with changes in body composition and overall body mass, as migratory fuel is

deposited and consumed during the course of the journeys. At that time of year, many normally diurnal species also become active at night. Such ‘phenotypic flexibility’ is evident whenever an individual switches from one life-history stage to another, and is an important way in which birds make the most of seasonally changing environments, while altering their appearance, body composition and behaviour to meet the needs of the time.

CHAPTER 10

Migration Timing

In the previous chapter, we saw how the annual schedules of different bird populations were adapted to the particular circumstances in which they live. This chapter is concerned with the proximate factors that influence the timing of migration in individual birds. It begins with some general points, and then moves on to the particular factors that operate in autumn and spring. As elsewhere in this book, I use the term autumn migration for the postbreeding movement towards wintering areas, even though in some species this migration begins in the latter half of summer. At both seasons, much has been learned about the control of migratory timing from studies conducted on captive birds, which offer better opportunities than wild ones for experimental studies.

OBLIGATE AND FACULTATIVE MODES

European researchers have long distinguished between obligate migration (formerly called 'instinct' or 'calendar' migration) and facultative migration (formerly called 'weather' migration). Broadly speaking, in the British Isles these two types of migration are associated with different species. In obligate migration, timing and other aspects are regarded as under firm internal (genetic) control, mediated by daylength changes. This genetic control gives a high degree of year-to-year consistency in the timing, directions and distances of movements. For the most part, each individual behaves in the same way every year, migrating at similar dates, in similar directions and often for similar distances. Typically, obligate

migrants leave their breeding areas each summer well before food supplies collapse, and while they still have ample opportunity to accumulate body reserves for the journey. To some extent, their behaviour can be regarded as ‘anticipatory’, in that they leave ahead of the onset of potentially lethal conditions. They tend to migrate long distances, often to the tropics or beyond, and frequently travel by night. Typical examples include the Cuckoo and Willow Warbler.

Although in such facultative migrants, the timing and distance of autumn movements may vary with individual circumstances, other aspects must presumably be under firmer genetic control, notably the directional preferences and the tendency to return at appropriate dates in spring. Compared with obligate migrants, facultative migrants tend to migrate shorter distances, and to travel by day, although exceptions occur. The two types of migrants thus have different distribution patterns in mid-winter. Whereas obligate migrants are usually concentrated in a distinct wintering area far from the breeding area, facultative migrants are often found in winter over the whole migration route from breeding to wintering areas, usually tailing off with increasing distance from the breeding area, but with marked annual variations.

In general, it seems that obligate migration occurs in populations whose food supplies in breeding areas are predictably scarce or absent in winter, giving little or no chance of survival there. In contrast, facultative migration occurs in populations whose food supplies in breeding areas vary greatly from one winter to another, according to weather, fruit crops or other variables. The distinction between obligate and facultative migration is useful because it captures the different degrees to which individual behaviour is sensitive to prevailing conditions, and hence varies from year to year. However, obligate and facultative migrants are perhaps best regarded, not as distinct categories, but as opposite ends of a continuum, with predominantly internal control (= rigidity) at one end and predominantly external control (= flexibility) at the other.

Another reason for not drawing a sharp distinction between the two categories is that many birds seem to change from obligate to

facultative mode during the course of their journeys, as the internal drive to migrate wanes with time and distance, and further migration becomes more directly dependent on local conditions (Terrill & Ohmart, 1984; Gwinner *et al.,* 1985; Terrill, 1990). Theoretically, the initial obligate phase of any journey might take the migrant across regions where the probability of overwinter survival is practically zero: where any individuals that attempted to winter there in the past were eliminated by natural selection. As migration continues into more benign areas, and survival probability rises, the bird switches to a facultative mode, in which it benefits by responding to local conditions, settling where food is readily available. The obligate phase would therefore be expected to take place more rapidly, on average, than the facultative phase, which involves longer and more variable stops. Such a two-stage migration, with obligate and facultative components, would also ensure that, in any particular year, the bird migrated no further than necessary. In some species, only the tail end of the migration maybe facultative, in others the entire journey. Most irruptive migrants, including Siskins and Waxwings, are near the latter end of the spectrum.

Arctic-nesting geese provide circumstantial evidence for a two-stage autumn migration, in which the first part is obligatory and the second part facultative. Geese need to leave the Arctic every year before their survival there becomes impossible, and they tend to depart en masse on about the same dates every year. But once they reach wintering areas, their movements become much more variable in timing and extent, depending largely on local conditions. They appear to change from a primarily endogenous migratory stage (obligate migration) to a stage when the stimulus for further migration is primarily environmental (facultative migration). In effect, as birds travel south in autumn, the drive to continue becomes increasingly dependent on prevailing conditions (Terrill, 1990).

Further support for the idea that migration is often two-stage comes from studies of captive songbirds, some of which show two

stages in migratory behaviour. The first stage is characterised by intense and continuous night-time activity, and the second by less intense activity, with numerous interruptions and greater variability (Helms, 1963). Later in the autumn or winter, nocturnal restlessness in various captive songbirds can be initiated or enhanced by restricting food or lowering temperature (Farner, 1955; Biebach, 1985; Gwinner *et al.,* 1985). These findings imply that such species could respond to adverse conditions by migrating at almost any time in the non-breeding season, but whether the captive birds reacted to temperature directly or through their energy needs and body condition was not clear.

On the return migration, the first part can be regarded as obligate but, once within the breeding range, migration again becomes more facultative in nature, enabling individuals of some species to settle wherever conditions are suitable that year. This is again most evident in species that exploit sporadic tree-seed crops (finches), caterpillar outbreaks (Brambling), local rodent peaks (mainly owls), particular wetland conditions (marsh and waterbirds) or snow-free patches on the tundra (waders and passerines). All such species tend to settle to nest each year in areas where conditions are most suitable, and vary in distribution from year to year (Chapter 19). They contrast with the majority of bird species, which return to the same breeding sites year after year (Chapter 13).

Role of dominance in facultative migrants

Because birds compete over food, and vary in dominance or feeding efficiency, some individuals could survive in autumn–winter conditions in which others would die unless they moved on. In facultative migrants, the subordinate sex and age groups typically migrate in greater proportions, at earlier dates, or extend further from the breeding areas than the dominants. Thus, in many bird species, adult females are more migratory than adult males, juveniles more than adults, and late-hatched young more than early hatched ones (Chapter 21). Such differences have led to the notion

that competition (or its effect on body condition) is involved as a proximate mechanism stimulating migration in those individuals least able to survive in local conditions (Gauthreaux, 1978).

Depending on circumstances, as mentioned above, the same individual might migrate in one year but remain in the breeding area in another (Nice, 1937). The commonest pattern is for a bird to migrate in its first year and not thereafter, but other sequences occur, presumably because foraging conditions in the breeding area vary from winter to winter (e.g. for the Blackbird, see Schwabl, 1983). If dominance were involved, the overall proportion of birds stimulated to migrate would depend on feeding conditions that year, with more birds from the dominant age groups departing in poor food years than in good ones. An effect of food supply mediated by social dominance was confirmed in captive birds in which subordinate individuals that lost out in aggressive interactions over food were most likely to accumulate fat and show migratory restlessness (Terrill, 1987). It may seem surprising that such losers can put on fat, but they seemed to do so through changes in physiology and behaviour, feeding for much longer each day than usual. The hormonal changes that stimulate migration in partial migrants are not yet understood, but the stress hormone, corticosterone, is probably involved (Wingfield, 2003).

THE MIGRATORY STATE

As most birds cannot forage while flying, the chief physiological change necessary for migration involves the accumulation of fat and other body reserves to sustain the bird and fuel its flight (Chapter 6). The main behavioural changes necessary for a bird to migrate involve an urge to depart given suitable weather, and a tendency to fly in one particular direction rather than any other. In captivity, diurnal migrants typically show migratory restlessness by day, and nocturnal ones at night.

Under natural daylengths, caged birds from obligate migratory populations develop fat reserves and migratory restlessness at

appropriate dates in autumn and spring, at about the same times as their wild counterparts in the same area. Evidently, the same factors that stimulate departure in wild birds trigger restlessness in captive ones kept on natural daylengths (Berthold, 1996). The role of daylength in promoting these processes (in association with an endogenous rhythm) is shown by the findings that: (1) captive birds experimentally exposed to photoperiods *longer* than natural days in spring develop migratory condition earlier than their wild counterparts; and (2) captive birds exposed to photoperiods *shorter* than natural days in late summer or autumn develop migratory condition earlier than their wild counterparts. As in the case of breeding, however, secondary factors also influence the timing of migration.

Food, fattening and restlessness

The role of feeding conditions in affecting the fattening rates, body condition and departure dates of migratory birds has been established in the field for a range of species from the Sedge Warbler (Bibby & Green, 1981) to Greylag Goose (van Eerden *et al.,* 1991). In general in these studies, individuals that could feed most rapidly also fattened most rapidly and left before others in the same population. Poor feeding conditions thus contributed to the variation in departure dates between individuals in the same season, and could delay the progress of whole populations in some years (Chapter 11).

The maximum fat levels accumulated by migratory birds are under genetic influence, and birds making long flights over areas where they cannot feed deposit more body fat than those making short flights. Little is known of what regulates fat deposition in individuals, but once an adequate level has been achieved, migrants normally leave at the first opportunity. This would be expected because, once acquired, fat reserves are expensive and risky to maintain, conferring in some species increased vulnerability to predation (Chapter 6). As they prepare for migration, birds have

often been caught and weighed, and whereas lean birds are usually re-caught on subsequent days as they gain weight, heavy (fat) ones are seldom re-trapped, suggesting that most have moved on (Bibby & Green, 1981; Yong & Moore, 1993).

Research on captive birds has confirmed that the motivation to depart on migration is related to body fat, as is the strength of directional preference (Dolnik & Blyumental., 1967; Yong & Moore, 1993; Sandberg *et al.,* 2002). In one study, four songbird species were caught on stopover at an oasis in Algeria, and kept in cages fitted with activity recorders (Bairlein, 1992). Lean individuals were usually active only during daytime, feeding as normal, whereas fat birds remained inactive by day without feeding but became active at night when they would normally have migrated. Birds with moderate fat reserves fed during the day and were also active at night. Nocturnal migratory activity was thus clearly associated with fat levels.

In another type of experiment, birds were trapped on autumn migration. Each was weighed, and then tested for directional preference in a circular cage. It was then fitted with a small chemi-luminescent light stick, released on its own one or two hours after sunset, and followed with binoculars until lost from view (Sandberg & Moore, 1996). Before their release, significantly more fat birds than lean ones showed migratory activity in cage tests. After release, all the fat birds flew out of sight in the migration direction, whereas the lean ones either stayed at their current location or took a direction opposite to the migration direction. Such findings were obtained in release experiments using Robins and Pied Flycatchers (Sandberg *et al.,* 1991). Similarly, in cage tests on Chaffinches and Snow Buntings, the heaviest (= fattest) individuals were the most likely to show a preferred direction (Bäckman *et al.,* 1997; Sandberg *et al.,* 1998). The fact that many lean birds preferred the opposite direction should not surprise us, because in the wild, temporarily reversed migration is not uncommon when lean birds encounter a sea coast or other barrier. It has been interpreted as an attempt to find more profitable feeding areas away from the crowded coast

(Chapter 4). Most of the above experiments were conducted at coastal localities, and the behavioural difference between fat and lean birds may be less marked at inland areas where feeding sites are plentiful (Sandberg & Moore, 1996). When migrating short distances through favourable terrain, departing individuals often show a wide range of fat levels, indicating no specific level at which departure is triggered (Schaub *et al.,* 2008). Such birds might then simply vary the length of their flights, according to their body reserves.

The general speed of migration depends not only on the flight speeds of the birds themselves, but also on conditions at stopover sites (which influence the feeding and fattening rates of individuals) and the weather encountered en route (Chapter 7). Warm conditions in spring favour the development of fresh food supplies, and in Europe are also associated with warm southerly tailwinds which favour migration. It is not surprising, therefore, that migratory journeys tend to be accomplished more quickly in warm springs than in cold ones (Forchhammer, 2002; Ahola *et al.,* 2004; Marra *et al.,* 2005; Huppop & Winkel, 2006). In autumn, cold conditions tend to reduce many kinds of food, and are also associated with northerly tailwinds which favour southward migration (Lack, 1960).

AUTUMN MIGRATION

In obligate migrants in which all individuals leave the breeding range, the dates of migration are in general fairly consistent from year to year, but while some species moult before leaving, others depart immediately after breeding and postpone moult until later in the year. Broadly speaking, in species which moult in breeding areas, the earliest juveniles finish moult and begin migration before the earliest adults; but in species that moult in wintering areas, adults generally leave before juveniles, as in many long-distance passerines, shorebirds and others (Chapter 21). In some species, sex differences in timing also contribute to the spread in departure dates within populations, as described in Chapter 21.

In some studies, marked individuals showed great year-to-year consistency in their arrival dates in staging or wintering areas. Those which arrived early with respect to other individuals in one year also arrived early with respect to other individuals the next year. In Tundra (Bewick's) Swans, Rees (1989) attributed this individual consistency to inherent variation in their response thresholds to daylength, but other explanations were possible, including variation in their abilities to feed and fatten for the journey.

In facultative migrants, the situation differs. Such populations generally moult after breeding, but individuals do not necessarily depart immediately after finishing moult. If conditions are favourable, some may linger longer in the breeding or stopover areas, leaving only when food supplies dwindle. As indicated above, mean autumn migration dates may therefore vary greatly from year to year, depending on local conditions, as may rates of travel. This situation is exemplified by most short-distance migrants, but especially by irruptive seed-eaters and by waterfowl and others affected by frost (Chapter 19). For example, the peak date for passage of Siskins through Falsterbo Bird Observatory in south Sweden between 1949 and 1988 varied from 15 August (in 1988) to 17 November (in 1958), the last date the station was manned that year (Roos, 1991). At another site, Siskins passed in largest numbers, and at the earliest dates, in years when birch seeds (their main autumn food) were scarce (Svardson, 1957; Chapter 19). Such facultative migrants evidently depart chiefly when deteriorating conditions encourage them to leave. Together with variable conditions on migration routes, this type of response gives wide variation in the dates that birds arrive at different latitudes in their potential wintering range, the more distant parts of which maybe reached only in occasional years.

Relationship between breeding, moult and autumn departure

Within populations, the timing of autumn departure is also influenced by preceding events in the annual cycle. Many birds lay a repeat clutch if the first is lost, or raise more than one brood in a year. Adult pairs get increasingly out of synchrony with one another through the season, and some breed much later into the summer than others in the same area. In species which moult in their breeding areas, individuals that finish breeding late also moult and migrate later. However, they may begin moult earlier with respect to a nesting cycle, well before their young have fledged, and may also replace their feathers more rapidly than earlier birds (Johnson & Minton, 1980; Morton, 2002). By these means, individuals breeding until late in the season reduce the delay in their migration.

Similar things happen in juveniles. In multi-brooded populations, young are produced in summer over periods of several weeks. Compared to early hatched young, later ones start to moult at a later date but at an earlier age, and may also replace their feathers more rapidly or less completely, as recorded, for example, in the Chaffinch (Dolnik & Gavrilov, 1980), Stonechat (Helm *et al.,* 2005) and various warblers (Berthold, 1988). In addition, while early young normally fatten for migration after completing moult, late birds may begin to fatten well before the end of moult. These differences between early and late birds again tend to lessen the delay in the migrations of late birds.

In experimental conditions, various songbird migrants started post-juvenile moult and autumn migration activity at a younger age if held under short photoperiods[†] They also moulted and fattened more rapidly, or showed more overlap between moulting and fattening, another time-saving adaptation in late birds, as found for example in Bluethroats (Lindström *et al.,* 1994) and Lesser Whitethroats (Hall & Fransson, 2001). The implication from these experiments was that the accelerated development of late young was promoted by the shortening days of autumn.

There are, however, costs to faster development. Feathers grown during a period of rapid moult are sometimes of poorer quality,

which could reduce a bird's chance of survival (Dawson *et al.,* 2000). Hence, the greater acceleration and overlap of different processes in late birds probably involves a trade-off. It saves time but only at the costs of additional daily energy need and reduced feather quality. Early birds can enjoy greater separation between the different processes, whereas in late birds, time-saving becomes paramount and separation less. The greater fat levels accumulated by late migrants may also make them more vulnerable to predation. While studied mainly in songbirds, links between breeding, moult and autumn migration timing are also apparent in other species, including various waterfowl (MacInnes, 1966; Black & Rees, 1984).

To sum up, in late-breeding adults, and in juveniles hatched late in the season, a response to shortening daylengths can speed up the moult, increase the overlap between breeding and moult (adults only) or between moult and migratory fat deposition, and increase the rate and extent of fat deposition, thereby reducing the delay in migration caused by late breeding. This acceleration of development in late season, known as the 'calendar effect' (Berthold, 1993), enables late birds to leave breeding areas before conditions deteriorate. However, in species which depart immediately after breeding, findings with respect to moult do not hold, because in these species, moult is postponed until after arrival in a staging or wintering area.

SPRING MIGRATION

Birds normally leave their wintering areas so as to reach their nesting areas in time to breed at the most favourable season. Many migrants winter so far from their breeding areas that they cannot judge conditions there from their positions in wintering areas. They can only leave their wintering areas at a time that natural selection has decreed is appropriate, using an internal timer combined with local conditions as a cue (Chapter 9). Among species wintering in the temperate zone, the main known environmental stimulus for spring migration (superimposed on an endogenous rhythm) is

increasing daylength, which promotes extra feeding, fattening and migratory restlessness at appropriate dates for the population concerned (Rowan, 1926; Wolfson, 1959; King, 1972). In species which moult in spring, this process is also initiated by increasing daylengths, as is gonad growth, each process occurring in appropriate overlapping sequence through the season (Gwinner, 1986, 1996; Berthold, 1996; Coppack & Pulido, 2004). The role of daylength has been shown repeatedly in experiments on captive birds, in which longer-than-natural photoperiods advance all spring-occurring processes, whether gonad growth, pre-nuptial moult or migratory fattening.

In many species that undergo a spring 'pre-nuptial' body moult into breeding plumage, this process also starts in winter quarters and proceeds through migration. However, the timing of this moult often varies greatly between individuals in the same population, much more than the start of migration. Among shorebirds seen at spring stopover sites, some individuals are in predominantly winter plumage, while others of the same sex at the same sites at the same time are in predominantly breeding plumage. Nutritional conditions may have a big influence on the timing and duration of this moult, as may inherent features (Battley, 2006; Chapter 15).

Conditions in wintering areas apparently affect the dates of spring migration. For example, many birds arrive at staging or breeding areas earlier in springs following good (= wet) conditions in African wintering areas than in springs following poor (= dry) conditions. This has been noted, for example, in the arrival dates of White Storks, Cuckoos and Barn Swallows in Iberia (Gordo & Sanz, 2008), of Barn Swallows in Italy (Saino *et al.,* 2004b), of Pied Flycatchers in England (Goodenough *et al.,* 2009), and of Cuckoos and Barn Swallows in Norway (Forchhammer *et al.,* 2002). Presumably, birds can fatten and migrate more rapidly in the good feeding conditions promoted by rain. In species which moult in winter quarters, such as the Barn Swallow, the process takes longer in dry years when food is scarce, which may in turn delay migration (van den Brink *et al.,* 2000). Similar delay, caused by a more

prolonged moult in certain years, has also been seen among Mallard in North America (Dugger, 1997).

Whatever the mechanism, the implication is that departure from winter quarters can be delayed by poor feeding conditions, which may in turn delay arrival inbreeding areas, and also affect subsequent reproduction (see Saino *et al.,* 2004a). In other species elsewhere, individuals that wintered in good habitats (= abundant food) departed earlier and arrived in breeding areas earlier than those that wintered in poor habitats, a further indication of the link between feeding conditions and individual migration dates (Marra & Holmes, 2001). This has been shown, for example, among Black-tailed Godwits individually colourringed so that they could be recognised in their wintering and breeding areas (Gunnarsson *et al.,* 2005).

As with autumn migration dates, individuals of some species have shown some consistency in spring migration dates from year to year, as measured either by their departure dates from wintering areas (for Tundra Swan, see Rees, 1989; for Bar-tailed Godwit see Battley, 2006) or by their arrival dates in breeding areas (for Barn Swallow, see Møller, 2001; for Greater Snow Goose, see Bêty *et al.,* 2004; for Black-tailed Godwit, see Gunnarsson *et al.,* 2006). Individuals that were early relative to other individuals in one year tended also to be early relative to other individuals in subsequent years. As in autumn, such consistency could have been due to inherent differences in migration timing between individuals, or to other differences between them, perhaps in the quality of their winter habitat and their abilities to feed and fatten. As individual birds tended to occur in the same places each winter, those in good habitats might be able to depart early every year (Gunnarsson *et al.,* 2006).

The partners in pairs of Black-tailed Godwits in Iceland showed remarkable synchrony in spring arrival dates, despite having wintered up to 1,900 km apart from one another (Gunnarsson *et al.,* 2004). One suggestion to explain this synchrony is that partners independently synchronise their arrival dates to the optimal time for

their own breeding site. It is more likely, however, that if birds have strong individual timetables for migration, some are likely to arrive consistently earlier or later than others. Mate formation and retention would then be a by-product of individual migration schedules that happened to coincide and allow pair formation in the first place (Gunnarsson *et al.,* 2004; Battley, 2006). It is not unusual among other birds for members of established pairs to arrive at their nesting places closer in time than expected by chance, another studied example being the White Stork (Tryjanowski *et al.,* 2004).

A 'calendar effect' may operate in spring, as well as in autumn, affecting the rate and extent of fattening, and the duration of stopovers. To give some spring examples, in Sedge Warblers and Reed Warblers studied on stopover in southern Israel, late birds gained weight faster and to a greater extent than earlier birds (Yosef & Chernetsov, 2004). The same was true for Red Knots migrating through Delaware Bay, in which the fattening rates increased by two or three times between mid-May and late May (Atkinson *et al.,* 2007). This seasonal trend could again have accelerated the migration of late birds within populations. But whether it arose from an inherent response to daylength (time of year), as in autumn, or from an increased food supply in late spring is an open question.

SPRING ARRIVAL AFFECTS AUTUMN DEPARTURE

Some long-distance migrants raise only a single brood each year and then depart from their breeding areas. In such species, the timing of arrival in breeding areas can influence the timing of all subsequent events up to postbreeding departure. This is because the breeding cycle, consisting of egg-laying, incubation and chick growth, is of fairly consistent duration, both from bird to bird and from year to year. So in springs when birds arrive early in their breeding areas, they can usually breed earlier and depart earlier in late summer. The whole sequence of events is thus affected by spring weather, leading to shifts in the whole breeding cycle from year to year (Nisbet, 1957; Sokolov *et al.,* 1999; Newton, 2008).

Consider the Common Swift, in which individuals depart soon after breeding, postponing their moult for winter quarters. Each pair leaves on migration within a few days after raising its brood. The date of departure is clearly determined primarily by the completion of breeding, which in turn is influenced by the date in May when eggs were laid (Lack, 1956). Since the latter is influenced by temperature, the mean date of departure of swifts in August depends on the weather in the preceding May.

More recently, year-to-year correlations between spring arrival or laying dates and autumn departure dates have also been noted among North European populations of the Bluethroat, Willow Warbler, Arctic Warbler, Sedge Warbler, Reed Warbler, Pied Flycatcher and Little Bunting, among others (Ellegren, 1990b; Sokolov *et al.,* 1999; Sokolov, 2001). The implication is that, in such single-brooded obligate migrants, autumn departure dates depend not so much on environmental conditions at the time, but on the completion of previous events in the annual cycle, whether the end of breeding or moult in adults or the end of growth or moult in juveniles, as the case maybe. In line with this, the timing of peak autumn migration in different years at Rybachy on the Baltic coast was related to the preceding April temperature in 15 species examined, emerging as statistically significant in five such species (Sokolov *et al.,* 1999). In none of these species was the timing of autumn migration related to prevailing autumn temperatures. Such close coupling between the timings of spring and autumn migration would not be expected in birds that can raise more than one brood each year, because with occasional nest failures, pairs get increasingly out of phase with one another. Nor would it be expected in some facultative migrants, in which individuals may linger in breeding areas well beyond the end of moult in autumns when the weather is warm or food is plentiful.

COMPARISON BETWEEN AUTUMN AND SPRING MIGRATIONS

In several respects, migration differs markedly between the two seasons. In autumn, birds leave their breeding areas under decreasing daylengths and temperatures, as conditions are deteriorating. In moving toward lower latitudes, they generally meet more clement conditions (except where they have to cross a large sea or desert). In spring, by contrast, most birds leave their same-hemisphere wintering areas under increasing daylengths, when conditions are improving or at least benign. In moving towards higher latitudes, they generally encounter progressively worsening conditions; they are often held up by bad weather, and may even have to backtrack for part of the route. It is normally some time after arrival in nesting areas that conditions improve enough to allow them to breed. In fact, environmental conditions, and the appearance of food supplies at particular latitudes, may have much more influence on the progress of spring migration than of autumn migration (Chapter 11).

In autumn, populations are large and juveniles are making their first migration; but in spring, populations are smaller and all participants have experienced at least one previous journey. This difference between seasons could influence the time taken over the journey and the extent of deviations from the primary direction, young birds in autumn being more prone to wind drift than older ones (Chapter 21). Moreover, autumn migration may in some species be interrupted for weeks or months at a time if the birds encounter rich feeding areas, but the spring journey is seldom broken for so long. The breeders of many species seem to travel more rapidly in spring than in autumn, most hold-ups in spring being caused by inclement weather.

The duration of migration seasons depends partly on how long individuals take over their journeys, and partly on the spread in their departure dates. In some species, the autumn migration season lasts longer than the spring one; in others, the spring season is more extended, especially in those species in which non-breeding immatures return up to several weeks later than breeding adults. In addition, some populations take different routes or use different

stopover sites in autumn and spring. The birds themselves are also in different physiological states at the two seasons. In autumn, the migrants travel with regressed gonads, and in spring with growing gonads, which leads to seasonal differences in hormonal states, which may in turn influence other aspects of migration. For reasons of physiology, experience and external conditions, therefore, the spring journey differs from the autumn one.

CONCLUDING REMARKS

Study of the proximate control of bird migration has revealed the crucial role of increasing daylengths in spring and to a lesser degree of decreasing daylengths in autumn in triggering migratory fattening. Changing daylengths also influence the rate of fattening and other events, leading to a general speeding up of processes later in a migration season. Although this may have costs, the benefit in autumn is in minimising delay in the departure of late birds from breeding areas, as conditions deteriorate. In spring, the benefit is in minimising delay in the return of late birds to their breeding areas.

While the primary control is by daylength (operating on an underlying endogenous rhythm), secondary factors are also involved, notably food supplies which influence the rate at which fat can be deposited, and previous events in the annual cycle which, if running late, can delay the onset of fattening and migration. A late moult in summer (in turn caused by late breeding) can delay departure from breeding areas, while a late or slow moult in winter can delay departure from wintering areas. This is further indication that migration does not occur at the optimal time in all birds, but is compromised by other events in the annual cycle, as well as by prevailing conditions.

There are still large gaps in our understanding. For example, although obligate and facultative migrants have long been distinguished by their behaviour, we still do not know exactly how they differ in control mechanisms. Similarly, while birds making long flights over sea or desert accumulate larger fat reserves for the

journey than birds migrating through favourable terrain, we still do not understand what regulates the maximum fat levels in different bird populations. Nor do we understand how departure is tripped once fat has achieved an appropriate level in the individual concerned.

† For examples, see Berthold, 1988; Gwinner, 1972; Jenni & Winkler, 1994; Berthold, 1996; Coppack *et al.,* 2001; Gwinner & Helm, 2003.

CHAPTER 11

Comings and Goings

As spring approaches, and days become longer and warmer, migratory birds begin to move from lower to higher latitudes in order to reoccupy their breeding areas. One species after another spreads northwards through Europe, progressively resettling areas abandoned since the previous year. When birds reach their home areas, they re-establish territories and pair up in preparation for breeding. This is followed by the periods of egg-laying, incubation and chick-feeding that comprise a nesting cycle, with some species nesting more than once during a single breeding season. After breeding is finished, the birds withdraw to lower latitudes, where they spend the non-breeding period. These large-scale distributional changes enable migratory birds to exploit the long days and abundant food available each spring and summer at high latitudes, yet avoid the short days and famines of winter.

LATITUDINAL TREND IN THE TIMING OF SPRING

The temperature of 10°C is often taken to indicate the start of spring conditions, suitable for rapid plant growth and insect activity. The spread of the 10°C isotherm from south to north through Europe is shown in Figure 113, based on the average figures gathered over a period of nearly 30 years. This particular isotherm takes more than four months to spread northeastwards through Europe, beginning in the southwest in around mid-January and reaching the extreme northeastern parts in early June. It takes almost as long to spread from the lowest to the highest parts of mountainous areas such as

the Alps, and approximately three months to spread from the southwest to the northeast of the British Isles. It provides a good indication of the onset of spring conditions in different parts of the continent, and the start of the breeding season for many birds.

The dates at which most bird species move northwards through Europe in spring depend partly on the food supplies that become available at successive latitudes. Migrating birds need food not only for daily maintenance, but also to fuel successive stages of their journeys (Chapter 6). There would normally be no advantage for migrating birds to arrive before their developing food sources, as they would then only lose body condition, and might even have to turn back (as sometimes happens; see Chapter 4). However, migration dates are largely an evolved response to past conditions (Chapter 15), so they cannot be expected to precisely match food supplies every year. In cold years, birds sometimes arrive 'too early', and many starve to death, as described in Chapter 23.

As some types of food become available earlier in spring than others, different species arrive at particular localities in fairly consistent sequence from year to year, and at roughly similar dates. Species that depend on spring thaw to release their food supplies (such as some waterfowl and waders) arrive earlier than those that rely on aerial insects (such as hirundines), and earlier still than those that depend on larval insects from later-developing leaves (such as some warblers).

In the first half of the 20th century, much attention was given, with the help of observer networks, to recording the northward advance of various bird species in spring (Fig. 115). In general, earlier migrants spread northwards more slowly than later ones. Five trans-Saharan migrants, namely the Barn Swallow, Willow Warbler, Common Redstart, Wood Warbler and Red-backed Shrike, arrived in southern Europe on the progressively later dates of 13 February, 5 March, 15 March, 1 April and 1 April respectively. They spread north through western Europe at average speeds of about 40, 46, 66, 70 and 88 km per day, and took around 109, 88, 61, 45 and 45 days to get from the southern to the northern parts of their breeding

ranges (Southern, 1938–41). Their northward progression generally kept step with particular isotherms—but different isotherms for different species. Of the five species studied, the Barn Swallow bred over the widest latitudinal range, and its period of spread over this range (109 days) more or less fitted expectations from measures of the northward advance of spring conditions shown in Figure 113.

The relationship between migration and isothermal advance presumably holds, because temperature gives a good indication of when each area becomes suitable for settlement, as food supplies become sufficiently available. It does not necessarily mean that species migrate in direct response to temperature, or that individual migrants travel north at the speed of 'isothermal lines'. Rather, the average rate of northward spread keeps step with particular isothermal lines—different lines in different species—in accordance with the development of their particular food supplies, with both temperatures and food supplies varying in rate of development from year to year.

The weather can vary widely from year to year, and many bird species travel more slowly and arrive in their breeding areas later in cold springs than in warm ones (Marra *et al.,* 2005; Ahola *et al.,* 2004). This annual variation is especially apparent in insectivores, such as the Barn Swallow and various warblers, whose food is clearly temperature-dependent, and in species that depend on snow and ice melt, such as some waterfowl and waders (Cooke *et al.,* 1995; Huin & Sparks, 1998). At particular localities, temperatures show more year-to-year variation in early spring than in late spring, and correspondingly, early arriving species typically show significantly wider annual variation in mean arrival dates than later-arriving ones (Fig. 120, Gilyazov & Sparks, 2002; Tryjanowski *et al.,* 2002). Disruptions in the usual arrival pattern can occur in years when a spell of bad weather falls within the normal arrival period (Elkins, 2005).

In some species, the effect of local food supplies on arrival seems to prevail over and above any temperature effect. The Brambling, for example, arrives at its Fennoscandian breeding areas earlier in

years of good spruce crops (Mikkonen, 1981). As the cones open, the seeds provide an early food supply, enabling newly arrived Bramblings to migrate and survive in their breeding areas until their main summer food (caterpillars) becomes available. In one area over a number of years, the size of the spruce crop, together with air temperature and snow cover, explained 89 per cent of the annual variation in Brambling arrival dates. This does not imply that Bramblings can predict the presence of spruce seed in their breeding areas from further south, for they could have enjoyed this abundant food source on migration, during their northward passage through the boreal forest.

REOCCUPATION OF LOCAL BREEDING AREAS

In spring, birds seem to be under pressure to return to breeding areas early, in order to compete for the best territories or nest sites, and to gain time, increasing their chance of raising young. By arriving early, single-brooded species may have time for a repeat nest if the first fails, and multi-brooded species may even fit in an additional brood. But there are limits to earliness, because, unless they have substantial body reserves, birds cannot survive in breeding areas until food becomes sufficiently plentiful there. Typically, among the early arriving species, individuals first concentrate in particular places where food is available, only later dispersing to their nesting areas as conditions permit. For example, Barn Swallows and other hirundines often initially appear in spring over wetlands, where midges first become abundant, and only later spread to their nesting sites in the surrounding countryside. Mountain species often appear first in valleys, moving up to higher ground as conditions improve. These ‘pre-breeding’ areas could be important in enabling birds to build up body condition in preparation for breeding. Later-arriving species seem to settle directly on their territories, especially those returning to areas they occupied in the previous year. Nocturnal songbird migrants, absent in the evening, can be found on their territories the following dawn,

when they start singing and chasing intruders, switching within a few hours from migration to reproductive mode.

In general, early arriving species experience a longer period between arrival and egg-laying than do later-arriving species. For example, Chiffchaffs arrive in southern England mainly in April but defer egg-laying until about a month later in May, whereas the closely related Willow Warblers arrive later, mainly in early May, and produce eggs only one or two weeks later. Similarly, within species, early arriving individuals tend to show a longer interval between arrival and egg-laying than those that arrive later (e.g. Dalhaug *et al.,* 1996; Tryjanowski *et al.,* 2004). Some late-arriving individuals can start nesting a few days after their arrival. There are occasional extreme examples, such as a male Wood Warbler which was caught and ringed during spring migration on the Isle of Man on 8 May. The following morning, less than 24 hours after ringing, the same bird had established a territory 205 km further north, in Scotland, and by that evening it had attracted a mate and started nest-building (Morton, 1986).

Arrival and occupation of territories

In any particular area, it is commonly found after detailed study that territories vary in quality: that is, in the reproductive benefits they confer upon their occupants. The quality of nesting habitat has often been assessed from measurements of cover, disturbance, local food supplies or proximity to good feeding areas (whichever was most relevant in the population concerned), or more directly from the feeding rates, survival or reproductive rates of previous occupants. On the basis of such assessments, places classed as best are generally occupied first each spring. As these places become taken, later arrivals are relegated to poorer sites. For example, Pied Flycatchers arriving in central Sweden in spring settled in deciduous areas in preference to coniferous (Fig. 122). In deciduous areas, food supply increased earlier in spring, the birds settled at greater

density, laid earlier and raised larger broods than in coniferous sites (Lundberg *et al.,* 1981).

Patterns of spring settlement, with the best areas occupied first, have been shown in many other European bird species, including the Great Reed Warbler (Bensch & Hasselquist, 1991), Collared Flycatcher (Wiggins *et al.,* 1994), Savi's Warbler (Aebischer *et al.,* 1996), Northern Wheatear (Currie *et al.,* 2000), Black-tailed Godwit (Gunnarsson *et al.,* 2005) and Black Kite (Sergio *et al.,* 2007). In some such species, the same sequence of territory settlement held year after year in the same area, even though the occupants changed, and even though some early settlers were displaced by former owners which returned later.

Arrival dates and breeding success

In many bird species, the earliest individuals to arrive in breeding areas tend not only to acquire better territories, nest sites or mates than later arrivals; they also lay earlier in the season, with larger clutches, and often achieve better nest success. Moreover, if their first nest fails, they have time to start another. Such relationships between arrival date, territory quality, mate acquisition, laying date and reproductive success have emerged in a wide range of bird species, both passerines and non-passerines, including raptors, waders and waterfowl (Newton, 2008). In some of these species, the latest individuals to arrive failed to acquire either a territory or a mate (there being more birds than territories and more males than females). And in some such species, such as the Great Reed Warbler, the earliest-arriving males acquired more than one mate, while the latest males remained unmated (Hasselquist, 1998).

While there are clear reproductive benefits in arriving early in breeding areas, there are also costs, such as bad weather early in the season, which may cause heavy losses among newly arrived birds (Chapter 23). Species that nest at high latitudes often risk untimely cold snaps or snowfalls that cut off their food supply. The earlier the birds arrive in spring, the more likely they are to experience such an

event. In contrast, birds that arrive later in the season are more likely to escape such cold snaps. The Barn Swallow illustrates these conflicting pressures, because like many other species, it benefits greatly from an early start to breeding, but suffers the costs of early arrival in cold seasons, which can cause heavy mortality (Møller, 1994, 2001). In this and other species, catastrophic losses early in the season can exert a measurable selection pressure on migration dates, which are partly under genetic influence (Chapter 15; Brown & Brown, 2000). Like many other aspects of timing, arrival date can therefore be viewed as a trade-off between opposing pressures. Early arrival gives better reproduction but increased risk of premature death, while late arrival gives poorer reproduction but reduced risk of premature death. The balance point is likely to change through time in response to climate change. At the same time, however, individuals vary, and some may be able to survive the cold when others could not, while other factors, such as adverse conditions en route, may sometimes delay the arrival of otherwise early birds. As is perhaps expected under conflicting selection pressures, in some species that have been studied, it was not the very earliest birds that bred most productively—they were just too early—but those that arrived slightly later but still before the majority, as found, for example, in Barnacle Geese over a number of years (Prop *et al.,* 2003).

POST-BREEDING RETREAT

Regional variation in the onset of winter conditions can again be tracked by following particular isotherms as they move from higher to lower latitudes, bringing colder conditions southwards across Europe (Fig. 123). In autumn, the 10˚C isotherm takes about four months to spread southward across the continent. Although not studied in detail, the autumn withdrawal of migratory birds from much of Europe occurs as expected, from north to south, as northern areas are generally vacated before southern ones.

Insufficient data are available to plot the withdrawal from much of a continent of any species, in order to establish how closely the process keeps step with moving isotherms. But the whole process can again take several weeks, or more than three months in species such as the Barn Swallow which breeds over a wide span of latitude. In multi-brooded species, low-latitude populations may still be present in their breeding areas when individuals from higher-latitude breeding areas pass through again, en route to winter quarters. Alternatively, although northern populations leave their breeding areas first, they have further to migrate, and may pass through southern breeding areas after southern populations have already left. The same is true for stopover sites. For example, on Heligoland Island, Northern Wheatears O. *o. oenanthe* from Europe pass mainly in late August–September, whereas those from Greenland O. *o. leucorhoa* occur mainly after mid-September, then outnumbering O. *o. oenanthe* (Bairlein, 2008). Most species show a single peak in passage with a long tail of latecomers, but many waders may show two distinct peaks, the first for adults and the second for juveniles (Nisbet, 1957). Again, populations from a wide span of latitude tend to show longer passage periods through southern localities than those from a narrower span.

There are exceptions to the general trend for the most northerly breeding populations to depart first. They include some single-brooded species, which spend about the same amount of time on their nesting areas at all breeding latitudes, but can both arrive earlier and depart earlier from southern than from more northern parts of the breeding range. For example, Arctic Terns nesting in the British Isles, at the southern end of the breeding range, arrive from late April, have raised a brood and are ready to leave again by mid-August. Other Arctic Terns do not arrive in their most northerly breeding areas in Svalbard until June, so they cannot leave much before late September. By the time the southward-migrating Arctic Terns from Svalbard have reached the latitude of Britain, most of the British breeders have already left. The breeding season is of similar duration in both areas, but is shifted several weeks later in

the far north, with effects on both migrations. Smaller single-brooded birds in which arrival, breeding and departure are shifted progressively later towards the north of Europe include the Swift and Pied Flycatcher. Swifts can leave the Middle East as early as June, the British Isles in August, but do not depart from northern Finland until September. Many other small species do not show this pattern, because they have longer breeding seasons in the south, raising more than one brood. Early departure from breeding areas also occurs in some species that breed in parts of southern Europe that are subject to a late summer drought, such as the Eurasian Reed Warbler, while their conspecifics from further north leave later (Akriotis, 1998). While high-latitude populations are the last to leave their breeding areas, the species as a whole may be seen at southern European localities later than at northern ones. This is evident, for example, in the Reed Warbler, Garden Warbler, Pied Flycatcher and Redstart (Bairlein, 2003).

As described in Chapter 10, patterns of autumn departure seem to differ between complete (obligate) migrants, in which all individuals leave every year, and partial (facultative) migrants, in which the proportions of individuals that leave, and their dates of departure, vary according to prevailing conditions. In obligate (often long-distance) migrants, individuals seem to leave their breeding areas as soon as they can after breeding, or after breeding and moulting, as the case maybe (Lack, 1960; Preston, 1966). In many such species, departure from breeding areas occurs well before local food supplies collapse. If birds do not have time to raise another brood, they probably benefit by leaving as soon as possible. Unlike the situation in spring when food is scarce but increasing, in late summer, food is plentiful but often decreasing, and weather is still fine. Birds probably therefore gain from migrating while conditions are still good, and before food supplies on staging areas have been depleted. They might also establish themselves in wintering areas at an early date, perhaps benefiting in competition for the best habitat. Hence, while in many species, spring arrival usually coincides fairly precisely with the reappearance of new food

supplies, autumn departure of complete migrants may precede the collapse of food supplies by up to several weeks (Schneider & Harrington, 1981). For trans-Saharan migrants, it might also pay to leave Europe relatively early, ensuring arrival on the southern edge of the Sahara while the Sahel zone is still green from summer rain. From September on, this zone dries rapidly and food supplies decline, making it a much less hospitable place for hungry migrants to make their first feeding stop after crossing the Sahara. In contrast, those species that winter further north, in the Mediterranean region, suffer no such penalty for late migration, because here rain falls mainly in winter, and gradually greens the land as it emerges from the summer drought.

Facultative migrants show less year-to-year consistency in autumn departure dates, and many individuals remain in breeding areas as long as food lasts, leaving up to several weeks later in some years than in others, and long after the end of moult (Chapter 10). This holds for some seed-eating finches, which, in years of good tree-seed crops, stay all winter or leave much later than in years of poor crops (Chapter 19). They can stay after snowfall, providing that seeds remain on the trees, whereas other finch species, which pick seeds from the ground, must leave by the first heavy snowfall. Likewise, many northern waterbirds leave as their wetland habitats begin to freeze over, which occurs much earlier in some years than in others. Moreover, because shallow waters freeze before deep ones, the shallow-water dabbling ducks usually migrate before deep-water diving ducks. In these facultative migrants, access to local food supplies seems to have a major influence on the timing and rate of southward migration, with birds lingering en route while food lasts, and travelling markedly shorter distances in some years than in others. In a sense, such species seem to be driven step by step along their migration routes by the onset of worsening conditions.

Competition for winter habitat

In species that compete for territories or feeding areas in winter, studies have shown the advantage of arriving early relative to other individuals, as in spring. For example, on the Exe estuary in southern England, Oystercatchers accumulated first on the two most preferred mussel beds where feeding was best (Goss-Custard *et al.,* 1984). But as more birds arrived and began to fight over feeding sites, latecomers progressively occupied the less favoured mussel beds. Adults arriving even later in the season displaced immatures already present on the favoured beds. Moreover, as mussel stocks declined on the favoured beds, more birds left, but in reverse order of their dominance rank, to feed on less preferred beds or in other habitats. In these Oystercatchers, therefore, the effects of arrival date on feeding location were modified by dominance relationships among age groups, but within age groups the benefits of early arrival relative to other individuals were still apparent. Further evidence of first arrivals taking the best habitats, and thereby having greater survival chances through the non-breeding season, emerged in a study of Ruddy Turnstones (P. Whitfield, in Wernham *et al.,* 2002).

In ducks, the advantages of early arrival in wintering areas are somewhat different, as found in several species wintering in the Camargue in southern France (Tamisier *et al.,* 1995). When dabbling ducks (Teal, Gadwall and Wigeon) first arrive in this area, they feed intensively to regain body condition. They then form pairs (mainly in January) and subsequently fatten for the spring migration (January-March). But females are in short supply, so that males which arrive and recover body condition earliest in the autumn are more likely to acquire mates, thus enabling them to breed the next spring. In addition, both sexes benefit from being paired, for they act together against unpaired ducks in competing for feeding sites.

We can draw three main conclusions from this chapter. First, migratory songbird species have been found to advance northward over the northern continents in spring at average rates of 40–150 km per day, in step with improving conditions, as reflected in the northward advance of particular isotherms. In general, early

migrating species progress more slowly than later ones. Barn Swallows, which breed over a wide span of latitude, take more than three months each year to recolonise all parts of their European breeding range. This rate is slower than the potential migration speeds of individual birds, which must often wait for weather and insect supplies to improve.

Second, many birds benefit from arriving in their breeding areas early with respect to other individuals, because they can then obtain better territories and mates than later arrivals, and often show better breeding success. However, if they arrive too early, they risk food shortage, and may sometimes die from late cold snaps. These conflicting selection pressures are likely to influence the average spring migration and arrival dates of different species. Nevertheless, species migrate at different dates from one another, depending partly on when their specific foods become sufficiently available at successive latitudes; and in general, many species arrive in particular localities earlier in warm springs than in cold ones.

Third, most migratory birds vacate the northern continents in autumn from north to south, in reverse order to that in which they colonised in spring. However, in some single-brooded migrants, southern-nesting populations (having completed their breeding earlier) leave their breeding areas before more northern ones. The potential benefits of early departure in late summer or autumn include better food supplies on the migration route and priority of access to prime wintering habitat.

The benefits of early arrival in breeding and wintering areas could lead to the whole breeding cycle of a species becoming earlier and earlier, if this process were not environmentally constrained in some way. The brake occurs mainly in spring, when birds cannot occupy breeding areas and start nesting until conditions become suitable. In addition, multi-brooded species gain from remaining in breeding areas later in summer than otherwise, if they could thereby raise another brood, even though this may delay their departure for wintering areas. Again, the birds face a trade-off between the advantages of extra reproduction and the disadvantages of a late

migration. The benefits of early arrival in wintering areas are perhaps most obvious in populations in which individuals occupy the same places throughout a winter, and thus gain priority of access to good habitat.

CHAPTER 12

Navigation

How birds find their way year after year from one part of the world to another is one of the most enduring mysteries of bird migration. More specifically, how do adult birds manage to return year after year to the same nesting and wintering localities, separated by hundreds or thousands of kilometres? How do young birds find their way on their first migration, unaided by adults, to areas totally unknown to them but specific to their population? And how do some pelagic birds, wandering over vast tracts of apparently featureless ocean, find their way year after year to their tiny breeding islands? It is not just a question of finding the way, for birds must also know where on their journeys to change direction or to accumulate extra body reserves in preparation for a long flight over sea or desert. The fact that birds can respond appropriately at specific places on their route implies that they possess some geographical sense—an ability to detect and react accordingly to conditions at particular locations.

To migrate effectively, birds need a sense of where they are, or need to be, a sense of direction, an ability to navigate from one place to another, and a sense of time, both seasonal and diurnal. In short, they need the equivalents of a map, compass, calendar and clock, together with a good memory, all packed into a brain that in some birds is no bigger than a pea. In the past 60 years, ornithologists have managed to unravel some of these mysteries, but others remain unresolved.

The ability of birds to navigate depends partly on their sensory capabilities. The eyesight of normally diurnal birds is better than

ours in the daytime, but probably much the same as ours at night. It is good enough to allow diurnal birds to fly in the dark through the open airspace, and to recognise the stars above and major topographical features, such as coastlines and mountains, below. Collisions with obstacles such as radio-masts occur mainly on dark misty nights, when vision is restricted. In addition, at least some bird species are able to perceive ultraviolet and plane-polarised light —facilities well beyond human capability.

Like many other animals, birds can also detect and respond to the earth's magnetic field. This is hard for us to understand, because we have no obvious magnetic sense ourselves. But recent research suggests that a bird's magnetic sense comprises two components— one based in the right eye, and the other near the nostrils (see box, p. 243). Other senses which some bird species might use in navigation include smell and hearing. Most birds seem to have a poor sense of smell, but there are exceptions, including petrels, in which the olfaction sense is well developed (Wenzel, 1991). In contrast, birds have a generally good sense of hearing, allowing individual migrants to detect the calls of other migrating birds at night. They seem also be able to detect ultrasound, the low frequency noises which we cannot hear but which travel over long distances. Birds also seem able to detect changes in barometric pressure, and to perceive wind direction and speed during flight, perhaps by reference to the ground below.

COMPASS ORIENTATION AND BI-COORDINATE NAVIGATION

Some of the earliest studies involved trapping large numbers of wild birds on autumn migration, transporting and releasing them in a distant location, and using the resulting ring recoveries to find where they went (Fig. 125). Such early experiments revealed that naive young birds behaved differently from experienced adults. Young birds on their first autumn migration proved unable to correct for their displacement, and failed to reach the normal wintering areas for their population. Instead, they continued on

their usual migratory heading for about the same distance they would normally travel from the capture site. The inference was that inexperienced birds migrated on the basis of innate information expressed as a direction and distance from the starting point, distance being controlled by the duration of migratory activity (Chapter 15). The innate information would be equivalent to an instruction like: ‘travel for six weeks towards the southwest’, or, in cases of non-straight routes: ‘travel for six weeks toward the southwest and then for five weeks toward the south-southeast’ (Wiltschko & Wiltschko, 2003). This system is known variously as clock-and-compass, bearing-and-distance or vector migration. In contrast to young birds used in displacement experiments, experienced adults that had travelled the route before were able to make the necessary corrections, and reach their former wintering areas. Homing towards a known site is more complicated than the ability to head only in a particular compass direction, because it involves true bi-coordinate navigation, requiring a map sense—an ability to head towards a specific point on the earth’s surface from some distant location (also known as goal orientation).

The biggest displacement experiments of this type involved Common Starlings *Sturnus vulgaris,* which migrate from northeast Europe west-southwestward in autumn through the Netherlands to winter in northern France and southern Britain. Over a period of years, the Dutch ornithologist Albert Perdeck (1958, 1967) caught more than 19,000 starlings in the Netherlands, released about 7,500 on site to act as controls, and transported 11,500 others by air 500 km south-southeast from the capture site for release in Switzerland (Fig. 126). The subsequent ring recoveries from translocated juveniles were on a line west-southwest of the release site and extended into southern France and northern Iberia. This indicated that the translocated juveniles had kept their inherent directional preference and normal migration distance, but had not corrected for their displacement. They therefore migrated parallel to the normal route, and wintered south of the regular wintering area for their population.

The adults, in contrast, corrected for their displacement, and after release headed northwest towards the normal wintering area with which they were familiar. They had evidently 'realised' they were off course at the release site, and took a different direction from usual in order to correct for this. The age-related (or experience-related) difference in behaviour occurred whether the birds were released in separate juvenile and adult groups or in mixed-age groups. Recoveries from subsequent years showed that, while juveniles tended to return to the new wintering areas reached after their displacement, both age groups continued to return to their original breeding areas (with which they were familiar). The conclusions were that: (1) autumn-migrating adult Common Starlings used true goal orientation (homing) to reach their wintering areas, whereas juveniles used one-directional orientation, moving on a fixed bearing for a fixed distance; and (2) juveniles were independently able to fix both their breeding and their winter quarters in their first year and return there in subsequent years by goal orientation.

Further evidence for inherent directional preferences came from other early field experiments, in which young birds of various species were held in their natal areas until all other individuals of their species had left. After their release, and from subsequent sightings and ring recoveries, the young were found to have migrated in the direction normal for their population. For example, 144 White Storks were taken from nests in the Baltic region and reared in western Germany. Released after all local migrant storks had passed, these birds showed a strong tendency to head south-southeast, the direction appropriate for the population from which they were drawn, but quite distinct from the southwest direction taken by storks local to the release area (Schüz, 1949).

All the above research was carried out at a time when such large-scale experiments were perfectly acceptable in the search for answers to puzzling questions, but it is unlikely that they would be conducted today in most European countries, where biologists act within the constraints of stringent codes of practice. More recent

displacement experiments have used smaller numbers of birds whose directional preferences were tested in orientation cages. In some experiments, young birds showed no change in directional preference after displacement, thus supporting (like the experiments above) the vector hypothesis (Hamilton, 1962; Mouritsen & Larsen, 1998). In other experiments, however, young birds appeared to change their preferred direction so as to correct for displacement, taking a bearing that would lead them to some place on the normal migration route (Rabøl, 1969a, 1994; Thorup & Rabøl, 2001; Åkesson *et al.,* 2001, 2005). Both adults and juveniles were involved in some long-distance displacements, and both corrected appropriately. Similar findings were obtained when naturally drifted migrants (including juveniles) were caught and tested in orientation cages, or tracked by radar (Evans, 1968; Chapter 14), and when birds were subjected to simulated displacement in a planetarium (Rabøl, 1992). The difference between adults and juveniles found in the earlier experiments was not therefore borne out in all subsequent ones, especially those involving substantial east–west displacements. More work is needed to explain these differences in research findings, but the distance, direction, speed or manner of displacement may have influenced the way that juveniles responded —whether they were shifted mainly by longitude or by latitude, or whether rapidly by air or more slowly by other means.

Other evidence for inherited directional preferences

The existence of innate migratory directions is further supported by those species in which juveniles migrate to wintering areas independently of adults. A striking example is provided by the European Cuckoo, in which the last young leave the breeding areas up to a month after the last adults have departed, yet they still find their own way to their African wintering areas. These young cuckoos also migrate independently of their various foster species, which in any case winter in a range of different areas. The same is true for other cuckoos, including the Shining Bronze Cuckoo, which

migrates from New Zealand 4,000 km over open water to winter on small Pacific Islands.

Yet other evidence for innate directional preferences comes from the ring recoveries of migrants, which in many species for both adults and juveniles lie on a straight-line route from the breeding area towards a staging or wintering area (for the Linnet, see Verheyen, 1955; for the Chaffinch, see Bairlein, 2001; for the Pied Flycatcher, see Mouritsen, 2001). Similarly, radio-tracking has shown that, in some species, each step of the migration follows a rather straight track, with only slight and temporary deviations from the overall direction. This was evident, for example, in studies on various thrushes, Whooping Cranes, Ospreys and Honey Buzzards (Cochran *et al.,* 1967; Kuyt, 1992; Thorup *et al.,* 2003). Other species, however, show much greater variation in directions between individuals, and less step-to-step consistency within a journey (Chapter 19). Final confirmation of the genetic control of migratory directions came from the cross-breeding experiments reported in Chapter 15, in which juveniles showed average directional preferences intermediate between those of their parents.

Both juvenile and adult birds may have the capacity for bi-coordinate navigation, but juveniles may use it only when they have learned the coordinates of particular breeding and wintering areas, or when they have drifted far off course, assessing their drift as they travel. The precise mechanism of goal-orientated navigation remains poorly understood, although various hypotheses have been proposed (Berthold, 1993).

Return of displaced adults to breeding sites

Further evidence for a map sense in birds comes from experiments in which breeding adults were taken from their nests, marked and released elsewhere. Frequent nest checks could then reveal whether and when the marked owners returned. Experiments on more than 50 species, from songbirds to seabirds, have shown some remarkable returns over distances varying from a few kilometres to

more than 5,000 km, depending on the species (Matthews, 1968; Wiltschko, 1992; Åkesson, 2003). Some non-migratory species, such as the Eurasian Tree Sparrow, returned only in small numbers and only from short distances of up to 10 km, perhaps using their knowledge of the local terrain (Wojtusiak, 1949). Other species returned after transportation over hundreds or thousands of kilometres, sometimes from areas which they could never have visited on their normal migrations, so they must have used more sophisticated means than prior knowledge (Matthews, 1968).

Returns from even longer displacement distances were reported from Laysan Albatrosses in the Pacific (Kenyon & Rice, 1958). Fourteen of 18 displaced adults returned to the breeding island in the mid-Pacific within 30 days, after having been transported between 2,116 and 6,629 km to six locations lying in different directions from the breeding colony. The fastest bird covered 5,148 km in ten days after release off the Washington coast, giving a mean speed of 515 km per day.

Return of displaced birds to wintering sites

All these experiments involved birds displaced from their nesting places, to which they presumably had a strong incentive to return, but similar experiments have involved the displacement of birds from their normal wintering sites. They showed that birds caught as adults were more likely to return in the same or a subsequent winter than birds caught as juveniles, and that the return of juveniles depended on how long they had spent at the site before they were caught and moved (Bellrose, 1958; Ralph & Mewaldt, 1975). For example, 30 adult and 69 juvenile Sanderlings were transported from Bodega Bay in California 200 km south. Overall, 60 per cent of adults but only 4 per cent of juveniles later returned and settled in Bodega Bay, either in the same or a subsequent winter (Myers *et al.,* 1988). The age difference was most apparent among birds moved in autumn (from which no juveniles returned), but was absent among birds moved in winter. By that time, the juveniles had apparently

been in Bodega Bay long enough to have become attached to the site, and they returned in the same proportion as adults which were familiar with the site from previous winters.

Overall, it seems that motivated birds can return to any site where they have previously lived, providing it lies within their capabilities. In general, migrants return successfully from longer distances, in greater proportions and at higher speed than non-migratory birds (Matthews, 1968; Wiltschko, 1992; Åkesson, 2003). Even within species, the return of displaced birds from long distances is more or less restricted to migratory stock, as shown by comparing the results from migratory and sedentary populations of the same species, such as the Herring Gull (Matthews, 1968). In most experiments, the proportions of individuals that returned declined with increasing distance of displacement, and allowing for distance, adults returned in greater proportions than juveniles. But whether migratory or non-migratory, young or old, many birds clearly have a map sense, which they can use at any time of year.

CUES USED IN DIRECTION-FINDING

The most obvious way in which birds and other animals find their way around on a day-to-day basis is by use of landmarks or other consistent features of their home areas. This could explain how some migrating birds manage to return to exactly the same nesting places year after year. But such features are useful only in familiar areas, and when moving over longer distances into unknown terrain, a reliable geographical reference system is needed for navigation. At least two types of factors can act as directional aids—celestial and geomagnetic (Emlen, 1975; Able, 1980; Wiltschko & Wiltschko, 1995, 2003). In migratory birds, the use of compasses based on the sun and stars and on magnetic information has been confirmed by experiment. But a prior requirement for using any compass is that the bird should ‘know’ beforehand—either by experience or inheritance—what direction it has to take. Also, effective use of any of these compasses requires a period of learning,

as well as frequent revision as the bird continually changes location while on migration. In other words, they all entail a combination of innate and learned components.

The main feature of celestial cues, such as the sun and stars, is that they appear to change position during each 24-hour cycle as the earth spins on its axis. In the northern hemisphere, the sun lies in the south and during the day moves through the sky on an arc from east to west, while at night, the stars rotate anti-clockwise around the geographical north, marked by the polar star. In the southern hemisphere, the sun lies in the north and moves on an arc from east to west, while the stars rotate clockwise around the geographical south unmarked by a specific star. In using the sun and related factors in direction-finding, therefore, birds in both hemispheres must allow for time of day. But the same is not necessarily true for star patterns if they are used solely to indicate geographical north or south, as these directions are given as the centre of rotation of the night sky, which is fixed. Timekeeping depends on the bird's 'internal clock', kept to time by the regular day–night cycle.

The height of the sun's arc through the sky varies with latitude and season, but it is always symmetrical with respect to true north or south. Its highest point in the sky at midday indicates due south in the northern hemisphere and due north in the southern hemisphere. That birds use the sun as a compass has been known for more than 50 years, beginning with some crucial experiments conducted by the German scientist Gustav Kramer (1951, 1952, 1957). Under a sunny sky, Common Starlings kept in circular wire cages during the migration period orientated in the same direction as free-living starlings. The angle they adopted towards the sun varied according to the time of day. If the sky became overcast, obscuring the sun, their directional preference disappeared. When their view of the sun's direction was changed using mirrors, the birds orientated at the same angle to the apparent sun as they would to the real sun (Fig. 131). These experiments confirmed that starlings made use of a sun compass, which gave accurate information only if regulated by

an internal clock, allowing adjustment of directional preference as the sun moved through the sky (the ‘time-compensated sun compass’). Additional experiments in which starlings were kept indoors under artificial cycles of day and night of the same duration as natural time, but out of phase, revealed clearly that, in order to orientate, the birds used both the sun’s position on the azimuth (direction from the observer) and the time of day. Given a simulated stationary sun, a caged migrant orientated at different angles to it according to the time of day, also confirming the effect of an internal clock.

The use of a sun-azimuth compass has now been confirmed experimentally in several bird species, and maybe common among diurnal migrants. However, simply seeing the sun provides a naive bird with little useful information. The bird must live at a site for some time and learn the way in which the sun moves across the sky, in order to use it subsequently as an effective directional aid. If experienced northern hemisphere birds are transported to the southern hemisphere, they orientate themselves incorrectly, interpreting the sun as if they were in the northern hemishere (indicating south rather than north). Regular trans-equatorial migrants must presumably be able to make the necessary adjustment, and one possible mechanism is explained later in this chapter.

Sky polarisation patterns change with respect to the sun’s position, and are particularly striking around the time of sunset. The ability of birds to detect these patterns has been demonstrated in experiments in which at least seven species of normally nocturnal migrants responded to manipulations of polarised light from the sky (Able, 1993). The birds were tested individually outdoors in otherwise normal conditions in cages covered by sheet polaroids (Able, 1989; Moore & Phillips, 1988; Phillips & Moore, 1992). In each case, the birds changed orientation as predicted by alterations in the alignment of the polaroids. However, the visual stimulus created by this procedure is quite unnatural, and birds sometimes orientated differently under artificial polarised light than they did

under naturally polarised sky light (Helbig & Wiltschko, 1989). Nevertheless, the experimental birds were clearly responding to polarised light as an orientation cue, rather than to the position of sunset (Helbig, 1991a).

The star compass

Providing that enough of the night sky was visible, nocturnal migrants proved able to use the stars as a guide. When tested in orientation cages, birds orientated correctly on clear starry nights, but became inactive or disorientated under overcast skies. They also became confused if star patterns were varied experimentally in a planetarium (Sauer, 1957; Sauer & Sauer, 1955, 1960; Emlen, 1967a, b). For example, when North American Indigo Buntings were tested in orientation cages under a natural starry sky during autumn migration, they preferred southerly directions. They maintained this southerly preference under an artificial star pattern imitating the natural sky in a planetarium. But when the artificial star pattern was changed by 180°, the birds changed their directional preference to the north. Under a static night sky, no obvious migratory restlessness occurred. Effective use of a star compass evidently involved learning, for captive Indigo Buntings lacking early experience of the night sky failed to orientate correctly in a planetarium (Emlen, 1967b, 1975). The same was found in other migratory species, such as the Garden Warbler (Wiltschko *et al.,* 1987). As with the sun compass, the ability and tendency to acquire the necessary knowledge was apparently innate.

With the star compass, the key factor was the rotation of the night sky about the Pole Star, and in experimental conditions, birds learned to respond to an extremely simplified and reduced star pattern, providing that it rotated about a single conspicuous star. Thus, nestling Indigo Buntings raised under an artificial sky with the star Betelgeuse (in the constellation Orion) as the point of rotation treated Betelgeuse as the Pole Star when subsequently tested.

The use of a star compass has now been demonstrated experimentally in at least six different bird species, and maybe widespread in nocturnal migrants. If the birds use the rotating star pattern only to define the positions of the poles, then as mentioned above, no correction for time of day is necessary. They may, however, gain further information from star patterns. As birds proceed on their journeys, lasting up to several weeks, some stars disappear below the horizon behind them, while others appear above the horizon in front, another indication that birds are unlikely to rely throughout on particular star patterns. Moreover, many bird species, such as the Lesser Whitethroat, change direction during their migration from Europe to Africa, heading first southeast into the Middle East, and then south-southwest into Africa. When shown northerly skies in a planetarium during the autumn migration season, individuals of this species headed southeast, but when shown skies characteristic of more southerly latitudes, they headed southwest (Sauer, 1957). This finding indicated that birds could respond appropriately to skies encountered at different points in their journey. In addition, Pied Flycatchers and Redstarts compensated by changing direction after a simulated east–west displacement in a planetarium, which again indicated an appropriate response to sky patterns (Rabøl, 1994).

Integrated use of celestial cues

Nocturnal migrants usually set off around dusk, when celestial cues related to the sun (such as sunset position, horizon glow and skylight polarisation pattern) are clearly visible and the star pattern is gradually emerging. They could therefore make use of all these celestial cues within a relatively short period. Radar observations reveal that migratory birds keep flying in the same direction during the transition from day to night or night to day (Myres, 1964). This finding implies that birds can switch between sun and stars for navigation, or that they rely on some other cue, such as the earth's magnetic field, to maintain their course. In addition, some arctic

species which prefer to migrate by night at lower latitudes necessarily migrate in daylight at high latitudes in summer when the sun never sets. Bright moonlight can make ground-based features more visible, but can apparently hinder the use of star patterns and produce the same disturbing effects as cloud (Sauer, 1957).

The magnetic compass

A second major system of bird orientation makes use of the earth's magnetic field. Imagine the earth as a hugely powerful magnet, whose magnetic north pole is situated fairly close to the geographic North Pole, and whose magnetic south pole is similarly close to the geographic South Pole.[†] Running through the atmosphere between the two magnetic poles are invisible longitudinal lines of magnetic force, which circle the globe rather like the segments of an orange (Fig. 132). The field lines leave the earth vertically at the Antarctic pole, then curve round the earth and re-enter its surface vertically at the Arctic pole. The magnetic vectors thus point upwards in the southern and downwards in the northern hemisphere, but lie parallel to the earth's surface at the magnetic equator. Hence, for any animal that can measure the inclination of the force lines, the earth's magnetic field can indicate latitude and direction (toward the equator or pole) within each hemisphere (except near the equator itself, where the force lines are horizontal and near the poles where they are vertical). The intensity of the magnetic field can also give positional information, for it declines progressively from pole to equator in each hemisphere. However, the magnetic field cannot give a reliable cue to longitude, so it cannot provide a firm basis for bi-coordinate navigation.[†]

The role of the geomagnetic field as a reference for migratory direction was later shown in juveniles of other species (Wiltschko & Wiltschko, 1995, 1999; Gudmundsson & Sandberg, 2000). Passerines were hand-raised without access to celestial cues and,

when tested during autumn migration, they headed in their population-specific migratory direction with the magnetic field as the only cue (Wiltschko & Wiltschko, 2003). It seemed that the geomagnetic field alone was sufficient to establish a migratory bearing, at least in temperate latitudes. Birds tested at higher latitudes, where the angle of magnetic inclination was steeper, needed to have observed celestial rotation (to fix north) in order subsequently to adopt the correct heading in relation to magnetic cues alone (Weindler *et al.,* 1996). Overall, the use of a magnetic compass has now been demonstrated experimentally in more than 20 bird species, including diurnal and nocturnal migrants in both hemispheres. Its use thus seems widespread, but partly in association with celestial information.

It has also been discovered that the avian magnetic compass is closely tuned to the intensity of the local ambient field (Wiltschko & Wiltschko, 1972). European Robins accustomed to the normal magnetic field in Frankfurt (0.46 gauss) initially gave random bearings in fields 26 per cent lower (0.35 gauss) or 48 per cent higher (0.68 gauss). However, if the birds were kept in altered fields for a few days, they could then orientate correctly in fields as low as 0.16 gauss or as high as 0.81 gauss. Clearly, they needed time to adjust to changed intensities. A similar sensitivity to altered field strengths was found in Whitethroats and Garden Warblers (Wiltschko & Merkel, 1971; Wiltschko & Gwinner, 1974). The birds' ability to adapt to a range of field strengths would permit them to adjust to the range of magnetic intensities that they would encounter at different latitudes during migration.

Trans-equatorial migrants using magnetic cues alone face two problems. First, the magnetic field is horizontal for some distance north and south of the equator, and hence ambiguous with respect to direction. Captive Garden Warblers in Germany that were experimentally exposed to horizontal force lines as their only directional cue became disorientated (Wiltschko & Gwinner, 1974). In the equatorial region, therefore, wild birds may have to use celestial cues to maintain an appropriate heading. However, beyond

the magnetic equator, if they are to revert to using the magnetic field, birds must adjust to the change in migratory inclination in order to continue heading south. Instead of migrating equatorward, as in the first part of their journey, they must change to migrate poleward in the second part. Birds that migrate across the magnetic equator have apparently developed a means to achieve this: captive Garden Warblers that were kept in a horizontal magnetic field for two days reversed their response system, so that they now headed poleward rather than equatorward, whereas untreated birds continued to show equatorward preferences until their migratory activity ended (Wiltschko & Wiltschko, 1992). It seems that the horizontal field of the magnetic equator itself serves as a trigger causing the birds to adjust their response to the changed magnetic inclination, and continue travelling in the same geographic direction. The same sort of change must presumably occur on the return journey in spring.

Between equatorial and polar regions, the earth's magnetic field represents a reliable and omnipresent reference for orientation, both in terms of directional and latitudinal information. Unlike celestial cues, it can give consistent information in all weather conditions, both day and night, and unlike the sun compass, it needs no correction for time of day. No wonder, then, that various kinds of migratory animals appear to make use of it. Although it is only just emerging how birds perceive the magnetic field (but see Box A), they are sensitive to both inclination and intensity, but apparently not to polarity (Wiltschko & Wiltschko, 1972). The main problems may arise in localised areas with magnetic anomalies where the force lines are distorted by magnetic material in the earth's crust. However, birds do not have to make use of magnetic information, as experiments have shown that they can use celestial cues alone to establish an appropriate direction (Rabøl & Thorup, 2006).

Response to specific areas

Many land birds that cross deserts or oceans accumulate the necessary fuel reserves just before embarking on the crossing, which may occur partway through their journey. Others change direction at particular points in their journeys. They evidently 'know' that they have reached an appropriate place either to accumulate large body reserves or change their heading, even though they may never have made the journey before. One possible mechanism involves the inherent time response: after a given period from the start of migration, the bird changes its behaviour. Another possible mechanism involves response to the specific conditions found at particular sites, whether celestial or magnetic. As mentioned above, Lesser Whitethroats showed different directional preferences under planetarium skies representing different points on their migration route (Sauer, 1957). They used the star patterns to indicate where to change their migratory direction. Other experiments using an artificial magnetic field implied that some birds can also use magnetic information to indicate regions where they must change direction, accumulate large fat reserves before crossing a barrier, or stop migrating.

BOX A. Current understanding of magneto-reception in birds.

Two means of magneto-reception have been proposed in birds: one involving interactions of light-dependent chemical processes with the ambient magnetic field, and another involving an iron-rich material (magnetite) which is sensitive to the intensity of the magnetic field.

The so-called 'radical pair' model postulates a light-dependent chemical compass based on direction-specific interactions of specialised photo-pigments with the magnetic field. Theoretical predictions had favoured the eyes as the site of such magneto-reception because their almost spherical shape would allow

receptors to be orientated in every possible direction, thus enabling birds to measure the precise direction of the force lines (Ritz *et al.* 2004). This prediction has been confirmed, with the surprising additional finding that receptors seem to be restricted to the right eye. Birds tested with their left eye covered were just as well orientated as binocular birds, whereas the same birds failed to show orientated behaviour when their right eye was covered (Wiltschko & Wiltschko 2007). The implication is that such magnetic information (like visual information) is processed primarily in the left hemisphere of the brain.

The second mechanism apparently involves magnetite, a specific form of permanently-magnetic iron oxide, which could react to the intensity of the ambient field. Magnetite has been detected in the bodies of many kinds of animals, and in birds has been found near the base of the upper mandible. Magnetite-based reception is not light-dependent, but is associated with the trigeminal nerve system which is also involved with olfaction. This receptor seems not to be involved in magnetic compass orientation, but is used instead in map-based navigation. Evidence has come from experiments in which birds were exposed to a rapid, high intensity magnetic pulse that was strong enough to re-magnetise single domain magnetic particles, but had no lasting effect on the photo-based receptor involving a radical pair mechanism. Such pulse re-magnetization altered the migratory orientation of adult birds that navigate using map-and-compass orientation, but had no effect on the orientation

of naïve young birds that undertake their first journey using only compass information (Munro *et al.* 1997a, b).

The two receptor systems could thus mediate different types of complementary information: a radical pair mechanism in the right eye could provide directional information, while magnetite receptors near the base of the upper mandible could measure magnetic intensity, and hence latitudinal position. One might say that birds have a compass in their right eye and a magnetometer in their beak. As this work is still in progress, findings should be regarded as provisional, but they indicate where research on magneto-reception in birds is pointing.

In other experiments, some juvenile Thrush Nightingales, caught in autumn in Sweden and exposed there to the geomagnetic conditions they would normally experience in northern Egypt, immediately accumulated high fat levels appropriate to the subsequent desert-crossing. This happened whether they were exposed to a step-change in magnetic field, as when they were switched suddenly from Swedish to Egyptian conditions, or to a gradually changing field, as they would normally experience on their migration. Both groups contrasted with control birds, exposed throughout to the geomagnetic conditions of southern Sweden, which accumulated much smaller fuel loads more slowly (Fransson *et al.,* 2001; Kullberg *et al.,* 2003). However, birds trapped late in the onset period of autumn migration accumulated a high fuel load irrespective of magnetic treatment. It seemed that the relative importance of endogenous and environmental factors in the fattening of individual birds was affected by time of season, as well as by geographical location (see also Chapter 10).

A further experiment indicated that adult Tasmanian Silvereyes might use magnetic conditions to signal when they had arrived in

breeding areas. Adults were tested near the midpoint of their south–north migration in southeast Australia. Birds exposed in captivity to artificially generated magnetic field values of inclination and intensity normally experienced near the start of their migration orientated north-northeast. In contrast, birds exposed to magnetic field values that they would experience near the end of their migration ceased to show any significant directional preference; in this respect, they acted as though they had arrived in their wintering areas (Fischer *et al.,* 2003). In contrast, no effects of changing the artificial magnetic field were noted on inexperienced young birds caught prior to their first migration.

These various experiments indicate that inexperienced birds on their first migration can detect and make use of the geomagnetic field to indicate when major changes are needed during their journeys. Such birds apparently have an inborn response to external geographic cues (especially geomagnetic cues) that are characteristic of certain latitudes or regions, and can use those particular conditions to trigger a halt to migration, or a change in direction or fattening regime (Beck & Wiltschko, 1988; Fransson *et al.,* 2001).

We thus have two potential mechanisms which could function in these ways. The first is an endogenous time programme which switches particular activities on and off at appropriate times in the migration cycle (Chapter 9). The second is a response to the celestial or magnetic conditions at particular latitudes or more specific regions, which can similarly trigger appropriate changes in migratory behaviour. How much these separate mechanisms act independently or in conjunction with one another is an open question, but different species would not necessarily be expected to respond to particular experiments in the same way.

Overview of orientation cues

To summarise so far, birds can use a number of different compasses for orientation during long-distance migrations, based on

information from the sun and related pattern of skylight polarisation, from star patterns and from the earth's magnetic field. After calibration, these different cues used by the same individual would normally give the same directional message. The use of the sun compass requires a time-compensation mechanism, through which the bird can allow for changes in the sun's position during the day, while the stellar rotation compass always gives the direction towards the geographical poles (Emlen, 1975). Geomagnetic compass courses are given by the angle of inclination (varying from horizontal at the equator to vertical at the poles). The reliability of these compasses might vary between regions, seasons and local conditions, so that for instance the sun compass cannot be used if the sky is totally overcast, the star compass might not be visible during the round-the-clock daylight in high-latitude summers, and a magnetic compass based on the angle of inclination is of limited use around the geomagnetic poles and the geomagnetic equator (Åkesson *et al.,* 2001). Magnetic cues seem often to be calibrated from celestial cues, using either stellar rotation to indicate geographic north, or polarised light patterns present at sunset and sunrise (Muheim *et al.,* 2006b). Use of all the known compasses employed by migratory birds seems to be modifiable by experience during early development, or during the course of particular journeys. Bi-coordinate navigation could be determined by any two non-parallel gradients, and in theory the different gradients could be provided by different types of cues: for example, one coordinate being based on a celestial cue and another on a magnetic cue. Given experience, latitude can be fixed by both celestial and magnetic cues, but longitude seems much more difficult to determine, as explained later.

Cue-conflict experiments

Which of several potential compasses is most important to a bird at a given time has been investigated in so-called 'cue-conflict' experiments. These involve presenting a bird with two (or more)

orientation cues at once, manipulating one of them while leaving others unchanged, and monitoring the response of the bird (Able, 1993; Muheim *et al.,* 2006a). A typical experiment might involve placing an orientation cage surrounded by electric coils outdoors under a clear night sky. In this situation, a bird in the cage would have access to two known orientation cues, the stars and the magnetic field. The coils can be used to shift the direction of magnetic north so that magnetic compass directions differ from star-based ones. If, as compared to control birds tested in an unaltered magnetic field, the birds experiencing the cue-conflict changed direction in line with the magnetic field shift, one would conclude that in this particular situation, magnetic information took precedence over stellar information.

Just such an experiment was conducted on three species of *Sylvia* warblers and European Robins captured on migration (Wiltschko & Wiltschko, 1975a, 1975b). When the directions of stellar and magnetic north were at variance, the birds seemed to orientate preferentially with respect to magnetic cues. The warblers changed direction during the first test in the conflict situation, but the robins did not shift until tested in cue-conflict for several consecutive nights (a finding later replicated on Robins elsewhere; Bingman, 1987). Robins apparently needed longer to work out the changed relationship between stellar and magnetic information.

In the findings from several cue-conflict experiments, magnetic cues overrode stellar cues, visual information at sunset overrode both of those stimuli, and polarised light (rather than sunset) was the relevant orientation cue used at that particular time of the day (Able, 1993). However, some studies produced results contrary to these general patterns, and experiments showed that birds could re-calibrate compass systems when they were exposed to conflicting information. In the wild, birds may regularly calibrate one compass against another. Young birds were found to use celestial information to calibrate an orientation response to the earth's local magnetic field (Weindler *et al.,* 1996; Bingham *et al.,* 2003). Once a bird had 'understood' the local geomagnetic field in relation to geographic

north and south, it could use magnetic cues to a greater degree in navigation.

In another experiment, thrushes caught on migration in North America were exposed to an experimentally deflected magnetic field during twilight, and then released and radio-tracked on their subsequent night flights (Cochran *et al.,* 2004; Cochran & Wikelski, 2005). Their tracks indicated that the thrushes re-calibrated their magnetic compass in relation to twilight cues, and then relied on their (mis-calibrated) magnetic compass for their nocturnal flight, apparently ignoring stellar cues. The experimental birds changed to normal orientation again on succeeding nights, apparently having re-calibrated their magnetic compass (correctly) back to north. Other experiments revealed that, for re-calibration, a view of the horizon at sunset was important, and no correction was made at other times of day or night (Muheim *et al.,* 2006b). Daily re-calibration of the magnetic compass against celestial cues could explain how birds cope with changes in magnetic declination during the route, as well as various local magnetic anomalies; it could also help birds operating with a magnetic inclination compass to cross the equator without becoming disorientated.

In practice, individual birds probably use information from several compass mechanisms, with emphasis on whatever cues are most reliable in the prevailing conditions, switching from one type of cue to another during the course of a journey, and continually calibrating one against another, depending on location, weather and light values (Wiltschko *et al.,* 1998; Muheim *et al.,* 2003). However, polarised light cues, visible at sunrise and sunset from the region of the sky near the horizon, may act as a common reference against which birds can calibrate both solar and magnetic cues (Muheim *et al.,* 2006b).

Other potential cues

From time to time, birds could make use of yet other directional cues, including auditory and olfactory ones (Keeton, 1980; Wallraff,

2003). For example, infrasound emanating from wind against mountain ridges or from waves breaking on shorelines can travel long distances, and could give strong directional cues to birds able to detect them. In addition, homing pigeons have proved capable of finding their way by smell, at least over short distances (Papi, 1989). However, it is not known how much birds make use of such potential cues, or of the distances over which they could do so. For most birds, it is unlikely that olfaction could work over more than a few tens of kilometres in a favourable wind.

Birds often behave in a way that suggests they can predict impending weather, for example by leaving before a storm arrives. One way in which they might do this is by monitoring barometric pressure, and experiments have suggested that pigeons have this ability. Such a pressure sense could assist migrants in maintaining their flight altitude, or in moving from areas of high to low pressure, or vice versa. By this means, in arid areas, birds could move towards areas where rain is falling, a frequently observed behaviour which has so far defied explanation (Chapter 20). Other, as yet unappreciated, environmental cues could provide birds with a geographical reference system. Various alternative means of navigation have been suggested, but have so far found no support in observation or experiment, and some would require levels of sensory perception well beyond those known in birds (for a review, see Berthold, 1993).

Observational evidence on orientation

Observations made directly or with radar have shown that birds prefer to migrate under clear skies, when sun or stars are visible (Chapter 5). On most occasions, nocturnal migrants seem to become disorientated when they enter low cloud, mist or rain and when neither sky nor ground is visible to them. When over land in these conditions, they normally settle, but when over the sea, they mill around in various directions gradually drifting downwind. However, a brief break in the cloud exposing the sky is enough to enable them

to get back on course. Such observations suggest that birds depend on celestial navigation and are not normally guided by cues from the earth's magnetic field alone. The additional fact that, during periods of mist or rain, migrating birds are attracted to lighthouses and other illuminated structures further implies that nocturnal migrants respond to visual cues. Nevertheless, at other times, birds that do fly in overcast conditions seem well orientated, in that their flight relative to the ground and air mass appears as straight and level as in birds flying on clear nights. Such behaviour might be expected if birds were migrating on magnetic cues.

That flying birds, both day and night, are influenced by the landscape below is well accepted, partly from the observation that migrants often follow coasts or other leading lines. When they can see the ground, birds might maintain direction in the same way as humans, by projecting a compass direction onto a series of landmarks, and heading successively toward them. This would enable birds to avoid drift by crosswinds, and so remain on course, at least over land. Correspondingly, drift is generally less marked in birds migrating over land than over water (Chapter 5). Use of land-based visual cues also provides continuity between night and day and allows the recognition of familiar areas. The difficulty of maintaining a straight course over water lacking any stable visual features may be another reason why many birds seem to avoid sea-crossings whenever possible.

Despite taking steps to avoid being drifted by crosswinds, birds sometimes do end up in localities far off their normal routes. Four types of evidence indicate that they can detect their displacement and attempt to get back on course. First, radar observations have revealed reoriented movements after drift has occurred (Myres, 1964; Evans, 1966; Able, 1977). Typically, the birds arrive under a crosswind, settle until the wind veers or slackens, and the next night head toward their normal route. Second, some radio-tagged birds tracked as they were displaced by wind subsequently redirected themselves to their normal route (for Whooper Swan, see Pennycuick *et al.,* 1996),[†] while other birds ringed as drifted

migrants were later recovered in localities closer too, or within, their regular range, including migration areas (Evans, 1968; for extreme examples, see Table C, Chapter 14). Third, known drifted birds trapped and tested in orientation cages did not head mainly in their normal migration direction, but in whichever direction would have got them back on their normal route (Evans, 1968; Able, 1977; Fitzgerald & Taylor, 2008). Such birds showed the same adjusted directional preferences as birds tracked at the same time by radar (Evans, 1968; Able, 1977). Fourth, birds caught on migration and transported 450 km westward off route compensated for their displacement when they were tested in orientation cages (Rabøl, 1969a, 1994). This was true for both juveniles and adults. Although other evidence reported above suggests that juveniles inherit only a general compass direction to guide them on their first journey, they nevertheless seem able to recognise and correct for any drift they have experienced. So unless they get far from land in prolonged adverse winds, land-bird migrants with a correctly functioning navigation system are unlikely to be drifted long distances off course before they reorientate.

When correcting for the effects of wind drift, birds take different directions in different regions, according to local geography. Migrants drifted from continental Europe to the east coast of Britain reorientated southeast, which would have got them back on their normal southwest route through western Europe (Evans, 1968), while those blown beyond the west coast over the Atlantic usually backtracked until they reached land, as seen by radar (Myres, 1964). Much of this reorientation by nocturnal migrants occurs in the daytime, when birds may often be able to see the coast from the altitude at which they normally fly.

Pelagic birds

Pelagic seabirds travel over vast stretches of apparently featureless ocean, yet return to their tiny nesting islands after long migrations lasting several months or after foraging trips of several days. The

use of tracking devices has enabled the movements of individual birds to be followed. After wandering in all directions over several days while searching for food, individuals have been found to return on a straight line to the breeding island, which is too far away to be visible (Weimerskirch *et al.,* 1993). This applies even to penguins, which remain on or below the water surface while at sea, and Emperor Penguins can walk in a straight line over featureless sea ice to their nesting areas for distances exceeding 100 km (Ancel *et al.,* 1992). Evidently, marine birds returning to their distant nesting places know the direction they should take from any point in the surrounding ocean.

Moreover, seabirds deliberately displaced from their nesting colonies can get back again quickly, as shown in the experiments reported earlier with Manx Shearwaters, Laysan Albatrosses and others (Kenyon & Rice, 1958; Matthews, 1968), and more recently using satellite-based radio-tracking of Cory's Shearwaters (Dali' Antonia *et al.,* 1995). When nearing their nesting islands, such birds may use their keen sense of smell to locate their colonies, and even their individual nest sites.

TIME SHIFTS

Although most northern hemisphere migratory birds winter south of their breeding areas, many have strong westerly or easterly components in their migrations. This holds, for example, in the many species that travel between breeding areas in Siberia and wintering areas in western Europe. In using celestial cues, long east–west migrations present greater navigational problems than north–south ones because east–west flights involve time shifts, as the birds pass through successive time zones. If long-distance migrants using celestial cues to navigate did not allow for time shifts during the course of their east–west journeys, they could make ever greater directional errors, and veer progressively further off course. The problem created by time shift is greatest at the highest latitudes, where the longitude lines are closest together, requiring more rapid

adjustment. Hence, a second presumed function of an internal clock is to measure the changes in timing of sunrise and sunset, as the bird flies long distances west or east. This is the most obvious way in which birds could detect changes in their longitudinal positions. Whether they do so remains an open question, but we are not aware of any other global cues that might allow the birds to achieve this. Displacement experiments with White-crowned Sparrows in arctic North America indicated that a combination of geomagnetic and celestial information might be used to define longitude, but the precise mechanism remained unclear (Åkesson *et al.,* 2005). This problem is in contrast to latitude (north–south position), which birds could determine more readily, either through the elevation of the sun at noon, the height of the centre of stellar rotation above the horizon or from the angle of magnetic inclination, all of which they can apparently sense. But whatever system birds use, they may be better able to fix their direction when stationary on the ground than during migratory flight, and major changes in direction normally follow stopovers in journeys when birds have had time to reassess their position.

RHUMBLINES AND GREAT CIRCLES

Another unresolved question concerns the extent to which birds travel on straight 'rhumbline' routes (also called loxodromes) or on great circle (orthodrome) routes. Navigationally, rhumbline routes are the most straightforward, because the bird could set off in the appropriate direction and maintain the same heading throughout its journey. If the route ran directly north–south, it would also be the shortest route between two points on the earth's surface and would not involve a time shift. However, if the journey had an easterly or westerly component, so that it involved crossing lines of longitude (as most routes do), a constant heading would still be the simplest but not the shortest route. A great circle route covers the shortest distance between two longitudinally separated points, but requires continual change in heading during the journey (Fig. 135). Great

circle routes are thus more demanding in their navigational requirements. They can be flown by aeroplanes fitted with sophisticated navigation equipment, but whether by birds remains an open question. It is at high latitudes, where the problems of time shift are most acute, that the distance savings on great circles are also greatest.

Evidence that any birds take great circle routes (other than north–south) is as yet rather slender. Use of radar on the coast of northern Siberia revealed the occurrence of an east-northeast post-breeding migration, suggesting direct flights between Siberia and North America, 1,800–3,000 km across the Arctic Ocean (Alerstam & Gudmundsson, 1999). If the migrants gradually changed their orientation to the right during these flights, as on a great circle route, they would travel first towards Alaska and neighbouring parts of Canada and eventually, continuing on the same great circle, they would reach South America. The commonest species involved were the Pectoral Sandpiper and Grey Phalarope, which winter on and near South American coastlines, respectively. This is one piece of evidence indicating that some long-distance migrants might travel along approximate great circle routes, but it will remain inconclusive until birds have been followed along more of the route. Ring recoveries from these or other candidate species are also insufficient to confirm travel by great circle routes. Only when not influenced by topographic features, important feeding sites or weather patterns would migrants be expected to follow either straightforward rhumbline or great circle routes, and this ideal may be quite rare.

Furthermore, among known orientation mechanisms, different compass systems allow different possibilities. To begin with the sun compass, as long as the birds do not compensate for the change in local time when travelling across longitudes, this compass would direct birds along migration routes that resemble great circle routes at high latitudes (Alerstam & Pettersson, 1991). In contrast, if birds did adjust for the longitudinal shift in time and reset their internal clocks regularly as they crossed longitudes, a sun compass would

direct them on a constant geographic rhumbline route. The star compass provides birds with geographic north–south information based on the rotation centre of the starry sky (see above). A migration route following a star compass would therefore also lead the birds along a constant geographic rhumbline route. On geomagnetic information, birds could use the inclination angle of the field lines to gain information about latitude as well as the direction towards the magnetic pole or equator. A migratory route based on geomagnetic orientation alone would lead birds along a constant magnetic course, a magnetic rhumbline (Alerstam & Gudmundsson, 1999), or possibly along so-called magneto-clinic routes, assuming the birds follow an apparent angle of inclination, a constant angle between the direction of the field lines and the heading of the bird. Hence, among the known mechanisms, only a sun compass with no compensation for changes in local time could lead birds along a track similar to a great circle route across longitudes.

One way in which birds might achieve an approximate great circle route, but using rhumbline navigation, would be to divide the journey into stages, with one or more appropriately positioned stop sites, flying straight from one to another, but making a directional change at each one. Such dog-leg routes are common among migrating birds, as they avoid long water-crossings or high mountains, or make use of refuelling sites that are somewhat off course. The journey is thus divided into successive stages with different main orientations. Most of the migrants that travel in autumn from western Europe to Africa migrate southwest into southern Iberia, and then take a more southerly course into Africa. Without this change in direction, they would end up over the Atlantic Ocean.

Overall, straight rhumbline routes based on constant compass headings appear more likely in many bird populations, and are consistent with the routes frequently recorded by ringing and radio-tracking. They also fit the experimental evidence (based mainly on songbirds) of a genetically fixed directional preference that steers

inexperienced juveniles towards their wintering areas (although they may change directions at specific points in their journeys). Clearly, more research is needed on the precise routes taken by long-distance migrants before their navigation systems can be more thoroughly assessed.

SOCIAL FACTORS

While the individuals of some bird species normally migrate singly, and separated from others of their kind, in many bird species individuals migrate in flocks, or at least maintain contact with other individuals by frequent calling. One advantage of migrating in flocks is that it could improve direction-finding, allowing for the emergence of skilled or experienced leaders or of collective decision-making leading to optimal 'mean directions'. This view was supported by observations showing that, as migrating Skylarks passed overhead, the directional scatter was found to decrease with the increase in group size (Rabøl & Noer, 1973). It was also supported by an experiment in which randomly assembled groups of three to six homing pigeons showed a reduction in both directional scatter and homing times compared with single birds (Tamm, 1980). In an even cleverer experiment, two groups of pigeons were experimentally manipulated to have different orientation preferences. When single individuals from each group were released together, their track was intermediate between the paths that the birds would have taken if they had been released individually (Burt de Perera & Guilford, 1999). In some species, therefore, individuals are clearly influenced in their migratory directions by their travelling companions. Moreover, in many bird species, young migrate from their natal areas at the same time as experienced adults, and in some species (notably cranes, swans and geese), the young travel in family parties with their parents. This raises the likelihood that, in some species, young birds learn migration routes from experienced ones, with appropriate knowledge passed down the generations by cultural transmission.

Other field research has also indicated that young individuals of some species can be influenced in migratory behaviour by the example of others. For instance, 754 young White Storks were transported from the Baltic region (from where storks normally migrate southeast) and released at migration time in western Germany (from where storks normally migrate southwest) (Schüz, 1950). In contrast to the experiment described earlier, in which the release of White Storks was made after the local birds had left, these releases were made while the local birds were still present. The resulting ring recoveries from the released birds showed a strong tendency toward the southwest, approximating the direction taken by the local storks, but contrary to the southeast direction prevalent in the homeland and taken by birds released after the local birds had left. Similar results were achieved in various waterfowl, inherent directional preferences again being overridden by social influences. This is in any case evident in the males of some duck species, which pair with females in wintering areas; each male then accompanies his partner to her natal area to breed, rather than returning to his own natal area (Chapter 13).

In addition, migration can be induced in non-migratory stock by the example of other migratory individuals of the same species. Eggs obtained from English non-migratory Mallards were hatched in Finland and the Baltic region (Pütz ig, 1938). The resulting 116 young were allowed free access to the local migratory Mallard. They gave 19 recoveries up to 2,300 km away, all within the normal winter range of the host population. In contrast, other English young released in autumn after the local young had left remained near the release points during winter. Once again, innate behaviour was apparently overridden by social influences, but remained dominant in the absence of conflicting peer pressure.

The knowledge that young geese, swans and cranes reach their specific wintering localities by accompanying their parents has been used to re-establish populations and migration routes in regions from which former populations had been eliminated (Ellis *et al.,* 2003). Captive-bred young were taught to follow ultralight or

microlight aircraft (in the same way that they would naturally follow their parents), and then, at the appropriate time, they were led on a long 'migration' to an appropriate wintering area. For example, young Whooping Cranes were taught to fly behind an ultralight plane, and released on former breeding areas in central Wisconsin. When the time came, the plane was used to guide these young from their release area 1,800 km southward to former wintering grounds in Florida that had not been used for many years. The cranes overwintered successfully there. In the spring, they returned unaided to their release area, and next autumn migrated unaided to their new wintering site. Apparently, one journey was enough to fix a migration route upon these young birds. Further releases were made subsequently and, at the time of writing (2008), the new population consists of around 69 individuals, including 11 nesting pairs. From 15 similar experiments conducted between 1990 and 2001, which also included Canada Geese and Trumpeter Swans, most of the birds reached a new wintering area chosen for them and returned on their own to their starting area next spring (Sladen *et al.,* 2002; Ellis *et al.,* 2003).

CONCLUDING REMARKS

In summary, the known navigational tools available to migrating birds include: (a) a celestial compass based on sun, skylight polarisation and star rotation patterns; (b) a magnetic compass based on the earth's magnetic field; (c) an internal clock, recording diurnal and longer-term time changes; (d) an inherited mean migratory direction and time programme, which together ensure that the bird flies in an appropriate direction for an appropriate time; and (e) a map sense used for homing to a previously experienced place. The latter also implies a good spatial memory.

Equipped with these navigation aids, a bird could use at least four different route-finding mechanisms:

1. In guiding or ‘follow the leader’, some birds might complete their migration by following other individuals which know the way, as in the waterfowl and cranes mentioned above. Providing the leaders were experienced, and the young could learn the routes, these routes could be passed on from old to young. However, any birds using this method would also benefit from a backup mechanism (such as clock-and-compass) in case they were left to travel on their own.
2. In piloting, a migration route is retraced by using a sequence of learned landmarks. This method would require birds to build a landmark-based map during a previous migratory journey, which could then be retraced during subsequent migrations. In theory, such landmarks could be visual, auditory, magnetic or olfactory. This is not a method for inexperienced migrants on their first journey, but it could help birds returning to a known area.
3. In clock-and-compass (vector) navigation, birds aim to head in a constant migratory direction (which may change once or several times during a journey) for an innately determined amount of time controlled by the internal clock. By this mechanism, birds could reach previously unknown but appropriate wintering areas. Theoretically, birds of all ages could use this orientation mechanism, which has been demonstrated experimentally in young passerines and others. With this facility alone, however, birds are unable to determine their position, and are therefore unable to correct for deviations, directional mistakes, over-flight or experimental displacement.
4. In bi-coordinate navigation, birds can sense at least two global coordinates forming a reliable grid through which they can determine their geographical position. Bi-coordinate navigation could provide continual positional feedback, enabling birds to correct for drift or directional mistakes. Theoretically, birds of all ages may have a map sense, but experimental evidence from several species

suggests that it is used primarily by experienced birds returning to a known area.

It seems also that birds have emergency strategies for when things go wrong—for example, when over the sea, land birds often reverse direction and retrace the route or, if the wind is too strong to fly back, they continue on the same heading or fly downwind until land appears. Migrants commonly experience wind drift during flight, and often compensate for this displacement at the time or during a later flight, showing that some course recording and correction is at work, even if they do not 'know' the coordinates of their migratory goal (Thorup & Rabøl, 2001). The fact that juvenile (as well as adult) birds can correct for drift may seem at odds with some of the displacement experiments discussed above, in which adults corrected the displacement and headed towards their former wintering areas, whereas juveniles continued on their usual direction and made no correction. However, naturally drifted juveniles, as well as adults, experience the drift and can see the ground below, whereas artificially displaced birds travel while boxed inside a vehicle or airplane and are unable to see the outside world. The method of lining up successive landscape features and flying from one to another is one obvious way of keeping on course in a crosswind.

In addition to these various route-finding mechanisms, birds seem also to possess a 'location response', through which they use magnetic or other conditions in specific regions as a cue to change their behaviour—to accumulate more fat than usual, to change direction or to stop migrating. This innate mechanism may operate in conjunction with the internal clock.

Perhaps the main message to emerge from research so far is that migratory birds have a number of orientation and navigation mechanisms available to them, and are not restricted to just one. As cues to compass directions, they can use celestial (sun, skylight polarisation and stars) or magnetic information (inclination and intensity of force lines). The sun compass must be time-compensated

to allow for time of day, so an important component of this mechanism is the bird's internal time sense. Almost certainly, birds also use known landmarks to recognise previous travel routes and home areas, and perhaps also to help maintain a straight course or detect drift. Effective use of all known compasses employed by migratory birds must be learned, and can be modified by experience, if necessary cross-checking them at points along a route. Some of the current pressing questions in bird navigation centre on the degree of development and nature of a map sense in young birds (to supplement the clock-and-compass mechanism), on the means of its encoding and inheritance, and on the extent to which migrants can travel on great circle as opposed to rhumbline routes. Despite an impressive range of navigation aids, and other migratory behaviour, things occasionally go wrong, and every year some migrating birds stray far off course, as discussed in Chapter 14.

†The current magnetic North Pole is situated at about 78°N, 103°W in northernmost Canada (Queen Elizabeth Islands), and the magnetic South Pole is at 65°S, 139°E (at the coast of the Antarctic continent at Wilkes Land). In wide regions around these poles, the horizontal component of the magnetic field is very small and the vertical component very steep, making magnetic orientation almost impossible there.

† Two magnetic parameters that vary in sufficiently different directions across the earth's surface in a largely predictable way are the angle of inclination and the magnetic field strength, so in theory these parameters could be used for bi-coordinate navigation, at least in some regions. However, in other regions these two parameters coincide, so they do not form a grid system. Furthermore, in areas with geomagnetic anomalies, where the magnetic parameters can be distorted by iron materials in the earth's crust, and in areas close to the geomagnetic poles where the field lines are vertical, such a bi-coordinate map might be difficult to use. Further difficulty arises from the fact that at particular localities, geomagnetic parameters change through time, undergoing a diurnal cycle resulting from

electromagnetic radiation from the sun, as well as other variation caused by occasional magnetic storms. They can also drift significantly during the life of a long-lived bird. Even the positions of the two magnetic poles change somewhat over the centuries with respect to true geographical north and south. On a much longer timescale, the polarity of the geomagnetic field has changed several times in geological history (with north and south reversing), so polarity has not formed a consistent source of reference through evolutionary time.

† One remarkable example of apparent reorientation concerned a radio-tagged juvenile Honey Buzzard migrating from Britain towards Africa. Caught by strong westerly winds, this bird was blown into mid-Atlantic more than 1,000 km from the European-African coastline. When winds abated, it flew directly east towards its normal route, but it died at sea still 363 km from the nearest land. By the time of its death, this young bird had spent more than 120 hours over water (www.roydennis.org/honeybuzzard).

CHAPTER 13

Site-fidelity and Dispersal

As revealed by ringing, individual migrants often return from their travels to breed in the same places year after year. Depending on species, many individuals use the same territories, and even the same nest sites, in successive years. This seems remarkable, considering the huge distances that some birds have travelled in the interim. Moreover, young birds tend to return and breed in the same general region where they were raised. These findings may apply more to one sex than the other, but hold for both territorial and colonial species. In addition, individuals of some bird species also winter in the same localities in successive years, and may even use the same refuelling sites each year on migration, while some waterfowl use the same moulting sites. Such site-fidelity is apparent in both resident and migratory populations, but in migrants it implies the existence of precise navigational skills and homing behaviour, through which individuals seek out, year after year, the same specific places hundreds or thousands of kilometres apart.

Birds that occur in the same places in successive breeding (or wintering) seasons are said to show strong site-fidelity, while those that breed (or winter) in different places in different years are said to disperse. But both site-fidelity and dispersal are concerned with the distances that separate different places of residence in the same individual. Other terms in frequent use include ‘homing’—the tendency to return to a previously occupied site, wherever it may lie—and ‘philopatry’—the tendency to reside in the area of birth, or to return there after a period of absence.

In studies of site-fidelity and dispersal in birds, it is useful to distinguish: (1) natal dispersal, measured by the distances between natal and first breeding sites; (2) breeding dispersal, measured by the distances between the breeding sites of successive years; and (3) non-breeding dispersal, measured by the distances between the wintering sites of successive years. In most bird species that have been studied, individuals move much greater distances between natal site and breeding site than between the breeding sites of different years. In many species, however, individuals may move large distances between their wintering sites in different years.

Site-fidelity and dispersal have been studied primarily with the help of ringing. Most studies have been conducted by researchers working in defined areas, ringing nestlings or adults in one year and noting their presence in the same area in a later year. Such records are invariably biased in favour of short-distance moves because, being confined to the study area, they are not balanced by the longer moves of other individuals which may have settled outside the area and remained undetected. Less biased information on dispersal distances can be gained from recoveries of ringed birds reported by members of the public. Even if all the birds are ringed in a particular locality, the recoveries are not confined to that locality, so can give a much more representative picture of dispersal distances. Although the natal sites are known precisely for birds ringed as chicks, the assumption usually has to be made that individuals of reproductive age recovered in the breeding season were in fact nesting, or had the potential to nest, at the localities where they were reported. Collectively, such records reflect the settling patterns of individuals with respect to the ringing site, regardless of their movements in the interim, which usually remain unknown.

BENEFITS AND COSTS OF SITE-FIDELITY

A bird might gain from nesting near where it was raised, and in returning to the same area each year, providing that conditions

permit. For one thing, it could benefit from local knowledge. This holds for both breeding and wintering areas, and at any sites where the bird might stop on migration. Familiarity and prior ownership might also give a bird an advantage in competitive interactions with other individuals, making it better able to defend its feeding and breeding sites against potential takers. Moreover, through long-term residence over many generations, populations tend to become adapted by natural selection to the conditions prevailing in their particular region. This is evident, for example, in the consistent inherent patterns of size and colour variation found within species across their geographical ranges. So by remaining in (or returning to) the same general breeding area year after year, individuals occupy regions to which both they and their likely breeding partners are best adapted. The benefits of local experience and of local adaptation, acting at the level of the individual, could thus be the main selective forces underlying site-fidelity in birds, where this is feasible.

Site-fidelity might also facilitate social cohesion. Many birds pair with the same partner each year, even though the sexes may live separately outside the breeding season. Partners can readily reunite if they share a common breeding site (like most birds) or a common breeding and wintering site (like some sea ducks, in which partners separate after egg-laying and reunite in wintering areas; Robertson & Cooke, 1999). The advantage of pairing with the same partner in successive years is that, in many species, this leads to better breeding success, as newly formed pairs (whatever their age) breed less well, on average, than more established ones (for a review, see Black, 1996).

Despite the frequent benefits of site-fidelity, dispersal from one site to another also has advantages. One is that birds can leave areas where conditions are poor or overcrowded to find somewhere better. Some birds occupy temporary habitats, such as ephemeral wetlands, which become less suitable over time, while others exploit patchy food sources, which are available in different places in different years. By moving from one good area to another, as

appropriate, individuals may thereby enhance their survival and reproductive prospects. Another advantage of dispersal is that it could reduce the chances of an individual pairing with a close relative, for in many birds, inbreeding can lower the production and viability of offspring (Greenwood *et al.,* 1978; Keller *et al.,* 1994).

There are clearly both benefits and costs to site-fidelity and dispersal, which are influenced by the ecological needs of the bird and by the environmental conditions in which it lives. In some circumstances, it pays to remain in (or return to) the same general area, in others to move elsewhere. Birds vary their behaviour accordingly, and some closely related species which exploit different types of environment or food can differ greatly in their dispersal behaviour, as discussed later.

NATAL DISPERSAL

The settling patterns of birds in relation to their natal sites are usually studied from birds ringed as nestlings and recovered in later breeding seasons. In many bird species, the numbers of recoveries tend to be greatest in the vicinity of the hatch site, and decline progressively with increasing distance. Typically, the recoveries come from all sectors of the compass, indicating no directional preference at the population level. Such dartboard settling patterns are shown for several species in Figures 137 and 138. These scattered patterns do not result merely from an inability of some migrants to re-find their home areas, because they also occur in sedentary species (such as the Sparrowhawk in Figure 137). Factors such as landscape structure, habitat and nest-site availability, and prior occupancy by other individuals can all influence how close to its natal site a bird is likely to settle.

Seabirds and other colonial species

In colonial species, as expected, natal dispersal is influenced by the distribution of colonies. Nevertheless, the settlement pattern is essentially the same as in other birds, with many individuals breeding in their natal or neighbouring colonies, and fewer individuals moving to colonies further away. This type of settling pattern holds for colonial land birds, such as the Sand Martin (Mead & Harrison, 1979a) and Lesser Kestrel (Negro *et al.,* 1997), and for a wide range of colonial seabirds, including gulls and terns, auks, shags and gannets, petrels, shearwaters and others (e.g. Brooke, 1978; Duncan & Monaghan, 1977; Harris, 1984; Swann & Ramsay, 1983; Halley *et al.,* 1995; Aebischer, 1995; Coulson & Nève de Mévergnies, 1992). Moreover, in some seabird species, many individuals settle to breed within the same part of a colony where they were raised. This finding is much more frequent than expected if individuals settled at random within their natal colony. It also occurs in a wide range of species, including skuas, auks, shags, shearwaters, and others (e.g. Richdale, 1963; Halley *et al.,* 1995; Klomp & Furness, 1992; Aebischer, 1995).

In any colony, then, breeders typically include some individuals raised within the colony and others that have moved in from elsewhere. The proportion of immigrants recorded in nesting colonies varies greatly between species and according to the prevailing circumstances. During the establishment and growth phases of a colony, immigration is high, so that most of the occupants have been raised elsewhere, whereas during a decline phase, the reverse maybe true (for seabirds, see Porter & Coulson, 1987; Phillips *et al.,* 1999; for geese, see Larsson *et al.,* 1988; Johnson, 1995).

In many seabird species, individuals are known to visit colonies for one or more years before they attempt to breed, supposedly acquiring experience and local knowledge while assessing the merits of potential nesting sites. The number of colonies visited by individuals during this pre-breeding phase seems to vary between species. Among Great Skuas nesting on Foula, virtually all ringed individuals seemed to visit only their natal colony in their pre-

breeding years, as none was recorded elsewhere (Klomp & Furness, 1992), but in European Storm-petrels and Atlantic Puffins, individuals regularly visited more than one colony, sometimes hundreds of kilometres apart, before settling to breed (Mainwood, 1976; Fowler *et al.,* 1982; Harris, 1984). One Puffin was ringed on the Treshnish Isles (Scotland) in late June and caught while visiting the Westman Islands (Iceland) 1,087 km away 21 days later (M. P. Harris, in Wernham *et al.,* 2002). By the time they start to visit colonies, some seabird species may have spent several years of their early life in distant seas, apparently without coming to land, yet they are still able to find their natal areas.

In some bird species, males and females disperse similar distances, but in many others, one sex moves further than the other, at least as a general tendency. The commonest pattern is for young females to move further between hatch site and breeding site than young males. This pattern has been found in a wide range of birds, including many passerines, owls and raptors, gallinaceous birds, shorebirds and colonial seabirds (Greenwood, 1980; Clarke *et al.,* 1997). However, in most migratory waterfowl, it is the males than move furthest (Rohwer & Anderson, 1988). In contrast to most other birds, pairing among waterfowl occurs in wintering areas, and the male then accompanies the female to her area of choice. Other species with male-biased dispersal include some shorebirds, such as phalaropes, that show ‘sex-role reversal’, with the female defending the territory or mate, and the male doing the incubation and chick care (Colwell *et al.,* 1988). Like many waterfowl, such shorebird species have a social system based on mate defence, but unlike many ducks, they form into pairs in breeding areas. Males also disperse further than females in some lekking species, such as the Great Bustard (Alonso & Alonso, 1992).

Competition and natal dispersal

While a tendency to disperse from the natal site seems inherent in birds, competition may influence the distances moved. In some

studies, the young moved further from their natal sites in years of high rather than low population densities (e.g. for the European Greenfinch, see Boddy & Sellers, 1983; for the Bearded Tit, see Cramp & Perrins, 1993), or moved further in successive years as a local population grew (e.g. Lesser Kestrel: Negro *et al.,* 1997). In other studies, the young moved further from their natal sites in years of low rather than high food supply (e.g. Common Kestrel: Adriaensen *et al.,* 1998; Tengmalm's Owl: Saurola, 2002). In yet other studies, young fledged late in the season dispersed further, on average, than young fledged earlier (e.g. Pied Flycatcher: Sokolov, 1997; Common Kestrel: Village, 1990). These various findings implied that dispersal distances may be 'density-dependent', and influenced by levels of competition, whether for territories, food or nest sites.

More detailed studies have revealed other patterns in the site-fidelity of breeders: (a) in most species, males are more likely than females to stay on the same territory from year to year (e.g. Greenwood, 1980; Jackson, 1994), possibly related to sex differences in territory acquisition and defence; (b) site-fidelity tends to increase with age (e.g. Harvey *et al.,* 1984; Thompson *et al.,* 1994; Aebischer, 1995), possibly related to the benefits of site-familiarity accruing through life; (c) individuals are more likely to change territories after a breeding failure than after a success (e.g. Shields, 1984; Jackson, 1994; Blums *et al.,* 2002), possibly related to site quality; (d) individuals tend to move to better territories (offering better breeding success) through early life (e.g. Matthysen, 1990; Newton, 2001), possibly related to improving status and competitive ability; and (e) change of territory is often associated with change of mate (e.g. Johnston & Ryder, 1987; Newton, 2001). Sex differences in the frequency of territory changes are accompanied by differences in the distances moved, and in most studied species, females moved more often and further than males. These various patterns have been confirmed in a wide range of studied species, but not in all.

Dispersal within a breeding season

Many birds raise more than one brood per season, or attempt a second nest nearby if the first fails. Some use the same nest site for a repeat brood: in particular, cavity nesters, whose sites are scarce. In most species, the same partners stay together for successive nests in a season, but in other species, some individuals change territories and partners, especially after nest failure, the female often moving further than the male. Such patterns have been described among House Sparrows (Sappington, 1977), Common Starlings (Feare & Burham, 1978) and Barn Swallows (Shields, 1984), among others.

Other species change location part way through a breeding season, in line with changes in food supplies or habitat suitability. This can happen over short distances on farmland, as crops grow and thicken, and birds vacate one field to find another with more acceptable vegetation structure (as found in the Skylark and Yellow Wagtail). But it also happens on a much larger spatial scale. For example, Penduline Tits studied in central Europe may raise first and second broods in different patches of riparian scrub as conditions change through the season, with movements generally greater than 0.5 km, and some extending up to 208 km (Franz, 1988). Yet other examples include the few species (such as the European Quail) that habitually stop and breed at two or more points on a migration route (Chapter 20). In some shorebirds, such as the Eurasian Dotterel and Kentish Plover, the females lay one clutch for the male to incubate, and then leave in search of another male to raise a second clutch. In the process, the females can travel hundreds of kilometres between nesting attempts.

LONG-DISTANCE DISPERSERS

The precise year-to-year homing behaviour shown by the species in Figure 142 is not universal in birds. It occurs chiefly where habitats remain fairly stable from year to year, and where returning birds can expect to survive and reproduce. It is less marked in species that

depend on habitats or food supplies which are available in different places in different years. This is the situation faced by some tundra-nesting species affected by variable patterns of spring snow conditions, in those waders and waterbirds that are affected by fluctuating water levels, in various desert species affected by irregular rainfall, in some boreal finches that exploit sporadic tree-seed crops or in those predatory birds that exploit locally abundant rodents (Chapter 19). Typically, the local population densities of all such species fluctuate greatly from year to year, in line with fluctuating habitat or food supplies. The speed with which local numbers rise and fall in response to changing conditions has led to the view that such species are nomadic, with individuals concentrating in different areas in different years, wherever conditions are good at the time. For some such species, ring recoveries have now confirmed that some individuals do indeed breed at hundreds or thousands of kilometres from their natal sites and in widely separated areas in different years (Chapter 19).

Similarly, among shorebirds, species which nest in habitats that normally remain stable from year to year, such as the Eurasian Oystercatcher and Common Sandpiper, show strong philopatry and site-fidelity, while species that nest in patchy and ephemeral habitats, or are affected by variable patterns of snow melt, such as the Curlew Sandpiper, Sanderling and Little Stint, show much less natal philopatry and less adult site-fidelity (Evans & Pienkowski, 1984; Tomkovich & Soloviev, 1994). Similar comparisons could be made among more southern waders, such as Black-winged Stilts, and various gulls and terns, some of the most nomadic being the Black and White-winged Black Terns. Species that show low site-fidelity also show low mate-fidelity, because pairing occurs annually on or near nesting areas and former partners do not normally move together to the same places.

NON-BREEDING DISPERSAL

In some bird species, once individuals have wintered in an area, they return from year to year with the same consistency as they return to their breeding localities. Most studies of winter site-fidelity, like breeding site-fidelity, have been conducted by individual researchers working in the same small areas year after year. So again, while such records are useful in confirming site-fidelity, most give little idea of the proportion of surviving birds that settle elsewhere. However, in some species, the proportion of individuals that returned to the same area in successive winters was again close to the expected annual (or over-summer) survival, implying that almost all surviving individuals were site-faithful. Annual return rates to particular wintering areas of 37–52 per cent have been recorded from various small songbirds, and of 77–95 per cent for various longer-lived shorebirds, which is more or less as expected from their annual survival rates (Fig. 142). More generally, return to the same specific wintering localities has been recorded by casual records for a wide range of passerines, raptors, gulls, waders, waterfowl and others, including many intercontinental migrants.

In winter, many birds base themselves on communal roosts, from which they range out into surrounding areas to feed. For example, Common Starlings and Barn Swallows can range more than 50 km from their winter roosts, so records of individuals several tens of kilometres apart in different winters may still represent ‘site-fidelity’ in a way that breeding season records at such distances would not. A survey of Eurasian Barn Swallows wintering in South Africa showed that nearly all ringed survivors returned to the same place, or to within 100 km of it, from year to year (Oatley, 2000). Similarly, many shorebirds are faithful to their roost sites in different years, and the median distance moved by ringed Dunlin trapped in different winters (14 km) was well within their daily travel range in large estuaries (Rehfisch *et al.,* 1996). Hence, the existence of communal winter roosts serving extensive feeding areas gives more flexibility to the notion of site-fidelity than do nesting territories in summer.

The fact that birds have greater freedom to move around in the non-breeding than in the breeding season raises problems in measuring site-fidelity, especially in migrants. In some species that show site-fidelity, such as the Blackcap, the numbers of birds at particular sites in the Mediterranean region have varied greatly from year to year, and from one part of a winter to another, depending on the size of the local fruit crops that provide their food. This fluctuation was apparently due largely to the behaviour of young birds which settled in their first year mainly in sites where fruit was plentiful, and partly to individuals (young or old) varying their length of stay from year to year, moving on each year once the local crops had been eaten (Cuadrado *et al.,* 1995). At any one time and place, both residents and transients are evident among wintering Blackcaps, but in varying proportions (Belda *et al.* 2007).

Some studies of migratory passerines in the tropics have reported high winter recurrence, suggesting that at least most surviving individuals have returned to their territories in successive years (e.g. Nisbet & Medway, 1972; Pearson, 1972; Kelsey, 1989). On the other hand, studies of related species in the Mediterranean region have generally reported lower return rates, indicating that many birds could have changed winter quarters within or between years (Herrera, 1978; Herrera & Rodriguez, 1979; Finlayson, 1980; Cuadrado *et al.,* 1995; Catry *et al.,* 2003). As the Mediterranean species depend more heavily on fruit in winter, it would not be surprising if they were less territorial and site-faithful than their tropical wintering equivalents which take more insects, and hence have a more consistent food supply. Moreover, some of the studies involved only territorial individuals (e.g. Kelsey, 1989), while others involved a mixture of territorial and non-territorial (or transient) ones (e.g. Cuadrado, 1995). Non-territorial individuals would be expected to show less site-fidelity.

Age-related differences

Outside the breeding season, when many birds move away from their nesting areas, juveniles often move further than adults, or stay away for longer. Some long-lived species, in which individuals do not breed until they are several years old, show a progressive change to shorter-distance moves or to shorter periods away from the breeding areas with increasing age (Chapter 21). Such patterns have again been noted in a wide range of bird species, including the Grey Heron (Olssen, 1958), Black Kite (Schifferli, 1967), Oystercatcher (Goss-Custard *et al.,* 1982), Herring Gull (Coulson & Butterfield, 1985), Common Guillemot (Birkhead, 1974), Great Cormorant (Coulson, 1961) and Northern Fulmar (Macdonald, 1977). This means that, as they age, some individual birds occupy different areas in successive winters or spend progressively less time in more distant wintering areas.

Comparison of breeding and non-breeding site-fidelity

Many bird species show greater fidelity to breeding than to wintering sites. This reflects not only spatial variation in wintering habitat from year to year, but also the fact that individuals of many species migrate in their first but not in subsequent years, or migrate different distances in different years. For example, White Storks show extreme fidelity to their breeding places, as they normally return year after year to the same nest sites; but they are much less faithful to particular wintering places. Four radio-tagged adults were tracked by satellite from Europe to their African winter quarters several times, one bird on nine successive journeys (Berthold *et al.,* 2002). These birds occupied different areas in Africa from year to year, depending on the rainfall (and presumably the food supply). One bird wintered in Tanzania in one year and further north in the Sudan in the second year, but then went as far as South Africa in the third year and Botswana in the fourth. Hence, this one individual wintered in successive years in places that extended from the northern tropics to the southern temperate zone (for discussion of other aspects, see Chapter 9).

Other species show less fidelity to their breeding areas than to their wintering areas. Examples include some arctic-nesting shorebirds, such as the Curlew Sandpiper and Sanderling, whose breeding sites may change from year to year according to snow-melt patterns (Tomkovich & Soloviev, 1994), but whose wintering sites are more consistent and used by the same individuals year after year (Elliott *et al.,* 1976; Evans, 1981).

To set against these patterns, other species show extreme site-fidelity in both breeding and wintering areas, while others exhibit little or no site-fidelity in either breeding or wintering areas, their behaviour at both seasons reflecting the unpredictability of their habitats and food supplies (Chapter 19).

FIDELITY TO STOPOVER SITES

Most migrants pause for refuelling several times during their journeys. Individuals of some species have been identified in successive years at the same staging sites, which they visit for at most a few days or weeks before moving on. Moreover, because some species take different routes on their outward and return migrations, individuals may use different stopping sites at the two seasons. This implies that some migratory birds remember the specific locations of several sites scattered over two continents, which they visit successively each year on a circuit that is repeated annually throughout their lives.

Most passerines migrate in abroad front over more or less continuously suitable habitat which provides a wide choice of potential stopping places. The turnover of birds at particular stopover sites is high, as individuals normally remain only for short periods (often less than one day), so the chances of recording particular individuals are low. Not surprisingly, therefore, most studies in which passerine migrants were trapped year after year at the same stopping sites have provided little or no evidence of individual year-to-year site-fidelity. Others gave small, but highly variable, proportions of re-traps, exceeding 10 per cent only in

extreme cases. Some of the low return rates may have been no greater than expected by chance, if birds had paused at random in suitable habitat encountered en route.

For other migratory birds, however, notably waterfowl and shorebirds, suitable refuelling places are often localised and far apart; and it is in such species that the highest recurrence rates have been recorded. Some shorebirds and geese have only one or two main stopover sites on their migration routes, so almost the entire population may stop at these sites on each journey. Not surprisingly, then, many ringed birds of these species are known to have visited the same staging sites year after year on migration (for shorebirds, see Pienkowski, 1976; Evans & Townsend, 1988; Wernham *et al.,* 2002). The minimum annual return rate of adult Sanderlings at a stopover site in southwest Iceland was 65 per cent, not very different from the estimated annual survival (Gudmundsson & Lindström, 1992). Similarly, among Greenland White-fronted Geese staging in two areas of Iceland, and seen in more than one season, 89 per cent were re-sighted within 4 km of the capture site from spring to the following autumn, 88 per cent from autumn to the following spring, 96 per cent from one spring to the next, and 100 per cent from one autumn to the next (Fox *et al.,* 2002). Again, the implication to be drawn from such high rates is that practically all surviving birds used the same sites in successive years. Among birds in general, however, such high stopover site-fidelity may be exceptional, and despite following the same route, many migrants may stop at different places in different years, either by choice or circumstance.

POST-FLEDGING DISPERSAL

Once they become independent of their parents, the young of many bird species disperse from their natal sites, for a time moving in various directions and progressing further from the natal site with increasing age. As birds hatched in particular localities gradually leave, others hatched elsewhere move in. This shifting and mixing

happens every year at this time regardless of local conditions. Yet post-fledging dispersal is the least conspicuous of all bird movements, for it occurs at a time when many birds are at their most silent and often moulting. They accumulate no special body reserves, and although they appear in a wider range of places than when nesting, no large-scale distributional change is evident at the population level. Evidently, the tendency to disperse is inherent and presumably endogenously controlled. However, the actual distances that individuals move maybe influenced by external conditions, as explained above, and in some species the young from early broods, with more time at their disposal, tend to wander over wider areas.

After a period of post-fledging dispersal, individuals of many sedentary species appear to stay in those areas thereafter, whereas individuals of migratory species depart for their winter quarters. For a few weeks in late summer, the pattern of ring recoveries in migrants is similar to that of natal dispersal, with no directional preference. Then, as the young age, recoveries are more directionally orientated and come from longer distances, as the initial centrifugal dispersal gives way to long-distance directed migration. This transition has been examined, for example, in Barn Swallows (Ormerod, 1991), Pied Wagtails (Dougall, 1992), Sand Martins (Mead & Harrison, 1979b), Willow Warblers (Norman & Norman, 1985) and Kestrels (Village, 1990). The change from random to directed movements is also evident among birds caught from the wild and tested in orientation cages (Shumakov, 2001).

On their return the next spring, migrants settle near their natal areas in the dartboard pattern described earlier, sometimes in the localities to which they dispersed in the post-fledging period. This was shown, for example, in Robins studied near Lake Ladoga in Russia (Zimin, 2001). In this area of 7 x 1.5 km, most local young were replaced by immigrants during the period of post-fledging dispersal. The immigrants stayed on their newly-acquired territories until they had completed moult, and then left on migration. Survivors from these summer immigrants returned the following spring to nest in the study plot, often in the very same territories

where they had moulted in the previous autumn. This behaviour revealed the exploratory nature of post-fledging dispersal, and its role in finding potential breeding places for a later year. In its effect on settling patterns, post-fledging dispersal was tantamount to natal dispersal. However, individuals of some resident species may have a second period of dispersal in spring.

SITE ATTACHMENT

Attachment of young birds to natal sites

The young of migratory birds must presumably learn the location of their natal area before they leave it, for only then could they return there after a long migration. This assumption has been confirmed experimentally in various species. When eggs or chicks were transferred from one area to another, tens or hundreds of kilometres away, the resulting adults were usually found breeding near their foster home rather than near their original home. The age of the birds at transference emerged as critical, because attachment to a locality occurred at a specific stage of development. In migratory passerines, this critical stage fell in the post-fledging period, between leaving the nest and leaving the area (Sokolov, 1997, 2000a). Individuals transferred after this age returned to their original natal homes, rather than their foster homes.

In another experiment, young Chaffinches released in a new area at less than 30 days old returned to the area in a subsequent year, while those older than 40 days returned mainly to their natal place after migration (Sokolov, 1997). Evidently, site imprinting in Chaffinches occurred between the age of 30 and 40 days, again mainly in the post-fledging period, before dispersal or migration. However, if Chaffinches were hand-reared without sight of the outside world and then released at 50 days old, some still returned to the release site in a later year. Hence, if they were denied the chance to learn attachment to a site at the usual age, they could do

so later. If they learned at the usual age, subsequent experience did not alter the preference established then. Site attachment in various other small passerines occurred in the age range 30–55 days, depending on species and rate of development (Sokolov, 2000a).

Attachment to a locality does not imply that we can expect all surviving young to breed there subsequently. They may return there initially in spring but, on finding breeding sites already occupied, they may have to move elsewhere. Alternatively, they may not return with exact precision to the natal area, but to somewhere nearby, perhaps to a place they located during their post-fledging dispersal before they left on migration (see above). These variations in behaviour give rise to the dartboard settling patterns discussed above.

Other experiments on site attachment have involved pelagic seabirds, in which individuals range over large areas of ocean before they return to their colonies several years later. As these birds tend to leave their colonies on migration soon after fledging, fixation to the natal site generally occurs in the late nestling period, or in burrow-nesting species when the young first emerge from their underground nest sites and are able to see the outside world (Fisher, 1971; Serventy *et al.,* 1989).

The tendency of young birds to breed near where they were raised has contributed to the success of conservation programmes in which certain bird species have been reintroduced to areas from which they were earlier eliminated. Even where young raised in the release area moved away after becoming independent, most of the survivors returned there to breed, leading to the establishment of a new local population. This has occurred in a wide range of migratory species, including waterfowl, raptors and seabirds (Newton, 1979; Kress & Nettleship, 1988; Cade, 2000). Again, the implication was that the young became fixated to the locality during their early life.

Attachment of young birds to wintering sites

The attachment of young migrants to specific wintering localities seems to occur soon after their arrival there. Samples of Dunlins that had arrived at a wintering site mainly in October were caught and moved 133 km to another site at different dates between November and December in four different years (Baccetti *et al.,* 1999). From the proportions that returned of the birds that were moved at different dates, the juveniles seemed to have become attached to the site by early December, within one or two months after arriving there. After this date, return rates were the same as those of adults, which showed no seasonal pattern, presumably because they had known the site from previous years. Similar findings from displacement experiments on Sanderlings were mentioned in Chapter 12.

Site-fidelity and dispersal patterns among birds clearly depend largely on the ecology of the species themselves, particularly on the level of year-to-year stability in their habitats and food supplies. In Chapter 1, dispersal was defined as a movement of no fixed direction; and in all the movement patterns described in this chapter (including post-fledging dispersal), the directions taken by individuals appear random (and centrifugal at the population level). Such movements by individuals could have consequences for the species as a whole. In particular, they influence patterns of abundance and distribution across the range; they enable depleted local populations to recover, vacated areas to be recolonised or new areas to be occupied, leading to range expansion. Dispersal movements also influence gene flow and genetic structure across the geographical range, facilitating or suppressing the development of locally adapted populations and subspecies. When the individuals within populations move only short distances from their natal sites to breed, local populations tend to include many closely related individuals. This process gives rise to considerable genetic substructuring across a wider region, and facilitates the development of local adaptations. On the other hand, when individuals disperse long distances, considerable genetic mixing occurs between birds in different parts of the range, which hampers

the development of local adaptations. Correspondingly, bird species with large geographical ranges in which individuals disperse over short distances tend to have many subspecies, whereas species in which individuals disperse over long distances between different breeding areas typically have few, if any, subspecies (Newton, 2003). This is evident among closely related species which differ in their dispersive behaviour, including finches, owls, raptors and waterfowl. In other words, dispersal patterns—which are adjusted to the environmental conditions to which populations are exposed—have both ecological and evolutionary consequences.

CHAPTER 14

Vagrancy

THE TERM VAGRANT CAN be applied to any species which turns up rarely. Thanks to their position in mid-latitudes off the edge of a continent and beside an ocean, the British Isles are ideally situated to receive vagrants from a large sector of the northern hemisphere. Our islands also have more bird-watchers than any similar-sized area on earth, some of whom are keenly interested in finding and recording rarities. As a result, more than half the bird species seen in the British Isles over the past two centuries are classed as rare visitors or vagrants, and newly recorded species continue to be added to the British and Irish lists year upon year (see the annual summaries in *British Birds* and *Irish Birds)*.

Outside the bird-watching community, little attention has been paid to vagrancy, partly because records are collected unsystematically (as they depend largely on the numbers and whereabouts of skilled observers), and partly because it has usually been assumed that vagrants are abnormal in some way or chance victims of unusual weather. Some apparent vagrants maybe escaped cage birds, derived from distant regions, while others may be free-living birds that have hitched a ride on a ship. But many vagrants belong to species which are not normally kept in captivity, and could not survive on a ship for days on end. Moreover, their occurrence often follows specific seasonal and location patterns, as they appear in particular weather conditions, in the same places and at about the same dates year after year, different species in mainly different places. Almost all vagrants are from migratory populations, and often in their first year of life. Evidently, recurring natural

processes underlie much of the vagrancy recorded among birds, adding interest to the subject.

Vagrancy can apparently result from: (1) normal dispersal, but over unusually long distances; (2) population growth or expansion, in which vagrants are noticed because populations are larger or breeding closer to the study area; (3) drift, in which migrants are blown off course by winds; (4) migration overshoots, in which individuals migrate in the normal direction but further than usual, appearing well beyond their usual breeding or wintering areas; (5) abnormal directional tendencies in which individuals migrate at the right time but in a wrong direction, including (6) mirror-image migration, in which birds migrate at a mirror angle to their normal direction (say southeast rather than southwest); and (7) reverse-direction migration, in which birds migrate in the opposite direction to usual for the time of year.

On a world scale, vagrants are often encountered on isolated islands off the fringes of continents, some of which are visited by a remarkable diversity of birds (which in turn attract bird-watchers). European hotspots include Heligoland off Germany (Gätke, 1895), the Northern Isles off Scotland (notably Fair Isle; Clarke, 1912; Dymond *et al.,* 1989), the Scilly Isles off southwest England (Flood *et al.,* 2007) and Cape Clear Island off southwest Ireland (Sharrock, 1973). These specially situated places, like others elsewhere, have often provided the first and sometimes only records of certain species for their particular regions. Of all the species added to the British List during the 20th century, about one-fifth were first seen on Fair Isle, which occupies less than 0.01 per cent of the total land area of the British Isles.

In the early years of migration studies, virtually all reliably recorded vagrants were shot and preserved as skins, some of which are still available for examination. As Harry F. Witherby, a leading British ornithologist of the early 20th century, used to remark: a specimen hit makes history, while a specimen missed remains a mystery. Subsequently, as guns gave way to binoculars, field guides and mist nets, many of the rarities were trapped, examined and

sometimes photographed before release, and nowadays field photographs and written descriptions by skilled observers have often proved sufficient to identify rare species unequivocally. Recent developments in digital photography have helped further, as has the increasing ability to record calls and produce sonograms for subsequent inspection. The development of ‘digiscoping’ (attaching a camera to a powerful telescope) has enabled good images to be obtained at greater distance than previously, so that identifications have come to rely not merely on notes taken at the time, but on quality images that can be studied at leisure and compared with previous photographs, descriptions and (if necessary) museum skins. Every year, papers are published in the bird literature describing how to distinguish in the field species and subspecies previously considered hard to separate. Birders are now routinely identifying vagrant subspecies, such as the Siberian Stonechat and Siberian Chiffchaff, which differ sufficiently from the native subspecies to be distinguished in the field. The use of the web and other means to advertise fresh sightings has also increased the numbers of observers able to see and photograph individual rarities. In view of the increasing numbers, expertise and mobility of observers, it is little wonder that the annual totals of recorded vagrants in the British Isles have risen greatly over the years, and that some species once classed as rarities are now regarded as regular visitors (Fig. 154)[†]

Vagrancy is even harder to detect in pelagic seabirds, because it depends largely on birds being sighted from land or washed up dead on shorelines (to which they may have been transported long distances by wind and waves). Pelagic birds sometimes fly far inland, either deliberately or accidentally during storms, which may explain some of the dead specimens found far from any sea coast. But with the growing popularity of ‘pelagic trips’ by bird-watchers, we can expect that the numbers of reported seabird vagrants around our islands will also increase in the coming years, and that some species currently regarded as rarities will prove to be frequent visitors.

In general, the longer a place has been studied, the greater the number of species recorded there. New species are continually added to local lists, and for the British Isles as a whole, more than 70 newly recorded species were added in the 25 years to 2005, an average of nearly three per year. The rate of addition would be expected to slow over time, as the cumulative total begins to level off, but bird distributions are changing all the time, bringing additional species within range. So who can guess how many species will be added to the British and Irish lists in the years ahead?

PROBABILITY OF ARRIVAL

Some species of vagrants occur in numbers every year, while others are seen less often, in extreme cases perhaps only once in several decades. Some appear in both autumn and spring, others mainly in spring, and yet others mainly or entirely in autumn (Fig. 156). Looking beyond the British Isles, arrivals follow several patterns. First, as expected, islands close to continents (such as Heligoland off Germany) receive many more vagrant birds than remote islands (such as Ascension in the mid-Atlantic). Second, on continents, the numbers of vagrant species which appear in particular localities, and their proportions in the overall numbers of species in those localities, decline with increasing latitude, matching the overall latitudinal decline in species numbers (Stevens, 1992). Third, the chance of any one species appearing in a given area generally declines with increasing distance from its regular range (Stevens, 1992). Fourth, body size is almost certainly relevant, not only because larger birds can last without food for longer than small ones, and are thus more likely to survive a difficult journey, but also because they are more conspicuous after arrival. Relative to their population sizes, vagrants of large species (such as ducks) seem to be recorded more often than smaller ones (such as warblers). This tendency is supported by analyses of long-distance sea-crossings compared to land-crossings (Robbins, 1980; McLaren *et al.,* 2006). For example, in western Europe, vagrants from Siberia, which have

travelled over land, include many more small passerines than vagrants from North America, which have crossed an ocean (Pfeifer *et al.,* 2007). However, there are specific exceptions to all these generalisations.

In post-fledging and other dispersal, recoveries of ringed birds tend to occur in all directions from the starting point, but fall off exponentially with increasing distance (Chapter 13). It seems that, while most birds disperse relatively short distances, occasional individuals disperse much further (more than ten times further than the average), with some moving beyond the regular range. It is presumably these extreme individuals that contribute most strongly to vagrancy. Because these dispersal movements are distinct from directional migration (Chapter 1), participants would be expected to occur in almost any direction from the regular range, and not just between their breeding and wintering areas. They would also be expected to occur mainly in the immediate post-breeding period, when most dispersal occurs. In the British Isles, dispersal vagrants are most likely to derive from species whose nearest breeding areas lie in western continental Europe, such as the Tawny Pipit and Melodious Warbler, although these same species may also occur at other times by other means.

Some waterbirds that breed early in the year in subtropical and Mediterranean latitudes seem to disperse mainly northwards after breeding, sometimes for hundreds of kilometres, as many southern wetlands dry out. Several species participate in these movements, including the Great White Heron, Squacco Heron and Black-crowned Night Heron, although this northward dispersal seems much less marked in Europe than in some other parts of the world. Some seabirds also move northwards in late summer, as exemplified by the numbers of Balearic and Cory's Shearwaters seen in British and Irish waters at this time of year.

EFFECT OF POPULATION SIZE

The overall abundance of a species is likely to influence the number of individuals that appear as vagrants in distant locations, even if nothing else changes (McLaren *et al.,* 2006; Pfeifer *et al.,* 2007). Several species whose populations have increased in eastern North America in recent decades, such as the Red-eyed Vireo and Ring-billed Gull, have appeared increasingly as vagrants in western Europe, but others have shown no such relationships (Robbins, 1980). In some studies, the numbers of vagrants that appear in distant localities each year have been related to annual variations in breeding success and population size in the regular range (Veit, 1997, 2000). The larger the late summer population, the more vagrants appeared in remote areas.

Range changes are also likely to alter the frequency with which vagrants occur in particular areas. Species which spread westward across Eurasia during the 20th century appeared with increasing relative frequency in Britain. Examples include the Red-flanked Bluetail, River Warbler, Greenish Warbler, Pallas's Warbler, Penduline Tit, Common Rosefinch, Rustic Bunting and Little Bunting.

It is hard to separate the effects of increasing population size over periods of decades from increasing numbers of observers, the latter never having been quantified. However, records have increased in the last half of the 20th century much more rapidly for some species than for others, while in yet other species, records have decreased. Examples of species whose occurrence is apparently decreasing in Britain include the Little Bustard and Pallas's Sandgrouse, the numbers of which are known to have declined in their regular range further east. Moreover, sustained observations over several decades at such well-watched places as Fair Isle surely indicate that some of the increases are real and not just a result of greater observer coverage and awareness.

The influence of wind on vagrancy is evident to any bird-watcher. Drift by crosswinds is one of the commonest ways in which migrants turn up in places off their normal routes, and often several species from the same region appear simultaneously. Almost every autumn,

on days with easterly winds, migrants that would normally pass down the western seaboard of continental Europe turn up on the east side of Britain, including some rarities (Chapter 5).

Arrivals of vagrants from more distant lands are likewise correlated with particular weather systems (Elkins, 2005). The appearance of Siberian birds in western Europe is associated with the occurrence of prolonged fine anticyclonic weather with easterly winds over the western half of Eurasia in September. These conditions have been much more prevalent in some years than in others, bringing unusually large numbers of far eastern vagrants in the autumns of 1975, 1982, 1992 and 2003 (Elkins, 2005). They included numbers of Pallas's Warblers and Yellow-browed Warblers, as well as occasional Radde's Warblers and Lanceolated Warblers, among others.

In contrast, the appearance of North American land birds in Iceland and western Europe follows prolonged westerly gales at appropriate latitudes, with unusually large numbers recorded in 1976, 1982, 1985, 1995, 2000 and 2005 (Elkins, 2008). These transatlantic vagrants include passerines, shorebirds and waterfowl, as well as gulls and terns, with more than 60 species in total having been recorded, and up to 42 species in one year (1995). The most frequent passerines include the Gray-cheeked Thrush, Blackpoll Warbler and Red-eyed Vireo, while the most frequent shorebirds are the Pectoral Sandpiper and White-rumped Sandpiper. Reflecting their normal migration periods, shorebirds appear in northwest Europe over a longer period (mainly July–November) than passerines (mainly late September–October). Westerly jet-stream winds high over the Atlantic can reach speeds of 250 km per hour, potentially bringing migrants over 5,000 km from Canada to Britain in less than 24 hours, but it is unlikely that many birds fly high enough to take advantage of them.

Smaller numbers of North American species turn up in western Europe in spring, when the main northerly migration occurs over land, rather than over the Atlantic as in autumn (winds being generally favourable over the Atlantic in autumn but not in spring).

This raises the question (discussed later) of whether the spring arrivals result from other types of movements. Some may have crossed in autumn and then overwintered in the Old World, passing through western Europe on their return journey (Nisbet, 1959b; Elkins, 2008).

The so-called North Atlantic Oscillation (NAO) is a measure of the atmospheric circulation over the North Atlantic. A positive NAO index represents a vigorous circulation in which westerly winds are frequent and strong, while a negative index indicates fewer and weaker westerlies. The number of North American vagrants recorded in Britain each year between 1987 and 2006 was broadly correlated with the NAO index, with most migrants found in years with a strong positive index ($r^2 = 0.33$, $P > 0.01$) (Elkins, 2008).

In some parts of the world, hurricanes can blow both land birds and seabirds far from their usual routes. Europe is not affected directly by hurricanes in the way that North America and Southeast Asia are, but tropical storms can influence transatlantic vagrancy. Many of the hurricanes that strike the southeastern USA veer northwards over land and then, greatly weakened, leave the continent further north travelling eastward over the Atlantic. As they meet cold air, they gather strength again, producing eastward-moving depressions with strong winds that could carry vagrants across the ocean to northwest Europe. A series of hurricanes in the Caribbean in autumn 2005 resulted in strong eastward-flowing winds further south than usual, conveying exceptional numbers of North American birds to the Azores. No fewer than 17 land-bird species and several wetland species appeared, including 41 White-rumped Sandpipers and 30 Chimney Swifts, as well as the first White-eyed Vireos recorded on the east side of the Atlantic (Hering & Alfrey, 2006). At the same time, other North American birds turned up in Iberia and the Canary Islands.

It is not just land birds that are susceptible to the effects of wind over water. Strong onshore gales offer the best prospects for bringing normally pelagic seabirds within view of coastal headlands.

Counts exceeding 10,000 birds per hour have been achieved at some sites, including rarities. In addition, small seabirds are also frequently blown far off course, sometimes for hundreds of kilometres, while some normally pelagic species, such as the Sabine's Gull and Grey Phalarope, sometimes appear at inland lakes (Elkins, 2005). Other small seabird species are occasionally found as 'wrecks' of dead and exhausted birds over land, the Little Auk being a frequent victim in Europe (Chapter 23).

Widespread mist over the sea can also cause disorientation, with migrants flying in various directions, as shown by radar (Alerstam, 1990b). If the mist is sufficiently widespread, birds could end up tens or even hundreds of kilometres from their normal routes, coming down and settling on the first land they encounter, to be recorded as vagrants.

OVERSHOOTING

Some birds follow their usual migration direction but travel too far, turning up at places beyond their regular range. In Europe, overshooting is most evident during spring migration, in stable anticyclonic conditions when temperatures are higher than usual, and winds are from the south (Elkins, 2005). In these conditions, birds may occur hundreds of kilometres beyond their normal breeding areas, as seen in the British Isles by the periodic appearance in spring of species that breed much further south or southeast, including the Alpine Swift, Woodchat Shrike, Eurasian Hoopoe, Rock Thrush, Subalpine Warbler, Black-headed Bunting and others. While migrating in the proper direction, overshooting birds may simply fail to 'switch off' their migration drive at the appropriate time, and continue travelling. Alternatively, they may switch off at an appropriate time, but under the influence of a strong tailwind, they travel too far. Spring overshoots sometimes occur relatively early in the year, at about the time they would have been expected in their normal breeding areas further south. Such

birds are usually male, and when closely examined, they are almost always found to be in their first year of life.

Some observers have suggested that overshooting could underlie the spring occurrence of some North American species in Europe. Most of the eastern North American coastline runs southwest–northeast. If one draws a line on a globe up the eastern seaboard from South Carolina to Newfoundland, and then extends that line, it reaches the British Isles. Hence, a bird heading northeast up the eastern seaboard in spring and overshooting into the North Atlantic could (on a great circle route) reach northwest Europe, providing it had sufficient body fuel and favourable winds. Correspondingly, nearly all the North American passerine vagrants that appear in the British Isles in spring breed well to the northeast in Canada. This phenomenon could thus account for the numerous spring records in Britain of North American sparrows, such as the White-throated Sparrow and Dark-eyed Junco, together with the Brown-headed Cowbird, Cape May Warbler and Cedar Waxwing, all appearing as though they were long-distance spring overshoots. The over-water journey is still more than 3,000 km, however, which is probably beyond the capability of most passerines, except under strong tailwinds. These conditions are relatively rare in spring, and many of the individuals that turn up in the British Isles at this season may have travelled on ships for at least part of their journey (Elkins, 2008).

In some bird species, juveniles on their first autumn journey show much greater spread in departure directions than adults of their species. Such an age difference has been reported from Swedish or Finnish ring recoveries for Spotted Flycatchers (angular spread 8–18° for adults, 13–23° for juveniles), Willow Warblers (9° for adults, 21° for juveniles), Honey Buzzards (8° for adults, 12° for juveniles) and others (Alerstam, 1990b). This difference between adults and juveniles is also obvious among birds tested in orientation cages, with juveniles again showing greater directional spread than adults (De Sante, 1973; Able, 1977; Sandberg *et al.,* 1991). If juveniles were to continue migrating on their more extreme directions, many

would end up well outside their usual migration route (Thorup *et al.,* 2007). However, it is not clear whether the juveniles that take an extreme direction suffer greater mortality and are then less represented in the adult samples, or whether they correct themselves further along the route, learn from their mistakes and perform better in later life. In any case, one plausible hypothesis is that some autumn vagrancy is simply a consequence of the wide directional spread normally existing within some bird populations and evident chiefly in juveniles. Such directional errors have been termed 'misorientation' (ability to follow a consistent direction, but not the most appropriate one), as opposed to 'disorientation' (inability to follow any consistent direction) (De Sante, 1983a). While both groups could in theory turn up in any direction from the usual range, in practice, 'misoriented' individuals seem to concentrate in specific directions, showing the two distinct types of pattern described below.

MIRROR-IMAGE MIGRATION

At a broad geographical scale, juveniles of many species appear annually in localities that imply they have followed a direction that is a mirror image of the correct direction. Mirror-image migration supposedly occurs when a departing bird takes a correct bearing with respect to the north–south axis, but chooses the wrong east–west (right–left) side of that axis. Instead of migrating southeast, say, the bird migrates southwest, with distance, timing and other aspects of the migration remaining unchanged. However, it is not obvious from normal orientation behaviour how this type of error could arise.

Supposed mirror-image migration has been studied mainly in North American warblers, about 30 species of which normally migrate towards the southeast, but have been recorded in autumn in California. Drift on westerly winds could not account for this pattern, for species would then be expected to occur in numbers proportional to their overall abundance, and over a much wider

span of latitude than is actually the case. Instead, such records are more confined geographically, and are more consistent with the hypothesis of mirror-image navigation (De Sante, 1973, 1983a, 1983b; Patten & Marantz, 1996). Moreover, vagrant Blackpoll Warblers *Dendroica striata* that were trapped and tested in orientation cages showed both the correct migratory direction and the mirror image of that direction (De Sante, 1973). The occurrence in western Europe in autumn of some central Eurasian species could also be attributed to mirror-image mis orientation, particularly those that normally migrate southeast or east then south to reach wintering areas in Southeast Asia. Possible examples include the Arctic Warbler, Greenish Warbler and Pechora Pipit. Other examples include vagrants of numerous species that breed in far eastern Siberia and normally migrate south-southwest to Southeast Asia, but occasionally follow a mirror-image route south-southeast down the west coast of North America. On this last route, the Eurasian Wigeon and Tufted Duck are regular, while many others are occasional (Robertson, 1980). Re-examination of off-route migration records elsewhere may yield other examples of possible mirror-image migration. In theory, mirror-image errors could occur among birds leaving their wintering areas, as well as in those leaving their breeding areas, and some spring vagrancy has also been attributed to this phenomenon (McClaren, 1981).

REVERSE-DIRECTION MIGRATION

If reverse-direction migration were a real phenomenon, rather than an untested hypothesis, it would influence which species were expected to arrive in particular areas by this mechanism. The vagrancy shadows of other species would fall elsewhere. Take as examples the Red-breasted Flycatcher and Collared Flycatcher, which have similar breeding distributions in Europe (although the former also extends further east). In autumn, most Red-breasted Flycatchers head southeast for southern Asia, whereas Collared Flycatchers head south for wintering areas in East Africa. The much

more frequent autumn occurrence of Red-breasted Flycatchers in northwest Europe (more than 2,000 records in Britain up to 1995) compared with Collared Flycatchers (19 records up to 1995) has been attributed to the reverse-direction migration of the former (Cottridge & Vinicombe, 1996). This difference in occurrence between these species is greater than expected from the respective sizes of their geographical ranges (and hence population sizes). And because almost all recorded individuals were juveniles in their first autumn, they must have arrived recently and not stayed over from some earlier time, which eliminates spring overshooting as the cause of their occurrence.

Similarly, birds that in autumn would normally migrate from northeastern North America southwestward across the continent to Central America could on reverse migration end up in northwest Europe. Examples of autumn species that might have arrived in this way in Britain include the Tennessee Warbler, Hooded Warbler and Sandhill Crane (Cottridge & Vinicombe, 1996). These species do not normally migrate over the western Atlantic in autumn, as do most of the North American autumn vagrants to Europe.

Another puzzle is that species migrating in an east–west direction seem more likely to reverse their migration than those migrating north–south or northeast–southwest (Thorup, 2004). This difference maybe related to the availability of orientation cues on different migratory axes, or to birds using mainly different cues on east–west and north–south axes. Furthermore, the very long distances covered by some displaced birds (up to twice the normal length of journey) suggest some fault in the birds' internal clock mechanism (Thorup, 2004). It may be the same faulty timing mechanism that leads them to take a spring direction in autumn. In any case, reverse-direction migration is presumably not the only means by which Siberian vagrants reach northwest Europe in autumn. If it were, some regular Siberian vagrants would never get here.

In considering reverse migration, remember that many birds on normal migration turn back temporarily if they reach unsuitable conditions for onward migration (Chapter 4). Others may get caught

up in strong winds from which they cannot escape. Such an event happened in eastern North America during 2005 when Hurricane Wilma passed northward in the autumn migration season, picking up many birds already on migration further south and depositing them in eastern Canada. Thousands of passerines and swifts were involved, many of which subsequently died (Dinsmore, 2006).

The proposed reality of reverse or mirror-image misorientation stems from observations that, in certain situations, specific large-angle misorientations seem more common than small or intermediate deviations from the normal migration course. We would also have to assume that specific large-angle misorientations occur much more commonly in some species than in others. Otherwise, it would be hard to explain why some species that breed far away turn up as frequently as they do. As yet, however, mirror-image and reverse-direction migration remain as unproven hypotheses of bird vagrancy. They nevertheless attract strongly held views on both sides.

NEW ROUTES AND RANGE EXPANSION

To what extent could bird vagrancy account for range expansion? The fact that regular migrants turn up in unexpected places much more often than non-migrants emphasises the connection between migration and vagrancy, as does the concentration of vagrant records in the normal migration seasons. Although migrants travel longer distances than non-migrants, and are often blown off course, they are not necessarily more likely to stay and establish themselves in new areas. When migrants arrive in a new area, they are usually in a migratory state, programmed to reorientate and continue their journeys. Ring recoveries confirm that many soon move on again (Table C, overleaf).

Nevertheless, vagrancy may occasionally lead to the colonisation of new areas. Many of the species now found on oceanic islands are likely to have descended from ancestors that were long ago blown off course by winds. Such a process supposedly led to the

colonisation of the New World by Old World Cattle Egrets (Maddock & Geering, 1994). It also led to the establishment of many species introduced to New Zealand on various oceanic islands to the south, involving water-crossings of up to 1,200 km (Williams, 1953). Other birds probably reach remote areas and breed there for a time, but without establishing a lasting population, such as the Fieldfare in Greenland (Salomonsen, 1951). Imagine the odds against two Spotted Sandpipers from North America reaching the same Scottish locality and nesting thousands of kilometres from their normal range. Yet it happened on at least one occasion (Wilson, 1976). Other vagrants to Britain have established territories, and occasionally paired up with local species and produced hybrid offspring, including the Pied-billed Grebe (with Little Grebe), Blue-winged Teal (with Northern Shoveler), Lesser Crested Tern (with Sandwich Tern) and North American Black Duck (with Mallard) (Newton, 2008).

In addition, some vagrants, having once wintered in an area, return there year after year, as in normal homing behaviour, with examples from Britain involving a King Eider (1986–91), Whistling Swan (1985–6), Wallcreeper (1976–7) and Yellow-browed Warbler (two examples: 1994–6 in Hampshire, 2000–1 in Cornwall). In addition, one North American Ring-billed Gull turned up in 13 successive winters in Stromness, Orkney, Scotland (Fraser & Rogers, 2002). Individuals of other species returned repeatedly in spring–summer, including an Ancient Murrelet, which normally occurs in the North Pacific but was seen off Lundy Island in three successive summers; and Black-browed Albatrosses from the Southern Ocean, which set up territories and displayed in Northern Gannet colonies over periods of 3 years (Bass Rock 1967–9), 3 years (Sula Sgeir, 2005–7), 23 years (Hermaness, 1972–95) and 35 years (Faeroes, 1860–94) respectively, all to no avail (a single long-lived albatross could have accounted for all the 20th-century records if it twice shifted colonies). Birds of other species were present more or less continuously over periods of years, such as two Steller's Eiders, one of which was repeatedly seen off South Uist between 1972 and

1984, while another made frequent appearances off Papa Westray in Orkney during the years 1974–84. These various birds were not ringed, but their individual identification was assumed because they occupied the same places in successive years.

TABLE C. Recoveries of vagrant birds ringed in Britain that suggest reorientation towards the regular range. (From Wernham et al., 2002)

Species	*Usual migration route*	*Subsequent recovery of vagrant*
Ring-necked Duck *Aythya collaris*	Breeds across Canada and the northern US and winters in southern States and Central America.	An adult male ringed at Slimbridge, Gloucestershire, 1 March 1977, was shot at Isertoq, southeast Greenland, in May of the same year, suggesting that it was heading to the regular breeding range.
Booted Warbler *Hippolais caligata*	Breeds in central Eurasia, and winters in India; nearest population to Britain breeds in Russia.	A juvenile ringed at Spurn, Yorkshire, on 16 September 1993 was recaptured at Wetheren, Belgium, on 5 October of the same year, suggesting that it had reorientated eastwards.
Penduline Tit *Remiz pendulinus*	Resident in much of continental Europe; nearest population to Britain breeds in Denmark.	An adult female ringed at Icklesham, Sussex, in October 1988 was recaptured at Kuismaren, Sweden, in May 1989, suggesting that it had reoriented towards the usual breeding range.
Rustic Bunting *Emberiza rustica*	Breeds from Sweden across northern Eurasia and winters in Southeast Asia; nearest population to Britain breeds at 60°N in Sweden.	A female ringed on Fair Isle, present there 12–19 June 1963, was recovered on the Greek island of Chios four months later, in October of the same year, suggesting that it had reoriented eastwards.
Red-breasted Flycatcher *Ficedula parva*	Breeds from eastern Europe across Eurasia, and winters in India and Southeast Asia.	An adult male ringed on Shetland on 6 September 1997 was trapped again in Norway 13 days later, suggesting that it had reoriented eastwards.
Barred Warbler *Sylvia nisoria*	Breeds from central Europe east to western Siberia and winters in East Africa.	A bird ringed in September 1978 on Fair Isle was recovered in February 1979 in Yugoslavia, indicating that it had reorientated eastward. Similarly, another ringed in Sweden on 26 August 1976 was recovered in Syria on 16 September 1976.

Other recoveries imply fidelity to off-route stopover sites by vagrants. An adult male Bluethroat was ringed on 17 May 1958 in Devon, southwest England, more than 300 km west of the usual migration route, and re-trapped at the same site on 5 May 1963.

Another first-winter male Bluethroat ringed at the same site on 21 September 1966 was re-trapped there on 14 September 1968. This suggests that, once having taken a particular migration route, at least some individuals repeat it in successive years, even though it may involve a detour.

It is, of course, almost impossible to distinguish a true vagrant (a bird well off the normal migration route) from a regular migrant on a route used by only a small number of individuals. The numbers of certain Siberian species in western Europe every autumn raises the question of whether their occurrence constitutes vagrancy or regular migration (Gilroy & Lees, 2003). If vagrancy is regarded as an accident, caused by adverse weather or faulty navigation, then it seems unlikely that the hundreds of Yellow-browed Warblers that have been found annually in northwest Europe in recent decades can be genuine vagrants. The annual appearance of both Yellow-browed and Pallas's Warblers is now as predictable as the occurrence of other regular migrants. These and other species, hitherto treated as accidental vagrants, might in fact be rare passage migrants en route to unknown wintering areas, whether long-standing or recently established. Both species seem to arrive slightly earlier in northern Britain than in the southwest, and occasional Yellow-browed Warblers have now been identified in West Africa in winter.

Genetically influenced deviations from the normal migration direction occasionally lead to the establishment of new migration routes and wintering areas, as shown by the Blackcaps which now migrate from central Europe to winter in Britain (Chapter 15). Such developments may also be occurring in Lesser Black-backed Gulls, which are wintering in increasing numbers on the east coast of North America, among Eurasian Wigeon and others on the west coast of North America, and among Ring-billed Gulls now wintering annually in very small numbers in western Europe (with at least five supporting ring recoveries).

Is it possible, then, that many of the vagrants which turn up in particular localities in increasing numbers are in the process of

establishing new migration routes and wintering areas, and that birds with appropriate deviant directions are gradually increasing in the population? This explanation could apply to Pallas's and Yellow-browed Warblers, which may once have reached western Europe through inherent 'flaws' in their directional preferences, but which were then favoured by selection and are now increasing in abundance. However, the alternative possibility cannot be excluded, namely that some individuals always migrated through western Europe, formerly in such small numbers that they passed unnoticed, but have now become more evident because of a general increase in their populations and in the numbers of bird-watchers. Pallas's Warbler is also extending its breeding range westwards, which could lead to more individuals reaching the British Isles.

In the case of small or inconspicuous species in little-known areas, we can seldom be certain that they have not always been there, although their numbers may have increased in recent years. The presence of an unknown population of Swinhoe's Storm-petrel in the northeast Atlantic may account for the appearance of individuals in northeast England. Several have now been caught at Tynemouth and identified from their DNA, including one individual in four successive years. Others have turned up elsewhere in the northeast Atlantic, and one caught on the Portuguese coast had a vascularised brood patch, but the nearest known nesting colonies occur on the other side of the Eurasian landmass, off Korea and Japan (Flood, 2009). Even vagrants of large species maybe difficult to identify if they resemble local birds. For example, another species identified from its DNA is the Southern (Brown) Skua, two individuals of which were picked up on different coasts of southern Britain during the winter of 2001/2 (Votier *et al.,* 2004). Different forms of this species breed on subantarctic islands and are hard to distinguish from the northern hemisphere Great Skua. They are probably regular visitors to the North Atlantic in the non-breeding season, but these were the first to be identified from the British Isles.

HUMAN-ASSISTED VAGRANCY

Not all apparent vagrants may have travelled unaided, for some types of birds can ride on ships. One documented incident involved the *Mauritania* as it began its seven-day transatlantic journey from New York to Southampton (England) on 7 October 1962 (Durand, 1963). On the morning of the second day, when the ship was 400–500 km out from New York and under heavily overcast skies, more than 130 birds of at least 34 species (mainly passerines but also woodpeckers) appeared on deck. The crew provided fruit and other types of food, which some of the birds ate. As the days passed, these birds gradually disappeared, and others arrived, but by 12 October, nine birds were still present as the ship passed southwest Ireland. At this point, a Yellow-shafted Flicker flew ashore. When the ship docked at Southampton on 15 October, four birds were still present, including two White-throated Sparrows, one Song Sparrow and a Slate-coloured Junco. The next day, a White-throated Sparrow was seen in a nearby park. The author mentioned similar incidents from other journeys, with birds spending varying amounts of time onboard.

TABLE D. Some transatlantic ring recoveries of vagrants between North America and the British Isles (excluding pelagic species and regular transatlantic migrants).

Species	*Ringing site*	*Recovery site*
Peregrine Falcon *Falco peregrinus*	New Brunswick, 18 July 1986	England, 24 December 1986
Caspian Tern *Sterna caspia*	Michigan, 14 July 1927	England, August 1939
Ring-billed Gull *Larus delawarensis*	New York, 21 June 1980	Ireland, 28 December 1981
Black-headed Gull *Larus ridibundus*	Finland, June 1996	Texas, January & November 2000
Northern Pintail *Anas acuta*	Labrador, 19 August 1948	England, 15 September 1948
	Labrador, 7 September 1951	England, 25 September 1951
	Prince Edward Is., 18 August 1969	Ireland, 29 January 1974
Blue-winged Teal *Anas discors*	New Brunswick, 26 July 1971	England, 10 October 1971
	Newfoundland, 11 September 1983	Ireland, 15 January 1984
	Quebec, 6 August 1982	Scotland, September 1982
American Wigeon *Anas americana*	New Brunswick, 5 August 1966	Scotland, 7 October 1966
	New Brunswick, 29 August 1968	Ireland, 12 October 1968
	Prince Edward Is., 30 August 1977	Ireland, 8 October 1977
	New Brunswick, 13 August 1986	Scotland, 21 September 1986
Green-winged Teal *Anas carolinensis*	New Brunswick, 22 August 1970	England, 2 January 1971
	Newfoundland, 22 September 1985	Ireland, 31 October 1985
Ring-necked Duck *Aythya collaris*	New Brunswick, 7 September 1967	Wales, 26 December 1967
Lapwing *Vanellus vanellus*	Cumbria, England, May 1926	Newfoundland, December 1927

EVIDENCE FROM RINGING

Some vagrants that turned up in the British Isles had been ringed, confirming their place of origin. In particular, there are now more than 30 records of ringed North American vagrants in Europe, with some in the British Isles (Table D). Such records mostly involve gulls and waterfowl, which typically have high recovery rates. In addition, at least one individual was known to return successfully to

the breeding range, namely a Ring-billed Gull ringed in Norway and recovered in Canada (Cottridge & Vinicombe, 1996). In the other direction, a Black-headed Gull was ringed as a fledgling in June 1996 in Finland, and subsequently seen in Fort Worth, Texas, in January 2000. Its metal ring was read through a telescope. The next winter, the bird was again back in Fort Worth, but it is not known where it spent the summer. These records show conclusively, for anyone who may have doubted it, that transatlantic vagrancy is a real and natural phenomenon.

CONCLUDING REMARKS

Different species are likely to reach the British Isles in different ways, and on the basis of different mechanisms, although some species may arrive in more than one way. Off-route displacement by inclement weather is usually little more than a temporary phenomenon for which birds are normally able to correct at a later date. Other types of vagrancy probably result from deliberate behaviour on the part of the birds which act on the basis of flawed instructions—some genetic or other change in the orientation or timekeeping mechanism which leads them to migrate in an atypical direction or for an unusually long time. In theory, more than one kind of genetically based flaw could occur simultaneously in the same population, with some individuals showing behaviour consistent with mirror-image migration, perhaps, and others with reverse-direction migration. It is seldom possible to say which theoretical mechanism might have brought particular vagrants to a given site. Nevertheless, the testing of directional preferences of vagrants in orientation cages has given clues to how those individuals might have arrived, as has the location itself, and more work of this type is needed. Some of the proposed mechanisms are no more than working hypotheses: uneven observer coverage throws doubt on some apparent examples of mirror-image and reverse-direction migration, so that neither mechanism can be considered as convincingly established.

The preponderance of juveniles among vagrants would be expected for several reasons, including theirinexperience and their greater dependence on compass orientation as opposed to the bi-coordinate navigation (= homing behaviour) used by adults (Chapter 12). Also, inherent errors in orientation and migratory timing would be expected more frequently in juveniles, because at that age, deviants from the norm would not have been exposed to the selective mortality provided by their first migration. For the most part, only successful individuals, behaving normally, are likely to reach adulthood, thus partly accounting for the preponderance of juveniles among vagrants.

Largely because of their rarity, vagrants from Siberia and North America excite particular interest among British and Irish bird-watchers. Not only do these two groups of migrants arrive from different directions, but the circumstances of their journeys are quite different. The Siberian birds originate in an area of fairly inactive atmospheric conditions, with prolonged anticyclones which in some years extend westward into Europe. On both their normal migration to Southeast Asia, and on their journeys to western Europe, they migrate primarily over land, and are easily able to rest and feed en route. They typically arrive in Europe some weeks after their normal departure dates from Siberia, having apparently undertaken a fairly leisurely journey. It seems inconceivable that they undertake this journey as a result of extreme weather over the whole route, and almost certainly do so as a result of ‘internal instructions’, flawed or otherwise. In contrast, many of the North American vagrants are species that naturally undertake a long, fuel-demanding over-water flight southward over the western Atlantic through a region of vigorous atmospheric conditions. They apparently become caught up in strong westerly winds, and get carried quickly and involuntarily far from their normal route. Their journey is unlikely to take more than a few days, and in strong winds may occasionally be accomplished in less than 24 hours. Unless they spend time on a ship, their flight is non-stop, but if pushed beyond the limit of their fuel reserves, many are likely to die

en route. Clearly, there is still much to be learned about bird vagrancy, and we in the British Isles are ideally situated to study it in more depth.

† Records of rare birds are vetted by the British Birds Rarities Committee established in 1959 in association with the journal British *Birds;* and any species new to the British Isles are also considered by the Records Committee of the British Ornithologists' Union, which is responsible for maintaining the 'British List'—the official record of all species seen here. In recent years, Irish records of rare birds have been considered instead by the Irish Rare Birds Committee, while the Irish List is maintained by Birdwatch Ireland.

CHAPTER 15

Evolution of Migration

MIGRATION MIGHT BE EXPECTED to occur wherever individuals survive or breed better by moving seasonally between different areas rather than staying in the same place year-round (Lack, 1954). The usual reason why breeding areas become unsuitable during part of the year is lack of food. Such food shortages occur for many birds because plant growth stops, and many kinds of invertebrates die, hibernate or become inaccessible under snow and ice. At high latitudes, daylengths also shorten so much in winter that many diurnal birds would have too little time to get enough food, even if it were available. Hence, the purpose of the autumn exodus from high latitudes is fairly obvious.

The reason why birds leave their wintering areas to return in spring is less obvious, because many wintering areas seem capable of supporting them during the rest of the year. But if no birds migrated to higher latitudes in spring, a large seasonal surplus of food would go largely unexploited. Under these circumstances, any individuals that moved to higher latitudes, with increasing food and long days, might raise more young than if they stayed at lower latitudes and competed with the resident birds. So whereas the advantage of autumn migration can be seen as improved winter survival, dependent on more available food supplies in winter quarters, the main advantage of spring migration can be seen as improved breeding success, dependent on better food supplies in summer quarters. Compared to survival, reproduction also has more stringent requirements in terms of specific food needs and predation avoidance.

While seasonal change in food supply is important for bird migration, this does not rule out the influence of other factors, such as reduced predation, parasitism or competition (for food or other resources). All these pressures may diminish with increasing latitude because of the general latitudinal decline in the total numbers of animals (species and individuals), whether these animals act as predators, parasites or competitors. At different times, all these factors have been suggested as contributing to the evolution of migration but on scant evidence, and it seems that none of them acquires the same importance as food supplies.

It would be misleading to divide bird species neatly into migratory and sedentary. As indicated already, both types of behaviour can be found in a single species or even in a single population. In the northern hemisphere, many widely distributed bird species are completely migratory in the north of their breeding range, completely resident in the south and partially migratory in between, with the proportions of birds leaving particular localities increasing northeastwards. Where populations are entirely migratory or entirely resident, their behaviour is usually regarded as obligatory and under firm genetic control, either migratory or resident, as the case maybe (Chapter 10). In contrast, partial migration can apparently arise in two different ways. In one way, ‘obligatory migratory’ and ‘obligatory resident’ individuals occur intermixed in the same area, and particular individuals exhibit the same behaviour throughout their lives. This situation is presumed to occur where migratory behaviour is genetically controlled, and where there is no overwhelming advantage in staying or migrating. In some years, perhaps, the migrants do best, while in others it is the residents who fare better, so that in the long term both types persist in the same breeding area (Biebach, 1983). However, the proportions of the two types may vary between areas depending on the severity of winter conditions, with more migrants in the more northern populations (Box B).

BOX B. The adjustment of obligate partial migration to local conditions

In genetically controlled partial migration, the advantage of each type of behaviour (residency or migrancy) depends partly on what other individuals do. If, over a period of years, more and more birds became resident (say), the time would come when far more birds stayed locally than the winter food supply would support. Competition would then increase, leading to greater mortality in the resident sector, eventually tipping the balance in favour of migration. In this way, changes in the relative advantages of the two types of behaviour could ensure that the ratio of residents to migrants in any one population was kept roughly in line with local winter conditions. The relative advantages of resident versus migrant may, of course, change over the years if environmental conditions altered, such as winter temperatures or winter food supplies in breeding areas (see Chapter 16 for examples). They may also differ between areas, giving rise to the situation in which, in many obligate migrants, greater proportions of individuals migrate from higher than lower latitudes. Obligate partial migration could thus be viewed as an ‘evolutionarily stable strategy’, because in the long term, with the appropriate ratio of migrants and residents in the local breeding population, the pay-offs for both genotypes (in terms of lifetime reproductive rates) are balanced, and in the prevailing conditions no one type can completely replace the other.

The situation in facultative migrants is different, as explained in the main text.

In the second way in which partial migration is thought to occur, the behaviour of each individual is optional (facultative), enabling it to behave differently in different circumstances, staying in the breeding area in years when conditions are favourable there, and leaving in other years (Chapter 10). This latter system can result in big year-to-year changes in the proportions of individuals that migrate from particular breeding areas, and the same individuals may behave differently in different years, depending on conditions. Examples include the Siskin and other irruptive migrants, in which, over a wide span of latitude, individuals can stay within the breeding range in winters when food is plentiful, but migrate south in other years.

ADAPTATIONS FOR MIGRATION

Although migration requires adaptations in morphology, physiology and behaviour, it is not hard to see how it might have evolved, because transitional or intermediate stages still occur. For instance, some bird species do not migrate at all, others travel only short distances, and yet others cover long distances. The full range of variation can be found among different populations of the same species, or even among individuals in the same population, as mentioned above. Further, the main adaptations needed for long-distance migration, such as seasonal fat reserves, timing mechanisms and orientation skills, are all found in less-developed form in non-migratory birds, as well as in other animals. These features are all necessary for effective migration to develop, but may have arisen independently in contexts other than migration.

Migration differs from other long-distance movements in that it involves a two-way journey in more or less fixed directions. An ability to perform a return movement is necessary before any

migration pattern (as just defined) can develop, but all birds have this ability over shorter distances, being able to return repeatedly to their nests and other places important to them. In resident populations, such movements are short and localised, but they provide a basis from which the longer return movements of migration might evolve. However, while short-distance moves could be performed entirely on the basis of learned landscape features as a bird gets to know its local area, return from long distances requires something more: namely, an ability to orientate by global signposts, as provided by celestial and magnetic cues. This facility is almost certainly inherent to some degree in all birds, because it is present in lower animals, including the reptiles from which birds evolved.

Similarly, it is not hard to imagine how, given a sense of location, directional preferences could evolve from random dispersal movements. In seasonal environments, any birds that move long distances after breeding are more likely to meet favourable conditions in some directions (towards lower latitudes) than in others. If they then survive better than other birds, and their directions are genetically influenced, directional preferences could over the generations become fixed by natural selection. Distances could also be fixed in this way, the birds from each population wintering wherever they can reach and survive best, taking account of the mortality costs of getting there and back. Only in populations (like some nomadic ones) in which, on balance, individuals are as likely to find food in one direction as in any other, is no directional preference likely to become fixed by natural selection.

All birds have timing mechanisms which ensure that breeding and moult occur at appropriate times of year, and in migrants, such mechanisms also promote migration at appropriate dates. Their annual cycles may be modified to some extent by altering the timing of breeding or moult to accommodate migration (Chapter 9). Similarly, many bird species accumulate body reserves in preparation for breeding or winter food shortages. In accumulating migratory fat, birds are again merely modifying a pre-existing

facility for a different purpose, rather than developing a completely new adaptation.

But one of the most remarkable structural differences found between resident and migratory birds concerns the brain. Compared with resident birds, migratory ones have a more highly developed hippocampus, the part of the brain associated with spatial memory. This difference is again evident between resident and migratory populations of the same species (Cristol *et al.,* 2003), and has obvious value for migrants, which have to find their way over long journeys.

For the most part, then, migratory birds do not possess any fundamentally different adaptations from residents, whether behavioural, physiological, morphological or other features. Migration simply involves the further development or modification of features already present in non-migratory populations. All migratory traits—including timing, direction and distance—are amenable to the action of natural selection, either independently or in association with other aspects. Moreover, all can be modified in an incremental manner, in which each small appropriate change brings benefits. This is a firm basis from which the different movement patterns of birds, and their associated adaptations, can be moulded by natural selection. Bird migration (like other types of bird movements) is made up of several components, each of which can be independently modified by natural selection to give the variety of movement patterns we see today.

THE GENETIC CONTROL OF BIRD MIGRATION

In considering the genetic control of migration, the main questions concern how a bird comes to migrate rather than stay in the same area year-round, to leave and return to its breeding area at particular dates rather than others, to fly in particular directions rather than others, and to stop migrating once it has reached a suitable wintering area it might never have seen before.

For many years, ideas on the role of natural selection in shaping bird migration patterns were based on little more than surmise. One indication of genetic control was the year-to-year consistency in all aspects of the migratory behaviour of particular populations, including the timing, directions and distances travelled. Such constancy through time suggested strongly that migratory behaviour had an inherited component.

In recent years, the role of genetic factors in the control of migration has been demonstrated unequivocally, mainly in a series of remarkable experiments by Peter Berthold and his colleagues, who found that Blackcaps and other songbirds could be raised in large numbers in captivity, enabling their migratory behaviour to be examined under controlled conditions (Berthold, 1995, 1999). In the wild, Blackcaps vary from completely migratory to completely sedentary in different parts of the range. The various migratory populations also differ in their migration dates and in the directions and distances flown. Most of these traits can be measured in captive birds by assessing the timings and amounts of migratory restlessness, a specific behaviour involving fluttering and wing-whirring which appears in caged birds for parts of each day or night at migration times. Directional preferences of individuals can be assessed by placing them in orientation cages, and checking their preferred headings. Both restlessness and headings can be recorded automatically, as described in Chapter 2.

A crucial finding was that when birds from different populations were crossbred, the offspring showed migration features that were intermediate between those of their parents. Moreover, if individuals with particular traits were selected and bred together, these traits became enhanced in future generations. This held for the timing and duration of migratory restlessness, and for directional preferences. The overriding implication was that all these aspects of migration were under genetic control; and because they could be changed in captive birds by artificial selection, they could also be changed in wild birds by natural selection, depending on the survival and reproductive benefits of different behaviours in the

local environment. The details of several key experiments are summarised below.

When Blackcaps with high levels of migratory restlessness were paired together, the trait persisted or increased in the offspring. Similarly, when individuals with low levels of restlessness were paired together, the trait persisted or decreased in the offspring. These findings confirmed that the amount of migratory restlessness in Blackcaps was to a large extent genetically pre-programmed (Berthold & Querner, 1981; Biebach, 1983). Starting with a partially migratory population, high or low levels of migratory restlessness (assumed to reflect migratoriness or sedentariness) could be selected to apparent uniformity within as few as three to six generations. After three generations of selecting and breeding from the least migratory individuals, sedentary behaviour was fixed in the population, but selection of the most migratory individuals over five or six generations was needed to produce an almost exclusively migratory stock. These experiments thus revealed not only the high heritability of migratory behaviour, but also how rapidly migratory behaviour could be changed in response to strong selection pressure. In nature, selection is seldom likely to be that strong, so substantial changes in wild Blackcaps would be expected to take somewhat longer, perhaps decades or more.

Timing and distance

In various warbler species, the number of nights (or days) that individuals showed migratory restlessness in captivity was found to correlate with the actual distance travelled by their populations. The more nights of migratory restlessness were shown by captive individuals, the longer the actual migration shown by their wild counterparts. This finding supported the view that migration was controlled in part by an endogenous time programme inherent within the bird (Chapter 9). Again, the timing of migratory activity, whether early or late in the season, or long or short in duration, could be influenced by selective breeding in captivity. The cross-

breeding experiment with Blackcaps, mentioned above, confirmed that migratory activity was a population-specific inherited characteristic. Restlessness began earlier and continued longer in one parent population than in the other (Berthold & Querner, 1981), while the first-generation hybrids showed intermediate patterns of behaviour (Fig. 170B). In another experiment, Blackcaps from a migratory population (southern Germany) were selected for later onset of migratory activity (Pulido *et al.,* 2001). After only two generations of artificial selection in captivity, the mean onset of migratory activity was delayed by more than a week.

Experiments involving the cross-breeding of different species also proved instructive. In southern Germany, the Black Redstart is a short-distance migrant, travelling about 1,000 km to Mediterranean winter quarters, whereas the Common Redstart is a long-distance migrant, travelling up to 7,000 km to tropical Africa. The young of both species hatch at about the same time in May–June, but the Common Redstart moults earlier and more rapidly in preparation for its longer journey, beginning in August. In captivity, this was reflected in the earlier appearance and longer duration of migratory restlessness in the Common Redstart compared with the Black Redstart, which showed only a brief period of restlessness in October–November. The Common Redstarts also became much heavier, through fat deposition, and retained their fat for much longer than the Black Redstarts. The two species were therefore ideal for cross-breeding experiments to elucidate the genetic control of these processes. In the event, hybrids between the two proved to be intermediate in all respects between their parent species: in the timing and duration of migratory restlessness, the timing of moult and the degree of fat deposition (Berthold, 1999). Yet again, the strong implication was that all these aspects were under genetic control.

By measuring migratory restlessness in different populations of Blackcaps and their hybrids, it emerged that non-migrants, short-distance migrants and long-distance migrants were part of the same continuum of variation in a single trait, as reflected in restlessness.

The response ‘migrate or not migrate’ was caused by a threshold which divided individuals into those above and below. Thus, all birds without measurable migration in the wild displayed activity levels in captivity at the low end of a range of values, below the limit of expression or detection (Pulido *et al.,* 1996). Similarly, the division between short-distance and long-distance migrants was associated with variation in the numbers of nights on which they showed appropriate behaviour. These findings have profound implications for the evolution of migration, because they suggest that ecologically significant transitions between resident or migratory, and between short- and long-distance migration, could come about by selection on a single trait: the duration of migratory restlessness. However, selection on other traits would be needed to change other behaviour, such as migratory direction and fattening, as discussed later.

Captive individuals with a low level of restlessness did not change to a high level of restlessness in subsequent years, although a proportion of individuals that initially showed a high level subsequently showed a lower level (equivalent to wild birds becoming less migratory in later life) (Berthold, 1993). In the Blackcap and Dark-eyed Junco, migratory behaviour (= high restlessness) was also expressed in a greater proportion of females than males, raising the possibility of sex-linked inheritance (Terrill & Berthold, 1989; Holberton, 1993). On this basis, sex differences in migratory tendency could result partly from genetic influence.

These various findings support the view that inborn, temporal patterns of migratory activity serve as time programmes that, together with inherited migration directions, enable inexperienced, first-time migrants to ‘automatically’ cover the distance between their breeding areas and their specific wintering areas. They help to explain why young birds, with no previous knowledge of a wintering area, can find their own way to an appropriate locality without help from experienced adults, although other behavioural responses may also be involved (Chapter 12).

Migratory directions

The finding that captive migrants, during periods of migratory restlessness, flutter in their cages towards an appropriate bearing suggested that migratory directions were also under genetic control. This idea could be easily tested on Blackcaps, because in the mid-latitudes of Europe this species shows a migratory divide, with birds from the western part of the continent migrating mainly southwest in autumn and those from the eastern part southeast. Moreover, the eastern populations migrate around the eastern edge of the Mediterranean to East Africa, so they must change their course (by about 60° clockwise) from southeast to south-southwest about halfway through their autumn journey. Western populations migrate southwest and winter mainly in the western Mediterranean region, so they have a shorter journey and do not need to change direction greatly en route.

It is not sufficient that birds merely inherit a directional tendency that allows them to reach winter quarters. They must also be able to reverse this direction in spring in order to return to their breeding areas. Such reversal in direction was demonstrated in tests of hand-raised Blackcaps and Garden Warblers (Helbig *et al.,* 1989; Gwinner & Wiltschko, 1980). In addition, evidence for an endogenously programmed change in direction part way through the migration period was found in experiments with naive young Garden Warblers and Pied Flycatchers (Gwinner & Wiltschko, 1980; Beck & Wiltschko, 1988). In autumn, captive individuals of these species orientated southwest, changing some days later toward south or south-southeast, but in spring they headed toward the north. These findings fitted with the loop migration recorded in wild Garden Warblers and Pied Flycatchers from central Europe, which in autumn migrate southwest through Iberia into Africa, but in spring travel on a more easterly route, heading northward from Africa through Italy (Fig. 191).

Further indications for genetic control of migratory directions in various other species stem from the findings that: (1) inexperienced

migrants tested in orientation cages showed regular species-specific and population-specific directional preferences, including in some species seasonal changes in directional preferences matching the course of migration in wild birds; (2) displaced first-time migrants (White Storks: Schüz, 1949; Starlings: Perdeck, 1958) showed migratory directions parallel to those of their parental populations (Chapter 12); and (3) many young birds (notably Cuckoos) migrate from Eurasia and tropical Africa independently of their parents (Chapter 12). All these findings indicate that such migrants possess pre-programmed migratory directions or directional sequences, although they may, of course, deviate from their genetically prescribed course in response to local topography, weather and other conditions (Chapter 5). In some populations, ring recoveries of migrating birds lie in such a narrow and straight line between breeding and wintering areas that a simple clock-and-compass system might be sufficient to account for this pattern, providing that the birds are also able to stay on course by correcting for directional errors and wind drift (Mouritsen & Larsen, 1998; Thorup & Rabøl, 2001).

Morphological features

The cross-breeding experiments with exclusively migratory Blackcaps from southern Germany (with long wings and high body weights) and poorly migratory Blackcaps from the Canary Islands (with short wings and low body weights) demonstrated a genetic influence on both characteristics. Wing lengths and body weights were intermediate in the hybrids (Berthold & Querner, 1982). Similarly, in a later study, hybrids between migratory and non-migratory Blackcap populations, from Moscow and Madeira, showed intermediate values between parental populations in wing length, wing shape and wing area, while in other variables they resembled either parent population (Fiedler, 2005).

Natural variability

Another interesting finding confirmed in captive birds concerns the level of individual variation in migratory restlessness and directions apparent within some populations. Among Blackcaps that breed in the Mediterranean region, some individuals are resident, while others travel mainly short distances up to 1,300 km. Correspondingly, migratory restlessness among captive individuals from this region varied by 100-fold from bird to bird. In contrast, Blackcaps that breed in Germany are wholly migratory, travelling distances from about 700 to 4,500 km to reach winter quarters which extend from southern France to the Ivory Coast. The amount of migratory restlessness displayed by captive individuals from this region varied by about sixfold (between about 150 and 900 hours), and occurred over generally longer periods than in the Mediterranean birds. In addition, migratory directions shown by ring recoveries from the Mediterranean population ranged from west through south to east, spanning an angle of about 180°, while equivalent directions in the German population spanned only about 90° (Berthold, 1996). The important point was that, despite big differences between populations, not all individuals in the same populations displayed identical migratory behaviour. Evidently, substantial variation existed within populations on which natural selection could act if necessary. Even in strictly resident bird populations, some individuals have shown low levels of migratory restlessness in spring and autumn, including tropical Stonechats (Helm & Gwinner, 2006).

A natural change in the migration of Blackcaps

A new migration route of west-central European Blackcaps to winter quarters in Britain and Ireland (as opposed to the western Mediterranean area) was discovered from ring recoveries (Berthold, 1995). Prior to 1960, Blackcaps were rare during winter in Britain and Ireland, but from the late 1980s, thousands of individuals

wintered regularly (Lack, 1986b). Ringing gave no indication that these wintering birds had been raised in the British Isles or Scandinavia, but showed instead that they came from west-central Europe (mainly southern Germany and western Austria). Many Blackcaps ringed during the breeding season in these areas began to be recovered in a west to northwest direction, including Britain and Ireland. However, not all migrants from these continental areas migrated northwest, for others continued to migrate in the traditional southwest direction.

The change may have started when a few individuals with an unusual directional tendency found themselves in a new area where they could survive the winter. These pioneers may have been individuals from the extreme end of a range of directional preferences already existing within the central European source population. Or they may have been mutant individuals with a new directional preference not previously expressed. Alternatively, they may have been individuals from a normal southeastward-migrating population with an inherent fault in their migration control system, which meant that they migrated in the reverse direction to normal for that time of year (that is, taking the spring direction in autumn and vice versa; see Chapter 14). But whatever the origin of the pioneers, it would not have been enough merely for them to have been blown off course, because the new route could not then have been inherited by their offspring.

Once the habit started, the selection pressures that favoured wintering of continental Blackcaps in the British Isles rather than Iberia could have included: (1) factors acting in the new wintering area, such as progressively milder winters or improved food supplies available from garden feeders and winter fruit bushes; (2) factors related to the location of the new wintering area, including a shorter migration distance and possibly an earlier return to the breeding areas; or (3) factors acting in the former Mediterranean wintering areas such as drought-induced declining food supplies. Other ringed Blackcaps from central Europe have been found in autumn further north in western Europe than the British birds, but have not yet

established wintering populations, possibly because the winters are still too cold for them at these higher continental latitudes.

After the spring equinox, Blackcaps wintering in the British Isles would experience longer days than those wintering in Iberia, which could have brought forward their reproductive development. Captive British-wintering Blackcaps showed migratory restlessness at a date that would enable them to arrive in their central European breeding areas by 1 April, whereas Iberian-wintering birds would not arrive until about 17 April. In addition, the mean testis size at the date of arrival was about 25 per cent greater in the British-wintering group than in the Iberian-wintering group. An early return could thus enable British-wintering Blackcaps to pair preferentially with one another, and perhaps raise an extra brood each year, thus speeding up the evolution of the new habit. A field study revealed that, on average, birds from British wintering areas did indeed arrive in central European breeding areas earlier than those from Iberian wintering areas, and were 2.5 times more likely to mate with one another than at random (the two groups being distinguished among breeding birds by isotope analyses; Chapter 2). The British-wintering birds also settled in the better habitat (as yet unoccupied by other Blackcaps), and produced larger clutches and broods (Bearhop *et al.,* 2005). In view of these findings, the British-wintering birds may eventually out-compete and replace the Iberian-wintering ones in this part of central Europe. Surprisingly, British-breeding Blackcaps have apparently not yet become partially resident. So far, only one recovery of a confirmed British-bred Blackcap has been obtained in Britain in winter, but this may well mark the start of a new habit. Meanwhile, most British Blackcaps continue to winter in Iberia and North Africa.

Heritability and other studies

Further evidence for the genetic control of various migratory traits has come from assessing the level of resemblance among closely related individuals, such as siblings or parents and their offspring.

Any resemblance between such closely related individuals is due partly to their shared genes. Significant heritability of traits was almost always apparent in birds studied in captivity, but less often discernible in birds studied in the wild (Pulido & Berthold, 2003). This difference probably arose because captive birds were kept in standard conditions, whereas wild birds were influenced by variable environmental conditions which also influenced migratory behaviour. In addition, samples sizes were generally lower for wild birds, and measurements were made less precisely. Taken overall, however, such studies provided further evidence for genetic influence on migratory traits, and increased the range of species encompassed.

Other field studies have provided a different type of evidence. For example, Cliff Swallows in mid-North America were exposed in 1996 to a severe cold snap in the middle of the spring arrival period, when insects became inactive. Many of the swallows that arrived early that year died, while others arriving after the cold snap survived (Brown & Brown, 2000). In later years, the mean arrival date of the whole population shifted later, as the population contained a smaller proportion of early arriving individuals. The cold snap seemed to have changed the genetic composition of the population in favour of later-arriving genotypes. Although in some years, early arrival gave better nest success, this advantage was apparently offset by the greater risk of mortality in occasional cold years, the resulting arrival dates being a compromise between these opposing selection pressures (Chapter 11).

CONCLUDING REMARKS

Most of the experimental research discussed above was concerned not with the origin of migratory behaviour, but with its modification and further development. It implies that, given sufficient underlying genetic variation and strong enough selection pressure, some wild birds could change their migratory habits within only a few generations in response to environmental change

(for more examples, see Chapter 16). Moreover, the fact that hybrids behave in a way that is intermediate between their two parents suggests control by several genes and not just one (for any behaviour controlled by a single gene would be expected to show an on–off pattern, according to whether or not a bird has the gene, giving no scope for intermediates).

In the experiments described, migratory activity was measured by the number of hours (or nights) of migratory restlessness shown by individuals. Birds drawn from resident, short- or long-distance populations all showed some migratory activity, and differed only in the amount. In other words, there was no sharp difference between residents and migrants. They merely lay at different points on a continuum of variation, presumably controlled as a single attribute by the same genes. This finding has important implications for the evolution of migration. It suggests that both obligate migrants and non-migrants could be widespread in bird populations, all of which could therefore be considered as partial migrants, differing only in the range of migratory activity represented. The frequency of birds with high migratory activity may be very low in populations classed as resident, while the frequency of birds with low activity maybe low in populations classed as migratory. Such variation in migratory activity (= partial migration) is clearly widespread in birds, providing a basis from which complete migratory or complete resident behaviour could be achieved or lost, depending on selection.

Such variation could account for many familiar aspects of bird movements: why, for example, occasional individuals of normally migratory species (such as the Barn Swallow) can be seen in breeding areas in winter, long after other individuals of their species have left; and why, even in the most sedentary of species, occasional ringed individuals are recovered in autumn or winter at long distances, all in a restricted direction south of their natal areas. This applies, for example, to the Reed Bunting and Stock Dove, in which movements exceeding 100 km have provided less than 1 per cent of

all recoveries from British-ringed individuals (Wernham *et al.,* 2002).

What is clear is that, once obligate partial migration has evolved, the whole gamut of behaviour from strictly resident to strictly migratory could develop in short-lived birds in much less than a human lifetime. If the propensity for resident or migratory behaviour exists in a population as a gradient rather than as a dichotomy (as research implies), selection to change from resident to migratory (or vice versa) could begin anywhere on the behavioural gradient, and would not necessarily depend on the prior presence of a few migratory individuals in an otherwise resident population (or vice versa).

As yet, findings on the genetic control of migration rest on studies from only a few species, and it is possible that not all populations or all aspects of migration could adapt so rapidly to altered conditions. In some species, reduced to low numbers, there may be insufficient genetic variation in a trait to allow any adaptation, whatever the selection pressure. In this situation, time would be needed for mutation to create yet more genetic variation on which selection could act. Whether a population could respond to a new selection regime would also depend on whether the trait under selection co-varies with other traits. If selection to change one trait beneficially brings concurrent detrimental changes in other traits, the resulting behaviour is likely to be a compromise. In terms of the length of journey, there are also limits to how many weeks of each year a bird could spend on migration and still have time to reproduce and moult, and how much body fuel it could carry for non-stop flights. These aspects act as constraints to evolutionary change in migratory behaviour, at least in the short term. They are discussed further in the next two chapters.

CHAPTER 16

Recent Changes in Migratory Bekauiour

CHANGES IN THE MIGRATORY behaviour of birds have attracted interest in recent years mainly in relation to climate change (Box C, overleaf) and other human impacts. In the British Isles and some other parts of Europe, bird distributions and numbers have been monitored for decades, as have the timing and routes of their migrations. Birds are therefore one of the best groups of organisms for assessing the effects of climate and other environmental change. Moreover, migratory species are perhaps more vulnerable to the effects of such change than are non-migrants, because they can be influenced by conditions in more than one location: in their breeding, migration and wintering areas.

Some recent changes in bird migratory habits are strikingly evident, in both Europe and elsewhere, with some species becoming less migratory and wintering at higher latitudes than previously, or arriving earlier and departing later from their breeding areas. Almost all these changes are probably associated with changes in food availability, or with climatic conditions that are likely to affect food availability, such as milder winters. Not all species have responded similarly, or to the same extent, and particular species have changed more in some regions than in others.

Many recorded changes in bird migratory behaviour appear to represent immediate behavioural (or 'facultative') responses to prevailing conditions, whereas others may reflect genetic changes brought about by natural selection. In every aspect of migration, there is scope for flexibility, through which individuals can adjust their behaviour to some extent according to prevailing conditions.

For example, the same birds might arrive in their breeding areas earlier in warm springs than in cold ones, or they might migrate further in cold winters than in mild ones. Birds clearly have considerable scope for adjusting their behaviour to prevailing conditions, without the need for modification of the genetic control mechanisms. On the other hand, every major aspect of migration has a genetic component (Chapter 15), so some recent changes in migratory behaviour may reflect genetic changes induced by natural selection. Although not hard to visualise, genetically based changes are difficult to demonstrate in the wild. We can return to this matter later, but will first examine the main types of change observed.

BOX c. Climate change.

Global climate change has been exhibited mainly by warming, resulting primarily from rising concentrations of 'greenhouse gases' in the atmosphere. These gases have increased since the pre-industrial era primarily because of human activities, especially the burning of fossil fuels, but also through deforestation and other changes in land cover. During the 20th century, land and ocean surface temperatures increased, spatial and temporal patterns of precipitation changed, and sea levels rose, while storms and other extreme weather events became more frequent. These changes have had profound effects not only on people, but also on plant and animal life, including migratory birds.

During the period 1750–2000, the atmospheric concentrations of carbon dioxide (the main greenhouse gas) rose by up to 35 per cent, methane by about 150 per cent and nitrous oxide by about 17 per cent. In consequence, the earth's surface warmed during the 20th

century by 0.4-0.8°C. Land areas warmed more than the oceans, and northern mid-to-high latitudes more than most other regions. Over the same period, mean annual precipitation rose by 5–10 per cent in the northern hemisphere and parts of Australia, but fell by 3 per cent over many subtropical land areas, including northwest Africa and parts of the Mediterranean region. The severity of droughts increased, especially in Africa.

Warming promoted sea-level rise through both the thermal expansion of seawater and the widespread melting of glacial land ice. Based on tide gauge records, and correcting for land movements, mean sea level rose by an average of 10–20 cm during the 20th century. Its main effect has been to reduce the areas of salt marsh and other coastal habitats, and to flood some former dry coastal areas, thus reducing the total land area.

Regardless of attempts to reduce greenhouse gas emissions, these changes are predicted to continue long into the future. Projected changes until the end of the 21st century include a further increase in global temperatures of 1.4–5.8°C, a rate without precedent in the past 10,000 years, to judge from long-term climate records based mainly on ice cores. Mean global precipitation is also projected to increase further, with some areas becoming wetter and others drier. Global mean sea level is projected to rise by 0.1–0.9 metres. Hence, all the physical and biological changes witnessed so far can be expected to continue long into the future, causing among other things, massive changes in the habitat distributions, numbers and

movement patterns of birds and other animals. These changes are already well under way

(Based mainly on the Third *Assessment Report* (2000) of the Intergovernmental Panel on Climate Change [IPCC])

CHANGE FROM MIGRATORY TO SEDENTARY

Over a wide range of latitudes, many bird populations have changed from migratory to sedentary in recent times. One example is the Eurasian Blackbird, in which the British and other west European populations have become progressively more sedentary during the last two centuries, as winters have mellowed (Berthold, 1993; Main, 2000). Another is the Lesser Black-backed Gull, which prior to 1940 was almost entirely migratory in the British Isles, only a few adults remaining year-round. But nowadays, large numbers of adults and immatures stay for the winter, feeding largely on rubbish dumps, which have increased the winter food supply (Hickling, 1984). Changes towards more sedentary behaviour have also occurred among Herring Gulls in Denmark (Petersen, 1984), Common Starlings in central Europe (Berthold, 1993), Chiffchaffs in Britain (G. Geen, in Wernham, 2002), Great-crested Grebes in the Netherlands (Adriensen *et al.,* 1993) and among Mute Swans and other waterfowl in eastern Europe (Švažas, 2001).

CHANGE FROM SEDENTARY TO MIGRATORY

Examples of changes from sedentary to migratory behaviour are less frequent, and have occurred mainly in species that have extended their breeding ranges northwards. For example, the European Serin was once restricted to the south of Europe where it is resident, but in the early 20th century it spread north, where it became

migratory. In more recent years, under milder winters, this migratory population reverted to partial residency (Berthold, 1999). Likewise, since the 19th century, many bird species have spread north in Fennoscandia, including the Northern Lapwing, Common Starling, Eurasian Blackbird and Dunnock. In their newly colonised breeding areas, they are essentially migratory, whereas further south they are partial migrants or residents.

SHORTENING OF MIGRATION ROUTES

So called 'short-stopping' has occurred in many species as more food has become available at higher latitudes in the wintering range, either through human action or climate change. Several populations of wild geese have responded in this way to agricultural changes or to the creation of protected areas where food crops are provided (Rutschke, 1990; Nilsson, 2006). For example, Greylag Geese breeding in Sweden formerly wintered mainly in Spain, but have now switched mainly to the Netherlands, a former stopover area; while White-fronted Geese breeding in northern Europe and western Siberia have progressively shortened their migrations so that greater proportions winter in continental Europe and smaller proportions in Britain (Wernham *et al.,* 2002). Other species of waterfowl have shortened their migrations, apparently in response to warmer winters, as waters which once froze now remain open. This has led to increased numbers of ducks, geese and swans wintering in northern and eastern parts of Europe, and to declining numbers of the same species wintering in the south and west, including the British Isles (Švažas, 2001). Similar change has occurred among waders wintering in Britain, with smaller proportions of birds reaching the west of the country than previously (Austin *et al.,* 2000).

Some Barnacle Geese have shortened their migrations in another way, by establishing nesting populations hundreds of kilometres south of their historic breeding range, nearer to wintering areas. Large numbers of Barnacle Geese now breed on the Swedish island

of Gotland and other sites around the Baltic and in the Netherlands, thus shortening the traditional migration route to Novya Zemlya by 1,300 km or more (Larsson *et al.,* 1988). Birds from the Greenland population wintering in the British Isles have also started to nest in Iceland, thus shortening their migration by more than 500 km. In a similar change, Whooper Swans now breed in Poland, about 800 km southwest of the main breeding range of that population. This type of change is more difficult to explain, but may in some cases be due to suitable habitat being created by human action, to the reoccupation of former range from which the species was eliminated in the past or simply to unprecedented population increase leading to an expansion of the breeding range into lower latitudes. Such changes occurred in particular individuals, some of which substantially changed their breeding or wintering areas from one year to the next, so at first they presumably represented facultative responses to prevailing conditions, rather than genetically driven changes.

Species which have expanded their breeding areas to higher latitudes in recent decades but retained the same wintering areas must necessarily have extended their migration routes. Eurasian examples include: (1) the Black-winged Stilt, which is expanding its breeding range northward (France, Ukraine, Russia) but still winters south of 40°N latitude; (2) the European Bee-eater, which has expanded northwards in almost all central European countries, yet still winters entirely in Africa south of the Sahara; (3) the Citrine Wagtail, which is expanding its breeding range from Asia westward into Europe, but still winters in India and Southeast Asia (Fiedler, 2003). These examples represent the sort of changes that must have occurred in many species after each glaciation, when ice receded, and plants and animals spread from lower to higher latitudes (Chapter 17).

In some other species, greater proportions of ring recoveries are now being obtained from the distant parts of migration routes than formerly, but it is hard to tell whether this is due to altered migration behaviour or to changed recovery opportunities along the

routes (Fiedler *et al.,* 2004). Over recent decades, hunting has declined much more in the northern and mid-latitudes of Europe than further south. This could affect the migratory behaviour of hunted species, as well as the distribution of reported rings.

CHANGES IN MIGRATORY DIRECTIONS

BREEDING IN THE WINTERING RANGE

Occasional individuals of some species have nested in their wintering range (through suspending their normal spring migration), leading in some cases to the establishment of new nesting populations. Examples include Eurasian White Storks and Bee-eaters now nesting in South Africa (Snow, 1978; Harrison *et al.,* 1997), and North American Barn Swallows nesting in Argentina, within the usual wintering range (Martinez, 1983). Among seabirds, Leach's Storm-petrels, which breed widely in the North Atlantic and Pacific, have been found breeding on an island off South Africa, and in potential nesting burrows on the Chatham Islands off New Zealand, within the wintering range of northern hemisphere birds (Imber & Lovegrove, 1982; Whittington *et al.,* 1999). This phenomenon involves individuals switching, under the influence of southern hemisphere daylengths, to an annual cycle appropriate to the southern hemisphere, a change which can be readily replicated in birds held under experimental conditions (Gwinner & Helm, 2003). It also involves change in the direction of migration to south–north in autumn and north–south in spring, instead of the other way round, as established recently for White Storks breeding in South Africa (Underhill, 2001). Considering the numbers of bird species that have conspecifics or closely allied forms breeding in equivalent habitat in the opposite hemisphere, this process may have been going on for millions of years (Snow, 1978; Newton, 2003).

The same type of directional change is shown by those northern hemisphere species which have been introduced into the southern hemisphere. These species have also reversed the direction of their spring and autumn journeys, as appropriate, so that they continue to winter in lower rather than in higher latitudes. This is true, for example, for the European Goldfinch and others introduced from Britain to New Zealand in the 19th century. In addition, Manx Shearwaters now breed on the west side of the Atlantic, in a region formerly visited only on migration (Storey & Lien, 1985).

MIGRATION TIMING

More information is available on timing than on any other aspect of migration. This is because many observers have kept records of the first and last individuals of migratory species seen each year in their home areas. For some localities, records extend back more than a hundred years, and for one area in Finland for nearly 300 years. Such observations provide an unrivalled source of information from which to examine change in the migration dates of birds.

In many northern hemisphere regions, including the British Isles, conspicuous spring events such as the bud burst and flowering of trees, the hatching of caterpillars or the spawning of frogs have occurred earlier over the past several decades; and the same holds for the spring arrival dates of migratory birds (Lehikoinen *et al.,* 2004). In fact, under the presumed influence of long-term climate warming, many birds now arrive in their breeding areas earlier in spring and depart later in autumn than in the past, spending from a few days to a few weeks longer per year in their summer quarters[†] Only a proportion of species have shown such changes, but some of the exceptions may result from observational deficiencies, for they refer to species that have undergone marked numerical declines over the period concerned. Decline makes it increasingly difficult to detect the earliest arrivals and latest departures, where first and last dates were the measures recorded.

Spring dates

Of 983 Eurasian bird populations in which first arrival or passage dates were monitored over time, 59 per cent showed no significant change, but 39 per cent had become significantly earlier, while only 2 per cent had become significantly later (Lehikoinen *et al.,* 2004). From 222 populations for which mean arrival or passage dates could be calculated over time, 69 per cent showed no change, while 26 per cent had become significantly earlier, and only 5 per cent had become significantly later. The overall average change of first arrival (or passage) date for all species and sites was 0.37 days earlier per year for first arrival/passage dates (equivalent to 18 days per 50 years), and 0.10 days earlier per year for mean arrival/passage dates (5 days per 50 years), both trends being statistically significant. While first arrival dates seem to have changed more than mean dates, they are more affected by long-term changes in bird numbers or observer numbers, so are probably less reliable.

Within the long-term trends, arrival and passage dates still fluctuated annually in line with local temperatures, with earlier arrival in warm springs than in cold springs (Figs. 180 and 181)

In comparing the changes that have occurred in the spring migration dates of different species, several widespread patterns have emerged:

Greater changes have occurred in the migration dates of early migrating species than of later ones (Lehikoinen *et al.,* 2004). This is associated with weather (including temperature) being more variable, and having changed more, earlier rather than later in the spring (for passage dates, see Sokolov *et al.,* 1998; for arrival dates at breeding sites, see Slagsvold, 1976; Loxton & Sparks, 1999).

Greater changes have occurred in the arrival dates of short-distance than long-distance migrants—presumably because short-distance migrants generally arrive earlier in spring (same

point as above), and have more flexibility in their migration timings (Tryjanowski *et al.,* 2002; Butler, 2003).

Greater changes have occurred in the arrival dates of small bird species than of large ones. This is possibly because the smaller species are more sensitive to annual temperature differences and their effects on food supplies.

Year-to-year arrival dates of early short-distance migrants were generally correlated with spring temperatures in the breeding locality, but such correlations were less obvious in later-arriving long-distance migrants (Tryjanowski *et al.,* 2002; Gienapp *et al.,* 2007). Moreover, where it was investigated, weather back down the route often showed a better relationship with arrival dates than did weather at the arrival location itself. For example, arrival dates of Barn Swallows in Britain were more closely correlated with air temperatures in France and Spain than with air temperatures in Britain (Huin & Sparks, 1998).

Spring weather has not changed everywhere in the same way. Correspondingly, the degree of change in bird arrival dates in breeding areas has varied across Europe, with arrival dates in most areas getting earlier as spring temperatures have increased, but later in other areas as springs have cooled.

Despite correlations between arrival dates and temperatures in the breeding area, much of the year-to-year variability in the arrival dates of many species remains unaccounted for. This is partly because arrival dates are also influenced by weather further down the migration route, as just mentioned, but also by other aspects of weather, such as wind. They are also affected by food supplies, which for some species can vary from year to year independently of weather (Chapter 11). Moreover, poor weather on one part of the route can stall migration, even though conditions may be favourable further along the route.

In view of the fact that, in most bird species, males arrive in breeding areas before females (Chapter 21), studies of migration timing based on first arrival dates concern males only. However,

studies of various songbird species migrating through some north European bird observatories in spring revealed that both sexes have responded to warmer springs, with males remaining ahead of females by about the same amount as in earlier years (Rainio *et al.,* 2007; Tøttrup & Thorup, 2008). On the other hand, a study of Barn Swallows in Denmark revealed that only males had started to appear earlier, while females arrived at about the same dates they did 30 years previously, so there was no advance in egg-laying (Møller, 2004).

Earlier arrival inbreeding areas could result from: (a) earlier departure from wintering areas; (b) wintering closer to breeding areas; (c) increase in the speed of spring migration (less stopover); or (d) combinations of these possibilities. All three sources of variation have been recorded in one species or another (Chapter 11), with migration speed recorded from the dates that migrants pass through successive observation sites in different years. Only facultative responses could account for the year-to-year variation in arrival dates seen in many migrants, but this need not exclude the possibility of progressive genetic change in response to longer-term climate warming (see Chapter 15).

Different bird populations have been exposed in spring to different degrees of climate change depending where and when they migrate (Sparks & Tryjanowski, 2007; Both & te Marvelde, 2007). This is because temperatures have changed differently in different parts of Europe, as well as differently at different times of the season. For example, southern populations of Pied Flycatchers still migrate at temperatures similar to those encountered 25 years ago, whereas nearly one-third of the total journey of their more northern counterparts crosses regions where temperatures are now higher than before (Both & te Marvelde, 2007).

Autumn dates

In general, changes in autumn migration dates over recent decades have been fewer in number, less marked and more variable than

changes in spring dates. Two patterns of change have emerged, involving either earlier or later departure from breeding areas over the years. In some single-brooded bird populations, earlier arrival in spring is followed by earlier breeding and moult, and subsequently by earlier departure from breeding areas in late summer or autumn (Chapter 10). The juveniles are affected as much as the adults, for being hatched earlier in the year than usual, they also reach migration age sooner. The situation differs in species in which individuals can have multiple nesting attempts in a season. Most such species have begun to leave later in recent years, spending longer in their breeding areas, with some individuals possibly squeezing in another nesting attempt (Bairlein & Winkel, 2001; Sparks & Mason, 2001; Jenni & Kéri, 2003; Lehikoinen *et al.,* 2004; Sokolov, 2006; Mesquida *et al.,* 2007).

ADDITIONAL OBSERVATIONS

Most of the studies mentioned above focus on particular species or groups of similar species, so it is hard to tell what proportions of British and Irish breeding bird species have changed their migratory habits in some way. However, in one analysis, 73 species provided enough ring recoveries from a sufficiently long period to examine changes in the lengths and directions of migrations. Some 51 (70 per cent) of these species showed no significant change in either respect during the 20th century, but in 15 species, movements had become shorter, in 5 they had become longer, while in 2 the movements had changed in other ways. Significant changes were found in British populations of songbirds, raptors, waders, waterfowl and seabirds (G. Siriwardena & C. Wemham, in Wernham *et al.,* 2002).

Regarding timing, long-term data from six English area bird reports were used to examine the first arrival dates in spring for a range of species (Sparks *et al.,* 2007). Of all 145 data series from 33 species, 50 per cent showed significantly earlier arrival in recent years, with the average advance over all species being 0.25 days per

year, or 12 days over 50 years. Species such as the Sand Martin became significantly earlier in all six areas, while others such as the late-arriving Spotted Flycatcher showed no significant change in arrival dates at any site. Arrivals often common species were related to March temperatures in both England and Spain (on the migration route), but temperatures fluctuated from year to year roughly in parallel in both areas. The same authors used data from three area reports to examine the last departure dates in autumn. Of 67 data series from 23 species, 30 per cent showed significantly later departure, with the average species delay being 0.16 days per year, or 8 days over 50 years. There was greater consistency between species in trends in first arrival dates than in trends in last departure dates, but in some species, trends in arrival and departure dates may have been masked by population declines (making first and last dates harder to detect reliably).

Temperature effects

Although arrival dates have been correlated with spring temperatures, either on migration routes or in breeding areas, it is uncertain to what extent temperature acts directly on the birds. Warmer weather is associated with other conditions that promote migration in spring, such as favourable tailwinds blowing from the south or southwest, good visibility and lack of rain (Chapter 5). In addition, warmth may reduce the thermoregulatory needs of the birds, allowing more of their daily energy intake to be devoted to migration, and for some species it may hasten development of food supplies (Chapter 11). All these associated factors could speed migration.

Few studies have examined arrival dates in relation to winds, but for Song Thrushes migrating through Rybachy in the southern Baltic, spring passage was significantly correlated with winds and rain over the route and with air temperatures in the winter quarters (Spain) (Sinelschikova *et al.,* 2007). In April, the main month of passage, tailwind frequency had increased over the preceding 40

years, accounting for 51 per cent of the variance in median passage dates. In this species, there was no relationship between passage dates and temperatures in the southern Baltic at the time of spring migration. Similarly, the arrival dates of wintering Bewick's Swans in England were associated with the number of preceding days with favourable winds (Rees, 1982). Hence, in some studies of bird arrival dates, temperature may have been associated with other factors that had more direct influence.

Genetic responses

Although all main aspects of migratory behaviour have heritable components (Chapter 15), genetic change is not easily demonstrated in birds living in the wild. But if individuals taken from the wild in different years express behavioural differences when held under identical conditions in captivity, these differences are likely to have a genetic basis. This conclusion is strengthened if the trend is maintained in captive-bred offspring from these individuals, unaffected by parental effects or experience in the wild, because only genetic effects are maintained through the generations. Such a test was made on samples of Blackcaps randomly collected as nestlings from south Germany and hand-raised each year over a 13-year period (Pulido & Berthold, 2004). Among these birds, autumn migratory activity in successive samples over the years was found to start later and decline in amount. In the wild, this would have been reflected in a later start and a shorter journey, precisely the result expected if the population had responded genetically to ameliorating conditions. So at least in this species, later departure and shorter migration may partly represent genetic responses resulting from natural selection. At the same time, spring arrival advanced in this population, possibly as a correlated response (Pulido, 2007).

Single selection events, such as spring storms, can cause rapid genetic change in the arrival dates of populations, as explained in Chapter 15, but counter-selection pressures in milder years could

rapidly reverse the situation and revert arrival dates back to their original state. Selection pressures must act consistently in the same direction over several generations if they are to have any more than temporary effects on the genetic composition of a population. Most selection probably acts to stabilise the behaviour of populations rather than to change it.

Timing mismatches

The timing of spring migration is influenced by weather conditions along the whole migration route, whereas the timing of egg-laying depends on conditions in the breeding area. Any discrepancy between conditions en route and in the breeding area can lessen the match between breeding and food supply. Moreover, in the breeding areas themselves, birds may respond more or less rapidly than their food organisms to climatic changes, so that birds no longer arrive and breed at the optimal time. An apparent example is provided by Pied Flycatchers nesting in the Netherlands and elsewhere, where climate change has advanced the food supply on which breeding depends, but spring migration has not advanced sufficiently to allow the flycatchers to make best use of this food supply, as they did in the past (Both & Visser, 2001). The birds have thereby suffered reduced breeding success, and in areas with the biggest mismatch between breeding and food supply, population levels declined by about 90 per cent over a 20-year period (Both *et al.,* 2006).

These examples raise a general point that the photoperiodic responses of many birds, through which their annual cycles are timed, may become less reliable predictors of seasonal change in food supplies, as climate change alters the timing of these supplies. This is not a new problem, as it is faced by all birds which expand their breeding ranges into different regions, but it may take a while for them to adjust genetically to new situations, during which time they could perform less well than usual, sometimes with effects on population levels.

CONCLUDING REMARKS

Many bird populations have clearly changed some aspect of their migratory behaviour during recent decades in response to changed conditions, with: (1) earlier arrival in spring, (2) earlier or later departure in autumn, (3) shortening or lengthening of migration routes, (4) directional changes and (5) reduced or enhanced migratoriness, as reflected in changes in ratios of resident to migratory individuals in particular breeding areas, and in the occurrence of wintering birds in regions where they were previously absent. Most examples of shifts toward increasing migratoriness involve species that have extended their breeding ranges to higher latitudes where successful wintering is impossible or risky.

These various observations, along with the breeding experiments described in Chapter 15, confirm that migration is a dynamic process, subject to continual change in response to prevailing conditions. It is uncertain how many of the changes observed in recent years involved genetic modifications and how many were facultative responses, occurring within the limits of existing flexibility. It is in any case difficult to separate genetic from facultative mechanisms, considering that the limits to flexibility may themselves by genetically controlled. Moreover, in any marked long-term change, both are likely to be involved, the birds responding initially by facultative means, and eventually by genetic change, as natural selection comes to bear. Facultative responses are relatively limited (though variable in extent between species), and if environmental conditions continue to change in the same direction, such responses may become inadequate to deal with the new conditions. Only genetic change may then enable the population to respond appropriately to conditions beyond the previous range. But whatever the basis of the observed changes, it is presumably in these various ways that birds continually adjusted their migration patterns to the massive climate changes of the past, and through which we can expect them to respond in future.

† For examples, see Loxton & Sparks (1999); Sparks (1999); Sokolov *et al.* (1998, 1999); Jenkins & Watson (2000); Bairlein & Winkel (2001); Sparks & Mason (2001); Sokolov (2001, 2006); Zalakevicius & Zalakeviciute (2001); Tryjanowski *et al.* (2002); Hüppop & Hüppop (2003); Jenni & Kéri (2003); Lehikoinen *et al.* (2004); Vahatalo *et al.* (2004); Stervander *et al.* (2005); Rubolini *et al.* (2007); Sparks *et al.* 2005, 2007.

†In examining arrival or passage dates in relation to spring weather, most researchers have used annual temperatures from localities on the migration route or in the breeding area. Others have used the winter–spring index of the North Atlantic Oscillation (NAO), a large-scale climatic phenomenon influencing regional weather (e.g. Hüppop & Hüppop, 2003; Vahatalo *et al.,* 2004; Stervander *et al.,* 2005; Zalakevicius *et al.,* 2006). The NAO is calculated as the difference in normalised monthly values of atmospheric pressure between the Azores (or Gibraltar) and Iceland. Positive values reflect warmer and wetter winter–spring weather (followed by earlier spring migration) in northwest Europe, while the same values indicate the opposite weather conditions and later arrival dates in southern Europe and northwest Africa. Negative values indicate the opposite conditions in both areas, with wetter conditions in the Sahel zone of Africa being of special significance to European–Afrotropical migrants.† Typically, most birds arrived in breeding areas about 2.5–3.3 days earlier for every 1°C increase in spring temperature (based on 203 regression analyses for different Eurasian bird populations; Lehikoinen *et al.,* 2004). At the Rybachy Bird Observatory in the southern Baltic, warm springs in the 1930s and 1940s, and again in the 1960s and 1980s, were associated with significantly earlier migration in many songbird species, while colder periods during the 1950s and 1970s were associated with later migration (Sokolov *et al.,* 1998).

CHAPTER 17

Glacial Legacies

Some curious aspects of current bird migration patterns can be best explained in terms of past conditions. At the height of the last glaciation, much of the northern hemisphere above about 50°N was covered with ice, and generally devoid of terrestrial life. Re-colonisation of this vast area by plants and animals followed the retreat of the ice, which began about 10,000–15,000 years ago and continues to this day. This means that some of the longest and most impressive of current bird migrations must have developed within this period, as birds spread gradually from lower to higher latitudes to occupy newly forming habitats. At the start of this process, when birds were confined to lower vegetated latitudes, in their 'glacial refuges', they may have been resident or perhaps shorter-distance migrants.

At this time, the ice in Britain extended south almost to Oxford, while land further south, including most of France, was covered with tundra, similar in character to that now found in the Arctic. Only south of the Pyrenees—in Iberia and North Africa—were there substantial areas of forest and scrub, capable of supporting the kinds of birds that now breed in such habitats over much of Europe. Moreover, the last 2.5 million years have seen more than 20 glaciations of varying severity, so that over this whole period, bird distributions and migration systems must have been in continual flux, and many populations are likely to have passed through alternating sedentary and migratory phases, each lasting for many thousands of years. The ability to migrate was perhaps ever-present in these populations, becoming suppressed or reactivated according

to prevailing conditions and the changing pressures of natural selection.

Consideration of past conditions sheds light on the old question of whether migration in present populations developed as resident birds found new wintering areas at lower latitudes, or new breeding areas at higher latitudes. It also provides plausible explanations for some otherwise puzzling aspects of current bird migration patterns, such as why some species take seemingly unnecessarily long and indirect routes between their breeding and wintering areas, how they came to undertake long flights over seas or deserts, or to show migratory divides, or chain and leapfrog patterns, as described in Chapter 18.

MIGRATION DEVELOPMENT TOWARDS HIGHER OR LOWER LATITUDES

In the development of migration, two scenarios have been proposed: (1) that the breeding range is the original year-round home of a population, while the wintering range is the secondary home, visited to enhance survival through the most difficult season; or (2) that the present wintering range is the original year-round home, while the breeding range is the secondary home, visited to enhance reproductive success. In theory, current migration patterns could have evolved in different species from either of these starting points. However, because most of the migration that we now observe developed as birds spread from low to high latitudes at the end of the last glaciation, range expansion and migration almost certainly developed hand in hand.

The process is evident in the northward expansion of the European Serin. This small finch is resident in southern Europe, but extended its breeding range northwards in the 19th and 20th centuries, becoming increasingly migratory in the newly colonised areas (Chapter 16). The same has held for other species elsewhere, including the Cattle Egret in North America. Such recent colonists show that, given suitable habitat, the occupation of higher latitudes,

and the associated development of migration, can occur within decades. The colonisation of new breeding areas is achieved by normal dispersal processes, and migration develops secondarily in response to conditions there. The inherent variation in migratory behaviour present within many bird populations provides the raw material on which natural selection can act to produce a predominantly migratory population from a predominantly resident one, or vice versa (Chapter 15). The latitude at which migration is favoured over residency is likely to vary between species, depending on their particular needs, but giving in many species a geographical gradient from wholly resident at the lowest breeding latitudes, through partially migratory, to wholly migratory at the highest breeding latitudes.

During the height of each glaciation, as explained above, most vegetation zones in the two northern landmasses were compressed into their southern parts, the more northern parts being mainly covered with ice. We can suppose that the post-glacial colonisation of northern regions involved a general northward movement of bird breeding ranges, associated with the northward advance of their required habitats, following ice melt. Bird species that were non-migratory could have remained so, or become migratory in the more northern of the areas colonised. Species that were migratory during the last glaciation (wintering at lower latitudes than their breeding refuges) could have moved both their breeding and wintering areas northward, or they could have retained the same wintering areas, and simply lengthened their migrations as their breeding range moved north. The latter scenario could have held in species that, throughout the glaciation until now, have continued to winter in tropical or southern hemisphere regions. The post-glacial northward movement of particular habitat types, making them increasingly remote from tropical wintering habitats, provides an example of how, over time, species could have adopted widely separated breeding and wintering areas.

In recent decades, genetic analyses have provided support for the view that migration developed in many species as they extended

their breeding ranges northward in post-glacial times. Parts of the DNA in organisms are thought to have no effects on the fitness of the individual but to change at fairly constant rates over time, owing to random mutations which alter the sequence of individual nucleotides along the length of the DNA molecule. By comparing this sequence in equivalent pieces of DNA (usually mitochondrial DNA) from individuals drawn from different parts of the breeding range, it is sometimes possible to work out the order in which different populations arose, and hence the historical pattern of range expansion.

Some species now live in areas that remained favourable during the glaciations, as well as at higher latitudes that they could have colonised only since glacial retreat. The majority of such species that have been studied show more variation in the mitochondrial DNA in the refugial than in the more recently colonised areas. Each species is assumed to have colonised from the edge of its refugial range, which would have restricted the number of initial colonists, and thereby reduced the genetic variation compared with the entire source population. Examples include the Greenfinch in Europe (Merilä *et al.,* 1997), and the Yellow Warbler and MacGillivray's Warbler in Central and North America (Klein & Brown, 1994; Milá *et al.,* 2000). Reductions in genetic variance with increasing latitude, assumed to result from post-glacial leading-edge spread, have also been described in plants, insects and mammals in both Eurasia and North America (Hewitt, 2000).

In some species, estimates have been made from mitochondrial DNA of both the dates and routes of post-glacial range expansion. Based on diversity patterns in mitochondrial DNA, Common Chaffinches appear to have spread from North Africa into southern Europe within the last 370,000 years or so, and spread further north through Europe only during the past 15,000–3,000 years, behind the retreating ice sheets (Baker, 2002). Only the more northeastern populations, breeding in the most seasonal environments, have become migratory.

Colonisation of wintering from breeding areas

The above discussion argues in favour of current migration systems developing as species spread from lower to higher latitudes, becoming more migratory as they reached increasingly seasonal environments. This is the situation that would have affected all those species that colonised high-latitude areas after the last glaciation, and is evident today in species that are still spreading north. However, we can imagine that the same process in reverse occurred repeatedly through the Pleistocene, at the start of each glaciation, as ice advanced southward. In those conditions, previously resident populations would need to become migratory from their breeding areas in order to survive the colder winters, before being driven entirely from their higher-latitude breeding areas by the advancing cold, and surviving only at the lowest latitudes. At these lower latitudes, in their glacial refuges, some species could have remained as migrants and others as residents, depending on winter food availability.

DEVELOPMENT OF MIGRATION PATTERNS

As a breeding population expands from lower to higher latitudes, and birds at the expanding front become increasingly migratory, more and more individuals are likely to concentrate for the winter in the original lower-latitude range. Theoretically, the resulting competition for the limited winter resources there could lead to one of four situations, depending on circumstances:

1. There could be a limit to the total numbers able to winter in the original range, preventing any further population growth and expansion of breeding range, so that the amount of wintering habitat restricts the extent of the breeding range.
2. If the winter immigrants from high latitudes are competitively superior to individuals in the original resident

population when the two types come together on their joint wintering area, the residents could break free of this competition by developing their own migration to areas beyond the current winter range (further south). Each winter, the original residents would then be replaced in their breeding area by the immigrants from further north. This scenario depends on the presence of suitable wintering habitat beyond the original range. It would give rise to a system of 'chain migration', in which breeding populations are seasonally replaced by wintering populations of the same species from higher latitudes (Chapter 18). In this way, populations from successive latitudes become migratory, but maintain the same south–north sequence in wintering areas as they do in breeding areas, with the whole series displaced southward in winter. Such chain migration is evident within a number of bird species that occur in Britain and continental Europe (Chapter 3).

3. If the winter immigrants were inferior in competition with those in the original resident population, the immigrant numbers could be held at a low level (as in 1 above), or they could break free of this competition by developing an even longer migration to winter in previously unoccupied areas beyond the original breeding range. This possibility again depends on suitable wintering habitat being available further south, but would then give rise to a system of 'leapfrog migration' in which the migrant population moves through the area occupied by the resident population to winter beyond it. In this way, populations of a species breeding at different latitudes reverse their sequence in winter, with those breeding furthest north wintering furthest south. Again, this is a common pattern in the migrations of many bird species that occur in winter over a wide span of latitude (Chapter 18).
4. Alternatively, if the immigrants were competitively superior, and no alternative winter habitat was available, they could

eliminate the original sedentary population completely. The species would then persist as a single population breeding at high latitude and wintering at low latitude in the original breeding range. The original breeding range would then become vacant for part of each year when the wintering population was away on its higher-latitude breeding range. This is another way in which a population could come to have separated breeding and wintering areas.

Greater fecundity is one way in which a migratory population could gain a competitive advantage over resident occupants in a shared wintering area where resources are limited. Even if the two populations competed on equal terms on their shared wintering range, with no difference in average survival rates, the population with the higher average breeding rate would in time increase at the expense of the other, either holding it at a much lower level or eliminating it altogether in their shared range. In many bird species, clutch sizes and nest survival rates increase with latitude (in association with the greater seasonal surge in food supplies and longer days found at high latitudes in summer), so we would often expect the higher-latitude populations of a species to be the most fecund.

This consideration may help to explain why many migratory birds do not breed in their wintering areas even though conditions seem suitable there year-round. For example, the Osprey does not breed in the tropics and subtropics of Africa and South America, even though the bulk of the northern continental populations winter there, and the immatures from these populations remain there year-round. Ospreys can obviously survive through the year at low latitudes, and the most likely reason they do not nest there is that they can achieve higher individual reproductive output by migrating to breed at higher latitudes, returning for the intervening winters. According to this view, residency does not evolve in tropical–subtropical regions, because competition from winter immigrants

would eliminate a resident sector in any population limited by winter food or other resources.

Intra-specific competition on the wintering grounds could thus have a major influence on the overall population sizes, distributions and migrations of birds (Bell, 2000). Through the process of post-glacial range expansion, and the associated development of migration, we have a possible explanation for two of the most familiar patterns of winter distribution found among migratory birds —the chain and leapfrog systems—as well as for the wide separation of breeding and wintering areas shown by some species. Another pattern, called 'telescopic' migration, occurs when the whole breeding population from a wide span of latitude concentrates for the winter in the southern part of the range (Chapter 18). This situation may occur where competition, or habitat availability, is insufficient to promote the development of the chain or leapfrog patterns, or it may represent a temporary situation which will eventually lead to chain or leapfrog patterns.

INDIRECT ROUTES TO DISTANT WINTERING AREAS

Birds would usually be expected to winter as close as possible to their breeding areas, and to take the shortest and most direct routes between the two. However, many birds take long roundabout routes, or use breeding and wintering areas that are separated by extraordinarily long distances, avoiding other apparently suitable areas that are much closer. Some roundabout routes might be explained on grounds of safety—for example, if the shortest route was more risky (say with unfavourable winds or a lengthy sea-crossing)—or on grounds of competition avoidance (if closer areas were already occupied by other populations of the same or similar species). However, these explanations seem unable to account for all such patterns, and almost certainly their explanation lies in past conditions. Imagine that, as a species expands its breeding range, it simply adds step after step to its already existing migration route. In this case, the route we see now could be interpreted largely as a

consequence of post-glacial colonisation history, as has long been appreciated (Thomson, 1926).

An apparent example is provided by the Northern Wheatear, which breeds across the whole width of Eurasia, from which it has colonised Greenland and northeast Canada in the west and Alaska in the east. Yet birds from the whole of this vast breeding range, extending round most of the northern world, converge on Africa to winter (Fig. 186). To reach their winter quarters, the Greenland–Canadian birds cross the Atlantic, which, at 2,500–4,000 km, may be the longest sea-crossing undertaken by a passerine (Chapter 8). The Alaskan birds first cross the Bering Sea and then travel via Siberia and the Middle East, covering a one-way distance of 15,000 km. If Northern Wheatears from Siberia and Alaska were to migrate instead to equivalent latitude in the New World that they occupy in Africa, they could halve their migration distances. If the east Canadian birds made this switch, they would save less on distance, but would travel by a mainly overland route rather than a transatlantic one. The Siberian–Alaskan birds would also save on distance if they went to Southeast Asia. Perhaps Africa is the only continent with suitable habitat for wintering Wheatears, but a more likely explanation is that the outlying populations have failed to evolve new routes. The problem with a switch from Africa to the Americas is that there are now no suitable intermediate routes, so no opportunity for gradual change. Thus, Wheatears from Siberia–Alaska would need a big directional change to reach Central or South America rather than Africa, while intermediate directions would land them in the Pacific. Similarly, any Northern Wheatears from northeast Canada would need a significant change in direction to end up in Central or South America, and any progressive shift by small step-changes would take them over the South Atlantic.

Similar patterns are apparent within the northern landmasses. For example, several bird species breed across almost the whole of northern Eurasia, but while some winter entirely in Africa, others winter entirely in Southeast Asia. African-wintering species include (besides the Northern Wheatear) the Willow Warbler, Spotted

Flycatcher and others, while Asian-wintering species include the Common Rosefinch, Arctic Warbler and Red-breasted Flycatcher, among others. In all these species, birds breeding furthest from their wintering areas face long migrations across a wide span of longitudes. Why do the European breeders of all these species not migrate south to Africa, and the Asian to southern and Southeast Asia, each making use of the nearest potential wintering areas? One possible explanation is that these species spread to breed across Eurasia in postglacial times from one end to the other, yet have kept their ancestral wintering grounds restricted to one end (Newton, 2008).

Such routes would presumably not persist unless they served their purpose in present conditions, but a difficulty in evolving (by gradual change) new routes to totally new wintering areas may largely account for their continuing existence. Perhaps, given enough time, they will change. Some species that now breed in both the Old and New Worlds have wintering areas in both, as shown by the Barn Swallow, Sand Martin, Osprey, Merlin and Peregrine, in addition to various waders and waterfowl. All these species can be assumed to have evolved in one of these regions, and spread to the other, where eventually they developed migration routes to separate wintering areas.

Apparently strange patterns are also evident on a smaller scale within Europe. Red-backed Shrikes migrating from Europe to Africa cross at the eastern side of the Mediterranean, including those from Spain which start their autumn journey by flying northeast then east. Some other summer visitors that breed in western Europe, such as the Marsh Warbler and Lesser Whitethroat, also migrate eastwards before turning south into Africa. Why do they not fly directly southwest through Spain into Africa like many other species? One possibility is again that these species survived the last glaciation only in southeast Europe–eastern Africa, and in post-glacial times spread to occupy for breeding first the eastern then western side of Europe. Perhaps in time, the western birds will evolve a new and more direct route through Iberia into western

Africa, but this would need a marked change in migratory direction, together with a longer trans-desert flight on the west side of Africa than is necessary on the east side.

For many years, the view that some migration routes retraced ancestral routes of spread was no more than plausible speculation, but recent DNA analyses have added support. For example, two subspecies of Willow Warblers *Phylloscopus trochilus* breed in Sweden—P. *t. trochilus* in the south and P. *t. acredula* in the north. The two subspecies meet at around 62°N. They differ morphologically, and show different migration routes, *trochilus* moving southwest into West Africa and *acredúla* southeast into eastern and southern Africa (Bensch *et al.,* 1999; Chamberlain *et al.,* 2000). They can also be distinguished by their DNA and by the isotope ratios in their feathers, reflecting the different wintering areas where moult occurs (Fig. 189). Their contact zone at about 62°N is paralleled in other bird and mammal species that breed in Scandinavia. Such examples are most readily explained by the post-glacial colonisation of Scandinavia along two routes, one from the southwest and the other from the east, over the northern end of the Baltic. In the region of the contact zone, the ice is known to have been unusually thick and lasted much longer than that to the south or north. This enabled areas to the north and south to be occupied sooner, but by different subspecies taking different routes. The two subspecies now migrate through Iberia and southeast Europe respectively, both of which were refuge areas during the glaciations. Similar patterns are apparent among some North American species subjected to DNA analyses (such as Swainson's Thrush; Ruegg & Smith, 2002). Such studies again suggest that many species have spread out from known glacial refuges and now maintain migration routes that take them through or near those areas.

MIGRATORY DIVIDES

While one explanation of migratory divides is that they represent the meeting point of populations that spread in post-glacial times

from different glacial refuges but have retained their ancestral migration routes, another possible explanation is that they evolved to circumvent barriers, such as seas or high mountain ranges. The two explanations are not mutually exclusive, for while divides may persist as post-glacial legacies, they may now serve a secondary role in directing birds around unfavourable areas. However, the taxonomic or genetic differentiation in many species on either side of the divide implies their long-terrn independent evolution, and hence their refuge-based origin. Once again, current migration routes reflect likely past colonisation routes.

Whatever their origin, we may now ask how migratory divides persist, given that directional preferences are inherited, and the populations on either side can (at least in theory) interbreed where they meet. The persistence of the divide may be due partly to the fact that migratory directions and distances inherited by hybrids are intermediate between those of their parents, and hence less effective in circumventing a barrier (Chapter 15). Such hybrids arising in the contact zone may then be less viable than the parental forms, so may not persist, contributing to the maintenance of the divide and the genetic integrity of each population.

One example of non-hybridisation concerns the Greenish Warbler, a rare visitor to Britain which breeds mainly in Asian forests. Populations spreading northwards in post-glacial times up the west and east sides of the high Tibetan plateau apparently met on the north side of the plateau in southern Siberia (Irwin *et al.,* 2001). During their previous isolation, the two forms had not only developed minor genetic differences (recognisable in the mitochondrial DNA), but also different songs. Where they meet on the north side, birds from the two populations do not react to one another's song, and so remain distinct without significant interbreeding. In effect, they behave there as different species, but are linked by a continuous population, each part interbreeding with its neighbours, forming a ring around the rest of the plateau. The two forms are assumed to migrate southward down the west and

east sides of the plateau respectively to reach their different wintering areas further south.

Another type of divide exists in populations in which some individuals take one direction to a wintering area, while others from the same place take a different direction to another wintering area. An example is provided by the central European Blackcaps, some of which began to migrate west-northwest to winter in Britain in the mid-20th century (Chapter 15). These birds differ from those that continue to migrate southwest to Iberia. Although birds from both types currently breed in the same general area, they show assortative mating, pairing with birds of their own directional preference much more often than expected by chance, owing mainly to a difference in the dates they arrive and pair up in breeding areas (Bearhop *et al.,* 2005). This divide in this area may be temporary, and in time one migratory genotype may gradually replace the other there, giving rise somewhere to a clear-cut divide separating west-northwest from southwest migrating populations.

THE CROSSING OF BARRIERS

It is easy to imagine how migration might evolve in species that have suitable areas for breeding and wintering adjacent to one another, enabling them to gradually lengthen the journey. But it is less easy to understand the origin of those migrations in which breeding and wintering areas are separated by hundreds or thousands of kilometres. How can birds from one part of the world come to winter in another part so far away when the intervening area is unsuitable?

The main difficulty is in explaining how land birds could evolve the ability to cross large stretches of sea or desert, which for most such species offer no opportunities for refuelling. If a species were to evolve such a migration today, it would entail not a gradual change in migration physiology but a big abrupt change, with markedly greater fat deposition and flight lengths. One obvious possibility is that barriers which are now wide, such as the Sahara desert, were

once narrow, so that a progressively longer migration could have evolved gradually over the generations as the barrier widened. Successive generations would then have been able to lengthen their flights bit by bit to match the need. The difficulty of evolving a migration over the Sahara (as it is now) may help to explain why most species known to have spread westward in Eurasia in historical times still return to traditional winter quarters in Southeast Asia, even though apparently suitable habitats exist at closer distance in Africa to the south.

Climate changes, with their effects on vegetation, could have led to the splitting of a once-contiguous vegetation type, in the way that the Sahara now separates scrub to the north and south, or the boreal forest in Asia now separates open tundra to the north from open steppe to the south. Alternatively, although a barrier may always have been wide, it may once have held more potential stopping places than are present now, perhaps more oases in the desert or more islands in the sea. If such stopping places disappeared gradually, this would again have allowed the progressive development of longer flights. This process is happening today as stopover sites are lost, either through climate change (as in the expansion of the Sahara) or by more direct human action in destroying already fragmented habitats.

Another question, applicable to even longer timescales than the Pleistocene glaciations, is how land birds evolved migrations over substantial sea areas where they could not stop to rest or feed. Many such migrations could have evolved gradually by progressive corner-cutting, as birds made first short then longer sea-crossings. For example, in the western Mediterranean, the shortest crossing of about 15 km is at Gibraltar, which most birds can cross without difficulty. But if birds left the east coast of Spain before reaching Gibraltar, they could achieve a more direct (shorter) route to North Africa, but only at the cost of a longer sea-crossing. Moving round the coast to southern France, the sea-crossing would be even longer, but the saving on overall distance even greater. Providing the birds, in evolutionary time, could make this change from short to long sea

crossings gradually, it would allow for the progressive development of other necessary adaptations, such as the accumulation of greater fat reserves. Nowadays, while some birds take the narrowest crossing at Gibraltar, others cross the Mediterranean at its widest parts, involving non-stop over-water flights of more than 1,000 km, and some even cross both the Mediterranean and Sahara in a single flight (Chapter 8). All stages in this hypothetical sequence of developments are still present today in different species, or in different populations of the same species.

Even more extreme examples of over-water flights occur elsewhere. Recall the Bar-tailed Godwits that breed in Alaska and migrate over the Pacific to winter in New Zealand. Again, it is likely that the ancestors of these birds once migrated down the Asian coastline and then to Australia (as other populations of Bar-tailed Godwits still do), and then evolved their present trans-Pacific route by progressive corner-cutting, making longer and longer non-stop over-water flights. In parts of the Pacific, island-hopping may also have helped. Steps in the evolution of long-distance barrier-crossing can be inferred from existing patterns of variation. They would allow gradual development of a long-distance migration system over hostile substrate, without the need for a sudden step-change in either direction or migratory fattening. This makes it easier to understand how such long and difficult migrations might have evolved, but it does not of course prove that they did evolve in this way.

Topographic influences

Sometimes a long roundabout migration route is of advantage, an end result in its own right, rather than a historical legacy or stage on the way to a more direct route. By taking a roundabout route, birds may avoid crossing an area of unsuitable habitat, even though such a crossing may seem within their capabilities. The detour may offer several benefits, such as: (1) reduced risk from adverse weather or predators; (2) reduced energy costs, despite the longer

journey (if, for example, winds are more favourable); or (3) suitable habitat in which the birds can stop and feed each day, thereby saving on fuel transportation costs. In the evolution of a number of common overland detour routes taken by birds, the saving on fuel transportation costs was probably paramount, as also in some loop migrations discussed below (Alerstam, 2001).

In Eurasia, major obstacles to migration, such as several mountain ranges, various deserts and the Mediterranean Sea, run west–east, roughly at right angles to the mainly north–south migration routes. While some birds migrate over these obstacles, others migrate to one side or the other to avoid them. Such avoidance gives another reason, in addition to the glacial legacy hypothesis, for a separation of autumn migration directions in Europe and elsewhere between southwest and southeast. Some 45 species of central European passerines from north of the Alps start their migration in a southwest direction, 10 in a southeast direction, while only 3 species converge southward toward Italy and the central Mediterranean. In addition, 13 species show a spread of directions between southwest and southeast, and 16 others show a migratory divide that to a large extent separates migrants moving southwest from those moving southeast (Bairlein, 1985c). Most of these species thereby avoid crossing the Alps.

In general, seasonal and other barriers may have at least three main consequences for bird migration: (1) they may stop onward movement altogether; (2) they may lead to genetically controlled or optional detours to get round the barrier; or (3) they may lead to modification of the fattening programme, ensuring that birds accumulate enough fuel beforehand to cross the barrier without any en route feeding.

LOOP MIGRATIONS

Many bird populations take markedly different routes on their outward and return journeys. So-called loop migrations have been described from observations and ring recoveries for passerines,

shorebirds, raptors, seabirds and others from several parts of the world. Some European species, such as the Pied Flycatcher, travel into Africa via Iberia, but return mainly by a more central route through Italy, the whole migration following an anticlockwise loop (Fig. 191). The same holds for the Willow Warbler, Garden Warbler, Common Whitethroat, Yellow Wagtail, Sand Martin and Barn Swallow. Other species, such as the Wood Warbler, return by a more westward route of their outward route through Italy, the whole migration following a clockwise loop. Yet other species, such as the Red-backed Shrike, travel south through the eastern Mediterranean region; but return further east mainly via Arabia, on another anti-clockwise loop. In association with the different routes, patterns of migratory fuelling may also differ between autumn and spring, depending on the numbers and spacing of stopping sites (Chapter 6).

Evidence that both the outward and return routes are under genetic influence comes from the directional preferences shown by loop migrants in captivity. These directions are not simply reversed between autumn and spring, but sometimes involve a consistent direction (corresponding to a straight route) at one season and a changing direction (corresponding to a long detour) at the other, as shown in young Garden Warblers and Pied Flycatchers in captivity (Chapter 15). In many populations that perform loop migrations, one route might be considered as the ancestral route, perhaps following the path of colonisation, and the other the derived route, evolved to shorten the distance or to avoid seasonally adverse conditions. Loop migrations show that selection pressures on the outward journey are sometimes different from those on the return journey, and that birds can adapt accordingly.

AN UNUSUAL FEATURE OF THE EURASIAN–AFRICAN MIGRATION SYSTEM

Most parts of the northern hemisphere support some bird species which migrate long distances to winter in the tropics and beyond.

Compared to the migration systems of North–South America and eastern Asia, the Eurasian–Afrotropical system has far fewer species overall. It also has an unusually small proportion of forest-dwelling species, and an unusually large proportion of scrub-dwelling ones. Excluding seabirds, the overall numbers of long-distance migratory species in the North–South American and eastern Asian systems are similar (about 338 species in both), whereas the Eurasian–Afrotropical system has only about 186 species. And whereas the North American forests hold about 112 species of longdistance migrants and the eastern Asian forests about 107 species, the west Eurasian forests hold only about 48 (Moreau, 1972; Rappole, 1995). Nearly all the North American and Asian species that breed in forests also winter in some type of forest, but only about six Eurasian migrants winter in forest, namely the European Honey Buzzard, Eurasian Golden Oriole, European Pied Flycatcher, Collared Flycatcher, Semi-collared Flycatcher and Wood Warbler. Of these, only the Wood Warbler winters primarily in humid evergreen forest, and all the others occur more commonly in open deciduous woodland. All the remaining Eurasian–Afrotropical migrants (apart from aquatic and coastal birds) winter in savannah, scrub or tall herbaceous vegetation such as reeds (Moreau, 1972; Böhning-Gaese & Oberrath, 2003).

Nevertheless, the current poverty of the west Eurasian forest avifauna cannot be attributed entirely to the effects of the Sahara desert as a barrier to spread. The forests in Europe were much more thoroughly obliterated by glaciations than were the forests of North America and eastern Asia. This process is known from fossil and other evidence to have eliminated large numbers of the plants and animals found in European forests in pre-glacial times (many of which still survive today in Asian forests, at least at the generic level). Among birds, extinctions are likely to have included migratory and resident species. No such catastrophe is likely to have affected scrub species, however, contributing to their predominance among current Eurasian–African migrants.

CONCLUDING REMARKS

It is clearly unwise to assume that, because some birds have altered their migrations in recent decades, all can do so. Nor can they readily change all aspects of their migrations. Most of the observed patterns of alteration involve gradual change, in which each incremental step is itself of benefit. Patterns that seem resistant to change include those that would involve a marked step-change in some feature, such as direction, to be viable, while the intermediate steps would be lethal. The birds may thus be locked into some genetically controlled patterns simply because the big step-changes needed to break free of them are unlikely to arise by a single mutation. Some extreme journeys of today, involving long flights over sea or desert, can most plausibly be explained by their gradual development, followed by eventual loss of the intermediate stages. Apparent legacies of the past are clearly evident in the migration routes and distribution patterns of many birds throughout the northern hemisphere. They represent carry-overs from an earlier stage in the earth's history, which may not now be ideal, but persist because they are not markedly disadvantageous under present conditions. They illustrate a general point that natural selection cannot start on a clean slate; it can only act on a pre-existing gene pool, evolved under different (historical) conditions.

Many of the ideas proposed in this chapter, although based on a firm observational foundation, are necessarily speculative, but they facilitate a fuller consideration of the evolutionary and ecological background to current migration patterns. They show how complex migration patterns might have arisen step by step, each of which brings benefits in its own right. They cannot be tested quantitatively in the field, so in a sense are less scientifically satisfying than are the quantitative or experimental studies that are possible for other aspects of migration. Yet they help us to understand how some otherwise puzzling aspects of current bird migration patterns might have developed, and if we disregard them merely because they cannot be formally tested, we risk ignoring some of the most

important evolutionary aspects of the subject. In the 1960s, almost all aspects of the evolution and genetic control of bird migration were speculative, and increasingly they have been confirmed or modified by experiment or by genetic studies. Already DNA analyses of certain species have helped to define post-glacial colonisation routes, and confirm that they match some current migration routes. Perhaps, in the coming years, other as yet intractable aspects of this subject will yield to ingenuity or new methodology.

CHAPTER 18

Geographical Patterns

Of all the types of movements undertaken by birds, regular seasonal migration is the most impressive, partly because of the enormous numbers of birds involved, and partly because of the huge geographical scale it encompasses. Associated with seasonal fluctuations in climate and food supplies, migration leads twice each year to massive changes in the distribution of birds over the earth's surface. High-latitude regions receive birds mainly in the breeding season, while lower-latitude regions support wintering birds from higher latitudes, as well as year-round residents. Some species occupy habitats over winter that they could not use for breeding, and then establish themselves in breeding areas that would not support them in winter. This applies, for example, to all Arctic-nesting shorebirds which occur in winter on coastal mudflats where, due to tidal flooding, nesting would be impossible; they then migrate north to breed on the Arctic tundra which is frozen and snow-covered for the rest of the year. Migration thus increases the numbers of species found in particular regions, even though some are present for only part of the year.

LATITUDINAL TRENDS

In general, the proportions of bird species that leave their breeding areas for the winter increase from low to high latitudes, as the contrast between summer and winter conditions widens (Newton & Dale, 1996a, 1996b). Progressing northward up the western seaboard of North Africa and Europe, the proportion of breeding

bird species which move out totally to winter further south increases from 29 per cent of species at 30°N (North Africa) to 83 per cent of species at 80°N (Svalbard), a mean increase of 1.3 per cent of breeding species for every degree of latitude (Fig. 193).

Let us examine winter conditions in more detail. In Europe, over much of the 20th century, mean January temperatures exceeded 10°C only in southern Spain; they lay within the range 0–5°C in much of western Europe, but fell below freezing and as low as -15°C in most of Fennoscandia, plunging to -20°C in Novaya Zemlya in the far north. Minimum winter daylengths were around 11 hours at 35°N in southern Europe but decreased to zero at the Arctic Circle. The season of plant growth lasted six to nine months at 35–50°? (mainly Spain and France), but shrank to less than three months in Svalbard, a mean decline in growing season of about one month for every 11° of latitude. In continental western Europe, most fresh waters north of 56°N (latitude of Copenhagen) froze in winter, remaining open for most of the time in Britain and Ireland. Much of the Baltic and Barents Seas also iced over during the course of the winter, closing these areas for seabirds. Throughout much of this region, however, temperatures are now rising as part of human-induced 'global warming'. Bird migration patterns are changing accordingly (Chapter 16), but they still relate to geographical gradients in prevailing conditions.

The converse of these latitudinal patterns is shown in Figure 194 as the proportions of the species wintering at different latitudes that move north for the summer. As expected, this proportion is greatest in the south: in western Europe, affecting 36 per cent of species wintering at 35°N (northernmost Africa), declining northward to 8 per cent of species wintering at 70°N (northernmost Norway, mostly seabirds), with none at 8o°N (Svalbard). The precise relationship varies somewhat between birds of different habitats, with aquatic species being especially responsive to freezing. In addition, 23 per cent of all species breeding in western Europe vacate the continent completely in autumn for the tropics, returning in spring (Newton & Dale, 1996a).

The proportions of all bird species that are migratory are correlated not only with latitude, but also with various climatic factors that vary with latitude, such as the temperatures of the hottest or coldest months, or the temperature difference between the hottest and coldest months (Newton & Dale, 1996a). These various measures are of course interrelated, but what matters is the extent of climatic difference between summer and winter. It is this difference that, for many birds, governs the difference in food supply between summer and winter at particular latitudes, and hence the difference in the ability of the local environment to support birds at the two seasons. Over a geographical temperature gradient, waterbirds experience a stepwise change in habitat suitability associated with the abrupt freezing of fresh waters below o°C, and of salt waters at a few degrees lower. Only in special conditions of surface agitation do waters remain open at lower temperatures, enabling species such as the Dipper to remain over winter on mountain streams at higher latitudes and altitudes than otherwise possible.

In some mid-latitude areas, while similar numbers of species maybe present in summer and winter, their composition changes somewhat between seasons, as some species from lower latitudes are present only in summer and other species from higher latitudes only in winter. In the British Isles, insectivorous swallows and warblers arrive from the tropics for the summer, whereas fruit-eating (or omnivorous) thrushes from further north and east arrive for the winter. Seasonal changes in bird communities in particular regions are thus tied to seasonal changes in the types of food available. For migrants often exploit seasonal abundances in both their breeding and non-breeding areas. It is a lifestyle that, for obvious reasons, is much more developed in birds than in most other animals.

MIGRATION AND DIET

Superimposed on the overall latitudinal trend is another related to diet. Broadly speaking, those species that are resident year-round in

a particular region exploit food supplies that are available there all year, whereas those that leave after breeding exploit foods that disappear then. In the northern coniferous forests, for example, residents include mainly species that feed directly from trees, on bark-dwelling arthropods (tits, tree-creepers, wrens), fruits and seeds (corvids, finches, tits), buds or other dormant vegetation (grouse), or that eat mammals and other birds (corvids, raptors and owls). Almost the entire resident land-bird fauna in boreal regions falls into one or other of these dietary categories, and many species are generalists, able to eat both plant and animal matter. Such flexibility enables some species to change their diets between seasons, for example eating mainly invertebrates in summer and seeds or fruits in winter. In contrast, species that depart for the winter include those which specialise year-round on active leaf-dwelling or aerial insects (warblers, hirundines) or which eat foods that become inaccessible under snow or ice (ground-feeding finches, thrushes, larks and pipits, some raptors, waterfowl and waders). Progressing southwards, as winters become less severe, the range of bird dietary types that remain for the winter increases, as a wider range of food types remains available year-round.

To illustrate in more detail the link between migration and seasonal food changes, consider the various European songbirds. Different species feed either on (1) insects or other invertebrates, (2) seeds and fruits, or (3) a mixture of both categories (Newton, 1995b). Of these food types, seeds and fruits are clearly much more available in winter at high latitudes than are insects. Within each dietary group, the proportion of migrants increases with latitude, following the general trend in birds as a whole. But at all latitudes north of about 35°N, a larger proportion of insect-eaters than seed-eaters leaves, while species with mixed insect-seed diets are intermediate. Furthermore, the insect-eaters generally move longer distances, many wintering in the tropics and some south of the equator (Fig. 197). The result is that insect-eaters are concentrated at more southern latitudes in winter than are seed-eaters from the same breeding areas. Among these general relationships, specific

exceptions occur, such as the seed-eating European Turtle Dove, which winters in Africa.

As a second example, consider the various European raptors (Newton, 1998a). Such species can be divided according to whether they eat primarily warmblooded prey (birds and mammals which remain active and available in winter at high latitudes) or cold-blooded prey (reptiles, amphibia and insects, which become inactive and unavailable in winter). Within each raptor dietary type, the proportion of migratory species again increases with latitude, but at any particular latitude, a larger proportion of the species that eat cold-blooded prey than of those whose prey is warm-blooded leaves for the winter, while species with mixed diets show intermediate patterns. Those species that eat coldblooded prey also migrate furthest. The reasons for this difference are fairly obvious, as species which eat cold-blooded prey and breed at high latitudes must winter in the tropics or in southern hemisphere temperate areas if they are to have access to the same type of prey year-round. All six insectivorous raptor species winter in Africa, four of them entirely (and two largely) south of the equator, where the seasons are reversed. They therefore live in almost perpetual summer, first north then south of the equator, in conditions in which they have easy access to their insect prey year-round. Such patterns again underline the link between migration and the seasonal changes in their specific food sources.

The overall effect of bird migration, then, is to alter the latitudinal distribution of birds between summer and winter, so that species numbers in the northern hemisphere are at their greatest in the northern summer, and in the southern hemisphere in the southern summer (northern winter). The entire assemblage of bird species that in spring-summer breeds north of 25˚N in North Africa and Europe extends in winter from northern Europe southwards at least as far as the southern tip of Africa at 35˚S (Fig. 198). Forty-eight species of Eurasian birds reach the southern Cape (Harrison *et al.,* 1997), and some seabirds extend into the seas beyond. They include three skua species, five tern species and Sabine's Gull.

ALTITUDINAL MIGRATION

By moving a few hundred metres down the sides of a mountain, some birds can achieve as much climatic benefit as by moving several hundred kilometres to lower latitudes, but without the extra winter daylength. Mirroring the latitudinal trend, with rising altitude, increasing proportions of breeding species move out for the winter, but in contrast to latitudinal migration, altitudinal movements can be in any directions that reach lower ground. They occur on mountain ranges worldwide, from the Himalayas to the Andes, and can involve a large proportion of local montane species. Some such species appear to be obligate migrants, the entire population leaving for the non-breeding season, whereas others appear to be partial migrants, with year-to-year variations in the proportions of individuals that move to lower ground. Altitudinal movements are not very conspicuous in the British Isles, because our mountains are too low, but some upland species move to lower ground for the winter and others during spells of hard weather. On the high tops of the Scottish Cairngorms, a few species are found year-round, such as Rock Ptarmigan, Raven and Golden Eagle, and several others breed there in summer. Altitudinal movements are more developed in the Alps and other high European ranges, as exemplified by the Snow Finch, Water Pipit, Citril Finch and others.

Bird species differ in the degree of separation of breeding and wintering ranges, from coincident (in year-round residents), through overlapping, to completely separate (Fig. 200). The greatest separation occurs in species that breed only at high latitudes in one hemisphere and winter only at high latitudes in the opposite hemisphere. The Arctic Tern is probably the most extreme example, breeding between about 50^{e} and 80°N and wintering between about 40° and 70°S, giving a 90° latitudinal gap between breeding and wintering ranges.

Despite the general relationship between sizes of breeding and wintering areas, nearly 70 per cent of species have a breeding range noticeably larger than their wintering range. The most extreme

example is the Lesser Grey Shrike *Lanius minor,* whose breeding range in Eurasia covers an area at least seven times greater than its known wintering range, which is centred on the Kalahari basin in southwest Africa. The fact that most land-bird migrants live at greater average densities in Africa than in Eurasia may reflect differences in the abilities of the two regions to support the birds at the times they are present. It might also result from a change in many species from territorial to flocking behaviour, or from sedentary to mobile, enabling birds to more effectively exploit local food abundances. But whatever the reason for the differences between sizes of breeding and wintering ranges, a similar phenomenon occurs in the New World, where migrants from large parts of North America concentrate each winter in a relatively small area in the northern neotropics.

Most arctic-nesting wader species switch from a widespread distribution on the tundra in summer to a linear distribution on coastlines in winter. They therefore breed only in a narrow span of latitude, mostly between 70° and 80°N, but in winter extend southwards over more than 95° of latitude between about 60°N and 35°S, the southern tip of Africa (Newton & Dale, 1997). Some shorebird species, such as the Ruddy Turnstone, can be found in winter on almost any rocky coast within this wide latitudinal span, while others, such as the Red Knot, maybe restricted to the relatively few sites where suitable conditions are found, but occur there in great numbers. As many waders change habitats between seasons, it is difficult to compare the sizes of their breeding and wintering ranges but, as a group, they show no relationship between the latitudinal extents of breeding and wintering ranges (Newton & Dale, 1997). Overall, then, the correlation between summer and winter range sizes is most apparent among species that occupy terrestrial and freshwater habitats year-round.

LONGITUDINAL AND LATITUDINAL MIGRATION PATTERNS

Longitudinal patterns

Within species, birds that breed furthest west in the breeding range tend to winter furthest west in the non-breeding range, and those that breed furthest east also winter furthest east. Allowing for the uneven distribution of landmasses, this holds in both the Old and New Worlds. It reflects the more or less parallel migrations of populations, as revealed by ring recoveries from most groups of birds (Moreau, 1972; Newton, 2008). It is illustrated for the Chaffinch in Figure 202.

Such more-or-less parallel migrations could be explained by the birds from different segments of the breeding range taking the shortest routes to their wintering areas at lower latitudes. Other factors being equal, any birds that deviate from the parallel pattern, crossing the routes of other populations, are likely to lengthen their journeys, and thus incur greater migration costs. By spreading populations across suitable habitat, parallel migrations also reduce competition among individuals, providing another selection pressure to maintain the pattern.

While most bird species seem to migrate on a broad front, some species travel along relatively narrow corridors, and seldom stray beyond them. Examples include some species of cranes, geese and shorebirds which travel between traditional widely spaced stopover and wintering sites. Some populations of geese remain separated from one another year-round as they move from different breeding localities along different flyways to their own traditional wintering areas. Examples include the Barnacle Goose and Pink-footed Goose, in both of which birds from three separate breeding areas have distinct migration and wintering areas (Fig. 203). This situation of narrow separated routes is no different in principle from the parallel but broad-front migration of most widespread bird species, except that the different breeding or wintering areas of the geese are localised and well separated.

In latitudinal distribution, at least three main patterns are found within species (Chapter 17). In the first pattern, of chain migration,

more northern (often larger) birds may replace others that breed further south, so that some of the same areas are occupied year-round, but by one population in summer and another from further north in winter (Fig. 205). The different populations thus maintain the same latitudinal position with respect to one another year-round, in that the population that breeds furthest north in the breeding range also winters furthest north in the wintering range. Some species that reveal chain migration within the British Isles were mentioned in Chapter 3; and on a wider European scale, other species exhibiting this pattern include the Goldfinch, Linnet, White Wagtail, Eurasian Sparrowhawk, Tufted Duck and Common Gull.

In chain migration, the distances maybe more or less similar among populations, even though these populations migrate between different areas, but in the other two latitudinal patterns, the high-latitude populations migrate furthest, with the greatest population differences occurring in leapfrog migrants. The past circumstances which may have given rise to these different latitudinal patterns were discussed in Chapter 17.

CONCLUDING REMARKS

The overriding role of food supplies in influencing the movement patterns of birds is evident from: (1) the link between migration and climatic seasonality, with increasing proportions of migrants in increasingly seasonal environments; (2) the relationship in different species between migration and diet; (3) within species, the regional variations in the proportions of birds that leave for the non-breeding season; (4) the locations of wintering areas; and (5) the precise seasonal timing of movements, so that birds are absent from breeding areas at a time when their particular foods are scarce there (Chapter 11). Some authors have stressed the role of climate and competition in influencing migration patterns, but both these factors are likely to act primarily through the food supply.

Migratory habits are so closely related to diet, and to the seasonal fluctuations in the food types involved, that it is hard to tell whether

any other factors influence migration beyond those that act through food (such as climate and competition). The main problem is that diet is related to virtually all aspects of the morphology, ecology and behaviour of birds, as well as to migration, so that almost any aspect of bird biology could seem to be relevant to migration through association.

In species that migrate between the northern and the southern hemispheres, the question arises why the same individuals do not breed twice in one year, in both summer and winter quarters. One reason in many species is that individuals moult while in winter quarters, a process that takes several weeks or months and could not be undertaken at the same time as breeding (the two processes being mutually exclusive in most birds; Chapter 9). Another reason is that many migratory species do not remain for long in the same place in the non-breeding period, but periodically move to other areas in response to changes in food supplies (Chapter 22). This exploitation of temporary abundances is one way in which individual migrants in the southern hemisphere could reduce competition with the local birds which, breeding at that time, are tied to fixed nesting areas. Neither explanation applies to all trans-equatorial migratory species, however, and there are still some that remain sedentary in both their breeding and wintering areas, and would seem able to breed in both, six months apart, but do not.

Appreciation of the large-scale, long-distance movements of birds highlights the conservation problems that migratory birds present. Depending on a series of areas, spanning a wide range of latitude, such species are vulnerable to human impact, not only in breeding and wintering areas, but also at crucial stopover sites en route. Nature reserves established in one region can be expected to protect some species for only a few weeks each year, before they move on. It underlines the needs for information on migration routes, and also for international collaboration in the conservation of migrants, a concept that long since led to concerted action for some groups of birds, such as waterfowl, in various parts of the world.

CHAPTER 19

Irruptions

One of the most striking features of most bird migration is its regularity. Most populations of birds migrate at about the same dates, in the same directions and for similar distances each year, with many individuals returning year after year to the same breeding and wintering localities. But consistency of movement is advantageous only in predictable environments, where birds can be sure of finding suitable conditions year after year in the same breeding or wintering areas. Other bird species exploit habitats or food supplies which vary unpredictably in distribution and abundance from year to year. Such species show greater flexibility in their movement patterns, concentrating in different areas in different years, wherever resources are plentiful at the time. They are often called nomadic or irruptive migrants to distinguish them from regular migrants. Their movements appear largely opportunistic (facultative) in nature, occurring in direct response to prevailing conditions (Chapter 10).

Irruptive migrants are discussed here in particular detail because of the light they shed on the role of food supplies in bird movements. Typical examples include: (1) boreal finches and others that depend on fluctuating tree-seed and fruit crops; (2) owls and others that specialise on cyclically fluctuating rodent populations; and (3) waterbirds that use ephemeral wetlands created by irregular rainfall. Most such species are hard to study because they breed mainly in regions with few people where the chances of obtaining ring recoveries are extremely small. And because of their nomadic behaviour, many are seldom in the same place long enough for

detailed study. For these reasons, an understanding of their movement patterns must be pieced together from snippets of information collected over many years, and scattered widely through the ornithological literature.

Among the specialist seed- and fruit-eaters, most individuals stay in the north in years when food is plentiful there, wintering within, or just south of, their breeding areas, but moving further south in years when food is scarce. The effect of widespread crop failure is often accentuated because the birds themselves tend to be numerous at such times, the result of good breeding and survival in previous years when food was plentiful (Lack, 1954; Berndt & Henss, 1967; Köenig & Knops, 2001). Any great imbalance between the birds and their food seems to stimulate large-scale emigration.

Food supplies

Every naturalist knows that tree-fruit crops vary greatly in size from year to year, and in some years fail completely. Fruiting depends partly on the natural rhythm of the trees themselves and partly on the weather. Trees of most species require more than one year to accumulate the nutrient reserves necessary to produce a fruit crop. In addition, for a good crop, the weather must ideally be fine and warm in the preceding autumn when the fruit buds form, and again in the spring when the flowers set. Otherwise, the crop is reduced or delayed for another year. In any one area, most of the trees of a species fruit in phase with one another, and often those of different species also fruit in phase, partly because they come under the same weather conditions. The result is an enormous profusion of tree fruits in some years and practically none in others: good crops are almost always followed by poor ones (Fig. 208; Köenig & Knops, 1998, 2000). Nevertheless, the annual seed crops of some tree species fluctuate less than others, with Scots Pine *Pinus sylvestris* producing smaller but more consistent crops than Norway Spruce *Picea abies,* and Alder *Alnus glutinosa* more consistent crops than Birch *Betula pendens* and B. *pubescens.*

Besides their total production, the timings of ripening and release of seeds are also important for seed-eating birds. Some tree species release most of their seeds within a short period in autumn, others more slowly over winter, and yet others in spring, or even more slowly over two or more years. Prolonged release occurs in some Pine *Pinus* and Larch *Larix* species, which can thereby provide food for seed-eaters even in non-cropping years. For most finches, the seeds are best available while they remain on the tree; once they fall to the ground, they are either rapidly removed by other animals or covered by snow. Among the European irruptive finches that depend on tree seeds, only the Brambling feeds chiefly on the ground in winter, although most others do so occasionally.

Bird species involved

Seed- or fruit-eating species that are known for irruptive migrations are listed in Table E (overleaf), along with their main food plants. Most species eat mainly different foods in summer and winter and, like most birds, migrate twice each year, away from the breeding range in autumn and back in spring. Some such species, such as the Common Redpoll and Eurasian Siskin, eat mainly seeds year-round, but different types of seeds at different seasons. Other species, such as the Bohemian Waxwing and Brambling, eat mainly insects in summer and seeds (or fleshy fruits) in winter. Waxwings and Bramblings tend to concentrate in summer in areas with insect outbreaks, the Brambling being fond of Autumnal Moth *Epirrita autumnata* caterpillars, which in some years infest birch trees (Enemar *et al.,* 1984; Lindström *et al.,* 2005). In contrast to all other species, crossbills and nutcrackers eat conifer seeds year-round (apart from Thick-billed Nutcrackers in Europe, which eat hazelnuts and other foods). These birds apparently make only one major movement each year, from regions where last year's crops were good to regions where the current year's crops are abundant (see later).

TWICE-YEARLY MIGRANTS

Twice-yearly migrants generally move towards lower latitudes in autumn and to higher ones in spring, but they may concentrate to breed and winter in different areas in different years, wherever food is plentiful at the time. Their local numbers therefore fluctuate greatly from year to year according to local food supplies, and in winter they may range between absence in years when appropriate tree seeds are lacking to thousands of birds per square kilometre in years when such seeds are plentiful. The bird species involved seem to move each autumn only until they find areas rich in food, and then settle (Svärdson, 1957; Newton, 1972; Jenni, 1987). In consequence, the distance travelled by most migrants varies from year to year, according to where the crops are good, and only when the migrants are exceptionally numerous, or their food is generally scarce, do they reach the furthest parts of their potential wintering range, as an ‘invasion’. The advantages of stopping in the first suitable feeding areas encountered are presumably that birds travel no further than necessary and do not pass over good feeding areas which might be the only ones available that year.

Other species also exploit the same foods as irruptive species, but do not depend so heavily on them, so they are less affected by the fluctuations in fruiting. Similarly, some of the species listed in Table E maybe irruptive in some parts of their range but not in others, depending on the breadth of the diet and the level of fluctuation in the total food supply. Populations that have access to a wide range of dietary items are less likely to experience a shortage of all types in the same year. Examples of species that behave as irruptive migrants in only parts of their range include the Eurasian Bullfinch, Wood Nuthatch, various titmice and Eurasian Jay. In other parts, they are either residents or regular migrants.

TABLE E. Documented year-to-year correlations between bird abundance and food supply in some seed-eating and fruit-eating birds. (Compiled from sources listed in Newton, 2008)

	Preferred winter food†	*Summer densities*	*Winter densities*	*Autumn emigration*
Great Spotted Woodpecker *Dendrocopos major*	Spruce, Pine and other seeds	+	+	+
Bohemian Waxwing *Bombycilla garrulus*	Rowan and other berries			+
Fieldfare *Turdus pilaris*	Rowan and other berries			+
Coal Tit *Parus ater*	Spruce seeds, insects			+
Great Tit *Parus major*	Beech seeds		+	+
Blue Tit *Parus caeruleus*	Beech seeds		+	+
Wood Nuthatch *Sitta europaea*	Spruce seeds			+
Brambling *Fringilla montifringilla*	Beech seeds	+	+	+
Eurasian Siskin *Carduelis spinus*	Birch, Alder, conifer seeds	+	+	+
Common Redpoll *Carduelis flammea*	Birch and Alder seeds	+		+
Arctic Redpoll *Carduelis hornemanni*	Birch and other seeds	+		+
Eurasian Bullfinch *Pyrrhula pyrrhula*	Various tree seeds and berries			+
Pine Grosbeak *Pinicola enucleator*	Rowan and other fruits		+	+
Common Crossbill *Loxia curvirostra*	Spruce and other conifer seeds	+	+	+
Two-barred Crossbill *Loxia leucoptera*	Larch and other conifer seeds	+	+	+
Parrot Crossbill *Loxia pytyopsittacus*	Scots Pine seeds	+	+	+
Eurasian Jay *Garrulus glandarius*	Oak seeds			+
Thick-billed Nutcracker *Nucifraga c. macrorhynchos*	Hazel and Stone Pine seeds			
Slender-billed Nutcracker *Nucifraga c. caryocatactes*	Siberian Stone Pine seeds, Brush Pine seeds			+

In common with local food supplies, local breeding densities of irruptive seed-eaters can vary greatly from year to year. For example, local densities of Common Redpolls in northern Sweden fluctuated about 39-fold over a 20-year period, with the highest densities coinciding with exceptionally good Dwarf Birch *Betula nana* crops, the low bushes and their seed-catkins protected under snow since the previous summer. Densities of Eurasian Siskins fluctuated between 6- and 50-fold in four different areas in parallel with the spruce cone crop (Fig. 210); while densities of Bramblings

fluctuated between 5- and 26-fold in three different areas in parallel with the abundance of Autumnal Moth caterpillars (Silvola, 1967; Lindström, 1987; Hogstad, 2000). In all these species, the increases in numbers from one year to the next were often far greater than could be explained by high survival and reproduction from the previous year, so must have involved immigration. Such observations led to the inference that year-to-year changes in local breeding densities were due primarily to movements—immigration or emigration, depending on local food conditions at the time.

Among populations of regular migrants, as shown by ringing, most surviving individuals return to breed in the same limited area year after year. In some of these species, the same also holds for wintering areas (Chapter 13). Among irruptive migrants, in contrast, return rates to the same study area are normally very low. For example, among Bramblings trapped in the breeding season in various areas, individuals were seldom or never caught in the same locality in a later year, so that each year's occupants were different from those the year before (Mikkonen, 1983; Lindström *et al.,* 2005; Hogstad, 2000). In one such study, only 7 (0.6 per cent) of 1,238 adults were re-trapped in the same area in a later year, and none of 1,806 juveniles, despite an annual trapping programme over many years (Lindström *et al.,* 2005). In other irruptive species, return rates were extremely low (all less that 8 per cent; Newton, 2008), compared with what would be expected from their annual survival rates. Again, the implication was that large proportions of individuals changed their nesting locations from year to year.

The small numbers of relevant ring recoveries available for irruptive species confirm that some individuals have indeed occurred in widely separated localities in different breeding seasons. Three Bramblings were found respectively at sites 280 km, 420 km and 580 km apart, one Northern Bullfinch at places 424 km apart (natal dispersal), two Common Redpolls at locations 280 km and 550 km apart, one Lesser Redpoll C. *cabaret* at sites 300 km apart (natal dispersal) and one Eurasian Siskin at places 120 km apart. On the other hand, some adult Siskins in south Scotland were found in

the same breeding area in successive years, despite large fluctuations in cone crops and breeding numbers from year to year (Shaw, 1990). Similar records are available for other irruptive finches in North America (Brewer *et al.,* 2000). Clearly, long-distance moves from one breeding area to another are not unusual in irruptive finches, and far more frequent than in most other bird species. In effect, most individuals of irruptive species settle in different areas each year as they return from spring migration.

Autumn emigration

Typically in irruptive species, the numbers of individuals undertaking migration, and the distances involved, vary greatly from year to year. Huge annual fluctuations are evident at migration watch sites, such as Falsterbo and Ottenby in Sweden, where the numbers of some irruptive species can vary from nil in some years to many thousands in other years (Fig. 211). During the 36 years from 1973 to 2008, the Eurasian Jay count in 29 years at Falsterbo was nil, but in 1977 it reached more than 16,000 individuals and in 1994 more than 19,000. Over the same period at the same site, Nutcrackers varied from nil in 14 years to 1,763 in 1995; Bohemian Waxwings from nil in 11 years to nearly 23,000 in 2004; Common Redpolls from nil in 2 years to more than 16,000 in 2000; Northern Bullfinches from nil in 2 years to more than 11,000 in 2005; and Common Crossbills from nil in 1973 to more than 15,000 in 1990 and more than 20,000 in 2002. These annual fluctuations were far greater than those recorded in more regular migrants (counts of which typically varied by two- to fourfold, occasionally up to tenfold, between years). Similar differences between irruptive and regular migrants have been recorded at other watch sites elsewhere in Europe (e.g. Dorka, 1966; Edelstam, 1972; Gatter, 2000).

The amount of autumn emigration has been related to food supplies in almost all seed-eating and fruit-eating species discussed here, being greatest in years when high bird densities coincide with poor seed crops (Table E). Different species that depend heavily on

the same seed or fruit crops as one another tend to irrupt in the same years. In Europe, they include the Blue Tit and Great Tit, which both feed heavily on Beech *Fagus sylvatica* mast, and the Common Crossbill and Great Spotted Woodpecker, which both feed heavily on spruce seeds. Where different tree species fruit in phase with one another, the numbers of participating species is increased further. Over much of boreal North America, conifer and other tree crops tend to fluctuate biennially, and in the alternate years with poor crops, several species that depend on them migrate to lower latitudes. The migrations of irruptive species are therefore much more regular in North America than in Europe and much more synchronised between species (Bock & Lepthien, 1976; Larson & Bock, 1986; Köenig & Knops, 2001). At least eight species of boreal seed-eating birds tend to irrupt together, even though they vary in the proportions of different conifer and broad-leaved tree seeds in their diets (Bock & Lepthien, 1976; Köenig & Knops, 2001). Over periods of years, however, different species of trees in the same area can drift in and out of synchrony with one another, affecting the movements of the birds that specialise on them.

Migration directions

As explained in Chapter 18, birds from different sectors of the breeding range normally migrate back and forth along roughly parallel routes, with birds from the western edge of the breeding range migrating to the western edge of the wintering range, and vice versa. However, this tendency is less marked in irruptive than in regular migrants, because irruptive migrants typically show a greater east–west component in their movements, and also greater directional spread, both from year to year and between individuals in the same year. Even individuals from the same brood may take markedly different directions from one another (Huttenen, 2004). In contrast to most migrants, moreover, irruptive species may end their journey at widely different places on the route each year. In any given year, birds from one part of the breeding range may stay in

the north if food permits, while those from another part may move far to the south, though not necessarily vacating the north completely. The following year, the pattern may differ. It is these behaviours that contribute to individuals turning up in widely separated areas in different winters. Most are at different points on the same migration axis, but some may end up in one winter far to the west or east of their position in a previous winter. Even within one winter, the birds may wander in various directions, and end up markedly to the east or west of their initial route.

The greater directional spread of irruptive, compared to regular, migrants is evident from observations at migration watch sites, and also from subsequent ring recoveries of birds trapped on migration. Typically, the recoveries of irruptive migrants ringed in autumn and recovered within subsequent winter months show two or three times as much angular spread as those of regular migrants. For example, from birds ringed at Rybachy in the southeast Baltic, winter recoveries of various non-irruptive species lay within an arc of 100° from the ringing site, but in irruptive species the spread was much greater: in the Eurasian Jay 198°, in the Bohemian Waxwing 237°, in the Brambling 188° and in the Eurasian Siskin 298° (Payevsky, 1994). Similar differences between irruptive and non-irruptive migrants have been noted elsewhere, the recoveries of some non-irruptive species being mainly confined to a narrow corridor from the ringing site (as shown for the Eurasian Linnet: Verheiyen, 1955; Chaffinch: Bairlein, 2001, and others; Chapter 12).

Correlations between numbers of birds and size of fruit crops in wintering localities have been documented in several species of irruptive migrants, as shown in Table E, but mostly in northern parts of the wintering range. Further south in the wintering range, such correlations would be expected to be weak or non-existent, because the birds reach the more distant localities only in exceptional years. In some years, seed crops are available there, but no birds turn up to use them, having already encountered and settled in good feeding areas further north. Conversely, irruptive migrants may turn up in distant areas in some years only to find

their favoured foods are scarce (as shown, for example, by the large numbers of Jays which irrupted into western Europe in 1983, a year almost devoid of acorns; John & Roskell, 1985).

Changes in wintering areas: evidence from ringing

Among the irruptive species studied, return to wintering sites in later years was even rarer than return to breeding sites. Despite some very large numbers ringed, return rates in different species were mostly nil or less than 1 per cent (Newton, 2008). Evidently, extremely few individuals of irruptive seed-eaters returned to the same localities in subsequent years. They showed little or no winter site-fidelity, compared with regular migrants (Chapter 13). Irruptive species also show greater turnover at particular sites within a winter than non-irruptive ones (for the Brambling, see Browne & Mead, 2003; for the Siskin, see Senar *et al.,* 1992), and some individuals may be continually on the move throughout the winter.

Most captures of the same individuals in successive winters occurred at localities on the same migration axis, as mentioned above (including some more than 3,000 km apart), but others included substantial east–west displacements. Extreme examples included a Bohemian Waxwing found in Poland one winter and in Siberia in a later winter (6,000 km apart), and a Common Redpoll found in Belgium in one winter and in eastern China in a later one (8,350 km apart). Another Common Redpoll was recorded in North America in one winter and in Eurasia in a later winter, having been ringed in Michigan and recovered near Okhotsk in Siberia, some 10,200 km to the northwest (Troy, 1983). All these birds are likely to have returned to the breeding range in the interim (though not necessarily to the same locality), and taken markedly different migration directions in the two years. Further records of this type are given in Box D.

BOX D. Examples of individuals of irruptive species found in widely separated areas in different winters (December–February).

Brambling *Fringilla montifringilla*.

Birds ringed in Britain or Belgium in one winter were recovered as far east as Turkey and the Balkans in a later one, while Bramblings ringed in Switzerland in one winter were recovered at various localities from Ireland to Greece and Georgia in a subsequent one. Similarly, many Bramblings that were ringed in western Europe (Belgium–Germany–Switzerland) at 5–15°E in one winter were re-trapped at a similar latitude (60–70°E) in a later winter (Jenni & Neuschulz, 1985; Zink & Bairlein, 1995). These various records involved up to 65° of longitudinal displacement between one winter and another, over distances up to 3,000 km.

Northern Bullfinch *Pynhula pynhula*.

Of 17 long-distance recoveries of birds ringed in Finland in winter, nine were at 550–1,000 km and eight at more than 1,000 km away in a later winter. Fifteen were between south-southwest (Hungary and Poland) and east (Russia) of the ringing site (including two at 1,920 km and 2,350 km east in Siberia), one was north-northeast and another north-northwest. Another three ringed in Sweden were found at 475–1,491 km, between northeast to southeast in a later winter (Cramp & Perrins, 1994). These records involved longitudinal displacements of up to 45°.

Eurasian Siskin *Carduelis spinus*.

Many were ringed in western Europe (Belgium, France or Iberia) in one winter and recovered as far east as Turkey and the Balkans in a later winter, at places up to 2,500 km apart; in addition, one ringed in Belgium in April was re-caught about 3,000 km to the southeast in Lebanon in the next November, while another ringed in Sweden in October 1980 was recovered 3,000 km to the southeast in Iran in January 1982 (Glutz von Blotzheim *et al.,* 1997). These records involved longitudinal displacements of up to 35º.

Common Redpoll *Carduelis flammea.*

Three ringed in Fennoscandia occurred in different winters at places 1,300, 1,500 and 1,800 km apart (Eriksson, 1970), and another caught in Hungary in February 1978 was recovered 3,300 km to the east-northeast in Siberia in March 1979 (Glutz von Blotzheim *et al.,* 1997). Even more remarkable are four movements between western Europe and eastern China, all exceeding 8,000 km: three from Belgium, Norway and Sweden to China, and one from China to Sweden respectively. In these four records, different wintering areas of the same individuals were separated by more than 110^0 of longitude and up to 8,350 km. In North America, ten redpolls were caught at localities 1,345–3,251 km apart in different winters, involving 8–43^0 of longitudinal displacement (Brewer *et al.,* 2000).

Redwing *Turdus iliacus.*

Many were ringed in Europe west of 10˚E in one winter and recovered east of 55˚E in a later winter, at places more than 3,000

km apart (Zink, 1981). Of Redwings ringed in winter in Britain, dozens were recovered in subsequent winters as far east as Italy, Greece and Turkey, and some as far east as Israel and Iran, at localities up to 5,000 km and up to 50^0 of longitude apart (Milwright, 2002). Even birds from the same brood have been recovered in widely separated localities in the same winter (Huttenen, 2004).

Fieldfare *Turdus pilaris*.

Many were found as far apart as Ireland and Italy, England and Turkey, or as Switzerland and Georgia, in different winters, at localities 2,000–3,000 km and up to 35° of longitude apart (Zink, 1981; Milwright, in Wernham *et al.,* 2002). Again, birds from the same brood have been recovered in widely separated areas in the same winter.

Bohemian Waxwing *Bombycilla ganulus*.

One ringed in Poland in February was recovered in the next winter 4,500 km further east in Siberia; a second was ringed in the Ukraine in one winter and recovered 6,000 km to the east in Siberia the next; a third was ringed in England one November and recovered about 3,200 km to the east in October three years later; and five ringed in various winters in Sweden were recovered in later winters in Russia (2,280–2,980 km) or Siberia (3,060 and 4,070 km). Many others were recorded west of 20˚E in one winter and 45–65˚E in another, at places more than 2,000 km apart (Zink, 1981). These

recoveries involved some longitudinal displacements exceeding 50^0. Other Waxwings have been found at the same place at intervals of one, two or three years, in successive irruptions.

Breeding in migration and wintering areas

It is not only the autumn distances that vary from year to year in irruptive seed-eaters. The same holds for the spring distances, with many individuals settling in different areas in different years, depending on food supplies. The Common Redpoll provides a striking example, for this species curtails its migration by up to several hundred kilometres to breed in southern Fennoscandia in some of the years when the spruce crop there is good. Once the seeds have fallen, the birds in some years move north with their young to their usual birch-scrub breeding areas, where they raise another brood. Such movements have not been proved by ringing, but have been inferred from the simultaneous changes in the populations of the two regions and, in particular, from the late arrival in these years of birds in the Birch areas with their free-flying young (Peiponen, 1967; Götmark, 1982). In most other years, with no early nesting, only the single later brood is raised.

Similar behaviour may sometimes occur in Eurasian Siskins, in which adults and recently fledged juveniles were in several years seen migrating northeast in May–July over the Courland Spit in the southern Baltic (Payevsky, 1994). Some of the adults were clearly paired at the time, and many trapped females had a shrunken brood patch, signalling a recent nesting attempt. The first females with brood patches usually appeared at this migration site towards the end of April. In the years 1984–7, some 23–91 per cent of adult females trapped in late April–July had brood patches, as did 35–86 per cent of yearling females (total females caught = 1,230). One juvenile caught in June 1959 had been ringed 25 days earlier, 760 km to the southwest, in Germany. While it could not be proved that

the adults among these Siskins went on to breed elsewhere in the same year, they clearly had enough time to do so. Some other irruptive species have been recorded breeding well to the south of their usual range in certain years, giving further evidence of variable spring settling patterns (Newton, 2008).

Conclusions on twice-yearly migrants

The most striking feature of irruptive seed-eaters, compared with regular migrants, is the flexibility of their movements. In both breeding and wintering areas, irruptive migrants typically show huge numerical fluctuations from year to year, and much less site-fidelity than regular migrants, as individuals may breed or winter in widely separated areas in different years. In most species, the ringing records from individuals in different years mostly lie at different points on the same migration axis (northeast–southwest in much of Europe), but some individuals show marked east or west displacement off this axis in different years. Typical irruptive migrants also show much more variation in their autumn migration dates and directions from year to year than do regular migrants, and make more frequent long movements within a winter. All these features are linked with the fluctuating and sporadic nature of the seed and fruit crops that provide their food. They contrast with the marked directional tendencies and strong homing and site-fidelity shown by birds that feed on more predictable food supplies, and that benefit from returning to the same familiar areas each year (Chapter 13).

ONCE-YEARLY MIGRANTS

Crossbills

Perhaps the most famous of irruptive migrants in the northern hemisphere are the crossbills, which feed year-round almost entirely

on conifer seeds obtained directly from the cones (Newton, 1972, 2006c). Three main boreal species are recognised: the Common Crossbill and the Two-barred Crossbill, which occur in coniferous habitat across much of Eurasia and North America, and the Parrot Crossbill, which occurs in the pine forests of northern Europe. Broadly speaking, these species differ in body and bill size, and specialise on different types of conifers: the Two-barred mainly on soft-coned species (such as larch), the Common Crossbill mainly on medium-coned species (such as spruce) and the Parrot Crossbill on the very hard, thick-scaled cones of Scots Pine. In addition, the Common Crossbill also varies in body and bill size from region to region across its extensive range, in association with the particular species of conifers that grow there (Newton, 2008).[†]

Annual cycle

In most years, Common Crossbills remain within the boreal forest, each year concentrating in areas where spruce cones are plentiful. In particular areas, their breeding numbers tend to fluctuate on a cycle of roughly two to four years, in line with the local cone crops (Fig. 217). The birds have one major period of movement within the summer of each year, as they leave areas where the previous year's spruce crop was good but is coming to an end, and concentrate in areas where the current year's crop is good but forming. Between these times, some birds concentrate temporarily in Scots Pine areas. It is chiefly at this period of transition, in summer, that Common Crossbills in Europe have been found with substantial fat reserves, which could be regarded as 'migratory fat' (Marquiss & Rae, 2002; Newton, 1972, 2006c). However, lesser movements occur at other times of year in relation to local changes in food availability, as seeds are shed or consumed, or as cones open and close.

Irruptions

In some years, when high populations coincide with poor Norway Spruce crops over wide areas, Common Crossbills leave the boreal forest, and sweep southwestward through Europe, appearing in many places that lack suitable conifer habitat. For example, between 1880 and 2000, Common Crossbills irrupted into Britain on at least 40 occasions, at intervals of one to nine years (Table F; Newton, 1972, 2006c). Each time, the birds appeared sometime during late May–October, mainly in June–July at the same time as the normal annual movement. The fact that trapped migrants differed slightly in bill dimensions from one irruption to another (Davis, 1964; Herremans, 1988; Edelaar & Terpstra, 2004) suggests that not all movements originated from the same region (or that not all bill-size categories were stimulated to move in the same years). Wide geographical separation in the source areas for different irruptions to Britain was supported by analyses of isotope levels in the feathers of irrupting Common Crossbills obtained in different years (Marquiss *et al.,* 2008). In years when the feathers of newly arrived birds in Britain had low deuterium values, average arrival dates were later, both of which suggested a more easterly origin. Some of the irruptions are likely to have started in Scandinavia and others further east, in the Urals or beyond.

Irruptive movements occur at about the same time as normal annual movements, but are more directional (towards the southwest) and cover much longer distances (with extremes at more than 5,000 km). Once on the move, irrupting crossbills spread over a wide area, some reaching the extreme southwest of Europe. Thousands of irrupting crossbills have now been ringed at trapping sites in central Europe, giving hundreds of recoveries (Newton, 1972, 2006c; Schloss, 1984). Almost all recoveries within the current cone year (June–May) were to the south and west (mostly southwest) of the ringing site, while many of those in later years were far to the northeast, in the boreal zone of northern Russia, almost all in a region west of the Urals between 57° and 62°N and 40° and 60°E (Fig. 218; Newton, 2006c). Overall, at least 29 adults caught on migration during different invasions through central

Europe have now been recovered back in the boreal forest to the northeast, one to three years later. None was found in northern boreal forest within the same spruce year as it was ringed in central Europe (Newton, 2006c). If the outward movement was stimulated by food shortage, birds would gain no advantage in returning to their area of origin before the next year's crop was ready. In addition to ring recoveries, observational evidence for eastward or northeastward return movements in the summers of non-invasion years is available from several localities (Newton, 2006c). The return movement is much less conspicuous than the outward one, perhaps because it involves smaller numbers of birds and is spread over more than one year. The main axis of migration is clearly northeast–southwest, as in most other seed-eaters, but unlike them, crossbills remained for a year or more before returning.

Most of the recoveries in northern Russia of migrant Common Crossbills ringed in central Europe relate to the invasions of only three different years (1959, 1963, 1990). Although large numbers of crossbills were ringed in the same central European sites in other irruption years, none was subsequently reported from northern Russia. The birds in these other years may therefore have originated from other parts of the boreal forest where recoveries were less likely.

If irrupting crossbills had remained in the regular range, they would almost certainly have starved, but by moving out, a proportion survived to return in a later year. The adaptive value of periodic mass emigration is presumably the same as in regular annual migration, namely the avoidance of food shortage. Those irrupting birds that find areas of seeding conifers may remain to breed. They usually move away after one breeding season, but some irruptions have resulted in the longer-term colonisation of new areas (for example, conifer plantations in Britain).

Ring recoveries imply that individual Common Crossbills have bred in widely separated areas in different years, taking the main breeding season in Norway Spruce areas as January-April inclusive. Movements of birds that were ringed between January and April of

one year and recovered in the same period in a later year are shown in Fig. 219. These birds were reported up to four years after ringing, with successive capture sites between 28 and 3,170 km apart, and including eight at more than 2,000 km. Although none of these birds was reported as nesting at the time of ringing or recovery, they were all within the usual breeding season from within potential breeding range. Moreover, no records have emerged of individuals in the same spruce locality in successive spruce years, which is not surprising, as good crops seldom occur in the same locality two years running. This contrasts with the situation in Pyrenean Mountain Pine forests, where seed crops are relatively stable from year to year, and where Common Crossbills are more sedentary, with many individuals trapped in the same place in successive years (Senar *et al.,* 1993). Similarly, colour-marked Scottish Crossbills were re-sighted in the same pine areas in successive years, or had moved over distances of at most a few tens of kilometres (Marquiss & Rae, 2002). The same may apply in other pine areas in Europe, most of which maintain local races of large-billed crossbills.

In Eurasia, where the Two-barred Crossbill feeds primarily on larch, it may not suffer such extreme fluctuations in food supply as the spruce-feeding Common Crossbill. This is because larch cones remain on the tree with some of their seeds for two to three years, so poor crops can be enhanced by carry-over from previous years. This may explain why this species is much less irruptive in western Eurasia than the Common Crossbill, and appears only in very small numbers south of the boreal zone. Irruptions into Scandinavia occur during cone failures in larch further east in Russia. They tend to occur from late summer, as new cones ripen, but at longer intervals than the two to four years recorded in North America (Bock & Lepthien, 1976; Larson & Tombre, 1989). Two-barred Crossbills have come to Britain mainly in the same years as Common Crossbills, though much less frequently and in much smaller numbers (Newton, 1972). The species is a rarity in Britain, but larger numbers than usual were seen in 1889, 1956, 1979, 1985–7, 1990 and 2008 (Cramp & Perrins, 1994; Harrop & Fray, 2008).

Following the irruption of Two-barred Crossbills in 1956, nesting was recorded in Sweden, 600 km east of the usual breeding range; and after the invasion of 1990, successful nesting was recorded near Berlin in 1991, some 1,700 km southwest of the usual breeding range (Newton, 2008).

Nutcrackers

Other irruptive seed-eaters include the Spotted Nutcracker of Eurasia and the Clark's Nutcracker of western North America. These species feed primarily on the fruits of various large-seeded pines, which they cache in the ground in late summer to eat during the ensuing winter and into the next breeding season. Their survival and breeding success vary from year to year in line with the size of seed crops (Lanner, 1996). Like crossbills, they make one major annual movement, in July–September (as the new cones form), with occasional irruptions outside the regular range. Having settled in appropriate areas, their strategy of living off food stores ideally requires continued residence until breeding is finished or until the next crop is ready. If they moved, they would lose access to their stores, and have no certainty of finding other foods. Like crossbills, Nutcrackers breed early in the year, and can rear their young entirely (or almost entirely) on seeds.

The Spotted Nutcracker *Nucifraga caryocatactes* has several subspecies, each occupying a different part of the range and depending on different tree species. The most widespread type is the slender-billed *N. c. macrorhynchos,* which occurs over most of Siberia, and depends on the seeds of the Siberian Stone Pine and, further east, the Korean Stone Pine. In northwestern Europe, where large-seeded conifers are absent, the thick-billed *N. c. caryocatactes* lives in mixed deciduous–coniferous areas, but depends in winter mainly on Hazel nuts, which it caches in late summer in the same way that other subspecies cache pine seeds. Further south, in the Alps, it also uses the hard-shelled seeds of Arolla Pine.

All these nutcrackers adjust to annual variation in local cone crops by redistributing themselves each year within the regular range (mainly July–September) and by exploiting alternative small-seeded conifers when their main food is scarce. However, in years when major food sources are scarce over wide areas, the birds leave their regular range in large numbers, and live as best they can off any suitable plant or animal material they can find.

The Siberian N. c. *macrorhynchos* performs the most spectacular irruptions, reaching in some years as far as western Europe, on journeys of several thousand kilometres. Thirty-one irruptions of this slender-billed form into Europe were recorded in the 250 years from 1750, at intervals of 1–33 (mean 8) years (Cramp % Perrins, 1994). In the 20th century alone, the figures were 13 irruptions, at intervals of 2–16 years (mean 7.7). Only in the largest irruption of 1968, which started as far east as Lake Baikal, did large numbers of birds reach Britain, a distance exceeding 7,000 km (Hollyer, 1970). Smaller numbers occurred in at least five other years. Again, not all invasions necessarily originated from the same region, that of 1911 coming from southeast Siberia, that of 1931 from northwest Siberia, and that of 1933 from central and northern Siberia (Formosov, 1933).

Like crossbills, nutcrackers may remain in invasion areas for up to a year, breeding if food supplies permit, and returning to the regular range when the next year's crop is ready. Small longer-term populations have been established after invasions in areas where suitable trees had been planted by foresters (Lanner, 1996). Following the invasion of 1968, colonies of Slender-billed Nutcrackers from Siberia became established in Finland and Belgium in areas where Stone Pines *Pinus sibirica* and P. *cembra* had been planted; and after the invasion of 1977, similar colonies were established in Sweden.

Those Thick-billed Nutcrackers *N. c. caryocatactes* that live in northern Europe move shorter distances to the south at times of food shortage, while those in the mountains of central Europe move mainly to adjacent lower ground. Big movements of central and

northern European birds do not usually coincide with one another, or with the bigger movements into Europe of Siberian Slender-billed Nutcrackers.

TABLE F. Autumns with irruptions of various seed-eating birds into the British Isles, 1900–2008. Brackets denote minor irruptions

Bohemian Waxwing: 1903, 1913, 1920, 1921, 1931, 1932, (1935), 1936, (1941), 1943, (1946), 1949, 1950, 1956, 1957, 1958, 1959, 1961, 1963, 1965, 1966, 1967, 1970, (1971), (1972), (1974), (1975), 1988, (1989), 1990, 1991, 1995, 1996, 1999, 2000, 2004, 2008.
Great Spotted Woodpecker: 1901, 1903, 1909, (1928), 1929, (1930), 1935, 1949, 1956, 1957, 1962, 1968, 1972, 1974, (1982), (1988), 1990, 1994, (1997), 1999, 2001, (2003).
Eurasian Jay: (1902), 1909, 1918, (1923), (1931), 1935, (1937), (1941), 1947, 1955, 1957, (1959), (1961), 1972, (1975), 1977, 1983, (1986), (1992), 1993, 1996, 2007.
Spotted (Slender-billed) Nutcracker: (1911), (1933), (1954), 1968, (1977), (1995).
Northern Bullfinch: 1906, 1910, (1913), 1921, 1934, (1953), (1959), 1968, 1975, 1980, 1986, 1989, 1994, 1999, 2001, 2004, 2005.
Siskin: 1901, 1905, 1909, 1919, 1921, 1949, 1953, 1959, (1960), 1961, (1962), 1965, (1969), (1974), 1975, 1977, 1980, 1983, (1984), 1985, 1988, (1991), 1993, (1994), (1995), 1996, (1997), (1998), 2000, 2002, 2007.
Common (Mealy) Redpoll**: 1910, 1913, 1923, 1931, (1943), (1945), (1946), (1953), 1961, (1963), 1965, (1970), 1972, 1975, 1984, (1985), (1986), 1990, 1995, 1997, 2002.
Common Crossbill: (1901), 1903, 1909, (1910), (1911), (1916), (1919), (1925), 1927, 1929, 1930, 1935, 1938, 1939, 1942, (1947), (1948), 1953, 1956, 1958, 1959, 1962, 1963, 1966, 1968, 1972, 1977, 1979, 1982, 1983, 1985, 1990, 1997, (2001), 2002, 2008.
Parrot Crossbill: (1901), (1909), (1916), 1927, 1929, (1930), (1939), 1947, (1949), (1953), (1956), 1962, (1963), 1966, 1968, (1972), (1975), (1981), 1982, (1985), 1990, 1997.
Two-barred Crossbill: (1901), 1903, 1907, 1909, 1910, (1911), 1914, (1925), 1927, 1929, (1930), 1942, (1947), 1948, 1953, 1956, 1959, (1962), 1963, 1966, 1972, (1979), (1986), 1987, 1990, 1997, 1999, (2001), 2002, (2003), 2008.
* Most invasions of Common Redpolls also contained some Arctic Redpolls *C. f. hornemanni*.

OVERVIEW OF SEED-EATERS

Regularity in irruptions

As the cropping patterns of many northern tree species are more regular than random, they would be expected to impart some regularity to large-scale emigration. Some evidence points to a cyclic rhythm in the irruptions of seed-eating species, notably the tendency to adopt a biennial pattern in several species in North America. In addition, a seven-year rhythm emerged in the influxes of Two-barred Crossbills in autumn to Finland between 1960 and 1988 (Larson & Tombre, 1989), and a three-to-five-year rhythm in the movements of Eurasian Jays in the Swabian Alps of southwest Germany during the period 1970–2000 (Gatter, 2000).

Such regularity reflects patterns in tree-seed production, but may not necessarily persist over longer periods, and in many areas irruptions seem irregular. However, irruptions have been studied chiefly in the reception areas, where the degree of regularity probably varies with distance from the breeding range. While every irruption might reach the nearest areas, only the largest would reach the furthest areas, as illustrated above for nutcrackers and others. Sometimes, invasions come not just in one year but in two or more successive years, hence the term 'echo flights'. But these might involve birds from different parts of the breeding range, thus obscuring any regularity there might be in more local breeding populations. For example, most invasions of the Pine Grosbeak into Germany came from the north, and the birds belonged to the European subspecies, but in 1892, a larger subspecies invaded from Siberia (Grote, 1937). Similarly, Redpoll invasions into central Europe in 1985 and 1986 were mainly long-billed *'holboellii'* types and hence probably came from within the range of the Larch in Siberia (Two-barred and Common Crossbills also came from this area in 1985). Moreover, as mentioned above, different Common Crossbill invasions to western Europe have involved birds with different bill sizes, isotope values and arrival dates, which also implies different areas of origin.

Invasions in Britain

During the 20th century, when invasions were increasingly well documented in Britain, they occurred in all species at irregular intervals (Table F). The most frequent visitors were the Bohemian Waxwing and Common Crossbill, with at least 28 and 25 major invasions respectively in the 100-year period. The least frequent was the Slender-billed Nutcracker, which is recorded to have reached Britain in numbers in only six years and in large numbers only in one (1968). For this species, Britain lies at the end of a very long migration route, exceeding 4,000 km. The relative infrequency of Mealy (Common) Redpoll and Northern Bullfinch irruptions (12 and 11 respectively) can be attributed to the Fennoscandian populations of these species moving mostly southeast rather than southwest, as shown by ringing (although some individuals of these species turn up in most years).

RODENT-EATERS

Irruptive movements are also shown by some owls and raptors which specialise on microtine rodents, such as voles and lemmings. The numbers of these small animals tend to fluctuate in regular three-to-five-year cycles, the peaks occurring in different years in different regions. The specialist bird species that prey upon them move around nomadically, concentrating to breed wherever such rodents are plentiful at the time. They tend to stay in particular areas for two to three years, during the increase phase of the cycle, but move elsewhere when numbers crash. Their invasions are most marked in the northern parts of continental Eurasia and North America. Regular invasions of Snowy Owls to the northeastern United States have now been documented for more than 120 years, occurring at average intervals of about four years (Newton, 2002). Irruptions of rodent-eaters are hardly felt in Britain, although three-to-five-year patterns have occurred in the autumn immigrations of Long-eared Owls from northern Europe (Harvey & Riddiford, 1996).

Far fewer movement records are available for other nomadic owl species, because the chances of recording marked individuals at

places far apartare low. However, in a study of Short-eared Owls in south Scotland, 21 breeders were tagged in 1976. Vole numbers then crashed, and only one of the tagged birds remained to breed in the area in 1977. Two others were reported in spring 1977 in nesting habitat 420 km and 500 km to the northwest, and the latter, at least, was proved to breed there (Village, 1987). In contrast, of seven breeders tagged in 1977, when vole numbers began to increase, three bred again in the same area in 1978. Hence, as in Tengmalm's Owls, individual Short-eared Owls seemed more likely to remain to breed in successive years when voles were increasing than when they were declining.

On the northern tundras, some species of skuas also exploit peaks in cyclic rodent populations, but it is yet unclear whether individuals change their breeding areas from year to year, or return to the same areas every spring but breed only when rodents are sufficiently plentiful. This latter pattern has been found in Pomarine and Long-tailed Skuas (Maher, 1970; Andersson, 1976).

DESERT BIRDS

Normally, desert species are able to remain within their regular range, in the wettest years penetrating deep into the driest areas, but at times of widespread drought, some species move out in search of food. This phenomenon is best illustrated by many Australian species which breed prolifically in the central deserts in wet years, and then move out to peripheral districts in dryer years. Nearer home, it is shown by the occasional westward movements of Rosecoloured Starlings, Pallas's Sandgrouse and others from the Asian steppes into western Europe, occasionally reaching the British Isles.

The irruptions of Pallas's Sandgrouse, which occurred from the steppes of Turkestan and Kazakhstan into western Europe in the spring–summers of 1859, 1863, 1872, 1876, 1888, 1890, 1899, 1906 and 1908 (with small numbers in some of the intervening years and subsequently), were attributed to seed shortage probably

resulting from prolonged drought. Again, after each of these irruptions there were occasional breeding records, some from as far west as Britain, with eggs found in Yorkshire in 1888 and young in Moray in 1888 and 1889. No substantial movements into Europe are known to have occurred subsequently, possibly because Asian populations have declined following the degradation of nesting habitat, and Pallas's Sandgrouse now occurs in the British Isles only as a rare and irregular vagrant.

WATERBIRDS

In much of the world, waterfowl are not normally regarded as irruptive, but especially in arid regions, they show many of the typical features: a tendency to concentrate temporarily wherever conditions are suitable, with some individuals occurring in widely separated areas in different years. In winter, they are also greatly influenced by prevailing temperatures, as individuals move to avoid areas where surface waters are frozen, and appear in numbers in the furthest parts of their wintering ranges only in exceptional years.

Although best studied in North America, counts and ringing have suggested similar distributional patterns among wintering ducks in Eurasia, but in the British Isles we are poorly situated to appreciate these movements. Lying at the ends of migration routes, we tend to get many species in large numbers only during cold spells in continental Europe. However, it is clear from ringing that: (1) some species of ducks take up to four months over their post-breeding migration, the bulk of the population moving more rapidly or further in some years than in others; (2) individuals may end up in widely separated places in different winters; and (3) spring settling patterns may also vary from year to year. As in North America, all these features have been linked with patterns in water levels, freezing and thawing, which influence the distribution of habitat and associated food supplies.

Dependent on shallow waters, Teal are clearly sensitive to local conditions, whether drought, flood or freeze, which involve them at

times in long movements or in residency for weeks on end, all manifest on a continental scale. Their spring settling patterns depend on the prevailing conditions when the birds arrive: ring recoveries are concentrated to the south and west parts of the breeding range in wet, cool years, and to the north and east in dry, warm years (when wetlands are dryer than average) (M. A. Ogilvie, in Wernham *et al.,* 2002). Common Pochards have been found in successive breeding seasons in places 200–600 km apart, and female Tufted Ducks in places up to 1,500 km apart, but most had moved much shorter distances (Blums *et al.,* 2002). In successive winters, individual Teal have been found at localities hundreds or thousands of kilometres apart, as have individual Common Pochards and Tufted Ducks (Wernham *et al.,* 2002). Extreme moves were shown by a Tufted Duck ringed in England one winter and recovered in Pakistan during a later winter, and by a Pochard ringed in England one winter and recovered 9,254 km away on the other side of the Eurasian landmass in a subsequent winter.

During hard winters, ducks appear in greater numbers than usual in southern and western parts of Europe. Ring recovery distances of several species (the Eurasian Wigeon, Teal, Northern Pintail, Common Pochard and Tufted Duck) were greater in cold winters than in mild ones, and greater in cold spells than in mild periods within winters (Ridgill & Fox, 1990). Such hard-weather movements were associated with greater mortality than usual, but this may have resulted partly from greater hunting pressure in southern Europe. Ice cover affects sea ducks as well as freshwater ones, and recent warmer winters have resulted in both types wintering further north and east than previously (Chapter 16).

CONCLUDING REMARKS

Coping with a boom-and-bust economy

Most irruptive migrants—especially the seed- and rodent-eaters—are specialists, taking a narrow range of food items which in particular areas fluctuate greatly in abundance from year to year, but differently in different areas. By changing breeding and wintering areas between years, irruptive migrants lessen the effects of the massive food shortages they would experience if they occupied the same areas every year. Nevertheless, they may still be exposed to a hugely fluctuating food supply, which can affect their survival and reproductive rates (Newton, 2006a).

Observations and ring recoveries give some idea of the enormous areas over which individual boreal seed-eaters or rodent-eaters may roam to find the food supplies necessary for their survival and reproduction. With their ability to move rapidly over long distances, these species can exploit a specialist niche in a way that other, more sedentary, animals could not. But because of the sporadic nature of their food supplies, only parts of their vast geographical ranges may be occupied at one time. Individual movements of hundreds or thousands of kilometres have been recorded between natal and breeding sites, and between breeding sites in successive years. However, most ring recoveries are supplied by members of the public, and refer to birds found dead, so carry the assumption that the birds were in fact nesting at the locality concerned.

Flexibility in migration behaviour

The advantage of strong endogenous control of migration, as shown by regular obligate migrants, is that it can permit anticipatory behaviour, allowing birds to prepare for an event such as migration before it becomes essential for survival, and facilitating fat deposition before food becomes scarce. But such a fixed control system is likely to be beneficial only in predictable circumstances, in which food supplies change in a consistent manner, and at about the same dates, from year to year. It is not suited to populations that have to cope with a large degree of spatial and temporal variability in their food supplies. It is these features of food supply which

probably result in irruptive migrants showing greater variations in autumn timing, directions and distances, selection having imposed less precision on these aspects than in regular migrants, and giving the birds more flexibility to respond to rapidly changing conditions. Both regular and irregular systems are adaptive, but to different types of food supplies, the one to consistent and predictable, and the other to inconsistent and unpredictable. Nevertheless, regular (obligate) and irruptive (facultative) migrants are best regarded not as distinct categories but as opposite ends of a continuum of migratory behaviour, with predominantly endogenous control (= rigidity) at one end and predominantly external control (= flexibility) at the other. Depending on the predictability and stability of its food supply, the same species may behave as a resident or regular migrant in one part of its range, and as an irruptive migrant in another.

† These different types of Common Crossbills also have recognisably different calls, and only rarely interbreed with one another, so to some extent they form distinct populations, but not sufficiently distinct to be classed as separate species. Depending on taxonomic fashion, the Scottish Crossbill, which is native to Highland pine forests, could be classed as a large-billed race of the Common Crossbill (as formerly), a small-billed race of the Parrot Crossbill (as sometimes mooted) or a separate species (as at present).

CHAPTER 20

Other Movements

Several variants on the basic outward–return migratory movement occur among European birds, each in a limited range of species. They include: (1) long movements within a winter (outside the usual migration seasons); (2) long movements within a breeding season; (3) moult migration; (4) dispersive migration; and (5) nomadism. These variants can all be related to the particular ecological circumstances faced by different species. They are described in the sections below.

MOVEMENTS WITHIN A WINTER

Some birds can make substantial movements in winter (December–February), often extending further from their breeding areas as the season progresses. Such movements may be regular, almost like different stages of a single journey, but separated by periods of up to several weeks. The separate moves occur at about the same dates each year, and each move is preceded by fat deposition to fuel the journey. Many of the species that breed in Eurasia and winter in Africa perform such staggered migrations, pausing for some weeks in the Sahel–Sudan zones (where some of them moult), before moving on further south (Chapter 22). In some species, these movements are apparently ‘obligate’ and consistent in timing from year to year, but in other species they seem ‘facultative’, varying in timing and extent with prevailing conditions, as in the irruptive migrants discussed in Chapter 19 (Lack, 1983; Herremans, 1998).

In Europe (as in Africa), facultative movements can take place at almost any time in the non-breeding season if feeding becomes difficult, with birds shifting further along their usual migration axis. Although irruptive migrants provide extreme examples, different species which obtain their food from water or the ground move in response to freezing temperatures. Their so-called 'weather movements' (or 'escape movements') occur as soon as waters freeze or snow covers the ground, cutting off food supplies. The dates of such movements vary between years, depending on the weather, and in mild winters may not occur at all. They are often extremely obvious, as large regions become evacuated within a matter of hours, and thousands of birds move out together. Counts made at such times include the 20,000 Eurasian Skylarks that passed westward over the Axe estuary in Devon on 28 December 1964; the 4,500 Northern Lapwings that passed southwest over Tring, Hertfordshire, during 50 minutes on 9 December 1967; and the 10,200 that passed in 2.5 hours over Portsmouth, Hampshire, on 30 January 1972 (Wernham *et al.,* 2002). Ducks and coots usually travel under cover of darkness, but weather movements are marked by massive overnight increases in their numbers on particular wetlands, following the onset of hard weather back along the migration route, or by the sudden abandonment of those same wetlands if they later freeze.

Some birds also migrate in response to predation and disturbance, not suddenly as in weather movements, but progressively over several days or weeks, making the cause harder to verify (Chapter 23). However, the banning of hunting in two coastal areas of Denmark resulted in waterfowl staying in larger numbers than in previous years, delaying their onward migration (Madsen, 1995). Over a five-year period, these two reserves became important staging areas, where most quarry species stayed up to several months longer each winter than in earlier years, and in marked contrast to other areas of Denmark still open to wildfowling. The accumulation of birds in the reserves was therefore attributed to individuals remaining there in the absence of disturbance, instead of

moving further down the migration route, as in previous years. Birds at coastal sites elsewhere have also been found to respond in the same way to natural predators, such as Peregrines, which, like human hunters, kill some individuals and continually disturb others, preventing them from feeding effectively (Chapter 23).

MOVEMENTS WITHIN THE BREEDING SEASON

When they are breeding, most bird species tend to remain resident in an area throughout the season, so that the whole breeding range is occupied in a consistent manner from spring arrival to autumn departure. There are, however, exceptions to this general pattern, in which individuals of some species nest in more than one locality each year. Typically, they raise a brood in one place, then migrate up to several hundred kilometres and raise another brood elsewhere. Among European birds, so-called itinerant breeding was first suspected in the European Quail, in which females arriving in Italy in June–July, apparently to breed, often showed regressing brood patches from an earlier nesting attempt, and were frequently accompanied by young no more than two months old. These young must have hatched from clutches begun in March, a date at which breeding would only have been possible further south—in North Africa. Reports of a general exodus of Quail from Tunisia in spring after breeding supported this view, and single birds ringed there in May and June were recovered two to three months later in Italy and Albania (Moreau, 1951; Cramp & Simmons, 1980). Similarly, late clutches in northern Europe during August–September could result partly from an influx in mid-summer of birds that had previously bred in the Mediterranean region. Apparently, males leave southern Europe soon after the females have laid, establishing new territories further north, where females join them later. Many females do not reach the most northern areas, so males predominate there (Aebischer & Potts, 1994). European Quail can mature and breed at three months old, so that young produced in the southern parts of the breeding range could breed the same summer in the more

northern parts, along with the adults on their second or third attempt. About half of the large numbers of Quail that bred in France in 1987 were judged to have hatched earlier in the same year (Hémon *et al.,* 1988). In the British Isles, Quail are scarce, but many more than usual turn up in occasional summers, such as 1870, 1893, 1947, 1952–3, 1964, 1970, 1983 and 1989, possibly in response to good breeding further south.

Other European birds are known on occasions to move up to several hundred kilometres between successive breeding attempts. They include some cardueline finches, such as the Common Redpoll and Siskin, which depend on different types of tree seeds (Chapter 19). Other carduelines have been found to move shorter distances (up to a few tens of kilometres) during a breeding season (Newton, 2000). Females of some waders move on to breed elsewhere after laying a clutch of eggs, leaving incubation and chick care to their mates. Examples include the Eurasian Dotterel, in which, after laying one clutch in Scotland, some females move on to Fennoscandia to lay another clutch for a different male. Some male Dotterels also move long distances during a breeding season, nesting first in Scotland and then, after nest failure, moving on for another attempt in Norway (D. P. Whitfield, in Wernham *et al.,* 2002). These movements have been confirmed by ringing.

Itinerant breeding enables species that could raise only one brood in a given locality to become multi-brooded, providing they can raise young to independence within a relatively short period. Species with long breeding cycles and prolonged parental care would not be expected to become itinerant breeders in seasonal environments, because they could not raise more than one brood each year. Itinerant breeding can be detected only when newly arrived adults have brood patches, recently fledged young or other signs of recent reproduction, and then proceed with a new nesting attempt. It is clearly rare or non-existent in the vast majority of well-studied European birds, although it has been described recently in some North American species which nest first in northern areas

and then further south following summer rains (Rohwer *et al.,* 2009).

Some wetland species perform long movements in summer after breeding, often to higher latitudes, apparently to escape drought. Such movements have most often been recorded among various herons and ducks (in which they merge with moult migration, described later). In addition, at least one non-wetland species performs extensive weather movements in summer. The Common Swift feeds on small high-flying insects which are available only in fine weather. As found by radar studies, Swifts escape cold rainstorms by flying clockwise into the wind around each depression, and returning behind it (Lack, 1956). In the process, they can travel up to 2,000 km. It is apparently mainly non-breeders that participate in these movements, but also some breeders, occasionally forming flocks of up to 50,000 birds. Nestling Common Swifts can survive without food for a week or more by becoming cool and torpid—an adaptation to parental absence which most other birds lack.

The pre-laying exodus of petrels

A different kind of 'within-season' movement occurs in some pelagic seabirds. Once they have returned to their breeding colonies, and re-established nest sites and pair bonds, many petrel and shearwater species leave their colonies for periods of days or weeks to feed up for egg production and incubation. In the process, they may travel to foraging areas hundreds or thousands of kilometres from the nesting colonies. For example, Manx Shearwaters from Skomer Island off Wales, which had been fitted with location-recording devices, flew up to 700 km from their nests during this two-week period to reach rich foraging areas (Guilford *et al.,* 2009), while longer movements were recorded for other species elsewhere (Phillips *et al.,* 2006).

Any body reserves the birds may have on first arrival at the colony have largely gone before the time of egg-laying, making it

necessary to accumulate fresh reserves. At that time of year, it may be more efficient to fly long distances to rich feeding areas elsewhere than to attempt to accumulate reserves nearby. Both sexes then need reserves to get back to the colony, the female also to produce the single large egg, and the male to undertake the first incubation stint (lasting several days). Later in the breeding cycle, birds tend to feed closer to the colony, as is shown by the shorter duration of their foraging trips and in some species confirmed by use of location-logging devices (Phillips *et al.,* 2006).

In some petrel species, both sexes participate in the pre-laying exodus, travelling independently of one another, but females are often away for longer than males. In other species, the journeys are made mainly or only by the females. The period away varies from a few days to several weeks, depending on the species and the distances involved (Warham, 1990). The females apparently form the egg while away and usually lay one or two days after their return, whether the male is back or not. This implies that fertilisation occurred when the partners were last together, up to several weeks earlier.

MOULT MIGRATIONS

In some waterfowl species, many individuals perform a 'moult migration' in summer, when they travel long distances from their nesting places to assemble in large numbers at traditional sites that offer security and food. They then become temporarily flightless, replacing all their large wing feathers simultaneously within the space of a few weeks. Body moult begins before flight feather moult and continues afterwards. Among geese, moult migrations are undertaken entirely by non-breeders and failed breeders, and moulting areas nearly always lie at higher latitudes than the nesting places, from a few tens to more than 1,000 km away. By leaving breeding areas to moult, non-breeders avoid competing with families which stay there; and by moving to higher latitudes where plants are at an earlier, more nutritious stage of their growth cycle,

these moulting geese benefit from a richer food source, as well as from longer days. After moult, the geese return to their breeding areas or migrate directly to their wintering areas.

Some moult migrations are far from trivial. In some duck species, individuals have been found by ringing to travel distances of more than 3,000 km from breeding to moulting sites, and some of the biggest concentrations hold tens of thousands or hundreds of thousands of individuals. In general, sea ducks perform longer journeys than freshwater ducks. Usually birds fly quickly and directly from breeding to moulting sites, and even sea ducks, which normally stick to the coast, sometimes fly long distances over land to take the shorter routes (Salomonsen, 1968). Some of the more impressive moult migrations among European ducks include the following:

Goosanders from much of northwest Europe migrate from their breeding areas to the shallow coastal waters of North Cape in northernmost Norway, forming a scattered concentration of about 35,000 birds (mostly males), from which they later move southward to their wintering areas. Drakes are virtually absent from breeding areas from June to October (Wernham *et al.,* 2002). Females leave their breeding areas much later than males, and move shorter distances to moult in various Scottish estuaries and inner firths, each holding perhaps 60–160 birds.

Common Scoters from breeding areas to the northeast migrate each summer to the west coast of Jutland in Denmark, where they reach more than 150,000 individuals. After moulting, some birds remain there, while others move on elsewhere, including to the seas off eastern Britain, but not necessarily as soon as moult has finished (Salomonsen, 1968).

It takes individual ducks three to five weeks to re-grow their flight feathers, depending on species, shelducks and geese four to six weeks, and swans about six weeks. However, some individuals arrive in moulting areas weeks before starting their wing moult, or leave long after finishing it, providing that food remains available, so that sites can be occupied by moulting birds for a total of two to four months. In various diving and dabbling ducks, the earliest arrivals in moulting areas are males, as mentioned above, but these are soon followed by non-breeding or failed females, leaving the successful females to hatch and tend their broods. Once their young are grown, some of the adult females also perform a moult migration, being last to arrive in moulting areas, while others remain in their breeding areas and moult their flight feathers there.

While some ducks migrate north of their breeding areas to moult, others moult at southern staging or wintering sites. For these species, therefore, the moult migration could be regarded either as an extra stage of the northward spring migration or as a stage of the southward migration, involving the same directional preferences. But for other species, the moult migration lies in a quite different direction, sometimes at right-angles to the normal migration axis. Moreover, because sites within the breeding range can attract birds from all directions, there is clearly no directional consistency between individuals using those sites. The birds can also periodically change their moulting sites in response to changes in water depths, or as established sites are destroyed, and new ones created, by human action. Given these facts, it seems unlikely that birds from different parts of the breeding range inherit different directional preferences for moult migration, especially considering that individual waterfowl can sometimes breed in areas hundreds of kilometres from where they were raised, or in widely separated places in different years (Chapter 13). Rather, they could learn the locations of favoured sites from other individuals, this knowledge being passed on by cultural tradition. The main features of favoured moulting sites are the security they offer at a time when birds are flightless, and a greater food supply than local breeders alone could

use. The food surplus arises either because local foraging habitat greatly exceeds local nesting habitat, or because in some high-latitude areas, the season is too short for the species concerned to breed there.

Various other wetland birds also gather in large concentrations to moult, and lengthy migrations are sometimes involved. This is true for coots and various grebes, all of which become flightless for a time. Up to 186,000 Black-necked Grebes have been counted at moulting time on Burdur Gölä in Turkey (Hagemeijer & Blair, 1997), and smaller numbers elsewhere, while 10,000–40,000 adult Great-crested Grebes have been counted in different years on the Dutch IJsselmeer (Piersma, 1988). In addition, Black Terns form a huge post-breeding concentration on the Dutch IJsselmeer (van der Winden, 2002), and Little Terns assemble at various sites on the Dutch coast, in the Venice Lagoon and the Nile delta (Tavecchia *et al.,* 2005). Ringing showed that most Little Terns at the Venice Lagoon were drawn from nesting colonies within 150 km of the site, but some travelled up to 500 km. Moulting concentrations have also been reported for divers, flamingos, cranes and auks, mostly at places away from nesting or wintering areas (Jehl, 1990; Cherubini *et al.,* 1996).

DISPERSIVE MIGRATION

The movements described so far in this chapter form additions to normal two-way directional migration, but dispersive migration largely replaces it. In many resident species, the newly independent young disperse in different directions from one another, gradually getting further away from their hatch sites in the ensuing weeks (Chapter 13). They then move back towards their natal areas as the next breeding season approaches. Such out-and-back movements implied by ring recoveries are apparent in a wide range of ‘resident’ species in the British Isles, including the Great Tit, Blue Tit, Song Thrush, Greenfinch, Chaffinch, Guillemot, Herring Gull, Great Black-backed Gull, European Shag, Great Cormorant, Grey Heron,

Common Buzzard, Mute Swan and others (Wernham *et al.,* 2002). They have also been confirmed in many species from repeated captures or sightings of marked individuals, and from radio-tracking (as in the Red Kite and Common Buzzard; Evans *et al.,* 1999; R. Kenward & S. Walls, in Wernham *et al.,* 2002). In all these species, birds moved outward from their natal or nesting areas after the breeding season, settled elsewhere over winter and then moved back in time for the next breeding season. Yet in other parts of their range, some of these same species perform directed migrations.

Because this dispersal is a back-and-forth seasonal movement, consistent in timing from year to year, it parallels migration. But at the population level, it differs from migration in that: (1) it is not directional (unless direction is imposed by landscape or coastline); (2) the movements are relatively short—mostly in the range of a few kilometres or tens of kilometres (but longer in some species); (3) ring recoveries drop off rapidly with increasing distance rather than concentrating in a specific distant wintering area; and (4) all or most individuals remain year-round within the breeding range of the species (although some seabirds may disperse far from their colonies to remote feeding areas). The term ‘dispersive migration’ seems appropriate for this type of movement, emphasising that it is seasonal, in various directions, and involves outward and return stages. It may enable individuals to seek out better feeding sites for the winter, or to exploit places that are suitable for wintering but not for breeding. Unlike directional migration, it is obviously not related to latitudinal climatically driven changes in food supplies.

The radio-tracking of individuals has provided much more detail than ring recoveries. It showed that young Common Buzzards started making long excursive flights from their natal nests when they were about 70 days old, after their feathers had hardened (Walls & Kenward, 1998). The young explored up to 25 km away, but for a time continually returned to their natal nests. About half the young dispersed right away from natal areas by their first October, moving longer distances than other young, which left later in winter or in spring. After leaving the natal area, each individual

established its own home range, but often changed locality more than once before settling in its eventual nesting place, at the latest in the third summer. In the spring of their early years, these birds made temporary visits back to their natal areas, earlier in each successive year until they bred, either there or, more frequently, where they had settled in winter (Walls & Kenward, 1998). Overall, patterns of outward–return movement each year, in which one sex moves further than the other and individuals spend longer each year in the natal (future breeding) area with increasing age, have all been recorded from dispersive migrants. They provide parallels with similar patterns in regular migrants wintering at lower latitudes (Chapter 21).

NOMADISM

Apparent nomadic movements occur in species which use sporadic habitats and food supplies, concentrating temporarily wherever conditions permit. As described in Chapter 19, they are exhibited by some boreal finches, which move around to exploit sporadic tree-seed crops, and by certain owls and raptors, which exploit the cyclic peaks of rodent populations. They are also shown by many desert bird species, which move around in relation to the irregular rainfall which generates their food supplies (Dean, 2004; Newton, 2008). Such species seem to show little year-to-year consistency in their movement patterns, but shift from one area to another, residing for a time in whichever parts of their range have plentiful food supplies. The areas successively occupied may lie in various directions from one another, and no one area is necessarily used every year. The birds themselves may in theory move at any time and in any direction between successive breeding sites, and over shorter or longer distances. However, much of what we 'know' about nomadic movements is based on observation and inference, as there are few or no relevant ring recoveries or other individual-based data.

In many such species, nomadic movements are superimposed on regular north–south migrations. The population is thus concentrated

at different latitudes at different times of the year, but is always patchily distributed, wherever food is available at the time. This is obvious in some seed-eating species such as the Redpoll and Siskin, and in some rodent-eaters such as Long-eared and Short-eared Owls (Chapter 19). Yet other bird species behave nomadically only in the non-breeding season, and return to the same localities to nest each year. Examples from among Eurasian–African migrants include the White Stork, Black Kite, Steppe Eagle, Lesser Spotted Eagle and Lesser Kestrel. Typically, these species specialise in their non-breeding areas on sporadic food sources, such as locusts and grasshoppers, emerging termites, large nesting colonies of Red-billed Queleas or Wattled Starlings, or small animals disturbed by grass fires. Some of these prey-species are accessible at the same localities for a short time every year, but others become available only in some years, after exceptional rainfall (Chapter 22).

One of the puzzles about nomadic birds, which seem to move in any direction from one breeding area to another, is how they find their way to suitable areas. One possibility is that they search at random, gradually settling wherever conditions are good, but this seems inefficient, and desert birds, in particular, may have other means of detecting areas where rain has fallen, responding perhaps to atmospheric pressure shifts, cloud formations or changing odours. As yet, though, it remains a mystery how birds find widely separated patches of temporarily favourable habitat in the vastness of the desert.

CONCLUDING REMARKS

The important point to emerge in this chapter is that migration is not always a simple two-season movement between fixed breeding and wintering areas. Some bird species move between three distinct areas: a breeding area, a late summer or autumn (often moulting) area, and a wintering area. Others move only when necessary, and no further than necessary, wintering much nearer to their breeding areas in some years than in others. Yet others seem to spend much

of their lives on the move, following the same route each year, pausing for a few weeks here and a few weeks there, before moving on. Their mobile lifestyle enables them to exploit short-lasting food supplies at different places at different times, as they occur (Newton, 1979; Lack, 1990; Pearson & Lack, 1992; Jones, 1995).

Other points to emerge are that not all bird movements are restricted to spring and autumn; and not all movements occur at the same times from year to year. The irregularity of some types of movements implies that they occur as a direct response to habitat and food conditions at the time. They are in no sense 'anticipatory', as is much regular seasonal migration. For the most part, movement patterns of nomadic species have been inferred from local numerical changes, and have been supported by abundant ring recoveries in only a very few species. This is not surprising in species which live mainly in areas where human population density is at best extremely low, and whose movements are so variable from year to year. More extensive use of tracking devices may change this situation in the coming years. In the meantime, many questions remain, notably: how do nomadic species know when and where to go; from how far away can they detect suitable conditions; how far do individuals move; and to what extent are their lifetime movements directional? Many birds classed as nomadic still have a north–south component in their movements, in line with latitudinal–seasonal trends in temperature and rainfall. Once again, we see different kinds of bird movements grading into one another, whether irruption and nomadism, or migration and dispersal. In any one population, however, one or two kinds usually prevail.

CHAPTER 21

Sex and Age Differences in Migration

Sex and age groups in bird populations sometimes differ in their migrations, as reflected in the proportions of each group that undertake migration, the timing of outward and return journeys, and the distances travelled. One or more such differences have been found in a wide range of birds, including passerines and non-passerines, land birds and seabirds. In some species, the differences are great, with little or no overlap between sex and age groups, while in others they appear minor, manifest chiefly in mean values, with extensive overlap. Information is of course limited to species in which the sex and age groups can be easily distinguished.

Sex differences in migration have been known for a long time. The Swedish taxonomist Linnaeus in 1758 named the Chaffinch *'Fringitta coelebs'* (meaning 'bachelor finch') because it was chiefly the males that stayed to winter in Sweden where he lived, while females moved to lower latitudes. Twenty-one years later in 1779, the English naturalist Gilbert White added another observation: 'For many years past, I have observed that, towards Christmas, vast flocks of Chaffinches have appeared in the fields…. when I came to observe them all narrowly, I was amazed to find that they seemed to me to be almost all hens.' With recent climate change, this difference is no longer so marked in either area, but subsequent bird-ringing has confirmed that male Chaffinches from northern Europe migrate, on average, less far than females. The same holds for the closely related Brambling, and for many other common songbirds (Newton, 2008).

Sex and age differences in migration can be linked with at least three aspects of species biology, namely: (1) the different roles of the sexes in breeding, which can influence their migration dates; (2) preceding events in the annual cycle, which can differ between sex or age groups and influence migration dates; and (3) body size and dominance, which often also differ between sex and age groups, and can be linked to migratory timing and distances. Particular species can differ in more than one of these aspects.

MIGRATORY TIMING AND BREEDING ROLES

Arrival in breeding areas

In most bird species, pair formation occurs in the breeding areas, with males arriving first to establish territories, where they are later joined by females (waterfowl and cranes excepted). The difference in mean arrival dates between the sexes is often greater in species that arrive early in the season than in those which arrive later, and within species it is often greater in warm springs when the population as a whole arrives early (e.g. Francis & Cooke, 1986). In some species, this sex difference also tends to increase with latitude, as journeys lengthen. In the Common Redstart, for example, the sexes arrive, on average, about 5 days apart on Mediterranean islands and 8 days apart in northern Europe, while in the Blackcap, the equivalent figures are 1 day versus 4 days, and in the Pied Flycatcher 8 days versus 11 days in first-year birds, and 5 days versus 10 days in older birds (Lundberg & Alatalo, 1992; Rainio *et al.,* 2007).

As it is the males in most species that compete for territories, they may gain more advantage than females in returning earlier in spring, a situation helped, perhaps, in those species in which males also winter nearer to breeding areas than females (Alerstam & Högstedt, 1982). Not being involved in territory establishment, females are under less pressure than males, and can arrive later,

closer to the time they begin nesting. This does not mean that females do not also compete among themselves—for example, for the most desirable territory-holding males. It is clear, therefore, that there are both costs and benefits associated with arrival time, and that males gain more from early arrival than females.

The sex difference in arrival date seems clearly related in some way to reproduction. Thus, in many species in which males migrate earlier than females in spring when their breeding is about to begin, the two sexes migrate at the same dates in autumn when breeding has finished. Examples include the Bluethroat (Ellegren, 1990a), Blackcap (Izhaki & Maitav, 1998b) and Red-backed Shrike (Tryjanowski & Yosef, 2002). Furthermore, in species in which females rather than males establish territories, it is the females that arrive first, as shown for example in various wader species, such as phalaropes and the Eurasian Dotterel (Myers, 1981).

In addition to the sex difference in arrival times, young adults nesting for the first time typically arrive in their breeding areas some days later, on average, than older and more experienced birds of the same sex (Newton, 2008). Two explanations have been offered, which are not mutually exclusive. The first is that, because young adults cannot compete effectively with older ones for nesting territories, they benefit from arriving later in the season, when most old birds have already settled, thereby saving energy that would otherwise be wasted on futile battles. On this basis, later arrival is under endogenous (genetic) control. Second, because of their inexperience and subordinate status with respect to older birds, young adults cannot feed as efficiently before departure from wintering areas, or at stopover sites en route, so are delayed on migration (Chapter 23). On this basis, later arrival results partly from the relative status and feeding skills of the individual under prevailing conditions. The same two explanations could apply to another finding, namely that in some species, older juveniles hatched early in the previous summer generally arrive earlier inbreeding areas than younger juveniles hatched later in the

previous summer (Jakober & Stauber, 1983; Bairlein, 2001; Sternberg & Grinkov, 2006).

Departure from breeding areas depends largely on when parental duties finish (even though some species may then moult before leaving). In many bird species, failed breeders leave their nesting areas earlier than successful ones, and in years of widespread breeding failure, as sometimes occur in arctic-nesting waders, postbreeding migration occurs noticeably earlier than usual. In addition, in some bird species, only one sex looks after the young, which frees the other sex to depart at an earlier date. This is evident, for example, in most duck species, in which the males play no part in parental care and leave their breeding places (for moulting sites) up to several weeks before the females and young (Chapter 20). Some wader species, such as the Curlew Sandpiper and Ruff, show a similar pattern, in that the females remain until their young are full-grown, allowing the males to leave the breeding areas some weeks earlier. In other waders, such as the Spotted Redshank and Grey Plover, the males raise the young to this stage, allowing the females to depart earlier. In yet other waders, such as the Lapwing and Black-tailed Godwit, both partners help to the same stage with parental care, and the two sexes migrate at about the same time. In these various species, therefore, post-breeding migration dates are clearly influenced by parental roles and preceding events in the annual cycle. Other bird species in which only one partner raises the young also show marked sexual divergence in autumn migration dates, the repetition of this pattern in different kinds of birds further emphasising the link between migration and breeding system.

After nesting in the Arctic, adult waders usually leave their breeding areas well before the juveniles, and moult at a migratory staging site or in winter quarters. In some species, the juveniles also progress more slowly on migration, taking longer and more frequent stops, or less direct migration routes (Saurola, 1981; Evans & Davidson, 1990; Baccetti *et al.,* 1999). Hence, in all these species from different taxonomic groups, the question of whether adults or

juveniles depart first on autumn migration is linked to whether or not they migrate immediately after breeding, and where and when they moult. The pressures are somewhat different between juveniles and adults, because, whereas the juveniles have a short body moult (or in some species no moult), the adults have a longer complete moult, including flight feathers. Again, the differences in timing between age groups are apparent mainly in mean values, for there is considerable overlap between adults and juveniles at the population level.

The Common Starling is resident in the British Isles, but in parts of Europe it has an unusual twin-peaked post-breeding migration, extending up to 1,200 km. In northeast Europe, some individuals migrate immediately after breeding either before their moult begins or in the early stages, while other individuals migrate in autumn after moult has finished. The two periods of movement are indistinguishable in direction and other aspects, and both involve mainly nocturnal flights (Kosarev, 1999). But juveniles participate mainly in the first period, moulting in their migration areas, while adults depart mainly in the second period, after moulting in their breeding areas. The post-breeding migration of the whole population therefore occurs in two distinctly separated periods (Fig. 245).

Migration and body size

The sex and age groups of a population often differ in body size. This may affect their ability to withstand cold and food shortage, as well as their dominance status and other features that could in turn influence their movement patterns. In most bird species, males are bigger than females, but in raptors, owls, some waders and others, females are bigger than males. In all these groups, the sex difference in body size varies from slight in some species to substantial in others, with no overlap between males and females. In most bird species, juveniles are also slightly smaller (as judged by weights and wing lengths) than older birds of the same sex.

The supposed greater ability of large individuals of a population to withstand cold has been proposed as an explanation of why, in so many bird species, males tend to winter at higher latitudes (nearer their breeding areas) than females, and why within the sexes, adults tend to winter at higher latitudes than juveniles. According to this proposition, because large birds have a lesser surface area-to-volume ratio than smaller birds of similar shape, they experience a lower rate of heat loss from the body, giving a better energy return on foraging. Also, if energy stores are proportional to body mass, larger birds should have greater body reserves relative to their daily energy needs, enabling them to fast for longer periods (Ketterson & Nolan, 1983). While this explanation of differential migration distances cannot be disproved, the differences in body size between the sex and age groups of many bird species are often small, possibly insufficient to have the effects on energy efficiency attributed to them. An alternative explanation is that migratory distances result from competition and dominance.

Migration and dominance relationships

In some bird species, as already described, more individuals stay in their breeding areas in winters when food is plentiful there than in winters when food is scarce, in mild winters than in cold ones, or in some habitats rather than others. It has been assumed that competition for food and other resources has an immediate influence on the proportions of birds that stay or leave each year, and the distances they travel (Chapters 10 and 19). Among Blue Tits in a breeding area in Sweden, the proportion of individuals that left for the winter increased from adult males (virtually none), through adult females, juvenile males and juvenile females (more than 40 per cent). In addition, more late-hatched juvenile males than early hatched juvenile males migrated (Smith & Nilsson, 1987). These proportions differed significantly between groups, and were associated with the known body size and dominance relations within the population, with adult males being the most dominant

and late-hatched juvenile females the least. Hence, in contests over feeding sites, late-hatched juvenile females would gain most from departing. The benefits of migration could extend further up or down the social hierarchy, according to prevailing conditions, accounting for annual variations in the proportions of birds leaving.

Not all migratory birds conform to the above patterns. Species that have given no indication of a sex difference in migration distances include the Sanderling and Grey Phalarope, in which females are larger than males (Myers, 1981), and the Eurasian Siskin, in which the sexes are about the same size (Payevsky, 1994). Nor is it the case that juveniles in all species migrate further than adults. Among Chaffinches, Bramblings and Eurasian Siskins that were ringed on autumn migration at Rybachy, adults were recovered at significantly greater distances than juveniles (Payevsky, 1994). Also, no age-related differences in wintering latitude were apparent from ring recoveries of the Barn Swallow (Wernham *et al.,* 2002), Osprey (Poole & Agler, 1987) and Mallard (Nichols & Hines, 1987). In fact, age-related differences in migration distances and winter distributions appear to be much less frequent than gender-based differences. But whether this is because age-related differences are smaller, and therefore harder to detect, or because they are really less frequent, remains to be seen.

DEFERRED AND GRADED RETURN TO BREEDING AREAS

In general among birds, age-related differences in migration patterns are most pronounced in species in which individuals do not breed until they are several years old (Chapter 9). Young birds may stay in their wintering areas beyond their first winter, returning to the breeding area in a later year (deferred return). In this way, the age groups are separated geographically in the breeding season, and the young birds, which would in any case not reproduce in their first year, avoid an unnecessary return journey. Alternatively, the immature individuals travel only part way from their wintering areas, passing the summer at sites en route to the breeding area,

with some species getting nearer year by year (graded return). They also tend to migrate later in spring and earlier in autumn than breeding adults. Eventually, these birds make a full return migration, and stay for the entire season, most settling to breed close to where they were hatched, and thereafter returning year after year (Chapter 13).

Age-related trends in the timing of migration have also been noted in raptors. For example, in the various eagle species that migrate through Israel each spring, the age groups pass in order of oldest first to youngest last, again spread over a period of several weeks (Shirihai *et al.,* 2000). Among some radio-tagged Lesser Spotted and Steppe Eagles, immature birds migrated later and more slowly than adults, arriving in breeding areas up to ten weeks later (Meyburg *et al.,* 1995b, 2001; Meyburg & Meyburg, 1999). As the immatures make no attempt to nest, they suffer no obvious penalty by arriving later and leaving earlier than older birds, and may benefit from migrating at a better time of year.

Similar patterns of (a) pre-breeding birds over-summering in 'wintering' areas, (b) returning partway towards breeding areas or (c) returning to breeding areas for a shorter time than nesting adults also occur in some waders. From wintering areas, immature birds left in increasing proportion, and progressively earlier each year, as they grew older, as shown in individually marked Oystercatchers, Grey Plovers and Avocets (Goss-Custard *et al.,* 1982; Evans & Davidson, 1990; Hötker, 2002). In one wintering population of Oystercatchers on the Exe estuary, individuals began to return to breeding areas from about the fourth summer on, but males did not begin to breed until ages five to eight, and females until three to six years (Goss-Custard *et al.,* 1982).

Comparing different wader species, a significantly greater tendency to over-summer in winter quarters occurs in those populations with the longest migratory flights that winter furthest from their breeding range (Summers *et al.,* 1995; Hockey *et al.,* 1998). Such latitudinal trends are also apparent in different populations of the same species, such as the Ringed Plover (Evans &

Davidson, 1990), and the same holds for some gulls, cormorants and others. Perhaps the longer journeys tip the balance in young birds in favour of staying rather than returning to the breeding range. In waders, over-summering in winter quarters also occurs significantly more often in species occupying coastal habitats in the non-breeding season than in those found at freshwater wetlands (Rogers *et al.,* 2006).

Deferred return to breeding areas may occur because young birds are unable to accumulate the fat reserves necessary for the return journey; alternatively, it could be an inherent feature that has evolved because young birds have no chance of breeding and benefit from avoiding the risks of long return flights (Chapter 9). These explanations are not mutually exclusive, and each may apply to different populations. The fact that over-summering in wintering areas seems commoner in populations that winter furthest from their breeding areas (on the southern continents) supports the evolutionary explanation; but the fact that some birds migrate only part way to their breeding areas (albeit still travelling hundreds of kilometres) supports the food-limitation hypothesis, with birds responding to conditions at the time. First-year birds that do not return to breeding areas normally show little gonad development, and no spring moult or pre-migratory fat deposition, but remain in drab winter plumage (Chapter 10). Their primary wing feathers are often heavily worn, and not in good condition for a long migration.

OTHER DIFFERENCES BETWEEN SEX AND AGE GROUPS

Males might arrive earlier than females in breeding areas because they winter closer to the breeding areas, begin their return migration earlier or travel faster. In some passerines and shorebirds, in which the sexes winter side by side in the same area, the males were found, on average, to fatten and leave first (Nisbet & Medway, 1972; Cramp, 1988; Bishop *et al.,* 2004; Catry *et al.,* 2004, 2005). Similarly, on stopover sites, males fattened more rapidly, on average, and stayed for shorter periods than females, thus making

more rapid progress (Lavée *et al.,* 1991; Morris *et al.,* 1994). If this happened at most stopover sites, the effect would be to widen the sex differences in migration timing as birds travel towards their breeding areas (Rainio *et al.,* 2007). These distinctions may again result from inherent differences between the sexes, or from the greater dominance of males, through which they gain access to better feeding areas. Whatever the explanation, in some species where females are larger than males, the opposite pattern applies, with females leaving wintering areas earlier and making more rapid migratory progress than males (Figuerola & Bertolero, 1998; Butler *et al.,* 1987; Newton, 2008).

Similar differences as occur between sexes also occur between age groups. In some species, juveniles take longer to fatten than adults, migrate with lower fuel loads, have more or longer stops, and take longer to complete their journeys (Newton, 2008). Such differences may again result partly from the reduced experience and social status of juveniles, compared with adults. When they leave their breeding areas, juveniles also show more spread in departure directions than adults (Chapter 14), and the two age groups sometimes migrate along partly different routes, with juveniles appearing in greater proportion than expected in coastal areas, perhaps through greater drift.

Some of these age-related differences can be clarified by specific examples. Among Savi's Warblers studied in Portugal, juveniles started migrating from early August and adults from late August, but both groups had left completely by early October (Neto *et al.,* 2008). In contrast to juveniles, adults showed a marked increase in weight and body fat from the end of August, and had significantly greater fattening rates. Accordingly, the estimated potential flight range in adults increased from 600 km in August to 1,500 km by September, extending in a few individuals to 2,750 km, which was enough for them to reach their tropical wintering areas without refuelling. In juveniles, fat levels remained small and roughly constant throughout the season, providing enough fuel for only 150 km of flight. This difference implied that juveniles migrated more

slowly than adults, stopping more frequently to refuel, at least in the early parts of their journey. The two age groups thus differed in spread of departure dates, migratory timing, fuelling and flight ranges.

CONCLUDING REMARKS

Overall, birds show various sex-related and age-related migration patterns, which are associated with mating and parental systems, annual cycle features and body size/dominance relationships, all of which can apparently modify the timing, distance, route and speed of migration within the constraints imposed by environmental conditions. Where species in the same family or genus differ in mating and parental systems, they also show corresponding differences in migration patterns. The fact that similar patterns recur in unrelated families emphasises the role of mating and parental systems in influencing sex differences in migration.

Some of the differences between age groups may at first sight seem strange. For example, among many partial and short-distance migrants, juveniles leave the breeding areas before adults and often migrate further, whereas in practically all migrants studied in spring, adults leave their wintering areas and arrive on breeding areas before juveniles. At each season, however, it is the dominant adults (especially males) that are able to pursue the optimal strategy, while other individuals are apparently predisposed by competition or other influences to behave otherwise. In autumn, the best strategy among the few partially migrant populations that have been studied is to stay in breeding areas as long as possible, preferably all winter, for in most years, resident individuals survive better than those that migrate, and also retain the best territories for breeding. In spring, the optimal strategy is to be among the first birds to return to breeding areas, for early birds secure the best of the remaining territories (Chapter 11). Clearly, there is still much to be learned about the factors underlying age and sex differences in

the migrations of birds, and some of the proposed explanations are as yet little more than informed guesses.

CHAPTER 22

Migrants in Africa

THE SEASONAL JOURNEYS THAT birds make between breeding areas in Eurasia and wintering areas in Africa south of the Sahara comprise one of the most impressive of the world's migration systems. Not only are huge numbers of birds involved, ranging from small warblers to large eagles, but most of them must make long and daunting journeys. Birds from the west of Eurasia cross the Mediterranean Sea and Sahara desert, while those from further east cross the deserts of southwest Asia and Arabia. Many of these same birds also negotiate high mountain ranges, such as the Pyrenees and the Alps. Yet every year in late summer, an estimated 4,000–5,000 million birds undertake this migration. Owing to human impacts mainly in breeding areas, Moreau (1972) felt that this represented only about one-third of their maximum numbers in post-glacial times, perhaps 3,000 years ago. These migrants cram into a geographical area in Africa less than half the size of their Eurasian breeding grounds, adding to an avifauna already rich in native species. This raises questions of how the seasonal visitors from Eurasia survive in what is apparently a very competitive environment. As so many of our summer visitors vanish into Africa each winter, it is relevant to examine the species involved and the conditions they encounter there.

THE BIRDS INVOLVED

About 186 land-bird species from Eurasia winter wholly or partly in Africa south of the Sahara, while 29 seabird species winter on the

seas and coasts, giving about 215 species altogether. However, from west to east across Eurasia, the numbers of species which migrate to Africa declines. The west Palearctic, the region lying to the north of Africa, produces about 193 species of migrants, the mid-Palaearctic between 45˚E and 90˚E about 178 (mainly the same) species, while the eastern Palaearctic, beyond 90˚E, produces only about 25 species, most of the longdistance migrants from this region travelling to southeast Asia or Australasia. In addition, other migrants of the same species (mainly waders) migrate to Africa from as far west as northeast Canada and Greenland; and yet others (mainly passerines) migrate to Africa from as far east as Alaska and the Yukon (Chapter 17). Some of these far eastern birds cover as much as 200˚ of longitude and more than 9,000 km before they reach Africa, and many then swing south to cross the equator and even the tropic of Capricorn. They include some of the most impressive of avian travellers, including the Amur Falcon, the Northern Wheatear and the tiny Willow Warbler.

The fact that so many species from the mid-Palaearctic make the long westerly flight to Africa, rather than southwards within Asia, is presumably due partly to the geography and climate of southern Asia. The area of land west of 70˚E with a genial winter is limited, as the Indian subcontinent covers only about 4 million km^2, compared with 21 million km^2 in Africa south of the Sahara. To the north of India, between 75˚ and 95˚E, lies the great mountain mass of Tibet, flanked on the south by the even higher Himalayas. The Tibetan plateau averages nearly 5 km above sea level and spans 2,000 km from north to south, while the Himalayan peaks rise to over 8 km and span another 200 km from north to south. This great mountainous area, much of which is snow-covered in spring, represents a formidable barrier to the north–south movements of migratory birds. Nevertheless, about 27 species and subspecies from the mid-Palaearctic do winter in India, mostly ‘leaking round the two ends of the Tibetan massif’ (Moreau, 1972). They include several species from the west Palaearctic that do not go to Africa, including the Scarlet Rosefinch and the Arctic Warbler. From the

east Palaearctic, nearly all the migrants move south-southeast into southern Asia, wintering from Burma eastward to Indonesia. Their journeys are far less arduous than those undertaken by birds entering tropical Africa from whatever source.

THE AFRICAN WINTERING AREAS

Africa is a vast continent, offering a wide spectrum of habitats from rainforest to dry desert. Ecological conditions there are governed much more by rainfall than by temperature. The alternation of wet and dry seasons is driven by the annual north–south movement of the Inter-Tropical Convergence Zone (ITCZ). This is a low-pressure zone that extends west–east across the continent where the northeast and southeast trade winds meet, and where rain falls on abroad front (Jones, 1995). During the northern summer, the ITCZ spreads from the equator slowly northward, bringing rain to the northern tropics, and then retreats southward again in autumn (Fig. 253). The wet season thus begins later and ends sooner further north, so that the length of the wet season and the total annual rainfall decline from the equator northwards. In West Africa, annual rainfall exceeds 2,000 mm near the equator but diminishes to less than 50 mm near the southern fringe of the desert. In addition, as the mean annual rainfall declines, the amount becomes more variable from year to year.

As the duration of the wet season and the overall rainfall both decline with distance north and south from the equator, the vegetation zones also mirror each other in the northern and southern tropics (Fig. 254). The region of almost year-round rainfall in equatorial West and Central Africa supports rainforest. Then, with decreasing rainfall towards both north and south, the vegetation becomes progressively shorter and sparser, as forest gives way first to broad-leaved deciduous woodland and then to increasingly sparse acacia savannah and grassland, and eventually to desert—the Sahara in the north and the Kalahari–Namib in the south. North of the equatorial rainforest, the woodland zone is known as the Guinea

zone, the wooded savannah as the Sudan zone and the sparser savannah grassland as the Sahel zone, which grades northwards into the Sahara. Where the rainforest has been cleared, it has given rise to a 'derived savannah' of remnant secondary forest and broad-leaved trees akin to the Guinea zone to the north.

The greatest exception to this broad latitudinal vegetational pattern within the continent is East Africa, where varied topography and twin rains combine to produce a complex mosaic of vegetation types from rainforest to semi-arid *Acacia* savannah. This complexity makes it harder in this region to discern clear latitudinal trends in rainfall or vegetation zones. Most importantly for the migrants, however, the seasons of maximum plant growth and associated insect life are six months apart between the northern and southern tropics.

Ecology of wintering areas

Throughout Africa, plant growth occurs in the wet season, so this is the time of greatest productivity and insect activity. North of the equator, the wet season occurs at the same time as the northern summer, when the Eurasian migrants are away in their breeding areas. So those Eurasian migrants that winter in the northern tropics of Africa are present there during the dry season, and experience progressively worsening conditions from the time they arrive (mainly in September) to the time they leave (mainly in March–April). The same is true for wetland birds, for during the rains, water collects in every hollow, and rising rivers may flood extensive areas. But as the dry season advances, these productive shallow waters progressively shrink and disappear. Towards the end of the dry season, in the Sudan and Guinea zones, grass fires become widespread. As the grasslands dry in roughly the order in which they were last wetted, a 'fire-belt' spreads systematically through large parts of the northern tropics each year in more or less regular pattern. Within this belt, the fires are localised at any one time, but over a period of weeks most of the terrain gets burned, and the belt

moves on. Small animals flushed out or injured by grass fires are exploited by a wide range of birds, including raptors, storks, rollers, bee-eaters and others, while the smaller insects carried into the air above are taken by masses of hirundines. These various species include many Eurasian migrants which are free to follow the fires across the continent, on a roughly similar schedule from year to year. In any one locality, however, the bonanza is short-lived, and in effect fires destroy many of the remaining food supplies. They affect especially the food available at ground level and, through scorching, also that in the lower trees and bushes. Yet despite the seasonally worsening conditions, many migrant species somehow maintain themselves in the Sahel zone throughout the northern winter, and are also able to fatten there in preparation for the spring desert-crossing.

In contrast to the migrants that stay in the northern tropics, those that move south of the equator, where the seasons are reversed, experience progressively improving conditions. The rains are starting as the first migrants arrive in late September and have hardly finished when they leave in March–April. However, they must still pass north through the arid Sahel zone on their return migration, getting their last chance to feed and fatten before a long desert-crossing. Not surprisingly, many fatten further south, in the more humid Sudan and Guinea zones, where the rains begin in March–April, rapidly increasing local food supplies. Such species may then over-fly the Sahel zone (where rain has not yet fallen) as well as the Sahara, apparently taking little or no further food until they reach North Africa.

Wetlands

North of the equator, the generally dry landscapes are alleviated by extensive shallow wetlands which occur patchily from west to east. The biggest are found mainly around the Senegal river (in Senegal), the upper Niger river (in Mali), the Lake Chad basin (in Chad) and the Nile–Sudd swamps (in southern Sudan). They provide

productive feeding areas year-round, even at the height of the dry season, leaving rich grassland and pools as they retreat. The seasonally inundated plains around Lake Rukwa, the Lake Victoria basin and the Wembere swamps in Tanzania also support large numbers of birds, including many Eurasian migrants. Each of these areas extends in the wet season over many thousands of square kilometres. South of the equator, equivalent wetlands include the Bangwelu swamps and the Kafue flood plain in Zambia, and the Okavango delta swamps in Botswana, again each extending in the wet season over many thousands of square kilometres.

Until recently, these various African wetlands comprised some of the largest expanses of fresh water on earth, covering an estimated 657,000 km^2 of West Africa, 208,000 km^2 of East and northern Africa, and 172,000 km^2 of southern Africa. However, most of these places are being rapidly reduced by drainage and other human impact, and now cover only a small part of the area they occupied as recently as the 1970s. Those in the northern tropics are the most important for Eurasian migrants, supporting huge numbers of herons, ducks and waders through the northern winter.

Overall, the numbers of Eurasian ducks counted between 1999 and 2004 on the three major wetlands in West Africa averaged 240,000 for the Senegal delta, 610,000 for the Inner Niger delta and 500,000 for the Lake Chad basin, with the most counted at one time in the three areas being 1.7 million (Troillet & Girard, 2006). Taking account of other wetlands in West Africa, the total regional duck population was estimated at 2.0–2.5 million. The Garganey was the most abundant Eurasian species, forming on average nearly 80 per cent of the total., the Northern Pintail comprised about 20 per cent, with much smaller numbers of Northern Shoveler (abundant only in the Senegal delta), Common Teal, Eurasian Wigeon, Common Pochard, Ferruginous Duck, Tufted Duck and Common Shelduck. In addition to all these immigrants, some 490,000 native African ducks were also counted (Girard, 2006).

In the seas off the western coast of Africa, two major upwelling areas occur in association with nutrient-rich cold-water currents, which support an abundance of sea life including birds. Off northwest Africa, the Canary and Guinea currents support around 20 species of wintering seabirds from European breeding colonies, including seven species of terns, and the younger age classes of Lesser Black-backed Gulls and Northern Gannets, among others. In the autumn, where this upwelling occurs, shoals of sardines move in from deeper water to spawn, providing rich pickings for the newly arrived seabirds. Off the southwest coast, the Benguela current supports about a dozen species from European breeding areas, including terns, skuas, petrels and others, in addition to large numbers of local breeding species. As the Eurasian species depart northwards to breed (the southern autumn), their place is taken by petrels and others from the Southern Ocean that migrate northwards from their nesting colonies far to the south to spend their non-breeding period off southwest Africa.

MOVEMENTS WITHIN AFRICA

The Sahel savannah zone that crosses the continent from west to east is particularly important for Eurasian land-bird migrants. It offers the first chance for them to feed and drink after crossing the Sahara in autumn and the last before crossing in spring, and in addition, many species spend the whole or part of the winter there (Moreau, 1972; Jones, 1995, 1999). The migrants arrive between August and November, depending on species, but mainly in September when many African birds (which have spent their breeding season there) are themselves beginning to retreat southward. At this time, the rains are finishing, the land is green and food is still plentiful, but as the country gradually dries out, feeding conditions deteriorate. Nevertheless, throughout the dry season, many of the dominant trees have leaves (supporting insects) or produce flowers and fruit, which many birds can use.

In West Africa, about one-quarter of all migrant species remain in the Sahel and Sudan zones for the whole winter in the local dry season ('Strategy 1' in Box E). Examples include some *Sylvia* warblers, which eat fruit as well as insects from leaves, and some ground-dwelling wheatears and chats, which eat small terrestrial insects (Pearson & Lack, 1992). They also include granivores, such as the Turtle Dove and Common Quail, for seeds remain available on the ground throughout the dry season, but disappear rapidly when rain causes them to germinate. It would make no sense for a ground-feeding seed-eater to move south of the equator in September to the austral summer.

BOX E. Migratory habits of Eurasian land-bird migrants in Africa. Some species occur in more than one category, usually where migration patterns differ between the west and east sides of Africa. (Mainly from Moreau, 1972, and Jones, 1999.)

Strategy 1: Wintering entirely in the dry-season conditions of the northern Sahel and Sudan savannahs.

Greater Whitethroat *Sylvia communis,* Lesser Whitethroat *Sylvia curruca,* Northern Wheatear *Oenanthe oenanthe,* Olivaceous Warbler *Hippolais pallida,* Bonelli's Warbler *Phylloscopus bonelli,* Subalpine Warbler *Sylvia cantillans,* Orphean Warbler *Sylvia hortensis,* Riippell's Warbler *Sylvia rüppellii,* Greater Short-toed Lark *Calandrala brachydactyla,* Tawny Pipit *Anthus campestris,* Red-throated Pipit *Anthus cervinus,* Bluethroat Luscinia *svecica,* Black-eared Wheatear *Oenanthe hispanica,* Ortolan Bunting *Emberiza hortensis,* Turtle Dove *Streptopelia turtur,* Common Quail *Coturnix coturnix,* Collared Pratincole *Clareola pratíncola,*

Black-tailed Godwit *Limosa limosa,* Short-toed Snake-Eagle *Circaetus gallicus,* Egyptian Vulture *Neophron percnopterus.*

Strategy 2: Wintering in dry-season conditions, first in the northern Sahel–Sudan savannahs and then further south in the Guinea and derived savannahs.

Barn Swallow *Hirundo rustica* (in West Africa), Tree Pipit *Anthus trivialis,* Woodchat Shrike *Lanius senator,* Common Nightingale *Luscinia megarhynchos,* Common Redstart *Phoenicurus phoenicurus,* Great Reed Warbler *Acrocephalus arundinaceus,* Melodious Warbler *Hippolais polyglotta,* Wood Warbler *Phylloscopus sibilatrix,* Willow Warbler *P. trochilus* (in West Africa), Garden Warbler *Sylvia borin.*

Strategy 3: Wintering in wet-season conditions, first in the northern tropics and then in the southern tropics (trans-equatorial migrants).

Sand Martin *Riparia riparia,* Tree Pipit *Anthus trivialis,* Great Reed Warbler *Acrocephalus arundinaceus,* Sedge Warbler *A. schoenobaenus,* Willow Warbler *Phylloscopus trochilus,* Garden Warbler *Sylvia borin,* Greater Whitethroat S. *communis,* Marsh Warbler *Acrocephalus palustris,* Thrush Nightingale *Luscinia luscinia.*

Strategy 4: Wintering entirely in wet-season conditions in the southern tropics, after passing rapidly through the northern tropics (trans-equatorial migrants).

Spotted Flycatcher *Muscícapa striata,* Collared Flycatcher *Ficedula albicollis,* Barn Swallow *Hirundo rustica,* Hobby *Falco subbuteo,* Red-footed Falcon *Falco vespertinus,* Common Cuckoo *Cuculus canorus,* Icterine Warbler *Hippolais icterina,* Eurasian Golden Oriole *Oriolus oriolus.*

Note: During their pause in northeast Africa, many migrants moult, including the Great Reed Warbler, Barred Warbler, Sedge Warbler, Olivaceous Warbler, Greater Whitethroat (eastern race, *icterops)* and Marsh Warbler (Pearson, 1973, 1990; Pearson & Backhurst, 1976).

A few species seem to fly directly to winter quarters in southern Africa, passing quickly through the northern tropics ('Strategy 4' in Box E). They include the Barn Swallow, Spotted Flycatcher, Icterine Warbler and Common Cuckoo. These species tend to leave Europe relatively early, pass through the northern tropics before the rains finish and reach the southern tropics as the rains begin. They thus spend the maximum time possible in wet-season conditions that sustain their food supplies. Some of them feed on the aerial or ground insects brought out by rain, and others on the flush of insects that appear on new leaves.

Most of the birds that migrate to East and southern Africa derive from Asian breeding areas at 30–90°E, but some migratory species that breed in western Europe move southeast in autumn (instead of southwest through Iberia) to join their conspecifics from Asia in the Middle East, before passing down the eastern side of Africa. Species that follow this route include the Thrush Nightingale, Lesser

Whitethroat, Marsh Warbler, Eurasian River Warbler, Olive-tree Warbler, Barred Warbler, Red-backed Shrike and Lesser Grey Shrike (Moreau, 1972; Pearson, 1990). Populations of these species from the whole breeding range thus spend the northern winter in eastern or southern Africa (although Lesser Whitethroats extend remarkably far west in Africa, being regular in northern Nigeria).

As in West Africa, many species that migrate to East Africa spend the first few weeks after arrival in the *Acacia* savannahs between 12°N and 15°N (Ethiopia–Sudan) in areas where it has recently rained, and some species moult there (Box E) (Pearson, 1973; Jones, 1995). They then move on in November–December as the dry season sets in. Some (mainly ground-feeders) winter in equatorial eastern Africa (Kenya–Tanzania) where the second wet season is just beginning (Lack, 1983), while others (mainly vegetation-gleaners) cross the equator to winter 2,000–4,000 km away in southern Africa (Pearson, 1990; Pearson & Backhurst, 1976; Lack, 1983; Jones, 1985, 1999). Like some species in West Africa, they thus perform a two-stage migration, with a two-month break between stages.

In some species, onward movements occur at about the same time every year, irrespective of local conditions, following a period of pre-migratory fat deposition. When visibility is poor at night, many of these birds are grounded, and some carry enough fat for a trans-equatorial flight to southern Africa (Pearson, 1990; Pearson & Lack, 1992). In other species, the onward movements maybe optional (facultative), as many more birds remain in northern Africa in wet than in dry years (Lack, 1983), and those that migrate display highly variable timing in their southward departure. Similarly, while some species (such as the Red-backed Shrike) arrive in the Kalahari basin of Botswana at about the same time every year, other species (such as the Great Reed and Sedge Warblers) show big year-to-year variations in arrival times depending on when the local rains begin (Herremans, 1994, 1998). In general, as a result of these various movements, the centre of gravity of the collective migrant population shifts southward within Africa during the course of the northern winter, but over a shorter mean distance in the west than

in the east. Some migratory species maybe on the move for much of the time between leaving their breeding areas in one year and returning there the next.

Both southward and northward migrations through East Africa seem to be channelled by mountains, and some west–east segregation of species is apparent, with some taking one route and others a different one. Some species show a strong passage mainly through Uganda (Willow Warbler, Garden Warbler, Red-backed Shrike), and others through eastern Kenya (Marsh Warbler, Greater Whitethroat, Thrush Nightingale). This segregation depends partly on breeding origin and partly on preferred habitat in Africa. Some species, such as the Marsh Warbler, seem to pass through Kenya on a front only about 100–200 km wide (Pearson & Lack, 1992). On their return northward journey in spring, many birds take a more easterly, coastal route, associated with the more humid conditions that characterise the season. The whole migration forms a loop, as shown for example in the Red-backed Shrike, Lesser Grey Shrike, Golden Oriole, Great Reed Warbler, Sedge Warbler, Willow Warbler, Garden Warbler, Spotted Flycatcher and Thrush Nightingale (Pearson, 1990; Pearson & Lack, 1992).

Whatever the particular migration strategies of different species, they all more or less conform to a single pattern, evident throughout Africa: north of the equator, birds follow the rain-belt northward from March to April onwards, returning southward in October–November as the rains withdraw; south of the equator, birds move further south with the rains from October to November, returning northwards in March–April. The pattern is essentially the same whether birds remain in the northern or southern tropics, or whether they cross the equator. It is also the same whether the birds are Eurasian–African migrants or intra-African migrants (Elgood *et al.,* 1973; Jones, 1985). All are subject to the same ecological pressures. The most obvious difference between the two groups is that the Eurasian migrants move much further north than the African ones, crossing the Sahara to breed in Europe and Asia. As the Eurasian migrants return to Africa in autumn, the African

migrants in the Sahel and Sudan zones begin to move further south (Jones, 1995, 1998). The extent to which the two groups replace each other ecologically, exploiting the same habitats and food types but at different times of year, awaits more study.

ECOLOGY OF MIGRANTS IN AFRICA

How can all these migrant birds be accommodated for more than half the year, and more densely than in their breeding areas, in lands already richly endowed with birds of their own? Despite their impressive numbers, the Eurasian visitors are in fact much less numerous overall than the native African birds, both as species and as individuals. Against 186 Eurasian migratory land-bird species, there are around 1,481 Afrotropical land-bird species, some of which are year-round residents and others seasonal migrants within Africa (Moreau, 1972). And against an estimated 4,000–5,000 million Eurasian migrants, there are an estimated 60,000–70,000 million native African birds. Nevertheless, in some areas the Eurasian visitors appear very abundant and may locally outnumber the native species. Of the African species, 409 inhabit evergreen forests, either lowland or montane, and another 74 are confined to montane non-forest habitats. Such habitats are barely used by Eurasian migrants, so the two communities hardly come into contact. It is the remaining 998 African species, occupying seasonal woodland, savannah and grassland, which interact with the 186 Eurasian immigrant species for part of each year (Moreau, 1972). These two groups comprise about 84 per cent and 16 per cent respectively of the total bird species that occupy these African habitats in the northern winter.

Distributions

As indicated already, the immigrant species do not by any means distribute themselves evenly over the continent (Fig. 260; Newton, 1995a; Hockey, 2000). Most species occur in the Sahel and Sudan

savannah belts, and southwards from these zones, the numbers of Eurasian migratory species progressively decline so that few reach the southern tip of Africa. It is as though the Eurasian species migrate no further within Africa than is necessary to find conditions that suit them.

Habitats

For the most part, the Eurasian migrants occupy habitats in Africa that are structurally similar to those they use in their breeding areas, and obtain similar foods in similar ways. The few migratory species from Eurasia that occur in evergreen forest include the Pied Flycatcher, Collared Flycatcher, Semi-collared Flycatcher, Wood Warbler and Eurasian Golden Oriole. All these species are found chiefly around edges and openings, and are most numerous in more open woodland or gallery forest, as also is the European Honey Buzzard. Most migrant passerine and raptor species live in the seasonal woodlands and savannahs (Lack, 1990; Leisler, 1992; Jones, 1999), where many of the passerines are found in scrubby or reedy areas. In some such areas, the Eurasian migrants may outnumber insectivorous resident species during certain times of year. As expected, waterfowl occur mainly in association with inland wetlands, and waders with inland wetlands or sea coasts, depending on species. The coastal species have such habitats almost to themselves, as they greatly outnumber the relatively few African species that occur there.

Mobility

A major difference between migrants and residents is their mobility. As they are not tied to nesting areas, the Eurasian migrants are free to roam around, exploiting temporary abundances of food in a way that most residents cannot. The same is true for intra-African migrants in their non-breeding season. Many migratory species thus pursue an itinerant lifestyle, periodically moving in relation to

seasonal changes in food supplies or even in relation to local flushes of food, such as those produced by patchy rainstorms (Sinclair, 1978; Liversidge, 1989; Leisler, 1992; Herremans, 1998). Typically, the birds move with the rain-belts, seldom staying for long in any one locality, and not appearing at all in drought years, but continually utilising food supplies that result from fresh rain, whether emerging termites, grasshoppers and locusts, or quelea colonies. In consequence, such migrants may occupy only part of their potential non-breeding range at any one time, avoiding certain areas altogether in some years.

In contrast to the migrants, many resident African species remain on territories year-round, and south of the equator, most African species, both residents and intra-African migrants, are breeding when the Eurasian migrants are present (Moreau, 1972). This limits how effectively the African birds can exploit transient food supplies, and hence their ability to compete for them with the visiting migrants. In effect, the Eurasian species tend to use temporary habitats and food sources which cannot be fully exploited year-round by local species. These habitats include seasonally flooded grasslands, drying pools, recently burned savannahs, nearly bare fields, and plantations and secondary growth in the forest zone (Thiollay, 1989).

Food

Within Africa, the majority of Eurasian land-bird migrants depend on arthropods, which are generally more abundant in the wet season (Morel, 1973; Lack, 1986a). Even in the dry season, however, the Sahel zone offers a reasonable abundance of insects, as trees and shrubs can be found throughout at every stage of leaf, flower and fruit production. Locally and temporarily, insects can be available in tremendous abundance, as for example around standing water, where for short periods at any time of year, masses of midges and lake flies coat the emergent vegetation, forming an important if temporary food source for small insectivorous birds, lasting for a

few days at a time. These short-lived insects are exploited by passerines and waders on both their northward and southward passages, enabling rapid fattening (Wanink & Goudswaard, 2000).

An important component in the insect flush associated with the wet season is the appearance everywhere of swarms of winged termites and ants. They are eaten by a wide range of birds which follow the rain-belts across Africa, from small warblers to large eagles. They are especially important to insectivorous falcons, and may account for the fact that four of the five migratory species winter mainly south of the equator. Hundreds of Lesser Spotted Eagles and other raptors have been found at localities where winged termites are temporarily available.

In contrast, plague locusts are only occasionally available in abundance (Moreau, 1972). These insects erupt after several years of drought, emerging immediately after heavy rain, their eggs having survived in the ground in the meantime. Once the larvae have eaten the local vegetation, they swarm and take wing, heading downwind to areas with low pressure where rain is falling. But in no part of Africa could locusts have ever provided a reliable source of food for birds, and however superabundant they may be at certain times and places, years pass without outbreaks anywhere. In the intervals, the surviving insects merely take their place among many other solitary grasshoppers, some of which are very abundant. Nowadays, locust outbreaks are usually controlled by pesticide applications, which presumably remove many other arthropods too.

Another important food source for some raptors and others is provided by Red-billed Queleas, small seed-eating birds that nest in dense colonies, millions strong. Colonies form after rain has fallen and grass has grown and seeded. In the northern tropics, they are available only for a few weeks after the migratory raptors first arrive, but in the southern tropics, they are accessible in one locality or another for much of the southern summer. Single nesting colonies, occupying only a few hectares of scrub, attract hundreds of migratory raptors and storks, which feed on the adults and chicks. At one large quelea colony in the Kruger National Park, Kemp

(2001) counted more than 1,000 eagles, the majority being Lesser Spotted Eagles, with smaller numbers of Steppe Eagles, Tawny Eagles, Wahlberg's Eagles and at least 100 Marabou Storks (the latter three species being intra-African migrants). In the same region at another large quelea colony, Pienaar (1969) counted 800–1,160 Steppe Eagles, 200–240 Wahlberg's Eagles, 300 Marabou Storks and many other species. At least 60 per cent of quelea nests were torn open by these birds. Other concentrations of raptors have been found at the smaller colonies of Wattled Starlings, which normally cover a few hectares or less. These birds move in after rain to exploit the resulting mass hatches of locusts or noctuid and other lepidopterous larvae. Many other raptor species are also attracted to local concentrations of rodents, which occur sporadically, again mainly in response to local rain.

Many of the migrant passerines eat fruit as well as arthropods, particularly of the shrubs *Salvadora persica, Maerua crassifolia, Balarites aegyptiaca* and *Zizphus mauritiaca* (Fry *et al.,* 1970; Moreau, 1972; Jones, 1995; Stoate & Moreby, 1995). Fruit crops vary greatly in size from year to year, but may remain available through the dry season, and are particularly favoured during the period of fat deposition for spring migration. Only the Common Quail and Turtle Dove are almost entirely granivorous in Africa, while the Short-toed Lark, Ortolan and Cretzschmar's Buntings eat both seeds and arthropods.

Within habitats, Eurasian visitors tend to segregate, spatially or ecologically, from closely related African species (Moreau, 1972; Thiollay, 1989; Lack, 1986a, 1987). The latter tend to be in different genera, and in arid areas are generally less abundant. The Eurasian migrants tend to differ from closely related African species in habitat, foraging behaviour or diet, which presumably reduces competition between them (Lack, 1986a; Rabøl, 1987; Salewski & Jones, 2006). More often than not, the Eurasian migrants exploit a wider range of habitats and food sources than the residents (Salewski & Jones, 2006). However, much depends on the species

and area concerned, and any superabundant food sources tend to be exploited by a wide range of species, both migrant and resident.

Temperatures

Conditions in African wintering areas are generally warmer than in European breeding areas, so individual migrants need less food per day in order to maintain themselves. The daily maintenance needs of individual birds were calculated at roughly 60 per cent, on average, of their breeding-grounds requirements (Moreau, 1972). For many species, the main problem is to keep cool. The mean temperature increase from breeding to wintering areas of 50 species of migrants was calculated at over 6°C. Extremes were provided by tundra-nesting species which experienced July temperatures of 5–1 0°C, and then migrated to tropical Africa, with January temperatures of around 20–30°C. In addition to these savings on daily maintenance costs, because the migrants are not breeding while they are in Africa, individuals have only themselves to feed.

Social systems

Moulting patterns

Many Eurasian–Afrotropical migrants moult in their breeding areas before they set off on their migration to Africa (Chapter 9). Some species may moult partly in breeding areas, stop during migration and resume once they reach their winter quarters. Other species do not begin moulting their flight feathers until they have reached Africa, either soon after their arrival or before they depart in spring. To complicate matters, within some species, different populations show more than one of these patterns, depending mainly on where they breed and where, within Africa, they spend the non-breeding period. For birds that remain in the dry northern tropics, food supplies are most abundant soon after they arrive, before the region

dries out: that is, between September and December, which is when they moult. In contrast, in equatorial and southern Africa, the rains become established later, and the majority of species wintering in these regions moult between December and April. These differences in moult timing, according to non-breeding area, are particularly evident among various species of shrikes and warblers (Jones, 1995).

CONCLUDING REMARKS

Traditionally, we think of our summer visitors as European birds that migrate to Africa each year to escape the northern winter. But they could equally be regarded as African birds that visit Europe each year to breed. Their annual cycles are adjusted to both regions, as illustrated in the timings of moults and movements. Most such species spend more of each year in Africa than in Europe, and some large species also remain there during their immature non-breeding years. The numbers and distributions of Eurasian migrants in Africa are greatly influenced by prevailing patterns of rainfall, which in turn influence habitats and food supplies. As rainfall patterns are broadly similar from year to year, so bird migration patterns remain largely the same, but with marked annual and regional variations. The total amount of rain in particular areas is itself highly variable from year to year, influencing food supplies, and hence the distributions and numbers of wintering migrants. As they are not breeding at the time, many migrants are able to move around within Africa, concentrating wherever rain has recently fallen, and exploiting the resulting food supplies. The migrants are clearly adapted to life there, occupying distinct niches, in which they live alongside native African species, some of which perform parallel movements within Africa.

To judge from measured mortality rates, less that half the migrants that leave Eurasia each autumn are likely return the following spring, probably fewer than 2,000 million individuals. However, the British Isles occupy only a tiny part of the total

breeding range of these birds, and to judge from recent counts, are likely to receive only about 16 million individuals each year. These summer visitors form around one-fifth of all the birds that breed in Britain and Ireland. Much of Africa is in the process of rapid change, as human and livestock populations expand, landscapes are increasingly degraded and habitats destroyed. Together with climate changes and frequent droughts, these human impacts are adversely affecting European migrants, as well as local species, a theme to which we shall return in Chapter 24.

CHAPTER 23

Population Limitation

In resident bird species, which live year-round in one place, population sizes are determined entirely by local conditions. But in migratory species, population levels may be influenced by conditions in breeding, migration or wintering areas, which can together span more than one continent. Problems in one area can affect the numbers of birds which appear in another. Migrants can also be killed in large numbers by adverse weather encountered on their journeys, a hazard to which resident species are not exposed. In recent years, as the numbers of many migratory bird species have declined, the question has arisen about the causes. Answering this question is important in the development of effective conservation measures.

During the course of a year, bird numbers normally fluctuate because of seasonal reproduction and mortality, but in discussing population limitation, we are usually concerned with breeding numbers (or densities). There are both biological and practical reasons for this. It is at the start of breeding that numbers reach their annual low; and it is upon breeders that all future additions to the population depend. In addition, it is when they are breeding that birds are most conspicuous and most closely tied to fixed localities, which makes them easier to count reliably. In some birds, such as arctic-nesting waterfowl and waders, any count must take place in the wintering areas, where the birds are concentrated and accessible. But for most bird species, our entire knowledge of year-to-year population trends is based on counts of breeders. So in this chapter, breeding numbers are implied unless stated otherwise

LIMITATION IN BREEDING OR WINTERING AREAS

The main limitation of migratory bird numbers might occur in either breeding or wintering areas, determined in the first place by the amount of habitat available. Consider the model in Figure 263. Seasonally breeding birds tend to reach peak numbers just after the nesting season, when young are produced. These numbers then decline over winter to reach their lowest level at the start of the next breeding season. It is usual to find that breeding habitats can only support a limited number of pairs, influenced by the available territories, nest sites or food supplies. Now imagine a situation in which the over-winter mortality is so great that too few birds are left at the end of the season to occupy all available nesting habitat (curve A in Figure 263). Under these conditions, given an appropriate sex ratio, every bird of appropriate age could find a place and breed. Such a population could be described as 'winter-limited', because to increase breeding numbers in the long term would entail some favourable change in the winter conditions experienced by the population.

The available data for migratory birds suggest that some populations are limited in wintering areas and others in breeding areas. This is evident from their long-term or year-to-year changes in numbers, which can be related to conditions in one area or the other (Newton, 2008). A good example of apparent winter limitation is provided by the Sedge Warbler, which breeds in Europe and winters in Africa south of the Sahara (Fig. 24). Over a number of years, the annual survival and breeding density, as measured in Britain, was related to rainfall in the Sahel zone of Africa, where this species spends the winter (or part of the winter). In this arid environment, rainfall largely determines the state of habitats, and the associated food supply for birds. High rainfall promotes good vegetation growth, which leads to high insect populations, and in turn to good over-winter survival among Sedge Warblers, and thus to high numbers returning to Britain in spring to breed. In years of poor rainfall, the reverse occurs. Similar relationships between

African rainfall and European breeding numbers have been found in several other species of trans-Saharan migrants, as discussed in Chapter 24.

In contrast, the Pied Flycatcher is a long-distance migrant which for much of the 20th century was apparently limited in its European breeding areas. It nests in tree cavities, and in many areas its natural breeding densities were greatly increased by providing nest boxes (Newton, 1994, 1998b). In one area of Finland, where virtually no flycatchers nested, the addition of nest boxes resulted in such huge uptake that flycatchers came to outnumber all other bird species in the woods concerned (von Haartman, 1971). Evidently, flycatcher breeding densities were usually limited by shortage of nest sites, many of the available tree cavities having already been taken by earlier-nesting tits and other birds. In areas where nest sites were in abundant supply, fluctuations in Pied Flycatcher breeding numbers were found to correlate with breeding success in the previous year. In general, increases in breeding densities from one year to the next followed good breeding seasons, when the young-to-adult ratios were high, while decreases in breeding densities followed poor breeding seasons (Fig. 265). In this species, therefore, conditions in breeding areas evidently overrode conditions in wintering areas in affecting breeding densities. This may have been true over much of Europe during the latter half of the 20th century, but more recently, Pied Flycatcher populations have declined in many areas despite a surplus of boxes. Conditions in Africa may have been responsible, but in some regions, nest success has also declined because of climate change, which has caused an increasing mismatch between arrival dates and food supply (Chapter 16).

If we assume that breeding rates are influenced primarily by conditions in breeding areas, and survival rates primarily by conditions in wintering areas, then inferences on summer or winter limitation could be made for other bird populations breeding in Europe (Newton, 2008). In at least 27 of these populations, to judge from long-term trends or annual fluctuations, breeding numbers were affected primarily by conditions in breeding areas, in 23

primarily by conditions in wintering areas, while 4 showed evidence of both breeding and wintering area effects. In some of the latter, long-term trends were associated with conditions in one area, and the year-to-year fluctuations about the trend with conditions in the other area. For example, in Dark-bellied Brent Geese wintering in western Europe, a long-term upward trend over the past 50 years has been associated with reduced hunting pressure and the establishment of winter refuges, enabling the population to recover from over-hunting in the past. Overall, this population increased from around 15,000 in 1955 to around 315,000 individuals in the late 1990s. Nevertheless, the great year-to-year fluctuations about this upward trend, evident throughout this period, were associated with predation in breeding areas, as described above. Some bird species may switch from summer-limited to winter-limited (or vice versa) as their numbers grow over a period of years, while others may be winter-limited in some years or areas and summer-limited in other years or areas. Each case must be judged individually, depending on time and place.

In some migratory species, breeding numbers declined for a time, and it was not immediately obvious whether the causes lay in breeding or wintering areas. However, where reproductive and survival rates were monitored in the same population during both periods of stability (or increase) and decrease, the comparison provided useful pointers to where the cause of the decline might lie. Where annual reproduction declined while annual survival stayed the same, the problem could be assumed to lie in breeding areas, but where survival had decreased, the problem could have lain in either breeding or wintering areas, depending on where the extra deaths occurred. Decline in a local population of Golden Plovers in Scotland was associated with a decline in survival rate but no change in reproduction (by implication a problem in wintering areas), while a decline in the British population of Northern Lapwings was associated with a decline in reproduction but no change in survival (by implication a problem in breeding areas) (Parr, 1992; Peach *et al.,* 1994). In not every species, however, can

decline in reproduction be confidently ascribed to conditions in nesting areas, for in geese and other species that breed partly on the strength of pre-existing body reserves, the problem may lie in wintering or migration areas (see later).

In yet other bird species, long-term population declines were associated with reductions in both breeding and survival. At times during the 20th century, White Storks suffered from reduced reproduction on the west European breeding grounds, caused by drainage and pesticide-induced food shortages, and also from reduced survival on West African wintering grounds, caused mainly by drought-induced and pesticide-induced food shortages (mainly locust control) (Dallinga & Schoenmakers, 1989; Kanyamibwa *et al.,* 1993). In recent decades, breeding numbers have also fluctuated in relation to weather in both Africa and Europe, which is thought to influence the amount of food available for breeding birds (Saether *et al.,* 2006). Thus, in any avifauna, we can expect to find at one time species whose numbers are changing mainly because of events in breeding areas, and others whose numbers are changing mainly because of events in non-breeding areas, or both.

Experimental evidence

Most evidence on the causes of population changes in migratory birds, as described above, is based on correlation and inference. Experiments are almost impossible to perform on regional scales, but sometimes widespread changes in land-use or legislation have been followed by widespread changes in bird numbers. Examples include the increases in many waterfowl and shorebird populations that followed the advent of protective legislation or other conservation measures from the mid-20th century, or the increases of bird of prey populations that followed reductions in the use of organo-chlorine pesticides between the 1960s and 1980s (Newton, 1979, 1998b; Cade *et al.,* 1988).

In addition, local population increases in migratory birds have followed local manipulations of potential limiting factors or the

introduction of specific conservation measures. For example, increases in breeding success and breeding density were associated with: (1) removal of predators, which benefited various ground-nesting ducks and waders (Duebbert & Kantrud, 1974; Duebbert & Lokemoen, 1980; Fletcher *et al.,* 2010); (2) provision of extra nest sites, which benefited many species of cavity-nesting and other birds with special needs (Newton, 1994, 1998b); (3) removal or exclusion of competing species, which gave Collared Flycatchers access to more nest sites (Gustafsson, 1988); (4) provision of extra nesting habitat following the establishment of nature reserves, which led to increases in the breeding numbers of several migratory species (Sills, 2007); and (5) change or intervention in destructive agricultural Proc.edures, which allowed Corncrakes and Stone Curlews to thrive and increase where they would otherwise have been eliminated (Green *et al.,* 1997; Green, 1999; Aebischer *et al.,* 2000). Similar measures have led to population increases in some resident bird species too, as has the provision of additional winter food (Newton, 1998b). All these planned experiments and conservation measures were restricted to local breeding populations. They imply that many migratory species were at that time and location limited by conditions in breeding areas, whether by quantity or quality of habitat, nest sites, interactions with competitors and predators, or agricultural operations.

CARRY-OVER EFFECTS

So far, I have discussed population limitation as it has occurred on either breeding or wintering areas. But in some species, carry-over effects are apparent, in that winter conditions can influence subsequent breeding success, and summer conditions can influence subsequent winter survival. These effects have been shown in a range of bird species, from small songbirds to raptors, waders and waterfowl (Newton, 2008). They can be felt at the level of both individual birds and the entire population. At the individual level, birds that are well-fed in winter and spring can accumulate

substantial body reserves, which support subsequent reproduction. Among Brent Geese in the Netherlands, females that had accumulated the greatest body reserves at a spring stopover site were more likely to return with young in the following autumn than females that had accumulated smaller reserves. Males generally accumulated smaller body reserves than females, adopted a less demanding role in parental care and showed no such relationship (Ebbinge & Spaans, 1995).

Other carry-over effects are apparent in smaller birds in which breeding is less heavily dependent on prior body reserves. Among colour-ringed Black-tailed Godwits, individuals that occupied the best wintering habitat were able to depart earlier on spring migration, and were then first to arrive in breeding areas. They thereby acquired the best nesting habitat, and subsequently had better breeding success, on average, than later-arriving individuals that had occupied poorer winter habitat. In this way, the effects of winter habitat carried through the whole annual cycle, from the British Isles to Iceland (Gill *et al.,* 2001; Gunnarsson *et al.,* 2005).

Individual Barn Swallows breeding in Italy were affected by conditions in African wintering areas, as judged from the satellite recording of the annual state of the rainfall-dependent vegetation. Years with good vegetation growth (and presumably insect activity) in African wintering areas were followed by earlier arrival and egg-laying in breeding areas, more second broods and an increase in the total seasonal production of young, compared with other years (Saino *et al.,* 2004b). This change was apparent in individual adults studied in consecutive breeding seasons. Similar carry-over effects from winter to summer, affecting migration dates and breeding, were described in another population of Barn Swallows nesting in Denmark (Møller & Hobson, 2004), and also in various songbirds in the New World (Marra & Holmes, 2001; Marra *et al.,* 1998; Bearhop *et al.,* 2004; Norris *et al.,* 2004; Studds & Marra, 2005, 2007).

Similarly, events in breeding areas can apparently affect subsequent survival in migration or wintering areas. One example is the Sand Martin mentioned above, in which heavy summer rain in

breeding areas was associated with the reduced survival of adults (Cowley & Siriwardena, 2005). Another concerns female Barnacle Geese, in which non-breeders (that had made no reproductive commitment) survived better than failed breeders, which in turn survived better than successful breeders. The annual survival rates in the three groups were 95 per cent (SE 3 per cent), 86 per cent (SE 2 per cent) and 82 per cent (SE 4 per cent) respectively (Prop, 2004). In other words, reproduction in these geese had a cost which was reflected in reduced survival. Among females that attempted to breed, variation in survival was explained largely by the date when they left their nests and could start feeding again. In successful breeders, this date followed hatching, and in failed breeders it followed clutch desertion. The later in the season that nest commitments ended, the lower the subsequent survival probability. This trend was attributed partly to body condition when intense feeding began again, partly to seasonal decline in the nutrient content of food plants and partly to the limited time available in late summer for pre-migratory fattening. In male geese, which played no part in incubation and were free to feed throughout, survival did not differ significantly according to breeding status.

Experimental evidence that reproduction could affect subsequent survival emerged when artificially increased brood sizes resulted in poor body condition, and in reduced survival of parents. This was demonstrated in field trials on Common Kestrels (Dijkstra *et al.,* 1990), Pied Flycatchers (Askenmo, 1979) and Collared Flycatchers (Cichon *et al.,* 1998), among others. The implication was that parents worked so hard to feed their enlarged broods that they lost body condition, with effects on their subsequent survival. Although poor body condition was experimentally induced in these studies, it confirmed that events acting at the time of breeding could influence the later survival of individuals.

There is another way in which carry-over effects at the population level are felt. In years when birds produce unusually large numbers of young so that post-breeding numbers are high, average mortality during the ensuing winter is often greater than usual. This could

result, for example, from greater competition for a limited food supply, causing more birds than usual to starve. Similarly, in years when winter mortality is higher than usual and breeding populations are low, mean breeding success is often greater than usual (Newton, 1998b). These tendencies have been best documented in resident species, but would be expected in migrants, too, if they were competing for some limited resource, such as territories, nest sites or food supplies. Among migrants, the percentage mortality over the non-breeding period has been shown to be 'density dependent' in this way (higher in years of high density) in several species, including the Sedge Warbler, Blackcap, Whitethroat, Willow Warbler, Pied Flycatcher, Common Redstart, Redshank, Mallard, Northern Shoveler and Barnacle Goose.[†] The main point to emerge from such studies is that, in migratory birds, the effects of events in breeding, migration and wintering areas cannot be considered totally in isolation, because events in one part of the year in one region can affect performance at a later time of year in another region.

LIMITATION ON MIGRATION

Migratory bird populations might also be influenced by conditions encountered during their journeys, either at stopover sites or during the flights themselves. In birds that travel long distances, migration can occupy a large part of each year, so it would not be surprising if much of the overall annual mortality occurred in this period. Nor would it be surprising if annual variations in this mortality influenced the year-to-year trends in breeding numbers.

The impact of migration mortality could depend largely on its timing. Heavy mortality on the autumn journey could be offset by improved survival of the remaining birds in winter, so that the effects of the migration losses were not evident in the subsequent breeding population. This would happen to some extent if winter survival were 'density dependent', because average survival rates

would then be higher in years with low numbers than in years with high numbers. But on the spring journey, there is little or no opportunity for heavy losses to be compensated in this way before nesting begins, so breeding numbers could be reduced accordingly. In other words, mortality on spring migration is likely to have much greater impact on subsequent breeding numbers than is similar mortality on the autumn journey (Newton, 2006b).

Food supplies and fattening rates

At migration times, birds must eat more than usual in order to accumulate the necessary body fuel (Chapter 6). They often concentrate in large numbers at stopover sites, increasing the potential for competition for available food supplies (Schneider & Harrington, 1981; Moore & Yong, 1991; Ottich & Dierschke, 2003). Depletion of these supplies can lower the feeding and fuelling rates of birds, especially of latecomers which arrive when little is left. For example, Tundra (Bewick's) Swans were studied at a staging site beside the White Sea, the last stop on the spring migration to the Siberian breeding grounds (Nolet & Drent, 1998). At this locality, the swans obtained their main food—tubers of Fennel Pondweed *Potamogeton pectinatus*— by upending, mainly during low tide. In the course of the staging period, the swans tended to forage at progressively lower water levels, indicating that they gradually depleted this food source, and exploited increasingly deeper parts of the tuber bank as the days went by. This depletion reduced the swans' main foraging period from 6.0 hours per tide on 20 May to 3.3 hours per tide on 28 May. The researchers calculated that this halving of feeding time must have greatly reduced refuelling rates during the staging period. Accordingly, swans arriving late stayed longer than those arriving early. It thus seemed important for the swans to arrive at this stopover site as soon after ice break-up as possible, because a month later, the tubers were largely eaten and any that remained began to sprout. The first swans to arrive could also leave the site first, and (in theory) reach the nesting grounds

earliest, secure the best territories and achieve the highest breeding success. The latest swans seen to leave this site would have arrived in the nesting areas too late to breed that year.

This study hinted at how competition for limited food supplies at a stopover site, used for no more than a few weeks each year, could have helped to regulate the swan population. The White Sea provides the only sizeable stopover site for swans on this part of the spring migration, so with severe food depletion there, the birds would be constrained in how much they could take advantage of improved conditions in breeding or wintering areas. In other words, this stopover site could have played a crucial role in limiting overall population size.

Observations of other species have also pointed to the importance of food supplies at migration times. During stopovers, as at other times, birds tend to accumulate at places where food is plentiful, and are more likely to stay and refuel there than at other areas where food is scarcer (Bibby & Green, 1981; Ottich & Dierschke, 2003; Dierschke, 2006). Repeated captures of birds during the fuelling Proc.ess have shown that rates of weight gain are often related to local food supplies, with individuals fuelling most rapidly where food is most plentiful (Fig. 270; Bibby *et al.,* 1976; Cherry, 1982; Prop & Deerenberg, 1991). Where fuelling rates are high, birds can then move on rapidly to the next site, so that food supplies influence stopover durations and (by inference) the overall speed of migratory journeys (Russell *et al.,* 1992). In Red Knots, fuelling rates were found to increase with latitude, in parallel with the greater food supplies available at higher latitudes in spring (Piersma *et al.,* 2005).

Rates of fuel deposition most commonly reported among birds were in the range 1–3 per cent of lean body mass per day. The average rates were much lower than the maximum rates recorded from individuals in the same populations, which exceeded 7 per cent of lean mass per day. Apparently, most individuals were constrained to feed at rates that were lower than needed to fuel at the maximum possible rate (Lindström, 2003). The provision of

supplementary food to migrants in field experiments led to increased rates of weight gain compared to unfed birds, as shown in studies of Bluethroats (Lindström & Alerstam, 1992), Whitethroats (Fransson, 1998), Robins (Danhardt & Lindström, 2001) and Garden Warblers (Bauchinger, 2002). These findings again implied that food could be limiting. In addition, it is commonly observed that fuel deposition rates or body weights of staging migrants decline in cold or wet weather, which would be expected to reduce their feeding rates (Ash, 1969; Ormerod, 1989; Schaub & Jenni, 2001).

These various observations point to the influence that feeding conditions en route can have on the migration and performance of individual birds. But the key question is whether events at stopover sites, through effects on survival and reproduction, can also affect population levels. Evidence for some species suggests that they can. The most telling example concerns the Red Knot, in which one population migrates each spring from southern South America to northern North America. These birds stop at Delaware Bay, which forms the last major refuelling place before the Arctic nesting grounds. While there, the birds feed mainly on the eggs of Horseshoe Crabs *Limulus polyphemus,* which spawn at this time. These eggs can be so abundant that they pile up on beaches, providing a rich nutrient source for staging shorebirds of many species. They have traditionally enabled Red Knots to approximately double their body weights from 90–120 g on arrival to 180–240 g on departure some two to three weeks later (Baker *et al.,* 2004). In recent years, the numbers of Horseshoe Crabs have been much reduced by human over-fishing (the crabs being collected largely as bait for other fish). From 1997 to 2002, increasing proportions of Knots staging in the bay failed to reach the minimum necessary departure mass of 180–200 g. Annual survival of adults fell by 37 per cent, and the proportions of immature birds by 47 per cent, leading to a halving of the population within a two-year period: from 51,000 individuals in 2000 to 27,000 in 2002, as counted in wintering areas. Of birds caught in Delaware Bay, known survivors were heavier at initial capture than birds not seen again. By 2004,

declines were apparent not only in Red Knots, but also in Turnstones and Sanderlings, which exploited the same food source. In subsequent years, food at Delaware Bay remained scarce, and Knot numbers declined further, reaching 18,000 during the period from 2005 to 2007 (Piersma, 2007).

The potential for population limitation on staging areas is perhaps especially acute in shorebirds and waterfowl, which in many regions have only a limited number of possible refuelling sites, often at widely spaced intervals along their migration routes. At many such sites, optimal food supplies are available only for short periods. This situation contrasts with many other bird species, which migrate through mainly favourable habitat, and would seem to have feeding opportunities at many places along their routes. Nevertheless, where weather extremes affect large areas, this can have repercussions on the population levels of many migratory species that pass through—for example, in the Sahel zone of Africa (Chapter 24).

Influence of predators, parasites and pathogens

The ability of birds to fatten for migration may also be constrained by factors other than food, such as predation, disturbance and parasitic diseases. At sites used by large numbers of small birds, raptors can also gather, increasing the ratio of predators to prey above the usual level. In this situation, Sparrowhawks and other raptors were calculated to remove about 10 per cent of all Chaffinches and Bramblings that passed through Falsterbo (Sweden) during a six-week period in autumn (Lindström, 1989). This mortality was significantly greater than expected if the total annual mortality had been evenly spread through the year. Birds of some species are thought to be especially vulnerable at migration times, because their increased body weight makes them less agile under attack from predators (Chapter 6). This supposition has been supported mainly by experimental studies on captive birds (Kullberg *et al.,* 1996; Lind *et al.,* 1999; Burns & Ydenberg, 2002). Not all species suffer from extra weight, however, because not all depend

on agility to escape predation. For example, Northern Wheatears simply hide behind a stone when a hawk passes, or ‘freeze’ so they cannot be seen. On seeing a Sparrowhawk, Wheatears on Heligoland Island remained ‘frozen’ for between 1 and 7 minutes, but occasionally up to 33 minutes. They thereby avoided predation, but lost potential feeding time, which reduced their fattening rates (Fig. 272). In this situation, lighter Wheatears were significantly more likely to be captured than heavier ones, possibly because the lighter ones were feeding harder and were less watchful (Dierschke, 2003). In another study, it was noted that falcons took the lightest individuals from among flocking waders (Bijlsma, 1990).

Whether predators catch heavy or light individuals, their main effect on fuelling migrants could usually stem, not from the numbers killed, but from the disturbance caused, which can affect a far greater number of birds. Clearly, one person walking over a coastal mud flat can interrupt the feeding of thousands of birds, as can a Peregrine flying over. Disturbance stops birds from feeding for a period, and if they take flight, it also increases their energy expenditure. In extreme cases, persistent disturbance can effectively exclude birds from feeding in places they might otherwise use, thus reducing the total habitat available to them and perhaps increasing competition in the remaining places (Cresswell, 2008).

Many people have doubted the importance of sport hunting or predation to migratory birds, because so few birds are killed at most staging sites. However, mortality is not the relevant measure here. Natural selection acts on individuals, and the question is how much higher the mortality would be on any individuals that did not adopt precautionary measures. To take a human analogy, relatively few people are killed by traffic in cities, but the existence of this risk is enough to influence the behaviour of almost everyone. Any individuals that habitually disregarded traffic would face premature death. The same holds for birds that do not take precautions against predation, even though taking such measures can adversely affect their performance in other ways.

Several mass-mortality events attributed to disease have been described in waterbirds concentrated at stopover sites (Newton, 1998b). An example was an outbreak of the H_5N_1 strain of 'bird flu' that killed many waterfowl, including rare Bar-headed Geese, on Qinghaihu lake in China in 2005 (Liu *et al.,* 2005). Species vary in their susceptibility to this virus: some die soon after infection, while others are relatively immune but can spread the virus. Migratory waterbirds subsequently carried the H_5N_1 virus elsewhere, including Europe and Africa (although wild birds seemed much less significant in the spread of this particular disease than the transport of infected poultry and poultry products; Gauthier-Clerc *et al.,* 2007). Other forms of avian influenza have been found in at least 105 wild-bird species (Olsen *et al.,* 2006), most commonly in waterfowl, terns and waders. The mixing of populations that occurs at stopover sites can facilitate the spread of these infections far and wide, continually introducing them to new areas, as shown in the recent increase of Lyme disease and West Nile virus in North America (Scott *et al.,* 2001; Rappole *et al.,* 2000; Malkinson *et al.,* 2002; Owen *et al.,* 2006).

Other mass mortalities among migrant waterbirds have been caused by botulism, a form of food poisoning resulting from a neuro-toxin produced by the bacterium *Clostridium botulinum.* This anaerobic bacterium thrives on rotting organic matter in shallow stagnant water or mud during warm weather. Invertebrates eating this matter or bird corpses are immune to the toxin, but they in turn are eaten by waterfowl and gulls, which subsequently die. In many recorded outbreaks, hundreds of thousands of birds have perished, and one event killed about a million waterfowl on the Caspian Sea in 1982 (Rocke, 2006). Other major outbreaks at sites in western North America during the 20th century killed varying numbers of birds, with estimates ranging from 65,000 at one site to a million at others. Apart from occasional mass-mortality events, the impacts of disease-causing agents on migratory birds remain largely unstudied. It is one thing to record the presence of a disease, but another to assess its impact on bird breeding numbers.

OTHER MIGRATION-RELATED MORTALITY

Migrants are sometimes exposed on their journeys to storms or other extreme weather events, which can kill large numbers of birds at a time. These mortalities may be classed as 'density independent', because the proportion of individuals killed probably does not vary in any systematic manner with overall population size. Some such events affect birds actually on migration, occurring when land birds encounter storms over water or over other terrain where they cannot take shelter. Heavy rain can saturate the plumage, increase body weight and cause the loss of body heat. These stresses, often coupled with disorientation, sometimes force migrants down, where they may perish through collision, drowning or chilling. Flying birds are also sometimes killed by hail or electrocution in lightning storms. Clearly, birds would best avoid flying at times of adverse weather. Usually they do, but occasionally they get caught out.

In-flight losses

Most recorded in-flight mortality incidents involved land birds that encountered storms over water or other places where they could not take shelter (Newton, 2007). The most extreme example on record involved a snowstorm in Minnesota, which is estimated to have killed more than 750,000 Lapland Buntings in one night. This storm occurred in March 1904 as the birds were on northward migration, and the following morning their bodies were counted in the snow on two large frozen lakes. However, bodies were reported from a much wider area, and it was considered that twice this number (1.5 million) may have been killed by the event (Roberts, 1907a, 1907b).

Considering that it is largely a matter of chance whether such extreme events are witnessed and documented, and that most probably occur over the sea, it is impossible to say how frequent they are, let alone what effect they have on populations. Although large numbers of birds may be killed, they may be drawn from a large part of the breeding range, with only small effects on local

numbers. Such catastrophes may become more common in future, as storms and other extreme weather events increase in frequency and severity under climate change. In addition to the major weather-induced catastrophes, other birds are presumed to die on migration because they drift too far off course, or run out of fuel in places where they cannot feed. Emaciated or dehydrated birds sometimes turn up in places where they have crossed seas or deserts.

Strong winds occasionally blow seabirds over land, resulting in 'wrecks' in which large numbers may die. Overland wrecks of Leach's Storm-petrels recorded in the autumns of 1891 and 1952 affected birds en route to wintering areas (Boyd, 1954). In 1952, at least 6,700 birds were picked up dead or dying in the British Isles, while others were found as far inland as Switzerland. Small numbers of storm-petrels were also involved. Wrecks of Little Auks in the British Isles have sometimes involved hundreds or thousands of individuals, as seen in 1895, 1900, 1910, 1912, 1950 and 1983 (review in Newton, 1998b). All these wrecks occurred between November and March, so may have mainly involved wintering rather than passage birds. Most also included other species. Juveniles predominated, and many appeared in poor condition, but it was never certain whether poor condition predisposed birds to the effects of strong winds, or whether the winds caused the poor condition by preventing feeding.

Weather-induced starvation

In some years, heavy mortality can also occur soon after migrants arrive in their breeding areas or when they are on passage, if warm spring weather suddenly reverts to winter cold. Most examples relate to swallows and other insectivorous species, but others concern waders affected by snowfalls or waterbirds affected by the re-freezing of newly opened water (Newton, 2007). To judge from the carcasses examined, the birds had simply starved to death, as they were light in weight and devoid of body fat. One such event occurred between 11 and 17 April 1966, when frost and snow killed

tens of thousands of Lapwings and other birds soon after they had arrived in their Fennoscandian breeding areas, causing in different localities 30–90 per cent reductions in subsequent breeding numbers (Vepsäläinen, 1968; Marcström & Mascher, 1979). These losses far exceeded the total annual mortality normally expected in Lapwings.

Other heavy mortality occasionally occurs at the end of the breeding season, when winter conditions return early, and affect birds before they have left on autumn migration or when they are on passage. An extreme event occurred in central Europe in 1931, when 'immense numbers of Swallows and House Martins, and some Sand Martins, numbed by the cold and unable to find food, sought shelter in bars, stables and houses where, in some cases, they congregated in great masses and were so inert that they could be picked up by hand' (Alexander, 1933). The 89,000 individuals that were collected live and transported by air for release in Italy 'were probably a small fraction of the total lost'. A similar event occurred in central Europe in 1974, again killing hundreds of thousands (possibly millions) of birds. Subsequent breeding numbers of House Martins in Switzerland fell by 25–30 per cent, and Barn Swallows by more than 50 per cent in part of Denmark (Bruderer & Muff, 1979; Møller, 1994). The latter were on migration through central Europe at the time of the cold snap.

Occasionally, Swifts have been unable to leave their north European breeding areas because of adverse weather. They usually leave south Finland by the end of August, but in the cold and wet late summer of 1986, around 2,000 remained into November and then died (Kolunen & Peiponen, 1991). Some were found dead in their roosts, while others were picked up too weak to fly. Scarcity of aerial insects apparently prevented the birds from accumulating fat for migration. Similar events occurred in 1918 and 1957, but in these years, delay was caused by late nesting resulting from cold weather in spring.

Some extreme weather events in breeding areas affected populations that happened to be under study at the time, so observers could record their effects on breeding numbers. Following

post-arrival losses in spring, local breeding numbers of various species fell by 25–90 per cent, and following heavy predeparture losses in autumn, subsequent breeding numbers fell by 25–50 per cent (Newton, 2007). After the most extreme events, populations probably took several years to recover. Among Common Sandpipers studied in the Derbyshire Peak District, temperatures in April when the birds arrived appeared to influence the overall annual survival, with the heaviest losses in the coldest years (Fig. 278).

Perhaps the most worrying structural threat to migrant birds, however, comes from the hundreds of wind turbines that are appearing across Britain and Europe, as well as in shallow coastal waters. Such turbines are known to kill migrants, especially those sited on major migration routes, as in southwest Spain (de Lucas *et al.,* 2007), or near to wetlands that attract concentrations of large migrating birds. A study at two large offshore wind farms in Denmark revealed that birds generally avoided the turbines by day, but species differed in their response (Petersen *et al.,* 2006). Divers and gannets were almost never seen flying among the turbines, whereas cormorants and gulls regularly flew between the rows of turbines or below the height of the rotor blades. At night, birds were less likely to veer off course, but many flew flew higher and well above the rotor blades. Overall, less than 1 per cent of geese and Common Eiders migrated close enough to the turbines to be at risk of collision (Desholm & Kahlert, 2005). Most of these observations were made in good weather, and more study is needed of how birds behave in thick mist. The main effect of the turbines, however, resulted not from collisions, but from the 'scarecrow' effect, deterring birds from feeding nearby, and hence reducing the potential feeding area, as evident especially in divers. As wind turbines continue to multiply in the years ahead, they could collectively begin to impose a heavier drain on migratory bird populations, either as a cause of direct mortality or by scaring birds from otherwise profitable feeding areas.

Oil installations are another source of bird mortality at sea, again mainly on nights with low cloud or mist. Attracted by the lights,

thousands of birds may circle around for hours at a time, moving on at dawn. Some birds become so exhausted by this Proc.ess that they fall in the water, while others settle on the rigs and stay for hours or days, to be periodically attacked by gulls and raptors or killed against the structure (Marquenie *et al.,* 2007). Other deaths occur at gas flares, up to several thousand per night having been recorded at individual rigs (Lid, 1977). The usual numbers are much lower, however, estimated at a few hundreds of birds per rig per year, which is a small proportion of the numbers passing (Bourne, 1979).

Many millions of birds fly over the North Sea each autumn, some moving down the continental seaboard and others crossing to Britain (Marquenie *et al.,* 2007). Illuminated platforms are visible from 3 to 5 km, so birds could currently encounter between two and ten platforms on their crossings, depending on the routes taken. On cloudy nights, the birds cannot see the stars, and their geomagnetic compass is upset by light at the red end of the spectrum. In an experiment at one platform, a change to lights with a lessened red component reduced the numbers of birds attracted by 50–90 per cent.

Estimating migration-related mortality

Most mortality estimates in birds are based on ringing, but the chance of obtaining recoveries varies along a migration route, which usually precludes arriving at reasonable estimates of migration-related mortality. However, some studies have yielded useful information. One involved Barnacle Geese migrating from Svalbard to Scotland in autumn (Owen & Black, 1991). By use of colour rings, researchers could record particular birds before they set off on migration, and then re-check the flocks after they had arrived in wintering areas in south Scotland. It was estimated that about 35 per cent of juveniles and 5 per cent of adults (half the annual total mortality) had been lost on this one journey. After arrival in wintering areas, the mortality of juveniles settled to a much lower level, similar to that of adults. Although this was deemed an unusual

year (owing to bad weather in breeding areas), similar estimates were obtained for marked Brent Geese migrating from northeast Canada to Ireland (33 per cent for juveniles, 5 per cent for adults; O'Briain, 1987), and for Greater Snow Geese migrating from Baffin Island to southern Canada (equivalent to 34 per cent per month for juveniles, 1 per cent per month for adults, but varying from year to year; Menu *et al.,* 2005). Among Pacific Brant Geese, migrating over the sea between western Mexico and Alaska, mortality was estimated from re-sightings of leg-banded birds at 9 per cent per month over the spring migration period, which was significantly lower than the 0–3 per cent estimated for other times of year (Ward *et al.,* 1997).

In theory, following radio-marked birds on their journeys can also provide information on migration-related mortality, providing death can be distinguished from radio failure or detachment. Of 19 juvenile Ospreys radio-tracked from Britain between 1999 and 2002, only ten seem to have survived the journey to Africa. Two died in the western Atlantic, four in the Sahara, and up to three elsewhere. With the latter three, however, only one fix was obtained of the last position so radio failure was possible. Of seven adult Ospreys tracked from Scotland, all survived the journey. Of eight young Honey Buzzards tracked from Britain between 2001 and 2008, two died in the Atlantic, while another probably died in Morocco. One adult Honey Buzzard survived. These records re-emphasise the hazards presented by long sea- or desert-crossings for these birds. And to these various estimates can be added the 34 per cent loss of juvenile raptors and 4 per cent loss of adult raptors while crossing the Sahara, described in Chapter 8.

A different method for estimating migration mortality was used on Black-throated Blue Warblers in the New World (Sillet & Holmes, 2002). The researchers were able to assess mortality during the summer period in New Hampshire, during the winter period in Jamaica and over the year as a whole respectively. They concluded that more than 85 per cent of apparent annual mortality occurred during migrations, giving a rate 15 times higher than at other times

of year. So whatever the causes of migration mortality, it can sometimes be substantial. We must assume that the net benefits of migration, in terms of improved year-round survival and reproduction, generally outweigh the costs in terms of mortality, otherwise the habit would not persist.

CONCLUDING REMARKS

From the information reviewed above, we can conclude that the year-to-year or long-term changes in the breeding numbers of some migratory bird species have been linked with conditions in either breeding or wintering areas. In a few species, such changes could be attributed to conditions at particular stopover sites, visited for at most a few weeks each year during migration. The latter circumstances are hard to study, so limitation at stopover sites could be more frequent than the few documented examples suggest. In the longer term, however, population limitation in migrants is probably a dynamic Proc.ess, involving breeding, wintering and migration areas.

We can also conclude that conditions in breeding, wintering or migration areas can have carry-over effects, becoming apparent at a later date in a different area. These effects occur both at the level of the individual (largely through body reserves) and at the level of the population (partly through body reserves and partly through density-dependent effects). In addition, the impact of weather-induced mortality events at migration times on migratory populations can be just as significant as the effects that severe winters sometimes have on resident species. Almost certainly, such mortality represents a major cost of migration in some bird species. As it becomes increasingly possible to study the same bird populations at different places on their annual journeys, our understanding of population limitation in migratory birds should increase greatly in the coming years. Such studies could become ever more important for the future conservation of migratory bird populations.

† Järvinen (1987); Stenning *et al.* (1988); Mihelsons *et al.* (1985); Owen & Black (1991); Baillie & Peach (1992); Whitfield (2003).

CHAPTER 24

Declining Migrants

From the earliest times, people across Europe have looked forward to the return each spring of summer visitors from Africa: the swallows and martins, cuckoos and swifts, warblers and nightingales, along with many others. In recent decades, many of these species have greatly declined. In this chapter, we will examine the current population trends of these species in the British Isles and at the environmental changes which could have influenced them. Could the problems lie in European breeding areas, on migration routes or in African wintering areas? This chapter extends the last, highlighting the difficulties of studying migratory species that winter outside Europe, and remain largely inaccessible or in unknown areas for much of the year.

About 54 land-bird species that nest in the British Isles winter entirely in Africa, or partly in Africa and partly in southern Europe, comprising about 28 per cent of all breeding species. Excluding seabirds, they include about 20 passerines (mainly warblers, swallows and martins), together with the Common Swift, Cuckoo, Wryneck, Turtle Dove, Nightjar, Corncrake and Spotted Crake, Common Quail, Garganey and several shorebirds and raptors. Most of our information on the population trends of these and other British birds comes from the nationwide monitoring programmes organised by the British Trust for Ornithology: the Common Bird Census, which began in the 1960s and, after a period of overlap, gave way in 1994 to the Breeding Bird Survey. The two schemes use different methodology, but the Breeding Bird Survey is less time-consuming, so attracts more participants, enabling a wider range of

randomly selected areas to be sampled. Both depend on volunteer observers, scattered across the country, making regular bird counts year after year.

Throughout the period 1967–2005, net population declines of 70 per cent or more were recorded in the Turtle Dove, Tree Pipit, Yellow Wagtail, Spotted Flycatcher, Northern Wheatear, Whinchat and in the rare Marsh Warbler (Table G). Smaller declines, but exceeding 50 per cent, were recorded in the Willow Warbler, Common Whitethroat, House Martin and Cuckoo. Many other species, including some that have increased in recent years, are still substantially below their 1960s level. The pattern of decline differed between species, the Common Whitethroat suffering a catastrophic crash mainly in one year, while others exhibited more gradual declines over ten or more years, with some subsequently recovering slightly and others not.

Comparing the figures for 1994–2005 with those from the longer period (1967–2005), it seems that the downward trends in some species accelerated (Table G). This is particularly noticeable in the Turtle Dove (58 per cent since 1994), Cuckoo (46 per cent since 1994), Tree Pipit (38 per cent since 1994), Yellow Wagtail (33 per cent since 1994) and Spotted Flycatcher (23 per cent since 1994). The limitations of the Common Bird Census meant that some species were not detected in adequate numbers before 1994, since when the Wood Warbler has declined by 60 per cent, the Pied Flycatcher by 43 per cent and the Swift by 20 per cent. In addition, the Red-backed Shrike and Wryneck, whose declines began decades earlier, effectively disappeared from Britain during this period, although occasional pairs may still nest.

TABLE G. Net population trend in bird species that breed in Britain and winter in Africa, as measured mainly by the Common Bird Census (CBC) and Breeding Bird Survey (BBS) of the British Trust for Ornithology. Minus signs without a figure indicate an unquantified decline inferred from other evidence.

Species	*Estimated % change 1967–2005 (CBC/BBS)*	*Estimated % change 1994–2005 (BBS)*
Common Sandpiper *Actitis hypoleucos*	-22[1]	-15
Turtle Dove *Streptopelia turtur*	-82	-58
Cuckoo *Cuculus canorus*	-59	-46
Nightjar *Caprimulgus europaeus*	-	+50
Swift *Apus apus*	-	-20
Sand Martin *Riparia riparia*	-9[1]	+23
Barn Swallow *Hirundo rustica*	+20	+28
House Martin *Delichon urbica*	-53	+7
Tree Pipit *Anthus trivialis*	-83	-38
Yellow Wagtail *Motacilla flava*	-70	-33
Nightingale *Luscinia megarhynchos*	-	+8
Common Redstart *Phoenicurus phoenicurus*	-20	-3
Whinchat *Saxicola rubetra*	-	-34
Northern Wheatear *Oenanthe oenanthe*	-	-16
Grasshopper Warbler *Locustella naevia*	-	+6
Savi's Warbler *Locustella luscinioides*	-58[2]	-53
Sedge Warbler *Acrocephalus schoenobaenus*	-28	+3
Marsh Warbler *Acrocephalus palustris*	-76[2]	-53
Eurasian Reed Warbler *Acrocephalus scirpaceus*	+108	+37
Blackcap *Sylvia atricapilla*	+144	+52
Garden Warbler *Sylvia borin*	-21	-16
Lesser Whitethroat *Sylvia curruca*	-15	-8
Common Whitethroat *Sylvia communis*	-62	+22
Wood Warbler *Phylloscopus sibilatrix*	-	-60
Chiffchaff *Phylloscopus collybita*	+26	+32
Willow Warbler *Phylloscopus trochilus*	-60	-31
Spotted Flycatcher *Muscicapa striata*	-84	-23
Pied Flycatcher *Ficedula hypoleuca*	-	-43

Such declines were not restricted to the British Isles, but also occurred in other west European countries. The Pan-European Common Bird Monitoring Scheme takes bird counts from 21 countries, and can supply annual trend data for 135 species, of which 44 are trans-Saharan migrants. Those species with the biggest population declines across the continent included, at the top of the list, the Ortolan Bunting (79 per cent decline between 1980 and 2005), followed by the Turtle Dove (66 per cent decline), Wryneck (63 per cent), Nightingale (63 per cent), Yellow Wagtail (61 per

cent) and River Warbler (56 per cent), and then by the Whinchat (55 per cent), Northern Wheatear (52 per cent), Spotted Flycatcher (50 per cent) and Tree Pipit (47 per cent). The Icterine Warbler, Wood Warbler, Willow Warbler and Pied Flycatcher showed long-term declines of 37, 27, 26 and 22 per cent respectively, and the Cuckoo of 12 per cent. Others showed smaller declines. It is thus clear that the recent population declines of Eurasian–African migrants are substantial, extend far beyond the British Isles and reflect a wider problem.

Many other European breeding birds have declined since the 1960s, including residents and short-distance migrants wintering within Europe. These declines have been attributed mainly to change in land use, especially agriculture and its associated pesticide applications, which have reduced the habitats and food supplies of many species. But in general, the long-distance migrants to Africa seem to have suffered more than the species that winter in Europe. They have declined in greater proportion and on average more markedly (Sanderson *et al.,* 2006). Europe-wide trends between 1970 and 2000 were analysed in 30 pairs of closely related species. In each pair, one species wintered in Africa and the other in Europe (e.g. Tree Pipit and Meadow Pipit, Whinchat and Stonechat). Significantly more negative trends emerged in the African-wintering species, regardless of breeding habitat. So why have the long-distance migrants suffered more than others? Could it be that in migrating through more areas, subject to different human impacts, they suffer more risks?

Other evidence for the importance of breeding habitat is available for various scrub and marshland species, which have generally declined in Britain over the past 40 years, but have increased locally where extra habitat has been provided through conservation measures. For example, following the conversion of 580 ha of arable land to wetland at Lakenheath in East Anglia, Reed Warblers increased within ten years from 6 to 780 pairs, Sedge Warblers from 7 to 150 pairs, Common Whitethroats from 10 to 76 pairs, Grasshopper Warblers from 0 to 10 pairs, Marsh Harriers from 1–2

to 7 nests, and Hobbies from 0 to 3 pairs (Sills, 2007). All these species winter entirely or partly south of the Sahara, but year-round resident species depending on the same habitats also increased at Lakenheath. Similarly, Nightingales at Bookham Common in Surrey increased from 1 to 14 singing males within 20 years following changed management that encouraged scrub development; and Common Whitethroats increased from 25 to 48 pairs within 10 years on the RSPB's experimental farm in Cambridgeshire, where hedgerows were allowed to grow taller and thicker. On a wider scale, the planting and subsequent felling of conifer forests has benefited some migratory species, including Willow Warblers, which colonise the young thicket plantations (Lack, 1933; Moss, 1978), and Tree Pipits and Nightjars, which occupy clear-felled areas within lowland forests (Burton, 2007; Langston *et al.,* 2007). In many other areas, these species have dwindled, causing a net decline over the past 40 years in Britain as a whole. As these various species increased after the local provision of extra habitat, could their general declines be due to widespread loss or degradation of breeding habitat?

Other species in which changes in numbers have been linked with events in breeding areas include the Pied Flycatcher, whose breeding densities during the 20th century almost invariably increased following the provision of nest boxes (Chapter 23). This finding implied that breeding densities were normally limited by a shortage of natural tree-cavity nest sites. In places where boxes were surplus to needs, year-to-year changes in Flycatcher breeding numbers were associated with the previous year's nesting success, again pointing to the importance of conditions in breeding areas (Fig. 265; Virolainen, 1984; Goodenough *et al.,* 2009). Likewise, Common Swifts in Britain nest mainly in the roofs of old buildings, and their recent decline has been attributed partly to the impact of building regulations and roof repairs on the number of potential nest sites (Clark, 2009). But where alternative sites have been provided, they have often been occupied.

Other Eurasian–African migrants that were affected adversely by changes in breeding areas include the Yellow Wagtail, which suffered mainly from the drainage of wet grasslands and the change from spring-sown to winter-sown grain (Newton, 2004); the Corncrake, which suffered in the early 20th century mainly from the introduction of mechanised grass-cutting (Norris, 1947; Stowe *et al.,* 1993); the Stone Curlew, which was affected adversely by various agricultural changes, including the conversion of down-land to arable; and the Turtle Dove, which suffered from the loss of tall scrub for nesting and of weed-seeds as a food source, the latter reducing the length of the breeding season and the seasonal production of young to a sufficient degree to account for the recorded rate of population decline (Browne & Aebischer, 2004). Most of these species have since increased in certain areas as a result of local conservation measures in which the detrimental changes brought by modern agriculture have been reversed. The same holds in Europe for yet other species affected by agricultural changes, including the Lesser Kestrel and Montagu's Harrier (Donázar *et al.,* 1993; Arroyo *et al.,* 2002; Newton, 2004). These various findings raise the possibility that long-term population changes in some European–African migratory species have occurred primarily through habitat and other changes in breeding areas.

CHANGES IN AFRICAN WINTERING AREAS

Over the past 40 years, changes have occurred not only in the landscapes of Europe, but also in those of Africa. In much of Africa north of the equator, rainfall during the northern summer largely determines the state of the vegetation and the extent of wetlands in the following dry season (Chapter 22). It thus influences the food supplies of many birds, whether they consume plant or animal matter. But rainfall also varies greatly from year to year, and over much of the region since the late 1960s it has in most years been well below former levels (Fig. 287). Rain-belts have extended less far to the north, so droughts have been most severe in the northern

Sahel zone, lying immediately south of the Sahara. Although only a proportion of Eurasian migrants winter primarily in the Sahel zone, all pass through on migration.

The importance of conditions at migration times were also apparent among White Storks breeding in eastern Europe, which migrate into East Africa. In this population, annual survival and population change were found to correlate with conditions on a major staging area in the eastern Sahel (Schaub *et al.,* 2005). The storks remained in this region for up to two months during their southward migration, and also fed there during their northward return. Annual variation in the rainfall-dependent condition of the vegetation in this region (assessed from satellite images) accounted for most of the annual variation in stork survival. Survival was high in years when primary production in the eastern Sahel was high, and lower in other years. In contrast, vegetation conditions further south in Africa, where some of the storks spent the winter, made no significant contribution to variations in annual survival. Some other points emerged from this 19-year study: for example, that annual survival fluctuated in parallel in adult and immature storks (even though many immatures remained well south of the breeding areas during summer), and also across a large part of the breeding range, despite regional variations in European habitats. The inference was again that Sahel conditions exerted the dominant influence on annual survival rates. These various studies indicate the importance of the Sahel zone even in species which spend much of the winter in more genial conditions further south.

In contrast to the east European population of White Storks, the west European population migrates to winter in West Africa, and has declined greatly since 1960. Annual variations in survival (measured from ringed birds) and subsequent reproduction (measured from nest studies) were both linked to annual rainfall in the western Sahel. Presumably winter food supplies influenced the body condition of adult storks in spring, which in turn affected their breeding success as well as their survival (Bairlein & Henneberg, 2000; Kanyamibwa *et al.,* 1993; Barbraud *et al.,* 1999). But this

population has also been affected by land drainage and other changes in breeding areas, and more recently has begun to winter in increasing numbers in southern Spain (Chapter 23).

Rainfall over Africa may also influence seabirds feeding offshore. High rainfall increases river flow, which washes more nutrients into estuaries, increasing productivity and fish supplies. Accordingly, among Common Terns nesting in Germany and wintering off West Africa, annual survival was better in years of high West African rainfall than in other years (Favero & Becker, 2006). Long-term declines have occurred in a number of other tern species wintering off West Africa, including Little Terns and Roseate Terns (although in the latter case, the large numbers caught and killed by small boys cannot have helped).

Comparisons of count data from different European countries showed that while year-to-year changes in the numbers of particular species were often correlated over large parts of the breeding range, there were, as expected, regional exceptions (Marchant, 1992; Sokolov *et al.,* 2001). The changes in breeding areas caused by intensive agriculture during the last few decades of the 20th century were much more severe in western than in eastern Europe. In addition, Europe-wide trends would perhaps not be expected in species whose west and east European populations winter in West and East Africa respectively, because the two regions have somewhat different weather patterns.

Overall, it is clear that climatic conditions up to several thousand kilometres south of breeding areas can affect the spring population levels of some species of trans-Saharan migrants that breed in Europe. Reduced rainfall in African wintering areas has been suspected as a major causal factor in the regional population declines of some European breeding species over the period 1967–2005, including several that nest in Britain.

Other factors acting in wintering areas

Serious droughts in the Sahel–Sudan zones have occurred in the past, as in the years 1911–16 and 1940–46, but without lasting ecological effects, as habitats quickly recovered when rainfall returned to normal. But in the latter half of the 20th century, the human and livestock populations in these regions multiplied more than tenfold, leading to impoverishment of grasslands, loss of trees and shrubs, increasing water abstraction and shrinkage of wetlands. All these changes have accentuated the Proc.ess of desertification, and many areas now hold little habitat for birds even in relatively wet years (Jones, 1985; Thiollay, 1989). The desert is expanding southward, and some climatologists believe that, owing to human activities, conditions in parts of the Sahel zone have now flipped to an alternative, more desert-like state.

Nearer the equator, more than 30 per cent of African forest was lost between 1970 and 2000, while cultivated land increased by 21 per cent (UNEP, 2002). Paradoxically, the felling of rainforest in West Africa may not have had entirely negative effects on European migrants, partly because few species winter in forest, and many more can use the more open secondary habitats (‘derived savannah’) that replace it (Morel & Morel, 1992; Leisler, 1992). However, the cultivation of rice and the irrigation of other crops has shrunk many wetlands used by migratory birds, reducing the surface area of Lake Chad, for example, from 25,000 km^2 to 1,350 km^2 since 1960 (UNEP, 2002). The spread in agriculture has also brought increased pesticide use, reducing the abundance of insects and other invertebrates, and directly poisoning many of the birds themselves (Thiollay, 1989; Mullié & Keith, 1993). Between 1969 and 1973, Thiollay (2006) made roadside counts of raptors over a large part of West Africa and repeated the counts over the same routes and season 30–35 years later. In national parks, numbers had been maintained, but outside the parks (in areas occupied by people), most species had greatly declined. These declines affected native African species as well as Eurasian migrants, suggesting that the causal factors lay in Africa. Among Eurasian migrants, the numbers of Common Kestrels had declined sharply, Montagu’s and Pallid

Harriers and Short-toed Eagles less so, while the numbers of Marsh Harriers and Booted Eagles had not changed significantly. On present knowledge, it is hard to assess the impact of human-induced changes in relation to those caused by weather patterns, but there can be little doubt that the landscape of much of northern Africa has been greatly degraded in the last few decades, reducing its ability to support birds and other wildlife.

HUNTING AND PREDATION

European–African migrants suffer much human-induced mortality on their migration routes, but there is no indication that this has increased in recent decades. The hunting of passing migrants in the Mediterranean region has been estimated to remove up to a staggering 1,000 million birds annually, mainly songbirds (Magnin, 1991; McCulloch *et al.,* 1992). If accurate, this figure would amount to about one-fifth of all the migrants estimated to leave Eurasia each autumn. Whatever the actual figure, there is no doubt that very large numbers of birds were killed every year. Hunting was particularly prevalent in southern France, Spain, Italy, various Mediterranean islands (notably Cyprus and Malta), Turkey, North Africa and the Lebanon. Through campaigns and legislation, attempts have been made to reduce this in recent decades. At least in the European Union countries north of the Mediterranean, legislation has been largely effective, despite repeated breaches and the continuing inclusion of thrushes and Turtle Doves as legal autumn quarry. The annual numbers of ringed birds reported from these areas are declining, but it is not known how much this reflects trends in migrant populations, hunting rates or ring reporting rates.

Nor is it known what effect hunting has on the breeding numbers of the target species. As hunting occurs mainly in autumn, it does not necessarily add to other mortality, as it could be offset to some extent by improved over-winter survival among the remaining birds. For example, if populations were limited by winter food supply, losses would be expected to be greatest in years with high

populations (relative to food supply), and up to a point, a reduction in numbers before the birds reached their wintering areas could then lessen the subsequent losses. In this case, autumn hunting would not have the large impact on population levels that might be expected from the numbers killed. This seems to be the case in Quail, in which the numbers caught each year in Egypt were related more to Sahel rainfall than to hunting pressure (Zuckerbrot *et al.,* 1980), with numbers declining in recent decades (Tucker & Heath, 1994). Similarly, the numbers of Corncrakes taken on the coast of Egypt in the autumns of 1993 and 1994 were estimated at about 9,000 and 14,000 respectively, but these numbers formed only 0.5–2.7 per cent of the total European stock (Baha el Din *et al.,* 1996). In contrast to autumn hunting, however, any spring hunting which occurs after winter losses have taken their toll is likely to add to previous mortality, and reduce subsequent breeding numbers. But whatever the effect of hunting in the Mediterranean region, it was unequivocally greater in the past, at a time when migrant populations were more stable than they are now.

There is also considerable hunting of migrants in Africa south of the Sahara. The emphasis seems to be on larger species, with reports of many European Honey Buzzards killed in Liberia, White Storks and Ospreys in Nigeria, White Storks and Cranes in Sudan, terns off West Africa, and many other species in these and other regions (Berthold, 1993). Some of these species are currently increasing in European breeding areas, while others are decreasing. However, as firearms become more widely available in Africa, we can expect that hunting of Eurasian migrants there will increase.

Natural predation

In some species, natural predation takes a considerable toll at migration times. Two falcon species specialise on Eurasian–African migrants. The Eleonora's Falcon nests mainly on rocky islands in the Mediterranean and off the west coast of Morocco, while the Sooty Falcon nests along the coasts of the Red Sea and Arabian Gulf, and

more sparsely in the deserts of the Middle East and northeast Africa. Both species breed late in the year, coinciding with the autumn migration, and raise their young on passing migrants. Three larger falcon species—the Peregrine Falcon in the Mediterranean region, the Barbary Falcon at scattered localities through the Sahara, and the Lanner Falcon in the southern Sahara—all nest early, at the time of spring migration, and exploit the northward-bound migrants. Unlike predation by the Eleonora's and Sooty Falcons, which coincides with the post-breeding peak in prey numbers, predation by the three larger falcons occurs close to the time of the pre-breeding low in numbers. It is thus more likely than autumn predation to influence subsequent breeding numbers, but its effects are almost certainly trivial.

Additional predation on migratory birds in the Mediterranean region is inflicted by the Giant Noctule Bat *Nyctalus lasiopterus* (Popa-Lisseanu *et al.,* 2007). This large bat has a wingspan of 46 cm (18 inches, about the same as a small crow) and hunts by aerial pursuit. It was suspected of eating nocturnal bird migrants because of the presence of feather fragments in its droppings. Subsequently, blood samples taken from live bats over the period March–October revealed that nitrogen (^{15}N) and carbon (^{13}C) isotopes changed seasonally in a manner expected if the bats had shifted from a diet of insects in summer to birds in autumn. In spring, when migrant numbers were lower, isotope values indicated a mixed diet of insects and birds. The virtual absence of birds from the diet in summer suggests that these bats specialise on passing migrants. However, the bats are so localised that it is again unlikely that they have any appreciable impact on the collective migrant population. Unlike human impacts, moreover, predation by all these species is a natural phenomenon, which migrants have presumably sustained without serious decline for millions of years.

Not all European–African migrants have been affected adversely by recent events. As mentioned above, some species showed no marked net change in numbers over the period 1967–2005, while others showed a substantial rise (Fig. 281; Table G). Major increases

occurred in the national breeding numbers of Ospreys and other birds of prey (viewed as recovering from past persecution, with Honey Buzzards and Hobbies perhaps also benefiting from climate change), of Blackcaps and Chiffchaffs (now probably wintering more in southern Europe than in Africa), and of Corncrakes and Stone Curlews (both subject to intensive conservation management in breeding areas). In other words, all these species seem to have benefited from improved conditions in Europe rather than in Africa, as have the others mentioned above in particular localities.

CONCLUDING REMARKS

For European–African migrants, conditions in breeding, migration and wintering areas have clearly deteriorated in recent years, largely through human impact. The situation may differ between species, with some affected mainly by conditions in Europe and others mainly by conditions in Africa. For yet others, conditions in both regions may have been involved, with events in European breeding areas causing long-term downward trends (through destruction of habitat and food supplies), and events in Africa causing the year-to-year fluctuations about the trend (through annual variations in rainfall and its effects on habitats and food supplies). Such a dual influence would fit the data for some species, such as the Barn Swallow and Sedge Warbler, but not for others, such as the Spotted Flycatcher and Cuckoo, which, as mentioned above, seem to have declined well below the levels that their current breeding habitats and apparent food supplies would support.

Differences in the timing and rate of decline between species may reflect differences in their wintering areas or in the mechanisms involved, and may be confounded by simultaneous changes in breeding areas in some species. For some species, African drought might be expected to reduce the food supply only in the year concerned, while for others, it might also lead to loss of the shrubby habitat on which they depend. Such shrubs could then take years to recover, or not, if human activity prevented it. However, the fact

that many declining species have recovered locally in Britain, in response to the creation or management of breeding habitat, suggests that these species could be helped by conservation measures taken here. For the time being, the jury is out on the role of different limiting factors, but future research may help to assess the relative importance of each in different species. Only then can meaningful conservation measures be put in place, in attempts to bring some of our summer visitors back to their former numbers.

Bird migration is such a remarkable phenomenon that it would be a tragic loss if some of the most impressive participants became so rare that they could no longer enrich the lives ordinary people. We are concerned here with the conservation not just of individual species, but with a spectacular biological phenomenon that for centuries has elicited a sense of awe and wonder in humankind.

---

[1] From Waterways Bird Survey, 1975–2005.

[2] From Rare Breeding Birds Reports.

Another source of information derives from 252 woods surveyed by RSPB workers and 153 woods surveyed by BTO workers in the 1980s and again in 2003–4 (Hewson *et al.*, 2007). All these woods were broad-leaved deciduous, and were widely distributed across Britain. In view of the different survey methods used, results from the two sets of woods on population changes between these two periods are given separately (RSPB first, BTO second) in the following list: Tree Pipit (-85 per cent* and -70 per cent*), Willow Warbler (-69 per cent* and -74 per cent*), Wood Warbler (-55 per cent* and -64 per cent), Common Redstart (-54 per cent and +8 per cent), Garden Warbler (-39 per cent and -26 per cent*), Spotted Flycatcher (-36 per cent and -70 per cent*) and Pied Flycatcher (-20 per cent and -25 per cent). Again, all species apparently declined over the study period, statistically significant changes being marked with an asterisk.

Another study of 13 areas of upland grassland, mainly in northeast England and Wales, suggested declines between the period 1968–80 and 2004 in the Northern Wheatear (–96 per cent), Whinchat (–95 per cent), Yellow Wagtail (–99 per cent) (all significant, $P<0.001$) (Henderson *et al.*, 2004). In addition, the rare Marsh Warbler declined by 76 per cent over the period 1967–2005, and the even rarer Savi's Warbler, restricted to southeast England, by 58 per cent.

CHAPTER 25

Postscript: British *Pioneers in Migration Studies*

To end this book, it seems appropriate to acknowledge some of those who went before. The early pioneers, who laid the foundations for the study of bird migration around the British Isles, were active at a time when few people were interested in natural history or had the opportunity to study it. Migration is scarcely mentioned in *The Origin of Species* by Charles Darwin (1858), and general appreciation of its importance came from field naturalists operating mainly in the last few decades of the 19th century. Two of the most significant in Britain were John Alexander Harvie-Brown (1844–1916) and John Cordeaux (1831–99), who in 1879 instigated a study of bird migration around the coasts of Britain, as observed at lighthouses and lightships (Harvie-Brown & Cordeaux, 1880). They were later joined by R. M. Barrington who organised similar watches at light stations around Ireland. At that time, it was known that nocturnal migrants were often attracted to lighthouses, where many were killed, thus providing a means of 'sampling' the passing birds. 'Forms of enquiry and letters of instruction' were sent to lighthouses around the British Isles, in the hope that the keepers would report their findings. Many did, and several lengthy reports were produced in a study which came to last nine years.

Harvie-Brown was born into a wealthy scottish land-owning family and was educated at the Universities of Edinburgh and then Cambridge, where he developed a lifelong friendship with Professor Alfred Newton, a distinguished zoologist and leading figure in British ornithology. Harvie-Brown became best known for a series of

regionally-produced volumes he wrote in mid-life (mainly with T. E. Buckley) on the vertebrates of Scotland. John Cordeaux had a somewhat different background, being the son of a rector in Leicestershire, with a love of wildfowling and natural history. To pursue his hobby, Cordeaux moved to south Humberside as a young man, later summarising his observations in a small book, *The Birds of the Humber District* (1873). In September 1874, at the suggestion of Alfred Newton, Cordeaux visited the pioneering migration-watcher Heinrich Gätke (1814–97) on Heligoland Island. The two became firm friends, and developed their mutual interest in bird migration via correspondence conducted over many years. A popular figure, Cordeaux became a 'gentleman farmer', with ample time to pursue his interests in 'nature and mankind'. He was described as 'a good sportsman and a fine specimen of the country gentleman, as well as a most genial companion' (Anonymous, *Ibis,* 1899: 665–6).

During his time in Edinburgh, Clarke was considered to have done more than anyone else to promote the study of ornithology in Scotland (Kinnear, 1938). In an article on British pioneers in ornithological research, David Lack ranked Clarke's *Studies in Bird Migration* third in the five most influential ornithological books published in Britain between 1899 and 1939 (Lack, 1959). He added that Clarke was 'the first to study visible migration in Britain, the first British ornithologist to watch regularly at lighthouses and on small islands, the discoverer, ornithologically speaking, of Fair Isle and the first to discuss the weather factors responsible for the arrival of night migrants'. He excelled at visual observation of migration, but made little attempt to integrate his findings with other aspects of migration research at the time.

Aware of Clarke's success on Fair Isle, the 'two Good Ladies' of Scottish ornithology, Evelyn Vida Baxter (1879–1959) and Leonora Jeffrey Rintoul (1878–1953), began to count migrants on the Isle of May in the Firth of Forth. From September 1907, they visited the island in both spring and autumn for 26 years, interrupted only by World War I. They described the effect of wind on bird movements,

suggesting that ‘deviation from the direct route is largely, perhaps mainly, due to drift’ (Baxter & Rintoul, 1918). One year after their last visit to the Isle of May, in autumn 1933, the first British Bird Observatory was established there, and is still running.

The study of wind effects, and other aspects of migration, was taken up by Kenneth Williamson (1913–77) when he became warden of the newly established Fair Isle Bird Observatory in 1948. He also emphasised the importance of drift, and studied the different weather systems that led to the appearance on Fair Isle of migrants and vagrants from different places. He had no formal scientific training, but had worked for a time in York museum, so on Fair Isle he introduced ‘field taxonomy’ into migration studies, getting people to examine birds in the hand in much greater detail than before, thereby helping to distinguish the migration periods and routes of different subspecies. He was an inspiration for the many bird-watchers who visited Fair Isle during his time there. In 1957, he accepted a position at the British Trust for Ornithology, initially as ‘migration officer’, but when the grant ended in the 1960s, he took charge of the bird population studies which developed under the newly instigated Common Bird Census. He held this post for the rest of his career.

Another remarkable British researcher of the mid-20th century was Reginald Ernest Moreau (1897–1970), who left school aged seventeen with no background in science or natural history, and took up a career in the civil service. After a few years, he was transferred to Egypt and later to Tanganyika (now Tanzania), in both of which locations he watched and studied birds. After premature retirement from the civil service in 1947, he was offered a room at the Edward Grey Institute (part of the Zoology Department at Oxford University) by its Director, David Lack, and from there Moreau continued his studies of African birds, editing the journal *Ibis* for 13 years on the side. In the migration field, he is known mainly for his work on the trans-Mediterranean–Saharan migration system, culminating in his book *The Palaearctic–African Migration System* (1972), in which he synthesised knowledge of the

migrations and wintering distributions of Eurasian migrants in Africa. During my own years at the Edward Grey Institute in Oxford in the 1960s, I interacted with Lack and Moreau on an almost daily basis. Together, they had a big influence on my own thinking on bird migration.

References

Able, K. P. (1977). The orientation of passerine nocturnal migrants following offshore drift. *Auk* 94: 320–30.

Able, K. P. (1980). *Mechanisms of orientation, navigation and homing.* In: *Animal migration, orientation and navigation* (Ed. S. A. Gauthreaux). Academic Press, London, 283–373.

Able, K. P. (1989). Skylight polarization patterns and the orientation of migratory birds. *J. Exp. Biol.* 141: 241–56.

Able, K. P. (1993). Orientation cues by migratory birds: a review of cue-conflict experiments. *Trends Ecol. Evol.* 8: 367–71.

Able, K. P. & Belthoff, J. R. (1998). Rapid 'evolution' of migratory behaviour in the introduced House Finch of eastern North America. *Proc.. R. Soc. Lond. B* 265: 2063–71.

Adriaensen, F. & Dhondt, A. A. (1990). Population dynamics and partial migration of the European Robin *(Erithacus rubecula)* in different habitats. *J. Anim. Ecol.* 59: 1077–90.

Adriaensen, F., Ulenaers, P. & Dhondt, A. A. (1993). Ringing recoveries and the increase in numbers of European Great Crested Grebes *Podiceps cristatus. Ardea* 81: 59–70.

Adriaensen, F., Verwimp, N. & Dhondt, A. A. (1998). Between cohort variation is dispersal distance in the European Kestrel *Falco tinnunculus* as shown by ringing recoveries. *Ardea* 86: 147–52.

Aebischer, A., Perrin, M., Krieg, M., Struder, J. & Meyer, D. R. (1996). The role of territory choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides. J. Avian Biol.* 27: 143–52.

Aebischer, N. J. (1995). Philopatry and colony fidelity of Shags *Phalacrocorax aristotelis* on the east coast of Britain. *Ibis* 137: 11–18.

Aebischer, N. J., Green, R. E. & Evans, A. D. (2000). *From science to recovery: four case studies of how research has been translated into conservation action in the UK.* In: *Ecology and Conservation of Lowland Farmland Birds* (Eds Aebischer, N. J., Evans, A. D., Grice, P. V. & Vickery, J. A.). British Ornithologists Union, Tring, Herts, 43–54.

Aebischer, N. J. & Potts, G. R. (1994). *Quail* Coturnix coturnix. In: *Birds in Europe: Their Conservation Status* (Eds Tucker, G. M. & Heath, M. F.). Birdlife International, Cambridge, 222–3.

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehikoinen, E. A. (2004). Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biol.* 10: 1610–17.

Å**kesson, S.** (2003). *Avian long-distance navigation: experiments with migratory birds.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). SpringerVerlag, Berlin, 471–92.

Å **kesson, S. & Hedenström, A.** (2000). Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.* 47: 140–44.

Åkesson, S., Karlsson, L., Walinder, G. & Alerstam, A. (1996). Bimodel orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* 38: 293–302.

Åkesson, S., Morin, J., Muheim, R. & Ottoson, U. (2001). Avian orientation at steep angles of inclination: experiments with migratory White-crowned Sparrows at the magnetic North Pole. *Proc.. R. Soc. Lond. B* 268: 1907–13.

Åkesson, S., Morin, J., Muheim, R. & Ottoson, U. (2005). Dramatic orientation shift of White-crowned Sparrows displaced

across longitudes in the high arctic. *Current Biol.* 15: 1591–7.

Åkesson, S. & Sandberg, R. (1994). Migratory orientation of passerines at dusk, night and dawn. *Ethology* 98: 177–91.

Akriotis, T. (1998). Post-breeding migration of Reed and Great Reed Warblers breeding in southeast Greece. *Bird Study* 45: 344–52.

Alerstam, T. (1978a). Analysis and a theory of visible bird migration. *Oikos* 30: 273–349.

Alerstam, T. (1978b). Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? *Oikos* 30: 405–8.

Alerstam, T. (1979). Optimal use of wind by migrating birds: combined drift and overcompensation. *J. Theor. Biol.* 79: 341–53.

Alerstam, T. (1988). Findings of dead birds drifted ashore reveal catastrophic mortality among early spring migrants, especially Rooks *Corvus frugilegus,* over the southern Baltic Sea. *Anser* 27: 181–218.

Alerstam, T. (1990a). *Bird Migration.* Cambridge University Press, Cambridge.

Alerstam, T. (1990b). Ecological causes and consequences of bird orientation. *Experientia* 46: 405–15.

Alerstam, T. (2001). Detours in bird migration. *J. Theor. Biol.* 194: 1–13.

Alerstam, T. (2003). *Bird migration speed.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 253–67.

Alerstam, T. & Gudmundsson, A. G. (1999). Bird orientation at high latitudes: flight routes between Siberia and North America across the Arctic Ocean. *Proc.. R. Soc. Lond. B* 266: 2499–505.

Alerstam, T. & Högstedt, G. (1982). Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scand.* 13: 25–37.

Alerstam, T. & Lindström, Å. (1990). *Optimal bird migration: the relative importance of time, energy and safety*. In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 331–51.

Alerstam, T. & Pettersson, S. G. (1991). Orientation along great circles by migrating birds using a sun compass. *J. Theor. Biol.* 152: 191–202.

Alexander, W. B. (1933). The Swallow mortality in central Europe in September 1931. *J. Anim. Ecol.* 2: 116–18.

Alonso, J. A., Alonso, J. C. & Nowald, G. (2008). Migration and wintering patterns of a central European population of Common Cranes *Grus grus. Bird Study* 55: 1–7.

Alonso, J. C. & Alonso, J. A. (1992). Male-biased dispersal in the Great Bustard *Otis tarda. Ornis Scand.* 23: 81–8.

Ancel, A., Kooyman, G. L., Ponganis, P. J., Gendner, J. P., Lignon, J., Mestre, X., Huin, N., Thorson, P. H., Robisson, P. & Le Maho, Y. (1992). Foraging behavior of Emperor Penguins as a resource detector in winter and summer. *Nature* 360: 336–8.

Andersson, M. (1976). Population ecology of the Long-tailed Skua *(Stercorarius longicaudus). J. Anim. Ecol.* 45: 537–59.

Andersson, M. (1980). Nomadism and site tenacity as alternative reproductive tactics in birds. *J. Anim. Ecol.* 49: 175–84.

Ankney, C. D. & MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459–71.

Arroyo, B. E., Garcia, J. T. & Bretagnolle, V. (2002). Conservation of Montagu's Harrier *Circus pygargus* in agricultural areas. *Anim. Conserv.* 5: 283–90.

Arzel, C., Elmberg, J. & Guillemain, M. (2006). Ecology of spring-migrating Anatidae: a review. *J. Orn.* 147: 167–84.

Ash, J. S. (1969). Spring weights of trans-Saharan migrants in Morocco. *Ibis* 111: 1–10.

Askenmo, C. (1979). Reproductive effort and return rate of male Pied Flycatchers. *Amer. Nat.* 114: 748–53.

Atkinson, P. W., Baker, A. J., Bennett, K. A., Clark, N. A., Clark, J. A., Cole, K. B., Dekinga, A., Day, A., Gillings, S., Gonzalez, P. M., Lalasz, M., Minton, C. D. T., Niles, L. J., Piersma, T., Robinson, R. A. & Sitters, H. P. (2007). Rates of mass gain and energy deposition in Red Knot on their final spring staging site is both time and condition dependent. *J. Appl. Ecol.* 44: 885–95.

Austin, G. E., Collier, M. P., Calbrade, N. A., Hall, C. & Musgrove, A. J. (2008). *Waterbirds in the UK 2006/7: The Wetland Bird Survey.* BTO/WWT/RSPB/JNCC, Thetford.

Austin, G. E., Peachel, I. & Rehfisch, M. M. (2000). Regional trends in coastal wintering waders in Britain. *Bird Study* 47: 352–71.

Baccetti, N., Serra, L., Cherubini, G. & Magnani, A. (1999). Timing of attachment to wintering site as revealed by experimental displacements of Dunlins *(Calidris alpina)*. *J. Orn.* 140: 309–17.

Bäckman, J. J., Pettersson, J. & Sandberg, R. (1997). The influence of fat stores on magnetic orientation on day migrating Chaffinch, *Fringilla coelebs*. *Ethology* 103: 247–56.

Baha el Din, S. M., Salama, W., Greene, A. & Green, R. E. (1996). Trapping and shooting of Corncrakes *Crex crex* on the Mediterranean coast of Egypt. *Bird Conserv. Int.* 6: 213–27.

Baillie, S. R., Balmer, D. E., Downie, I. S. & Wright, K. H. M. (2006). Migration watch: an internet survey to monitor spring migration in Britain and Ireland. *J. Orn.* 147: 254–9.

Baillie, S. R. & Peach, W. J. (1992). Population limitation in Palaearctic–African migrant passerines. *Ibis* 134: 120–32.

Bainbridge, I. & Minton, C. D. (1978). The migration and mortality of the Curlew in Britain and Ireland. *Bird Study* 25: 39–50.

Bairlein, F. (1985a). Body weight and fat deposition of Palaearctic passerine migrants in the central Sahara. *Oecologia* 66: 141–6.

Bairlein, F. (1985b). Efficiency of food utilisation during fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin. Oecologia (Berl.)* 68: 118–25.

Bairlein, F. (1985c). Offene Fragen der Erforschung des Zuges paläarktischer Vogelarten in Africa. *Vogelwarte* 33: 144–55.

Bairlein, F. (1991a). Nutritional adaptations in the longdistance migratory Garden Warbler *Sylvia borin. Proc.. Int. Orn. Congr.* 20: 2149–58.

Bairlein, F. (1991b). Body mass of Garden Warbler *(Sylvia borin)* on migration: a review of field data. *Vogelwarte* 36: 48–61.

Bairlein, F. (1992). Recent prospects on trans-Saharan migration of songbirds. *Ibis* 134: 41–6.

Bairlein, F. (1996). Fruit eating in birds and its nutritional consequences. *Comp. Biochem. Physiol.* 113A: 215–24.

Bairlein, F. (1998). The effect of diet composition on migratory fuelling on Garden Warblers *Sylvia borin. J. Avian Biol.* 29: 546–51.

Bairlein, F. (2001). Results of bird ringing in the study of migration routes. *Ardea* 89 (special issue): 7–19.

Bairlein, F. (2003). *Nutritional strategies in migratory birds*.In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 321–32.

Bairlein, F. (2008). The mysteries of bird migration—still much to be learnt. *Brit. Birds* 101: 68–81.

Bairlein, F. & Henneberg, H. R. (2000). Der Weissstorch *(Ciconia ciconia)* im Oldenburger Land. Isensee, Oldenburg.

Bairlein, F. & Totzke, U. (1992). New aspects on migratory physiology of trans-Saharan passerine migrants. *Ornis Scand.* 23: 244–50.

Bairlein, F. & Winkel, W. (2001). *Birds and climate change.* In: *Climate of the 21st Century: Changes and Risks* (Eds Lozan, J. L., Grasse, H. & Hupfer, P.). Wissenschaftliche Auswertungen, Hamburg, 278–82.

Baker, A. J. (2002). The deep roots of bird migration: inferences from the historical record preserved in DNA. *Ardea* 90: 503–13.

Baker, A. J., Gonzalez, P. M., Piersma, T., Niles, L. J., de Lima Serrano do Nascimento, I., Atkinson, P. W., Clark, N. A., Minton, C. D. T.,

Peck, M. K. & Aarts, G. (2004). Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc.. R. Soc. Lond. B* 271: 875–82.

Balança, G. & Schaub, M. (2005). Post-breeding migration ecology of Reed *Acrocephalus scirpaceus,* Moustached *A. melanopogon* and Cetti's Warblers *Cettia cetti* at a Mediterranean stopover site. *Ardea* 93: 245–57.

Barbraud, C., Barbraud, J.-C. & Barbraud, M. (1999). Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis* 141: 469–79.

Battley, P. F. (2006). Consistent annual schedules in a migratory shorebird. *Biol. Lett.* 2: 517–20.

Battley, P. F., Piersma, T., Dietz, M., Tang, S., Dekinga, P. & Hulsman, K. (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proc.. R. Soc. Lond. B* 267: 191–5.

Bauchinger, U. (2002). Phenotypic flexibility of organs during long-distance migration in Garden Warblers: implications for migratory and reproductive periods. PhD thesis, Technical University, Munich.

Bauchinger, U., Hoff Van t, T. & Biebach, H. (2007). Testicular development during long-distance spring migration. *Hormones & Behaviour* 51: 295–305.

Bauchinger, U. & Klaassen, M. (2005). Longer days in spring than in autumn accelerate migration speed of passerine birds. *J. Avian Biol.* 36: 3–5.

Baxter, E. V. & Rintoul, L. J. (1918). The birds of the Isle of May: a migration study. *Ibis* 1918: 247–87.

Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., Berthold, P. & Farnsworth, K. (2005). Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* 310: 502–3.

Bearhop, S., Hilton, G. M., Votier, S. C. & Waldron, S. (2004). Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proc.. R. Soc. Lond. B* 271 (suppl. 4): 215–18.

Beck, W. & Wiltschko, W. (1988). Magnetic factors control the migratory direction of Pied Flycatcher *(Ficedula hypoleuca* Pallas). *Proc.. Int. Orn. Congr.* 19: 1955–62.

Beekman, J. H., Nolet, B. A. & Klaassen, M. (2002). Skipping swans: fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick's Swans *Cygnus bewickii. Ardea* 90: 437–60.

Belda, E. J., Barba, E. & Monros, J. S. (2007). Resident and transient dynamics, site fidelity and survival in wintering Blackcaps *Sylvia atricapilla:* evidence from capture–recapture analyses. *Ibis* 149: 396–404.

Bell, C. P. (2000). Proc.ess in the evolution of bird migration and pattern in avian ecogeography. *J. Avian. Biol.* 31: 258–65.

Bellrose, F. C. (1958). The orientation of displaced waterfowl in migration. *Wilson Bull.* 70: 20–40.

Bellrose, F. C. (1967). Radar in orientation research. *Proc.. Int. Orn. Congr.* 14: 281–309.

Benhamou, S., Bonnadonna, F. & Jouventin, P. (2003). Successful homing of magnet-carrying White-chinned Petrels released in the open sea. *Anim. Behav.* 65: 729–34.

Benkman, C. W. (1987). Food profitability and the foraging ecology of crossbills. *Ecol. Monog.* 57: 251–67.

Benkman, C. W. (1990). Intake rates and the timing of crossbill reproduction. *Auk* 107: 376–86.

Bensch, S., Andersson, T. & Åkesson, S. (1999). Morphological and molecular variation across a migratory divide in Willow Warblers *Phylloscopus trochilus. Evolution* 53: 1925–35.

Bensch, S. & Hasselquist, D. (1991). Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus:* the effect of variation in territory attractiveness. *J. Anim. Ecol.* 60: 857–71.

Bensch, S. & Hasselquist, D. (1999). Phylogeographic population structure of Great Reed Warblers: an analysis of mtDNA control region sequences. *Biol. J. Linn. Soc.* 66: 171–85.

Bensch, S. & Nielsen, B. (1999). Autumn migration speed of juvenile Reed and Sedge Warblers in relation to date and fat loads. *Condor* 101: 153–6.

Berndt, R. & Henss, M. (1967). Die Kohlmeise, *Parus major,* als Invasionsvogel. *Vogelwarte* 24: 17–37.

Berndt, R. & Winkel, W. (1979). Verfrachtungs—Experimente zur Frage der Geburtsortsprägung beim Trauerschnapper *(Ficedula hypoleuca). J. Orn.* 121: 281–6.

Bernis, F. (1975). Migration of Falconiformes and *Ciconia* spp. through the Straits of Gibraltar. Part 2. *Ardeola* 21: 489–580.

Berthold, P. (1973). Relationships between migratory restlessness and migration distance in *Sylvia* species. *Ibis* 115: 594–9.

Berthold, P. (1984). The control of partial migration in birds: a review. *The Ring* 10: 253–65.

Berthold, P. (1988). The control of migration in European warblers. *Proc.. Int. Orn. Congr.* 19: 215–49.

Berthold, P. (1993). *Bird Migration. A General Survey.* Oxford University Press, Oxford.

Berthold, P. (1995). Microevolution of migratory behaviour illustrated by the Blackcap *Sylvia atricapilla:* 1993 Witherby Lecture. *Bird Study* 42: 89–100.

Berthold, P. (1996). *Control of Bird Migration.* Chapman & Hall, London.

Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70: 1–12.

Berthold, P. (2001). *Bird Migration: A General Survey.* Second edition. Oxford University Press, Oxford.

Berthold, P. & Querner, U. (1981). Genetic basis of migrating behaviour in European warblers. *Science* 212: [77–9.]

Berthold, P. & Querner, U. (1982). Genetic basis of moult, wing length, and body weight in a migratory bird species *Sylvia atricapilla. Experientia (Basel)* 38: 801–2.

Berthold, P., Gwinner, E. & Klein, H. (1972). Circannual Periodic bei Grasmückken I. Periodic des Körpergewiches, der Mauser und der Nachtunruhe bei *Sylvia atricapilla* und *S. borin* unter verschiedenen konstanten Bedingungen. *J. Orn.* 113: 170–90.

Berthold, P., Kaatz, M. & Querner, U. (2004). Long-term satellite tracking of White Stork *(Ciconia ciconia)* migration: constancy versus variability. *J. Orn.* 145: 356–9.

Berthold, P., Helbig, A. H., Mohr, G. & Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360: 668–70.

Berthold, P., van den Bosch, W., Fiedler, W., Kaatz, C., Kaatz, M., Leshem, Y. & Querner, U. (2001). Detection of a new important staging and wintering area of the White Stork *Ciconia ciconia* by satellite tracking. *Ibis* 143: 450–5.

Berthold, P., van den Bosch, W., Jakubiec, Z., Kaatz, C., Kaatz, M. & Querner, U. (2002). Long-term satellite tracking sheds light on variable migration strategies of White Storks *(Ciconia ciconia)*. *J. Orn.* 143: 489–95.

Bêty, J., Giroux, J.-F. & Gauthier, G. (2004). Individual variation in timing of migration: causes and reproductive consequences in Greater Snow Geese *(Anser caerulescens atlanticus)*. *Behav. Ecol. Sociobiol.* 57: 1–8.

Bibby, C. J., Green, R. E., Peplar, G. R. M. & Peplar, P. A. (1976). Sedge Warbler migration and reed aphids. *Brit. Birds* 69: 384–99.

Bibby, C. J. & Green, R. E. (1981). Autumn migration strategies of Reed and Sedge Warblers. *Ornis Scand.* 12: 1–12.

Biebach, H. (1983). Genetic determination of partial migration in the European Robin *(Erithacus rubecula)*. *Auk* 100: 601–6.

Biebach, H. (1985). Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* 41: 695–7.

Biebach, H. (1990). *Strategies of trans-desert migrants.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 352–67.

Biebach, H. (1991). Is water or energy crucial for trans-Saharan migrants? *Proc.. Int. Orn. Congr.* 20: 773–9.

Biebach, H. (1992). Flight-range estimates for small trans-Sahara migrants. *Ibis* 134 (suppl.): 47–54.

Biebach, H. (1998). Phenotypic organ flexibility in Garden Warblers *Sylvia borin* during long-distance migration. *J. Avian Biol.* 29: 529–35.

Biebach, H. & Bauchinger, U. (2003). *Energetic savings in organ adjustment during long migratory flights in Garden Warblers* (Sylvia borin). In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 269–80.

Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J. & Schmidt, D. (2000). Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. *Ibis* 142: 623–34.

Biebach, H., Friedrich, W. & Heine, G. (1986). Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69: 370–9.

Bijlsma, R. G. (1990). Predation by large falcon species on wintering waders on the Banc d'Arguin, Mauritania. *Ardea* 78: 75–81.

Bingman, V. P. (1987). Earth's magnetism and the migratory orientation of European Robins.*Auk* 104: 523–5.

Bingman, V. P., Budzynski, C. A. & Voggenhuber, A. (2003). *Migratory systems as adaptive responses to spatial and temporal variability in orientation stimuli.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 457–70.

Birkhead, T. R. (1974). Movement and mortality rates in British Guillemots. *Bird Study* 21: 241–53.

Birkhead, T. (2008). *The Wisdom of Birds. An Illustrated History of Ornithology*. Bloomsbury, London.

Bishop, M. A., Warnock, N. & Takekawa, J. Y. (2004). Differential spring migration by male and female Western Sandpipers at interior and coastal stopover sites. *Ardea* 92: 185–96.

Black, J. M. (1996). *Partnerships in Birds. The Study of Monogamy*. Oxford University Press, Oxford.

Black, J. M. & Rees, E. C. (1984). The structure and behaviour of the Whooper Swan population wintering at Caerlavarock, Dumfries and Galloway, Scotland: an introductory study. *Wildfowl* 35: 21–36.

Blem, C. R. (1990). Avian energy storage. *Current Orn.* 7: 59–113.

Blomqvist, S., Holmgren, N., Åkesson, S., Hedenström, A. & Pettersson, J. (2002). Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia* 133: 146–58.

Bluhm, C. (1988). Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. *Current Orn.* 5: 123–85.

Blums, P., Nichols, J. D., Hines, J. E. & Mednis, A. (2002). Sources of variation in survival and breeding site fidelity in three species of European ducks. *J. Anim. Ecol.* 71: 438–50.

Boano, G., Bonardi, A. & Silvano, F. (2004). Nightingale *Luscinia megarhynchos* survival rates in relation to Sahel rainfall. *Avocetta* 28: 77–85.

Bock, C. E. & Lepthien, L. W. (1976). Synchronous eruptions of boreal seed-eating birds. *Amer. Nat.* 110: 559–71.

Boddy, M. & Sellers, R. M. (1983). Orientated movements by Greenfinches in southern Britain. *Ringing & Migration* 4: 129–38.

Böhning-Gaese, K. & Oberrath, R. (2003). Macroecology of habitat choice in long-distance migratory birds. *Oecologia* 137: 296–303.

Bojarinova, J., Ilves, A., Chernetsov, N. & Leivits, A. (2008). Body mass, moult and migration speed of the Goldcrest *Regulus regulus* in relation to the timing of migration at different sites of the migration route. *Ornis Fenn.* 85: 55–65.

Bolshakov, C. V. (2003). *Nocturnal migration of passerines in the desert-highland zone of western central Asia: selected aspects.* In:

Avian Migration (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 225–36.

Bolshakov, C. V. & Bulyuk, V. N. (1999). Time of nocturnal flight initiation (take-off activity) in the European Robin *Erithacus rubecula* during spring migration: direct observations between sunset and sunrise. *Avian Ecol. Behav.* 2: 19–50.

Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H. P. & Dell'Omo, G. (2005). Orientation in the Wandering Albatross: interfering with magnetic perception does not affect orientation performance. Proc.. *R. Soc. Lond. B* 272: 489–95.

Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature* 44: 81–3.

Both, C. & te Marvelde, L. (2007). Climate change and timing of avian breeding and migration throughout Europe. *Clim. Res.* 35: 93–105.

Both, C., Sanz, J. J., Artemyev, A. V., Blaauw, V., Cowie, R. J., Dekhuizen, A. J., Enemar, A., Järvinen, A., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Silverin, B., Slater, F. M., Sokolov, L. B., Visser, M. E., Winkel, W., Wright, J. & Zang, H. (2006). Pied Flycatchers travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date. *Ardea* 94: 511–25.

Both, C. & Visser, M. E. (2001). Adjustment to climatic change is constrained by arrival date in a longdistance migratory bird. *Nature* 411: 296–8.

Bourne, W. R. P. (1959). Notes on autumn migration in the Middle East. *Ibis* 101: 170–76.

Bourne, W. R. P. (1979). Birds and gas flares. *Mar. Pollut. Bull.* 10: 124–5.

Bourne, W. R. P. (1980). The midnight descent, dawn ascent and re-orientation of land birds migrating across the North Sea in autumn. *Ibis* 122: 536–40.

Bourne, W. R. P. (1983). A satellite view of bird migration between Iceland and Scotland. *Sea Swallow* 32: 80–82.

Boyd, H. (1954). The 'wreck' of Leach's Petrels in the autumn of 1952. *Brit. Birds* 47: 137–63.

Branson, N. J. B. A., Ponting, E. D. & Minton, C. D. T. (1979). Turnstone populations on the Wash. *Bird Study* 26: 47–54.

Bregnballe, T., Frederiksen, M. & Gregersen, J. (1997). Seasonal distribution and timing of migration of Cormorants breeding in Denmark. *Bird Study* 44: 257–76.

Brewer, D., Diamond, A., Woodsworth, E. J., Collins, B. T. & Dunn, E. H. (2000). *Canadian Atlas of Bird Banding,* Volume 1. Canadian Wildlife Service, Ottawa.

Bromley, R. G. & Jarvis, R. L. (1993). The energetics of migration and reproduction of Dusky Canada Geese. *Condor* 95: 193–210.

Brooke, M. de L. (1978). The dispersal of female Manx Shearwaters *Puffinus puffinus. Ibis* 120: 545–51.

Brookes, B. (2008). House Martins eating elderberries. *Brit. Birds* 101: 384.

Brosset, A. (1984). Oiseaux migrateurs européens hivernant dans la partie guinéenne du Mont Nimba. *Alauda* 52: 81–101.

Brown, C. R. & Brown, M. B. (2000). Weather-mediated natural selection on arrival time in Cliff Swallows *(Petrochelidon pyrrhonata). Behav. Ecol. Sociobiol.* 47: 339–45.

Browne, S. J. & Aebischer, N. J. (2004). Temporal changes in the breeding ecology of European Turtle Doves *Streptopelia turtur* in Britain, and implications for conservation. *Ibis* 146: 125–37.

Browne, S. J. & Mead, C. J. (2003). Age and sex composition, biometrics, site fidelity and origin of Brambling *Fringilla montifringilla* wintering in Norfolk, England. *Ringing & Migration* 21: 145–53.

Bruderer, B. (1971). Radarbeobachtungen über den Frühlingszug in Schweizerischen Mittelland. *Orn. Beob.* 68: 89–158.

Bruderer, B. (1997a). The study of bird migration by radar. Part 1. The technical bases. *Naturwissenschaften* 84: 1–8.

Bruderer, B. (1997b). The study of bird migration by radar. Part 2. Major achievements. *Naturwissenschaften* 84: 45–54.

Bruderer, B. (1999). *Three decades of tracking radar-studies on bird migration in Europe and the Middle East.* In: *Migrating Birds Know No Boundaries* (Eds Leshem, Y., Mandelik, Y. & Shamoun-Baranes, J.). International Centre for the Study of Bird Migration, Latron, Israel, 107–41.

Bruderer, B. & Boldt, A. (2001). Flight characteristics of birds: 1. Radar measurements of speeds. *Ibis* 143: 178–204.

Bruderer, B. & Jenni, L. (1990). *Migration across the Alps.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 60–77.

Bruderer, B. & Liechti, F. (1999). Bird migration across the Mediterranean. *Proc.. Int. Orn. Congr.* 22: 1983–99.

Bruderer, B. & Muff, J. (1979). Bestandesschwankungen schweizerischer Rauch- und Mehlserchwalben, insbesondere im Zusammenhang mit der Schwalbenkatastrophe in Herbst 1974. *Orn. Beob.* 76: 229–34.

Bruderer, B., Steuri, T. & Baumgartner, M. (1995). Short-range high-precision surveillance of nocturnal migration and tracking of single targets. *Isr. J. Zool.* 41: 207–20.

Bryant, D. M. & Jones, G. (1995). Morphological changes in a population of Sand Martins *Riparia riparia* associated with

fluctuations in population size. *Bird Study* 42: 57–65.

Budeau, D. A., Ratti, J. T. & Ely, C. R. (1991). Energy dynamics, foraging ecology, and behaviour of pre-nesting Greater White-fronted Geese. *J. Wildl. Manage.* 55: 556–63.

Burns, J. G. & Ydenberg, R. C. (2002). The effects of wing loading and gender on the escape flights of Least Sandpipers *(Calidris minutilla)* and Western Sandpipers *(Calidris mauri)*. *Behav. Ecol. Sociobiol.* 52: 128–36.

Burt de Perera, T. B. & Guilford, T. (1999). The orientational consequences of flocking behaviour in homing pigeons, *Columbia livia. Ethology* 105: 13–23.

Burton, N. H. K. (2000). Winter site-fidelity and survival of Redshank *Tringa tetanus* at Cardiff, south Wales. *Bird Study* 47: 102–12.

Burton, N. H. K. (2007). The influences of restock age and habitat patchiness on Pipits *Anthus trivialis* breeding in Breckland pine plantations. *Ibis* 149 (suppl. 2): 193–205.

Busse, P. (2000). *Bird Station Manual.* SE European Bird Migration Network, University of Gda sk, Poland.

Butler, C. J. (2003). The disproportionate effect of global warming on arrival dates of short-distance migratory birds in North America. *Ibis* 145: 484–95.

Butler, P. J., Bishop, C. M. & Woakes, A. J. (2003). *Chasing a wild goose: post-hatch growth of locomotor muscles and behavioural physiology of migration of an Arctic goose.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 527–42.

Butler, P. J., Woakes, A. J., Bevan, R. M. & Stevenson, R. (2000). Heart rate and rate of oxygen consumption during flight of the Barnacle Goose, *Branta leucopsis. Comp. Biochem. Physiol. A* 216: 379–85.

Butler, P. J., Woakes, A. J. & Bishop, C. M. (1998). Behaviour and physiology of Svalbard Barnacle Geese *Branta leucopsis* during their autumn migration. *J. Avian Biol.* 29: 536–45.

Butler, R. W., Kaiser, G. W. & Smith, G. E. J. (1987). Migration chronology, length of stay, sex-ratio, and weight of Western Sandpipers *(Calidris mauri)* on the south coast of British Columbia. *J. Field Orn.* 58: 103–11.

Cabot, D. & West, B. (1973). Population dynamics of Barnacle Geese in Ireland. *Proc.. R. Irish Acad.* 73: 415–43.

Cade, T. J. (2000). *Progress in translocation of diurnal raptors.* In: *Raptors at Risk* (Eds Chancellor, R. D. & Meyburg, B.-U.). Hancock House Publishers, Washington, DC, 343–72.

Cade, T. J., Enderson, J. H., Thelander, C. G. & White, C. M. (1988). *Peregrine Falcon Populations: Their Management and Recovery.* The Peregrine Fund Inc., Boise, ID.

Calmaestra, R. G. & Moreno, E. (2000). Ecomorphological patterns related to migration: a comparative osteological study with passerines. *J. Zool. Lond.* 252: 495–501.

Carbone, C. & Owen, M. (1995). Differential migration of the sexes of Pochard *Aythya ferina:* results from a European survey. *Wildfowl* 46: 99–108.

Carmi, N. & Pinshow, B. (1995). Water as a physiological limitation to flight duration in migrating birds: the importance of exhaled air temperature and oxygen extraction. *Isr. J. Zool.* 41: 369–75.

Carmi, N., Pinshow, B., Porter, W. P. & Jaeger, J. (1992). Water and energy limitations on flight duration in small migrating birds. *Auk* 109: 268–76.

Carpenter, F. L. & Hixon, M. A. (1988). A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 90: 373–8.

Casement, M. B. (1966). Migration across the Mediterranean observed by radar. *Ibis* 108: 461–91.

Catry, P., Campos, A., Almada, V. & Cresswell, W. (2004). Winter segregation of migrant European Robins *Erithacus rubecula* in relation to sex, age and size. *J. Avian Biol.* 35: 204–9.

Catry, P., Catry, I., Catry, T. & Martins, T. (2003). Within and between-year winter-site fidelity of Chiffchaffs *Phylloscopus collybita. Ardea* 9: 213–20.

Catry, P., Lecoq, M., Araujo, A., Conway, G., Felgueiras, M., King, J. M. B., Rumsey, S., Salima, H. & Tenreiro, P. (2005). Differential migration of Chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. *J. Avian Biol.* 36: 184–90.

Cavé, A. J. (1983). Purple Heron survival and drought in tropical West Africa. *Ardea* 71: 217–24.

Chamberlain, C. P., Bensch, S., Feng, X., Åkesson, S. & Anderson, T. (2000). Stable isotopes examined across a migratory devide in Scandinavian Willow warblers *Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula* reflect their African winter quarters, *Proc.. R. Soc. Lond. B* 267: 43–8.

Chan, K. (1994). Nocturnal activity of caged resident and migrant Silvereyes (Zosteropidae: Aves). *Ethology* 96: 313–21.

Cherry, J. D. (1982). Fat deposition and length of stopover of migrant White-crowned Sparrows. *Auk* 99: 725–32.

Cherubini, G., Serra, L. & Bacceti, N. (1996). Primary moult, body mass and moult migration of Little Tern *Sterna albifrons* in NE Italy. *Ardea* 84: 99–114.

Cichón, M., Olejniczak, P. & Gustafsson, L. (1998). The effect of body condition on the cost of reproduction in female Collared Flycatchers *Ficedula albicollis. Ibis* 140: 128–30.

Clapham, C. (1979). The Turnstone populations of Morecambe Bay. *Ringing & Migration* 2: 144–50.

Clark, J. (2009). The flying enigma. *BTO News* 281:10–11.

Clarke, A. L., Saether, B.-E. & Røskaft, E. (1997). Sex biases in avian dispersal: a reappraisal. *Oikos* 79: 429–38.

Clarke, W. E. (1912). *Studies in Bird Migration.* Volumes 1 & 2. Oliver & Boyd, Edinburgh.

Cochran, W. W. & Kjos, C. G. (1985). Wind drift and migration of thrushes: a telemetry study. *Illinois Nat. Hist. Survey Bull.* 33: 297–330.

Cochran, W. W., Montgomery, G. G. & Graber, R. R. (1967). Migratory flights of *Hylocichla* thrushes in spring: a radiotelemetry study. *Living Bird* 6: 213–25.

Cochran, W. W., Mouritsen, H. & Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304: 405–8.

Cochran, W. W. & Wikelski, M. (2005). *Individual migratory tactics of New World Catharus thrushes.* In: *Birds of Two Worlds* (Eds Greenberg, R. & Marra, P. P.). Smithsonian Institution, Washington, DC, 274–89.

Colwell, M. A., Reynolds, J. D., Gratto, C. L., Schamel, D. & Tracy, D. M. (1988). Phalarope philopatry. *Proc.. Int. Orn. Congr.* 19: 585–93.

Cooke, F., Rockwell, R. F. & Lank, D. B. (1995). *The Snow Geese of La Pérouse Bay.* Oxford University Press, Oxford.

Coppack, T. & Pulido, F. (2004). Photoperiodic response and the adaptability of avian life cycles to environmental change. *Adv. Ecol. Res.* 35: 131–50.

Coppack, T., Pulido, F. & Berthold, P. (2001). Photoperiodic response to early hatching in a migratory bird species. *Oecologia* 128: 181–6.

Corso, A. (2001). Raptor migration across the Strait of Messina, southern Italy. *Brit. Birds* 94: 196–202.

Cottridge, D. M. & Vinicombe, K. (1996). *Rare Birds in Britain and Ireland. A Photographic Record.* Collins, London.

Coulson, J. C. (1961). Movements and seasonal variation in mortality of Shags and Cormorants ringed on the Farne Islands, Northumberland. *Brit. Birds* 54: 225–35.

Coulson, J. C. & Butterfield, J. (1985). Movements of British Herring Gulls. *Bird Study* 32: 91–103.

Coulson, J. C., Butterfield, J., Duncan, N., Kearsey, S., Monaghan, P. & Thomas, C. (1984). Origin and behaviour of Great Black-backed Gulls wintering in northeast England. *Brit. Birds* 77: 1–11.

Coulson, J. C. & Nève de Mévergnies, G. (1992). Where do young Kittiwakes *Rissa tridactyla* breed, philopatry or dispersal? *Ardea* 80: 187–97.

Cowley, E. (1979). Sand Martin population trends in Britain, 1965–1975. *Bird Study* 26: 113–16.

Cowley, E. & Siriwardena, G. M. (2005). Long-term variation in survival rates of Sand Martins *Riparia riparia:* dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study* 52: 237–51.

Cramp, S. (1985). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 4. Oxford University Press, Oxford.

Cramp, S. (1988). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 5. Oxford University Press, Oxford.

Cramp, S. (1992). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 6. Oxford University Press, Oxford.

Cramp, S. & Perrins, C. M. (1993). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 7. Oxford University Press, Oxford.

Cramp, S. & Perrins, C. M. (1994). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volumes. 8–9. Oxford University

Press, Oxford.

Cramp, S. & Simmons, K. E. L. (1977). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 1. Oxford University Press, Oxford.

Cramp, S. & Simmons, K. E. L. (1980). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 2. Oxford University Press, Oxford.

Cramp, S. & Simmons, K. E. L. (1983). *Handbook of the Birds of Europe, the Middle East and North Africa.* Volume 3. Oxford University Press, Oxford.

Cresswell, W. (2008). Non-lethal effects of predation on birds. *Ibis* 150: 3–17.

Cristol, D. A., Reynolds, E. B., Leclerc, J. E., Donner, A. H., Farabaugh, C. S. & Ziegenfus, C. W. (2003). Migratory Dark-eyed Juncos, *Junco hyemalis,* have better spatial memory and denser hippocampal neurons than non-migratory conspecifics. *Anim. Behav.* 66: 317–28.

Croxall, J. P., Silk, J. R. D., Phillips, R. A., Afanasyev, V. & Briggs, D. R. (2005). Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* 307: 249–50.

Cuadrado, M. (1995). Winter territoriality in migrant Black Redstarts *Phoenicurus ochruros* in the Mediterranean area. *Bird Study* 42: 232–9.

Cuadrado, M., Senar, J. C. & Copeti, J. C. (1995). Do all Blackcaps *Sylvia atricapilla* show winter site fidelity? *Ibis* 137: 70–5.

Currie, D., Thompson, D. B. & Burke, T. (2000). Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe. Ibis* 142: 389–98.

Curry-Lindahl, K. (1958). Internal timer and spring migration in an equatorial migrant, the Yellow Wagtail *(Motacilla flava). Ark Zool.*

11: 541–57.

Curry-Lindahl, K. (1963). Molt, body weights, gonadal development and migration in *Motacilla flava. Proc.. Int. Orn. Congr.* 13: 960–73.

Dalhaug, L., Tombre, I. M. & Erikstad, K. E. (1996). Seasonal decline in clutch size of the Barnacle Goose in Svalbard. *Condor* 98: 42–7.

Dall Antonia, L., Dall Antonia, P., Benvenuti, S., Ioalè, P., Massa, B. & Bonadonna, F. (1995). The homing behaviour of Cory's Shearwaters *(Calonectris diomedea)* studied by means of a direction recorder. *J. Exp. Zool.* 198: 359–62.

Dallinga, J. H. & Schoenmakers, S. (1989). *Population changes of the White Stork Ciconia ciconia since the 1850s in relation to food resources.* In: *White Stork: Status and Conservation* (Eds Rheinwald, G., Ogden, J. & Schulz, H.). Dachverband Deutscher Avifaunisten, International Council for Bird Preservation, Bonn, 231–62.

Danhardt, J. & Lindström, Å. (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Anim. Behav.* 62: 235–43.

Darwin, C. (1859). *The Origin of Species.* John Murray, London.

Dau, C. P. (1992). The fall migration of Pacific flyway Brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43: 80–95.

Davies, J. C. & Cooke, F. (1983). Annual nesting production in Snow Geese: prairie droughts and arctic springs. *J. Wildl. Manage.* 47: 291–6.

Davis, P. (1964). Crossbills in Britain and Ireland in 1963. *Brit. Birds* 57: 477–501.

Davis, P. (1966). The great immigration of early September. *Brit. Birds* 59: 353–76.

Dawson, A., Hinsley, S. A., Ferns, P. N., Bosser, R. H. C. & Eccleston, L. (2000). Rate of moult affects feather quality: a

mechanism linking current reproductive effort to future survival. *Proc.. R. Soc. Lond. B* 267: 2093–8.

de Lucas, M., Janss, F. E. & Ferrer, M. (Eds) (2007). *Birds and Wind Farms.* Quercus, Madrid.

De Sante, D. F. (1973). An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California. Unpub. PhD dissertation, Stanford University, CA.

De Sante, D. F. (1983a). Annual variability in the abundance of migrant landbirds on southeast Farallon Island, California. *Auk* 100: 826–52.

De Sante, D. F. (1983b). Vagrants: when orientation or navigation goes wrong. *Point Reyes Bird Observatory Newsletter* 61: 12–16.

Dean, W. R. J. (2004). *Nomadic Desert Birds.* Springer, London.

Demey, R. & Fishpool, L. D. C. (1994). The birds of Yapo Forest, Ivory Coast. *Malimbus* 16: 100–22.

den Held, J. D. (1981). Population changes of the Purple Heron in relation to drought in the wintering area. *Ardea* 69: 185–91.

Derégnaucourt, S., Guyomarc h, J.-C. & Belhamra, M. (2005). Comparison of migratory tendency in European Quail *(Coturnix c. coturnix),* domestic Japanese Quail *(Coturnix c. japonica)* and their hybrids. *Ibis* 147: 25–36.

Desholm, M. (2003). How much do small-scale changes in flight direction increase overall migration distance? *J. Avian Biol.* 34: 155–8.

Desholm, M. & Kahlert, J. (2005). Avian collision risk at an offshore wind farm. *Biol. Lett.* 1: 296–8.

Diamond, J. M., Karasov, W. H., Phan, D. & Carpenter, F. C. (1986). Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature* 320: 62–3.

Diehl, R. H., Larkin, R. P. & Black, J. E. (2003). Radar observations of bird migration over the Great Lakes. *Auk* 120:

278–90.

Dierschke, V. (2003). Predation hazard during migratory stopover: are light or heavy birds under risk? *J. Avian Biol.* 34: 24–9.

Dierschke, V. (2006). Factors determining stopover decisions in migrating passerines on an offshore island. *Acta Zool. Sinica* 52 (suppl.): 594–8.

Dierschke, V., Schmaljohann, H. & Mendel, B. (2005), Differential timing of spring migration in Northern Wheatears: hurried males or weak females? *Behav. Ecol. Sociobiol.* 57: 470–80.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. (1990). Brood size manipulations in the Kestrel *(Falco tinnunculus):* effects on offspring and parent survival. *J. Anim. Ecol.* 59: 269–85.

Dinsmore, S. J. (2006). The changing seasons: weatherbirds. *N. Amer. Birds* 60: 14–26.

Dittman, T. & Becker, P. H. (2003). Sex, age, experience and condition as factors affecting arrival date in prospecting Common Terns, *Sterna hirundo. Anim. Behav.* 65: 981–6.

Dolnik, V. R. (1963). A quantitative study of vernal testicular growth in several species of finches *(Fringillidae). Dokl. Akad. Nauk USSR* 149: 370–2.

Dolnik, V. R. (1990). *Bird migration across arid and mountainous regions of Middle Asia and Kazakhstan.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 368–86.

Dolnik, V. R. & Blyumental, T. I. (1967). Autumnal premigratory and migratory periods in the Chaffinch *Fringilla coelebs* and some other temperate zone passerine birds. *Condor* 69: 435–68.

Dolnik, V. R. & Gavrilov, V. M. (1980). Photoperiodic control of the molt cycle in the Chaffinch *(Fringilla coelebs). Auk* 97: 50–62.

Donázar, J. A., Negro, J. J. & Hiraldo, F. (1993). Foraging habitat selection, land-use changes and population decline in the Lesser Kestrel *Falco naumanni*. *J. Appl. Ecol.* 30: 515–22.

Dorka, V. (1966). Das jahres- und tageszeitliche Zugmuster von Kurz- und Langstreckenziehern nach Beobachtungen auf den Alpenpässen Cou/Bretolet (Wallis). *Orn. Beob.* 63: 165–223.

Dougall, T. W. (1992). Post-fledging dispersal of British Pied Wagtails *Motacilla alba yarrellii*. *Ringing & Migration* 13: 21–6.

Dow, H. & Fredga, S. (1983). Breeding and natal dispersal of the Goldeneye, *Bucephala clangula*. *J. Anim. Ecol.* 52: 681–95.

Dowsett, R. J. & Fry, C. H. (1971). Weight losses of trans-Saharan migrants. *Ibis* 113: 531–3.

Dowsett-Lemaire, F. & Dowsett, R. J. (1987). European Reed and Marsh Warblers in Africa: migration patterns, moult and habitat. *Ostrich* 58: 65–85.

Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T. (2003). Pay-offs and penalties of competing migratory schedules. *Oikos* 103: 274–92.

Drost, R. (1938). Über den Einflus von Verfrachtungen zur Herbstzugzeit auf den Sperber *Accipiter nisus* (L.). *Proc.. Int. Orn. Congr.* 9: 502–21.

Duebbert, H. F. & Kantrud, H. A. (1974). Upland duck nesting related to land use and predator reduction. *J. Wildl. Manage.* 38: 257–65.

Duebbert, H. F. & Lokemoen, J. T. (1980). High duck nesting success in a predator-reduced environment. *J. Wildl. Manage.* 44: 428–37.

Dugger, B. D. (1997). Factors influencing the onset of spring migration in Mallards. *J. Field Orn.* 68: 331–7.

Duncan, W. N. M. & Monaghan, P. (1977). Infidelity to the natal colony by breeding Herring Gulls. *Ringing & Migration* 1: 166–72.

Durand, A. L. (1963). A remarkable fall of American landbirds on the 'Mauritania', New York to Southampton, October 1962. *Brit. Birds* 56: 157–64.

Dymond, J. N., Fraser, P. A. & Gantlet, S. J. M. (1989). *Rare Birds in Britain and Ireland.* T. & A. D. Poyser, Calton.

Eastwood, E. (1967). *Radar Ornithology.* Methuen, London.

Ebbinge, B. S. (1985). Factors determining the population size of arctic-breeding geese wintering in western Europe. *Ardea* 73: 121–8.

Ebbinge, B. S. & Spaans, B. N. (1995). The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105–13.

Edelaar, P. & Terpstra, K. (2004). Is the nominate subspecies of the Common Crossbill *Loxia c. curvirostra* polytypic? Morphological differences among years at a single site. *Ardea* 92: 93–101.

Edelstam, C. (E**d.)** (1972). *The Visible Migration of Birds at Ottenby, Sweden.* Vår Fagelvärld Sonderh, Sweden.

Elgood, J. H., Fry, C. H. & Dowsett, R. J. (1973). African migrants in Nigeria. *Ibis* 115: 1–45.

Elkins, N. (1988). *Weather and Bird Behaviour.* T. & A. D. Poyser, Calton.

Elkins, N. (2005). Weather and bird migration. *Brit. Birds* 98: 238–56.

Elkins, N. (2008). Further thoughts on the transatlantic vagrancy of landbirds to Britain and Ireland. *Brit. Birds* 101: 458–77.

Ellegren, H. (1990a). Autumn migration speeds in Scandinavian Bluethroats *Luscinia s. svecica. Ringing & Migration* 11: 121–31.

Ellegren, H. (1990b). Timing of autumn migration in Bluethroats *Luscinia svecica* depends on timing of breeding. *Ornis Fenn.* 67: 13–

17.

Ellegren, H. (1991). Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scand.* 22: 340–8.

Ellegren, H. (1993). Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scand.* 24: 220–8.

Ellegren, H. & Fransson, T. (1992). Fat loads and estimated flight ranges in four *Sylvia* species analysed during autumn migration at Gotland, south-east Sweden. *Ringing & Migration* 13:1–12.

Elliott, C. C. H., Waltner, M., Underhill, L. G., Pringle, J. S. & Dick, W. J. A. (1976). The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. *Ostrich* 47: 191–213.

Ellis, D. H., Sladen, W. J. L., Lishman, W. A., Clegg, K. R., Duff, J. W., Gee, G. F. & Lewis, J. L. (2003). Motorised migrations: the future or mere fantasy? *Bioscience* 53: 260–4.

Emlen, S. T. (1967a). Migratory orientation in the Indigo Bunting, *Passerina cyanea.* Part 1: Evidence for use of celestial cues. *Auk* 84: 309–42.

Emlen, S. T. (1967b). Migratory orientation in the Indigo Bunting, *Passerina cyanea.* Part 2: Mechanism of celestial orientation. *Auk* 84: 463–89.

Emlen, S. T. (1975). *Migration: orientation and navigation.* In: *Avian Biology,* Volume 5 (Eds Farner, D. S., King, J. R. & Parkes, K. C.). Academic Press, London, 129–219.

Emlen, S. T. & Emlen, J. T. (1966). A technique for recording migratory orientation of captive birds. *Auk* 83: 361–7.

Enemar, A., Nilsson, L. & Sjöstrand, B. (1984). The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. *Ann. Zool. Fenn.* 21: 321–38.

Eriksson, K. (1970). Ecology of the irruption and wintering of Fennoscandian Redpolls *(Carduelis flammea* Coll.). *Ann. Zool. Fenn.* 7: 273–82.

Erni, B., Liechti, F., Underhill, L. G. & Bruderer, B. (2002). Wind and rain govern the intensity of nocturnal bird migration in central Europe—a log-linear regression analysis. *Ardea* 90: 155–66.

Erskine, A. J. (1979). Man's influence on potential nesting sites and populations of swallows in Canada. *Can. Field-Nat.* 93: 371–7.

Esler, D. & Grand, J. B. (1994). The role of nutrient reserves for clutch formation by Northern Pintails in Alaska. *Condor* 96: 422–32.

Evans, I. M., Summers, R. W., O Toole, L., Orr-Ewing, D. C., Evans, R. D., Snell, N. & Smith, J. (1999). Evaluating the success of translocating Red Kites *Milvus milvus* to the UK. *Bird Study* 46: 129–44.

Evans, P. R. (1966). Migration and orientation of passerine night migrants in northeast England. *J. Zool. (Lond.)* 150: 319–69.

Evans, P. R. (1968). Reorientation of passerine night migrants after displacement by the wind. *Brit. Birds* 61: 281–303.

Evans, P. R. (1981). *Migration and dispersal of shorebirds as a survival strategy.* In: *Feeding and Survival Strategies of Estuarine Organisms* (Eds Jones, N. V. & Wolff, W. J.). Plenum Publishing Co., New York, 275–90.

Evans, P. R. & Davidson, N. C. (1990). *Migration strategies and tactics of waders breeding in arctic and north temperate latitudes.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 387–98.

Evans, P. R. & Pienkowski, M. W. (1984). *Population dynamics of shorebirds.* In: *Behaviour of Marine Animals, Volume 5: Shorebirds, Breeding Biology and Populations* (Eds Burger, J. & Olla, B. L.). Plenum Press, New York, 83–123.

Evans, P. R. & Townsend, D. J. (1988). Site faithfulness of waders away from the breeding grounds: how individual migration patterns are established. *Proc.. Int. Orn. Congr.* 19: 594–603.

Farner, D. S. (1955). *The annual stimulus for migration: experimental and physiologic aspects.* In: *Recent Studies in Avian Biology*(Ed. Wolfson, A.). University Illinois Press, Urbana.

Farnsworth, A., Gauthreaux, S. A., Jr & van Blaricom, D. (2004). A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. *J. Avian Biol.* 35: 365–9.

Fasola, M., Hafner, H., Prosper, J., van der Kooij, H. & Schogolev, I. V. (2000). Population changes in European herons in relation to African climate. *Ostrich* 71: 52–5.

Favero, M. & Becker, P. H. (2006). Effects of the North Atlantic Oscillation and El Niño Southern Oscillation on return rates, body mass and timing of migration of Common Terns *Sterna hirundo* breeding in Germany. In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 405–9

Feare, C. J. & Burham, S. (1978). Lack of nest site tenacity and mate fidelity in the Starling. *Bird Study* 25: 189–91.

Ferns, P. N. (1975). Feeding behaviour of autumn passage migrants in northeast Portugal. *Ringing & Migration* 1: 3–11.

Ferrer, M., de la Riva, M. & Castroviego, J. (1991). Electrocution of raptors on power lines in southwestern Spain. *J. Field Orn.* 62: 181–90.

Ferrer, M. & Janss, G. F. E. (Eds) (1999). *Birds and Power Lines. Collision, Electrocution and Breeding.* Quercus, Madrid.

Fiedler, W. (2003). *Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 21–38.

Fiedler, W. (2005). Ecomorphology of the external flight apparatus of Blackcaps *(Sylvia atricapilla)* with different migration behaviour. *Ann. N.Y. Acad. Sci.* 1046: 253–63.

Fiedler, W., Bairlein, F. & Koppen, U. (2004). *Using large-scale data from ringed birds for the investigation of effects of climate change on migrating birds: pitfalls and prospects.* In: *Birds and Climate Change. Adv. Ecol. Res.,* Volume 35. Elsevier, London, 35–49.

Figuerola, J. & Bertelero, A. (1998). Sex differences in the stopover ecology of Curlew Sandpipers *Calidris ferruginea* at a refuelling area during autumn migration. *Bird Study* 45: 3134–319.

Finlayson, J. C. (1980). The recurrence in winter quarters at Gibraltar of some scrub passerines. *Ringing & Migration* 3: 32–6.

Fischer, J. H., Munro, U. & Phillips, J. B. (2003). *Magnetic navigation by an avian migrant?* In: *Avian Migration* (Eds Berthold, P., Gwinner E. & Sonnenschein, E.). Springer-Verlag, Berlin, 423–32.

Fisher, H. I. (1971). Experiments on homing in Laysan Albatrosses (*Diomedea immutabilis). Condor* 73: 389–400.

Fitzgerald, T. M. & Taylor, P. D. (2008). Migratory orientation of juvenile Yellow- rumped Warblers *(Dendroica coronata)* following stopover: sources of variation and the importance of geographic origins. *Behav. Ecol. Sociobiol.* 62: 1499–1508.

Fletcher, K., Aebischer, N., Baines, D., Foster, R. & Hoodless, A. (2010). Experimental evidence that predator removal on moorlands can be used as a tool for bird conservation. *J. Appl. Ecol.* In press

Flood, B. L., Hudson, N. & Thomas, B. (2007). Essential guide to birds of the Isles of Scilly. Published by the authors, St Mary's, Scilly Isles.

Flood, R. L. (2009). 'All-dark' *Oceanodroma* storm-petrels in the Atlantic and neighbouring seas. *Brit. Birds* 102: 365–85.

Fogden, M. P. (1972). Pre-migratory dehydration in the Reed Warbler *Acrocephalus scirpaceus* and water as a factor limiting migratory range. *Ibis* 114: 548–52.

Forchhammer, M. C., Post, E. & Stenseth, N. C. (2002). North Atlantic Oscillation timing of long and short-distance migration. *J. Anim. Ecol.* 71: 1002–14.

Formosov, A. N. (1933). The crop of cedar nuts, invasions into Europe of the Siberian Nutcracker *(Nucifraga caryocatactes macrorhynchos* Brehm) and fluctuations in the numbers of the Squirrel *(Sciurus vulgaris* L.). *J. Anim. Ecol.* 2: 70–81.

Förschler, M. I., Förschler, L. & Dorka, U. (2006). Population fluctuations of Siskins *Carduelis spinus,* Common Crossbills *Loxia curvirostra,* and Citril Finches *Carduelis citrinella* in relationship to flowering intensity of Spruce *Picea abies. Ornis Fenn.* 83: 91–6.

Fowler, J. A., O'Kill, J. D. & Marshall, B. (1982). A retrap analysis of Storm Petrels tape-lured in Shetland. *Ringing & Migration* 4: 1–7.

Fox, A. D., Glahder, C. M. & Walsh, A. J. (2003). Spring migration routes and timing of Greenland White-fronted Geese—results from satellite telemetry. *Oikos* 103: 415–25.

Fox, A. D., Hilmarsson, J. Ó., Einarsson, O., Walsh, A. J., Boyd, H. & Kristiansen, J. N. (2002). Staging site fidelity of Greenland White-fronted Geese *Anser albifrons flavirostris* in Iceland. *Bird Study* 49: 42–9.

Francis, C. M. & Cooke, F. (1986). Differential timing of spring migration in Wood Warblers (Parulinae). *Auk* 103: 548–56.

Fransson, T. (1986). The migration and wintering area of Nordic Spotted Flycatcher *Muscícapa striata. Vår Fågelvarld* 45: 5–18.

Fransson, T. (1995). Timing and speed of migration in North and West European populations of *Sylvia* warblers. *J. Avian Biol.* 26: 39–48.

Fransson, T. (1998). A feeding experiment on migratory fuelling in Whitethroats *Sylvia communis*. *Anim. Behav.* 55: 153–62.

Fransson, T. & Jakobsson, S. (1998). Fat storage in male Willow Warblers in spring: do residents arrive lean or fat? *Auk* 115: 759–63.

Fransson, T., Jakobsson, S., Johansson, U. S., Kullberg, C., Lind, J. & Vallin, A. (2001). Bird migration—magnetic cues trigger extensive refuelling. *Nature* 414: 35–6.

Fransson, T., Jakobsson, S. & Kullberg, C. (2005). Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. *J. Avian Biol.* 36: 6–11.

Franz, D. (1988). Migration of the Penduline Tit *(Remiz pendulinus)* during the breeding period—range, frequency and ecological importance. *Vogelwelt* 109: 188–206.

Fraser, P. A. (1997). How many rarities are we missing? Weekend bias and length of stay revisited. *Brit. Birds* 90: 94–101.

Fraser, P. A. & Rogers, M. J. (2002). Report on scarce migrant birds in Britain in 2000. *Brit. Birds* 95: 606–30.

Fraser, P. A. & Rogers, M. J. (2004). Report on scarce migrant birds in Britain in 2002. *Brit. Birds* 97: 647–64.

Fraser, P. A. & Rogers, M. J. (2005). Report on scarce migrant birds in Britain in 2002. *Brit. Birds* 98: 73–88.

Fraser, P. A., Lansdown, P. G. & Rogers, M. J. (1999). Report on scarce migrant birds in Britain in 1997. *Brit. Birds* 92: 618–58.

Fry, C. H., Ash, J. S. & Ferguson-Lees, I. J. (1970). Spring weights of Palaearctic migrants at Lake Chad. *Ibis* 112: 58–82.

Fry, C. H., Ferguson-Lees, I. J. & Dowsett, R. J. (1972). Flight muscle hypertrophy and ecophysiological variation of Yellow Wagtail *Motacilla flava* races at Lake Chad. *J. Zool.* 167: 293–306.

Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R. & Bingman, V. P. (2006). Daytime naps in night-migrating birds: behavioural

adaptation to seasonal sleep deprivation in the Swainson's Thrush, *Catharus ustulatus*. *Anim. Behav.* 72: 951–8.

Fuller, M., Holt, D. & Schueck, L. (2003). *Snowy Owl movements: variation on a migration theme.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 359–66.

Galushin, V. M. (1974). Synchronous fluctuations in populations of some raptors and their prey. *Ibis* 116: 127–34.

Garvin, M. C., Szell, C. C. & Moore, F. R. (2006). Blood parasites of Nearctic-Neotropical birds during spring trans-gulf migration: impact on host body condition. *J. Parasitol.* 92: 990–6.

Gätke, H. (1895). *Heligoland as an Ornithological Observatory. The Result of Fifty Years Experience.* David Douglas, Edinburgh.

Gatter, W. (2000). *Vogelzug und Vogelbestände in Mitteleuropa.* AULA-Verlag, Wiebesteim.

Gauthier, G., Bêty, J. & Hobson, K. A. (2003). Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. *Ecology* 84: 3250–64.

Gauthier-Clerc, M., Lebarbenchon, C. & Thomas, F. (2007). Recent expansion of highly pathogenic avian influenza H_5N_1: a critical review. *Ibis* 149: 202–14.

Gauthreaux, S. A., Jr (1972). Behavioural responses of migrating birds to daylight and darkness: a direct visual study. *Wilson Bull.* 84: 136–48.

Gauthreaux, S. A., Jr (1978a). *Importance of daytime flights of nocturnal migrants: redetermined migration following displacement.* In: *Animal Migration, Navigation and Homing* (Eds Schmidt-Koenig, K. & Keeton, W. T.). Springer-Verlag, Berlin, 219–27.

Gauthreaux, S. A., Jr (1978b). *The ecological significance of behavioural dominance.* In: *Perspectives in Ornithology, Vol. 3* (eds P. P. G. Bateson & P. H. Klopfer). Plenum Press, New York, 17–54.

Gauthreaux, S. A., Jr (1991). The flight behaviour of migrating birds in changing wind fields: radar and visual analyses. *Amer. Zool.* 31: 187–204.

Gauthreaux, S. A., Jr (1999). *Neotropical migrants and the Gulf of Mexico: the view from aloft.* In: *Gatherings of Angels: Migrating Birds and Their Ecology*(Ed. Able, K. P.). Cornell University Press, Ithaca, NY, 27–47.

Gauthreaux, S. A., Jr, Belser, C. G. & van Blaricom, D. (2003). *Using a network of WSR-88D weather surveillance radars to define patterns of bird migration at large spatial scales.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 335–46.

Gibbons, D. W., Reid, J. B. & Chapman, R. A. (1993). *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T. & A. D. Poyser, London.

Gienapp, P., Leimu, R. & Merila, J. (2007). Responses to climate change in avian migration time—microevolution versus phenotypic plasticity. *Clim. Res.* 35: 25–35.

Gifford, C. E. & Odum, E. P. (1965). Bioenergetics of lipid deposition in the Bobolink, a trans-equatorial migrant. *Condor* 67: 383–403.

Gill, J. A., Clark, J., Clark, N. & Sutherland, W. (1995). Sex differences in the migration, moult and wintering areas of British-ringed Ruff. *Ringing & Migration* 16: 159–67.

Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W. & Sutherland, W. (2001). The buffer effect and large-scale regulation in migratory birds. *Nature* 412: 436–8.

Gill, R. E., Piersma, T., Hufford, G., Servrancky, R. & Riegen, A. (2005). Crossing the ultimate ecological barrier: evidence for an 11,000 km-long nonstop flight from Alaska to New Zealand and eastern Australia by Bar-tailed Godwits. *Condor* 107: 1–20.

Gill, R. E., Jr, Tibbits, T. L., Douglas, D. C., Handel, C. M., Mulcahy, B. J., Battley, P. F. & Piersma, T. (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc.. R. Soc. B* 276: 447–57.

Gilroy, J. J. & Lees, A. C. (2003). Vagrancy theories: are autumn vagrants really reverse migrants? *Brit. Birds* 96: 427–38.

Gilyazov, A. & Sparks, T. (2002). Change in the timing of migration of common birds at the Lapland nature reserve (Kola Peninsula, Russia) during 1931–1999. *Avian Ecol. Behav.* 8: 35–47.

Girard, O. (2006). *Anatidae wintering in the Inner Niger Delta, Mali.* In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 228–9.

Gladwin, T. W. (1963). Increase in the weights of Acrocephali. *Bird Migration* 2: 319–24.

Glutz von Blotzheim, U. N. (1966). Das Auftreten des Seidenschwanzes *Bombycilla garrulus* in der Schweiz und die von 1901 bis 1965/66 West und Mitteleuropa erreichenden Invasionen. *Orn. Beob.* 63: 93–146.

Glutz von Blotzheim, U. N. & Bauer, K. M. (1997). *Handbuch der Vögel Mitteleuropas, Band 4, II Passeriformes, Fringillidae (5 Teil).* Akademische Verlagsgesellschaft, Wiesbaden.

Glutz von Blotzheim, U. N., Bauer, K. M. & Bezzel, E. (1975). *Handbuch der Vögel Mitteleuropas. Band 6 (Charadriiformes).* Akademische Verlagsgesellschaft, Wiesbaden.

Glutz von Blotzheim, U. N., Bauer, K. M. & Bezzel, E. (1977). *Handbuch der Vögel Mitteleuropas. Band 7 (Charadriiformes).* Akademische Verlagsgesellschaft, Wiesbaden.

Goodenough, A., Elliot, S. L. & Hart, A. G. (2009). The challenges of conservation for declining migrants: are reserve-based initiatives during the breeding season appropriate for the Pied Flycatcher *Ficedula hypoleuca? Ibis* 151: 429–39.

Gordo, O. & Sanz, J. J. (2008). The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *J. Orn.* 149: 199–210.

Gorney, E. & Yom-Tov, Y. (1994). Fat, hydration condition, and moult of Steppe Buzzards *Buteo buteo vulpinus* on spring migration. *Ibis* 136: 185–92.

Goss-Custard, J. D., Clarke, R. T. & Le V. dit. Durell, S. E. A. (1984). Rates of food intake and aggression of Oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe Estuary. *J. Anim. Ecol.* 53: 233–45.

Goss-Custard, J. D., Le V. dit. Durell, S. E. A., Sitters, H. P. & Swinfen, R. (1982). Age-structure and survival of a wintering population of Oystercatchers. *Bird Study* 29: 83–98.

Götmark, F. (1982). Irruptive breeding of the Redpoll, *Carduelis flammea,* in south Sweden in 1975. *Vår Fågelvarld* 41: 315–22.

Goudie, A. S. & Middleton, N. J. (2006). *Desert Dust in the Global System.* Springer-Verlag, Berlin.

Green, M. (2004). Flying with the wind—spring migration of Arctic-breeding waders and geese over south Sweden. *Ardea* 92: 145–59.

Green, M. & Alerstam, T. (2000). Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. *J. Avian Biol.* 31: 215–25.

Green, M., Alerstam, T., Clausen, P., Drent, R. & Ebbinge, B. S. (2002). Dark-bellied Brent Geese *Branta bernicla bernicla,* as recorded by satellite telemetry, do not minimise flight distance during spring migration. *Ibis* 144: 106–21.

Green, R. E. (1999). Survival and dispersal of male Corncrakes in a threatened population. *Bird Study* (suppl. 46): 218–29.

Green, R. E., Tyler, G. A., Stowe, T. J. & Newton, A. V. (1997). A simulation model of the effect of mowing agricultural grassland

on the breeding success of the Corncrake *Crex crex*. *J. Zool. Lond.* 243: 81–115.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140–62.

Greenwood, P. J., Harvey, P. H. & Perrins, C. M. (1978). Inbreeding and dispersal in the Great Tit. *Nature* 271: 52–4.

Grenquist, P. (1947). Über die Biologie des Hakengimpels. *Orn. Fenn.* 24: 1–10.

Grote, H. (1937). Der sibirische Hakengimpel *(Pinicola enucleator stschur* Port.) in Deutschland. *Orn. Monatsber.* 45: 83–5.

Grubb, T. G., Bowerman, W. W. & Howey, P. W. (1994). *Tracking local and seasonal movements of wintering Bald Eagles* Haliaeetus leucocephalus. In: *Raptor Conservation Today* (Eds Meyburg, B.-U. & Chancellor, R. D.). Pica Press, London, 347–58.

Gudmundsson, A. G. & Lindstrom, Å. (1992). Spring migration of Sanderlings *Calidris alba* through SW Iceland—where from and where to. *Ardea* 80: 315–26.

Gudmundsson, A. G. & Sandberg, R. (2000). Sanderlings *(Calidris alba)* have a magnetic compass: orientation experiments during spring migration in Iceland. *J. Exp. Biol.* 203: 3137–44.

Gudmundsson, G. A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. & Åkesson, S. (1995). Examining the limits of flight and orientation performance: satellite tracking of Brent Geese migrating across the Greenland ice cap. Proc.. *R. Soc. Lond. B* 261: 73–9.

Gudmundsson, G. A., Lindström, Å. & Alerstam, T. (1991). Optional fat loads and long-distance flights by migrating Knots *Calidris canutus,* Sanderlings *C. alba* and Turnstones *A. interpres. Ibis* 133: 140–52.

Guilford, T. C., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S. & Perrins, C. M. (2008).

GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150: 462–73.

Guilford, T. C., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., Collett, M., Freeman, R. & Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx Shearwater *Puffinus puffinus:* insights from machine learning. *Proc.. R. Soc. B* 276: 1215–23.

Guillemain, M., Elmberg, J., Arzel, C., Johnson, A. R. & Simon, G. (2008). The income-capital breeding dichotomy revisited: late winter body condition is related to breeding success in an income breeder. *Ibis* 150: 172–6.

Gunnarsson, T. G., Gill, J. A., Atkinson, P. W., Gelinaud, G., Potts, P. M., Croger, R. E., Gudmundsson, G. A., Appleton, G. F. & Sutherland, W. J. (2006). Population-scale drivers of individual arrival times in migratory birds. *J. Anim. Ecol.* 75: 1119–27.

Gunnarsson, T. G., Gill, J. A., Petersen, A., Appleton, G. F. & Sutherland, W. J. (2005). A double buffer effect in a migratory shorebird population. *J. Anim. Ecol.* 74: 965–71.

Gunnarsson, T. G., Gill, J. A., Sigurbjornsson, T. & Sutherland, W. J. (2004). Pair bonds: arrival synchrony in migratory birds. *Nature* 431: 646.

Gustafsson, L. (1988). Inter- and intraspecific competition for nest-holes in a population of the Collared Flycatcher *Ficedula albicollis. Ibis* 130: 11–15.

Gwinner, E. (1968). Circannuale Periodik als Grundlage des jahreszeitlichen Funktionswandels bei Zugvögeln. Untersuchungen am Fitis *(Phylloscopus trochilus)* und am Waldlaubsänger (P. *sibilatrix). J. Orn.* 109: 70–95.

Gwinner, E. (1972). Adaptive functions of circannual rhythms in warblers. *Proc.. Int. Orn. Congr.* 15: 218–36.

Gwinner, E. (1981). *Circannual rhythms: their dependence on the circadian system.* In: *Biological Clocks in Seasonal Reproductive Cycles* (Eds Follett, B. K. & Follett, D. E.). Wright Publishers, Bristol, 153–69.

Gwinner, E. (1986). *Circannual Rhythms.* Springer-Verlag, Berlin.

Gwinner, E. (1990). *Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 257–67.

Gwinner, E. (1996). Circadian clocks in avian reproduction and migration. *Ibis* 138: 47–63.

Gwinner, E., Biebach, H. & von Kries, I. (1985). Food availability affects migratory restlessness in caged Garden Warblers *(Sylvia borin). Naturwissenschaften* 72: 51–2.

Gwinner, E. & Helm, B. (2003). *Circannual and circadian contributions to the timing of avian migration.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 81–95.

Gwinner, E. & Wiltschko, W. (1980). Circannual changes in migratory orientation of the Garden Warbler, *Sylvia borin. Behav. Ecol. Sociobiol.* 7: 73–8.

Haapanen, A. (1966). Bird fauna of Finnish forests in relation to forest succession. *Ann. Zool. Fenn.* 3: 176–200.

Haas, W. & Beck, P. (1979). Zum Frühjahrszug paläarktischer Vögel über die westliche Sahara. *J. Orn.* 120: 237–46.

Hagemeijer, W. J. M. & Blair, M. J. (Eds) (1997). *The EBCC Atlas of European Breeding Birds. Their Distribution and Abundance.* T. & A. D. Poyser, London.

Hagner, S. (1965). Cone crop fluctuations in Scots Pine and Norway Spruce. *Stud. For. Svec.* 33: 2–21.

Haila, Y., Tiainen, J. & Vepsäläinen, K. (1986). Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland. *Ornis Fenn.* 63: 1–9.

Håke, M., Kjellén, N. & Alerstam, T. (2003). Age-dependent migration strategy in Honey Buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103: 385–96.

Hall, K. (2008). Visible migration of Bitterns. *Brit. Birds* 101: 691–4.

Hall, K. S. S. & Fransson, T. (2001).Wing moult in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis. Ibis* 143: 580–6.

Halley, D. J., Harris, M. P. & Wanless, S. (1995). Colony attendance patterns and recruitment in immature Common Murres *(Uria aalge). Auk* 112: 947–57.

Hamilton, W. J. (1962). Does the Bobolink navigate? *Wilson Bull.* 74: 357–66.

Hansen, L. (1954). Birds killed at lights in Denmark 1886–1939. *Vidensk. Medd. fra Dansk naturh. Foren.* 116: 269–368.

Harris, M. P. (1966). Breeding biology of the Manx Shearwater *Puffinus puffinus. Ibis* 108: 17–33.

Harris, M. P. (1970). Abnormal migration and hybridisation of *Larus argentatus* and *L. fuscus* after interspecies fostering experiments. *Ibis* 112: 488–98.

Harris, M. P. (1984). *The Puffin.* T. & A. D. Poyser, Calton.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V. & Brown, C. J. (1997). *The Atlas of Southern African Birds.* Volumes 1 & 2. Birdlife South Africa, Johannesburg.

Harrop, H. & Fray, R. (2008). Two-barred Crossbills in the Northern Isles in July and August 2008. *Birding World* 21 (8): 329–39.

Harrop, H. R., Mavor, R. & Ellis, P. M. (2008). Olive-tree Warbler in Shetland: new to Britain. *Brit. Birds* 101: 82–8.

Harvey, P. H., Greenwood, P. J., Campbell, B. & Stenning, M. J. (1984). Breeding dispersal of the Pied Flycatcher *(Ficedula hypoleuca). J. Anim. Ecol.* 53: 727–36.

Harvey, P. V. & Riddiford, N. (1996). An uneven sex ratio of migrant Long-eared Owls. *Ringing & Migration* 11: 132–5.

Harvie-Brown, J. A. & Cordeaux, J. (1880). Report on the migration of birds in the autumn of 1879. *Zoologist* 38: 161–204.

Hasselquist, D. (1998). Polygyny in Great Reed Warblers: a long-term study of factors contributing to male fitness. *Ecology* 79: 2376–90.

Hebrard, J. J. (1971). The nightly initiation of passerine migration in spring, a direct visual study. *Ibis* 113: 8–18.

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* 342: 353–61.

Hedenström, A. (2004). Migration and morphometrics of Temminck's Stint *Calidris temminckii* at Ottenby, southern Sweden. *Ringing & Migration* 22: 51–8.

Hedenström, A. & Alerstam, T. (1998). How fast can birds migrate? *J. Avian Biol.* 29: 424–32.

Hedenström, A. & Pettersson, J. (1987). Migration routes and wintering areas of Willow Warblers *Phylloscopus trochilus* ringed in Fennoscandia. *Ornis Scand.* 64: 137–43.

Hedenström, A., Alerstam, T., Green, M. & Gudmundsson, G. A. (2005). Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behav. Ecol. Sociobiol.* 52: 308–17.

Heitmeyer, M. E. (1988). Body-composition of female Mallards in winter in relation to annual cycle events. *Condor* 90: 669–80.

Helbig, A. J. (1991a). Dusk orientation of migratory European Robins, *Erithacus rubecula*— the role of sun-related directional information. *Anim. Behav.* 41: 313–22.

Helbig, A. J. (1991b). SE migrating and SW migrating Blackcap *(Sylvia atricapilla)* populations in Central Europe: orientation of birds in the contact zone. *J. Evol. Biol.* 4: 657–70.

Helbig, A. (1996). Genetic basis, mode of inheritance and evolutionary changes of migratory direction in Palearctic warblers (Aves: Sylviidae). *J. Exp. Biol.* 199: 49–55.

Helbig, A. J., Berthold, P. & Wiltschko, W. (1989). Migratory orientation of Blackcaps *(Sylvia atricapilla):* population-specific shifts in direction during the autumn. *Ethology* 82: 307–315.

Helbig, A. J. & Wiltschko, W. (1989). The skylight polarization patterns at dusk affect the orientation behavior of Blackcaps, *Sylvia atricapilla. Naturwissenschaften* 76: 227–9.

Helm, B. (2003). Seasonal timing in different environments: comparative studies in Stonechats. PhD thesis, Ludwig-Maximilian University, Munich.

Helm, B. & Gwinner, E. (2006). Migratory restlessness in an equatorial non-migratory bird. *PLoS Biol.* 4: 611–14.

Helm, B., Gwinner, E. & Trost, L. (2005). Flexible seasonal timing and migratory behaviour: results from Stonechat breeding programs. *Ann. N.Y. Acad. Sci.* 1046: 216–27.

Helms, C. W. (1963). The annual cycle and Zugunruhe in birds. *Proc.. Int. Orn. Congr.* 13: 925–39.

Hémon, Y. A., Saint-Jalme, M. & Guyomarc'h, J. C. (1988). Structure et fonctionnement des populations reproductrices 'français' de cailles des blé. *Bull. Mensuel de l'Office National de la Chasse* 127: 29–32.

Henderson, I., Holt, C. & Vickery, J. (2007). National and regional patterns of habitat association with foraging Barn

Swallows *Hirundo rustica* in the UK. *Bird Study* 54: 371–7.

Henderson, I. G., Fuller, R. J., Conway, G. J. & Gough, S. J. (2004). Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study* 51: 12–19.

Hengeveld, R. (1993). What to do about the North American invasion by the Collared Dove? *J. Field Orn.* 64: 477–89.

Henny, C. J. (1973). Drought displaced movement of North American Pintails into Siberia. *J. Wildl. Manage.* 37: 23–9.

Hering, J. & Alfrey, P. (2006). Die Azoren als Rettungsanker für verdriftete nearktische Vogelarten—Herbst 2005. *Limicola* 20: 65–90.

Herremans, M. (1988). Measurements of moult of irruptive Common Crossbills *(Loxia curvirostra curvirostra)* in central Belgium. *Le Gerfaut* 78: 243–60.

Herremans, M. (1993). Seasonal dynamics in sub-Kalahari bird communities with emphasis on migrants. *Proc.. Pan-Afr. Orn. Congr.* 7: 555–664.

Herremans, M. (1994). Fifteen years of migrant phenology records in Botswana. A summary and prospects. *Babbler* 28: 47–68.

Herremans, M. (1998). Strategies, punctuality of arrival and ranges of migrants in the Kalahari basin, Botswana. *Ibis* 140: 585–90.

Herrera, C. M. (1978). Ecological correlates of residence and non-residence in a Mediterranean bird community. *J. Anim. Ecol.* 47: 871–90.

Herrera, C. M. (1981). Fruit food of Robins wintering in southern Spanish Mediterranean scrubland. *Bird Study* 28: 115–22.

Herrera, C. M. & Rodriguez, M. (1979). Year-to-year site constancy among three passerine species wintering at a southern Spanish locality. *Ringing & Migration* 2: 160.

Hewitt, G. M. (2000). The genetic legacy of the Quaternary ice ages. *Nature* 405: 907–13.

Hewson, C. M., Fuller, R. J. & Day, C. (2005). An investigation of habitat occupancy by the Nightingale *Luscinia megarhynchos* with respect to population change at the edge of its range in England. *J. Orn.* 146: 244–8.

Hewson, C. M., Amar, A., Lindsell, J. A., Thewlis, R. M., Butler, S., Smith, K. & Fuller, R. J. (2007). Recent changes in bird populations of broad-leaved woodland. *Ibis* 149 (suppl.): 14–28.

Hickling, R. A. O. (1984). Lesser Black-backed Gull numbers at British inland roosts in 1979–80. *Bird Study* 31: 157–60.

Hildén, O. & Saurola, P. (1982). Speed of autumn migration of birds ringed in Finland. *Ornis Fenn.* 59: 140–3.

Hjort, C., Pettersson, J., Lindström, Å. & King, J. M. (1996). Fuel deposition and potential flight ranges of Blackcaps *Sylvia atricapilla* and Whitethroats *S. communis* on spring migration in the Gambia. *Ornis Svecica* 6: 137–44.

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314–26.

Hockey, P. A. R. (2000). Patterns and correlation of bird migrations in sub-Saharan Africa. *Emu* 100: 401–17.

Hockey, P. A. R., Turpie, J. K. & Velásquez, C. R. (1998). What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *J. Avian Biol.* 29: 325–30.

Hogstad, O. (1967). Density fluctuations of *Carduelis spinus* in relation to the cone crops of Norway Spruce. *Sterna* 7: 255–9.

Hogstad, O. (2000). Fluctuation of a breeding population of Brambling *Fringilla montifringilla* during 33 years in a subalpine birch forest. *Ornis Fenn.* 77: 97–103.

Holberton, R. L. (1993). An endogenous basis for differential migration in the Dark-eyed Junco. *Condor* 95: 580–7.

Holland, P. K. & Yalden, D. W. (1991). Population dynamics of Common Sandpipers *Actitis hypoleucos* breeding along an upland river system. *Bird Study* 38: 151–9.

Hollyer, J. N. (1970). The invasion of Nutcrackers in autumn 1968. *Brit. Birds* 63: 353–73.

Hötker, H. (2002). Arrival of Pied Avocets *Recurvirostra avosetta* at the breeding site: effects of winter quarters and consequences for reproductive success. *Ardea* 90: 379–87.

Hübner, C. E. (2006). The importance of pre-breeding sites in the Arctic Barnacle Goose *Branta leucopsis. Ardea* 94: 701–13.

Huin, N. & Sparks, T. H. (1998). Arrival and progression of the Swallow *Hirundo rustica* through Britain. *Bird Study* 45: 361–70.

Huin, N. & Sparks, T. H. (2000). Spring arrival patterns of the Cuckoo *Cuculus canorus,* Nightingale *Luscinia megarhynchos* and Spotted Flycatcher *Muscicapa striata. Bird Study* 47: 22–31.

Hüppop, O. & Hüppop, K. (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proc.. R. Soc. Lond. B* 270: 233–40.

Hüppop, O. & Winkel, W. (2006). Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *J. Orn.* 147: 344–53.

Huttenen, M. J. (2004). Autumn migration of thrushes over eastern Finland: a comparison of visible migration and ringing recovery patterns. *Ringing & Migration* 22: 13–23.

Imber, M. J. & Lovegrove, T. G. (1982). Leach's Storm Petrels *(Oceanodroma l. leucorhoa)* prospecting for nest sites at the Chatham Islands. *Notornis* 29: 101–8.

Irwin, D. E., Alstrom, P., Olsson, U. & Benowitz-Friederichs, Z. M. (2001). Cryptospecies in the genus *Phylloscopus* (Old World leaf warblers). *Ibis* 143: 233–47.

Izhaki, I. & Maitav, A. (1998a). Blackcaps *Sylvia atricapilla* stopping over at the desert edge; physiological state and flight-range estimates. *Ibis* 140: 223–33.

Izhaki, I. & Maitav, A. (1998b). Blackcaps stopping over at the desert edge; inter- and intra-sexual differences in spring and autumn migration. *Ibis* 140: 234–43.

Izhaki, I. & Safriel, U. N. (1989). Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54: 23–32.

Jackson, D. B. (1994). Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, UK. *Ibis* 136: 463–73.

Jakober, H. & Stauber, W. (1983). Phenology of a population of Red-backed Shrike *(Lanius collurio)*. *J. Orn.* 124: 29–46.

Järvinen, A. (1987). Key-factor analyses of two Finnish hole-nesting passerines: comparisons between species and regions. *Ann. Zool. Fenn.* 24: 275–80.

Jehl, J. R. (1990). *Aspects of the molt migration.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 102–13.

Jenkins, D. & Watson, A. (2000). Dates of first arrival and song of birds during 1974–99 in mid-Deeside, Scotland. *Bird Study* 47: 249–51.

Jenni, L. (1987). Mass concentrations of Bramblings *Fringilla montifringilla* in Europe 1900–1983: their dependence upon beech mast and the effect of snow cover. *Ornis Scand.* 18: 84–94.

Jenni, L. & Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *J. Avian. Biol.* 29: 521–8.

Jenni, L. & Kéri, M. (2003). Timing of autumn bird migration under climate change: advances in longdistance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. B* 270: 1467–72.

Jenni, L. & Neuschulz, F. (1985). Schweizerische Ringfunds von Bergfinken *Fringilla montifringilla:* ein Beitrag zum Problem der Masseneinfluge. Orn. *Beob.* 82: 85–106.

Jenni, L. & Winkler, R. (1994). *Moult and Ageing of European Passerines.* Academic Press, London.

Jenni-Eiermann, S. & Jenni, L. (1996). Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. *Func. Ecol.* 10: 62–72.

Jenni-Eiermann, S. & Jenni, L. (2003). *Interdependence of flight and stopover in migrating birds: possible effects of metabolic constraints during refuelling on flight metabolism.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 293–306.

John, A. W. G. & Roskell, J. (1985). Jay movements in autumn 1983. *Brit. Birds* 78: 611–37.

Johnson, C. & Minton, C. D. T. (1980). The primary moult of the Dublin *Calidris alpina* at the Wash. *Ornis Scand.* 11: 190–5.

Johnson, D. H. & Grier, J. W. (1988). Determinants of breeding distributions of ducks. *Wildlife Monographs* 100: 1–37.

Johnson, S. R. (1995). Immigration in a small population of Snow Geese. *Auk* 112: 731–6.

Johnston, V. H. & Ryder, J. P. (1987). Divorce in larids: a review. *Colonial Waterbirds* 10: 16–26.

Jones, P. (1985). *The migration strategies of Palaearctic passerines in West Africa.* In: *Migratory Birds: Problems and Prospects in Africa* (Eds MacDonald, A. & Goriup, P.). International Council for Bird Preservation, Cambridge, 9–21.

Jones, P. J. (1995). Migration strategies of Palaearctic passerines in Africa: an overview. Isr. *J. Zool.* 41: 393–406.

Jones, P. (1999). *Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change.* In: *Dynamics of Tropical Communities* (Eds Newberry, D. M., Prins, H. H. T. & Brown, N. D.). Blackwells, Oxford, 421–47.

Jones, P., Vickery, J., Holt, S. & Cresswell, W. (1996). A preliminary assessment of some factors influencing the density and distribution of Palaearctic passerine migrants in the Sahel zone of West Africa. *Bird Study* 43: 73–84

Jordano, P. (1987). Frugivory, external morphology and digestive system in Mediterranean sylviid warblers, *Sylvia* spp. *Ibis* 129: 175–89.

Jukema, J. & Piersma, T. (1987). Special moult of breast and belly feathers during breeding in Golden Plovers *Pluvialis apricaria. Ornis Scand.* 18: 157–62.

Kaiser, A. (1999). Stopover strategies in birds: a review of methods for estimating stopover length. *Bird Study* 46 (suppl.): 299–308.

Kanyamibwa, S., Bairlein, F. & Schierer, A. (1993). Comparison of survival rates between populations of the White Stork *Ciconia ciconia* in central Europe. *Ornis Scand.* 24: 297–302.

Karasov, W. H. & Pinshow, B. (2000). Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. *Physiol. Biochem. Zool.* 73: 335–43.

Keeton, W. T. (1980). Avian orientation and navigation: new developments in an old mystery. *Proc.. Int. Orn. Congr.* 17: 137–57.

Keller, L. F., Årcese, P., Smith, J. N. M., Hochachka, W. M. & Stearns, S. (1994). Selection against inbred Song Sparrows during a natural bottleneck. *Nature* 372: 356–7.

Kelsey, M. G. (1989). A comparison of the song and territorial behaviour of a long-distance migrant, the Marsh Warbler *Acrocephalus palustris,* in summer and winter. *Ibis* 131: 403–14.

Kemp, A. (2001). Concentration of non-breeding Lesser Spotted Eagles *Aquila pomarina* at abundant food: a breeding colony of Red-billed Queleas *Quelea quelea* in the Kruger National Park, South Africa. *Acta Ornithol. Jena* 4: 325–9.

Kenyon, K. W. & Rice, D. W. (1958). Homing of Laysan Albatrosses. *Condor* 60: 3–6.

Kerlinger, P. (1989). *Flight Strategies of Migrating Hawks.* University of Chicago Press, Chicago.

Kerlinger, P. & Moore, F. R. (1989). Atmospheric structure and avian migration. *Current Orn.* 6: 109–42.

Ketterson, E. D. & Nolan, V. (1983). The evolution of differential bird migration. *Current Orn.* 1: 357–402.

King, J. R. (1961). The bioenergetics of vernal premigratory fat deposition in the White-crowned Sparrow. *Condor* 63: 128–42.

King, J. R. (1972). Adaptive periodic fat storage in birds. *Proc.. Int. Orn. Congr.* 15: 200–17.

King, J. R. & Farner, D. S. (1965). Studies of fat deposition in migratory birds. *Ann. N.Y. Acad. Sci.* 131: 422–40.

Kinnear, N. B. (1938). William Eagle Clarke. *Ibis* 1938: 548–52.

Kjellén, N. (1992). Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scand.* 23: 420–34.

Kjellén, N. (1994). Differences in age and sex ratio among migrating and wintering raptors in southern Sweden. *Auk* 111: 274–84.

Kjellén, N. (2008). Falsterbo Bird Observatory website at www.falsterbofagelstation.se.

Kjellén, N., Håke, M. & Alerstam, T. (2001). Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *J. Avian Biol.* 32: 57–67.

Kjellén, N. & Roos, G. (2000). Population trends in Swedish raptors demonstrated by migration counts at Falsterbo, Sweden, 1942–97. *Bird Study* 47: 195–211.

Klaassen, M. (1995). Water and energy limitations on flight range. *Auk* 112: 260–2.

Klaassen, M. (2003). *Relationships between migration and breeding strategies in Arctic breeding birds.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 237–49.

Klaassen, M. (2004). May dehydration risk govern longdistance migratory behaviour. *J. Avian Biol.* 35: 4–6.

Klaassen, M., Beekman, J. H., Kontiokorpi, J., Mulder, R. J. W. & Nolet, B. A. (2004). Migrating swans profit from favourable changes in wind conditions at low altitude. *J. Orn.*145: 142–51.

Klaassen, M. & Biebach, H. (2000). Flight altitude of trans-Sahara migrants in autumn: a comparison of radar observations with predictions from meteorological conditions and water and energy balance models. *J. Avian Biol.* 31: 47–55.

Klaassen, M., Kvist, A. & Lindström, Å. (1999). How body water and fuel stores affect long-distance flight in migrating birds. *Proc.. Int. Orn. Congr.* 22: 1450–67.

Klaassen, M., Lindström, Å., Meltofte, H. & Piersma, T. (2001). Arctic waders are not capital breeders. *Nature* 413: 794.

Klaassen, M., Lindström, Å. & Zijlatra, R. (1997). Composition of fuel stores and digestive limitations to fuel deposition rate in the long-distance migratory Thrush-Nightingale *Luscinia luscinia. Physiol. Zool.* 70: 125–33.

Klein, N. K. & Brown, W. M. (1994). Intraspecific molecular phylogeny in the Yellow Warbler *(Dendroica petechia),* and implications for avian biogeography in the West Indies. *Evolution* 48: 1914–32.

Klomp, N. I. & Furness, R. W. (1992). The dispersal and philopatry of Great Skuas from Foula, Shetland. *Ringing & Migration* 13: 73–82.

Köenig, W. D. & Knops, J. M. H. (1998). Scale of mast seeding and tree-ring growth. *Nature* 396: 225–6.

Köenig, W. D. & Knops, J. M. H. (2000). Patterns of annual seed production by northern hemisphere trees: a global perspective. *Amer. Nat.* 155: 59–69.

Köenig, W. D. & Knops, J. M. H. (2001). Seed crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.* 70: 609–20.

Kolunen, H. & Peiponen, V. A. (1991). Delayed autumn migration of the Swift *Apus apus* from Finland in 1986. *Ornis Fenn.* 68: 81–92.

Korpimäki, E. & Norrdahl, K. (1991). Numerical and functional responses of Kestrels, Short-eared Owls and Long-eared Owls to vole densities. *Ecology* 72: 814–25.

Korpimäki, E., Lagerström, M. & Saurola, P. (1987). Field evidence for nomadism in Tengmalm's Owls *Aegolius funereus. Ornis Scand.* 18: 1–4

Korschen, C. E. (1977). Breeding stress of female Eiders in Maine. *J. Wildl. Manage.* 41: 360–73.

Kosarev, V. (1999). Summer movements of Starlings *Sturmus vulgaris* on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 30: 99–109.

Kramer, G. (1951). Eine Neue Methode zur Erforschung der Zugorientierung und die bisher damit erzeilten Ergibnisse. *Proc.*.

Int. Orn Congr. 10: 269–80.

Kramer, G. (1952). Experiments on bird orientation. *Ibis* 94: 265–85.

Kramer, G. (1957). Experiments on bird orientation and their interpretation. *Ibis* 99: 196–227.

Krapu, G. (1981). The role of nutrient reserves in Mallard reproduction. *Auk* 98: 29–38.

Krapu, G. L., Eldridge, J. L., Gratto-Trevor, C. L. & Buhl, D. A. (2006). Fat dynamics of arctic-nesting sandpipers during spring in mid-continental North America. *Auk* 123: 323–34

Krapu, G. L., Iverson, G. C., Reinecke, K. J. & Boise, C. M. (1985). Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. *Auk* 102: 362–8.

Kress, S. W. & Nettleship, D. N. (1988). Re-establishment of Atlantic Puffins *(Fratercula arctica)* at a former breeding site in the Gulf of Maine. *J. Field Orn.* 59: 161–70.

Kullberg, C., Fransson, T. & Jakobsson, S. (1996). Impaired predator evasion in fat Blackcaps *(Sylvia atricapilla)*. *Proc.. R. Soc. Lond. B* 263: 1671–5.

Kullberg, C., Lind, J., Fransson, T., Jakobsson, S. & Vallin, A. (2003). Magnetic cues and time of season affect fuel deposition in migratory Thrush Nightingales *(Luscinia luscinia)*. *Proc.. R. Soc. Lond. B* 270: 373–8.

Kuyt, E. (1992). Aerial radio-tracking of Whooping Cranes migrating between Wood Buffalo National Park and Aransas National Wildlife Refuge, 1981–4. Canadian Wildlife Service, occasional paper no. 74: 1–53.

Kvist, A. & Lindström, Å. (2000). Maximum daily energy intake: it takes time to lift the metabolic ceiling. *Physiol. Biochem. Zool.* 73: 30–6.

Kvist, A. & Lindström, Å. (2003). Gluttony in migratory waders—unprecedented energy assimilation rates in vertebrates. *Oikos* 103: 397–402.

Lack, D. (1933). Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *J. Anim. Ecol.* 2: 239–62.

Lack, D. (1954). *The Natural Regulation of Animal Numbers.* Oxford University Press, Oxford.

Lack, D. (1956). *Swifts in a Tower.* Methuen, London.

Lack, D. (1959). Some British pioneers in ornithological research, 1859–1939. *Ibis* 101: 71–81.

Lack, D. (1960). The influence of weather on passerine migration. A review. *Auk* 77: 171–209.

Lack, D. (1963). Migration across the southern North Sea studied by radar. Part 5. Movements in August, winter and spring, and conclusion. *Ibis* 105: 461–92.

Lack, P. C. (1983). The movements of Palaearctic landbird migrants in Tsavo East National Park, Kenya. *J. Anim. Ecol.* 52: 513–24.

Lack, P. C. (1986a). Ecological correlates of migrants and residents in a tropical African savanna. *Ardea* 74: 111–19.

Lack, P. C. (1986b). *The Atlas of Wintering Birds in Britain and Ireland.* T. & A. D. Poyser, Calton.

Lack, P. C. (1987). The structural and seasonal dynamics of the bird community in Tsavo East National Park. *Ostrich* 58: 9–23.

Lack, P. C. (1990). *Palaearctic–African systems.* In: *Biogeography and Ecology of Forest Bird Communities* (Ed. Keast, A.). SPB Academic Publishing, The Hague, Netherlands, 345–56.

Landys, M. M., Piersma, T., Vesser, G. H., Jukema, J. & Wijker, A. (2000). Water balance during real and simulated long-distance migratory flight in the Bartailed Godwit. *Condor* 102: 645–52.

Langston, R. H. W., Wotton, S. R., Conway, G. J., Wright, L. J., Mallord, J. W., Currie, F. A., Drewitt, A. L., Grice, P. V., Hoccom, D. G. & Symes, N. (2007). Nightjar *Caprimulgus europaeus* and Woodlark *Lullula arborea*–recovering species in Britain? *Ibis* 149: 250–60.

Lank, D. B. & Ydenberg, R. C. (2003). Death and danger at migratory stopovers: problems with 'predation risk'. *J. Avian Biol.* 34: 225–8.

Lanner, R. M. (1996). *Made for Each Other. A Symbiosis of Birds and Pines*.Oxford University Press, Oxford.

Larson, D. L. & Bock, C. E. (1986). Eruptions of some North American boreal seed-eating birds, 1901–1980. *Ibis* 128: 137–140.

Larson, T. & Tombre, I. (1989). Cyclic irruptions of Two-barred Crossbills in Scandinavia. *Fauna Norv. Ser. C Cinclus* 12: 3–10.

Larsson, K., Forslund, P., Gustafsson, L. & Ebbinge, B. S. (1988). From the high arctic to the Baltic: the successful establishment of a Barnacle Goose *Branta leucopsis* population on Gotland, Sweden. *Ornis Scand.* 19: 182–9.

Lavée, D., Safriel, U. N. & Meilijson, I. (1991). For how long do trans-Saharan migrants stop at an oasis? *Ornis Scand.* 22: 33–44.

Lehikoinen, E,. Sparks, T. H. & Zalakevicius, M. (2004). Arrival and departure dates. In: 'Birds and climate change'. *Advances in Ecological Research* 35: 1–28

Leisler, B. (1992). Habitat selection and coexistence of migrants and Afrotropical residents. *Ibis* 134 (suppl. 1): 77–82.

Leisler, B. & Winkler, H. (2003). *Morphological consequences of migration in passerines.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 175–86.

Lensink, R., van den Bijtel, H. J. V. & Schols, R. M. (1986). Invasion of Redpolls *Carduelis flammea* in the Netherlands in 1986.

Limosa 62: 1–10.

Leshem, Y. & Yom-Tov, Y. (1996a). The magnitude and timing of migration by soaring raptors, pelicans and storks over Israel. *Ibis* 138: 188–203.

Leshem, Y. & Yom-Tov, Y. (1996b). The use of thermals by soaring migrants in Israel. *Ibis* 138: 667–74.

Lid, G. (1977). Fugler brennes ihjel av gassflaminer i Nordsjøen. *Fauna* 30: 185–90.

Liechti, F. (2006). Birds: blowin by the wind? *J. Orn.* 147: 202–11.

Liechti, F. & Bruderer, B. (1998). The relevance of wind for optimal migration theory. *J. Avian Biol.* 29: 561–8.

Liechti, F., Bruderer, B. & Paproth, H. (1995). Quantification of nocturnal bird migration by moonwatching: comparison with radar and infrared observations. *J. Field Orn.* 66: 457–68.

Liechti, F., Klaassen, M. & Bruderer, B. (2000). Predicting migratory flight altitudes by physiological migration models. *Auk* 117: 205–14.

Liechti, F. & Shaller, E. (1999). The use of low-level jets by birds. *Naturwissenschaften* 86: 549–51.

Lincoln, F. C. (1935). The migration of North American birds. US Department of Agriculture, Washington, DC, Circular No. 363: 1–72.

Lind, J., Fransson, T., Jacobsson, S. & Kullberg, C. (1999). Reduced take off ability in Robins due to migratory fuel load. *Behav. Ecol. Sociobiol.* 46: 65–70.

Lindström, Å. (1987). Breeding nomadism and site tenacity in the Brambling *Fringilla montifringilla*. *Ornis Fenn.* 64: 50–6.

Lindström, Å. (1989). Finch flock size and risk of hawk predation at a migratory stopover site. *Auk* 106: 225–32.

Lindström, Å. (1991). Maximum fat deposition rates in migrating birds. *Ornis Scand.* 22: 12–19.

Lindström, Å. (2003). *Fuel deposition rates in migrating birds: causes, constraints and consequences.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 307–20.

Lindström, Å. & Alerstam, T. (1986). The adaptive significance of reoriented migration of Chaffinches *Fringilla coelebs* and Bramblings *F. montifringilla* during autumn in southern Sweden. *Behav. Ecol. Sociobiol.* 19: 417–24.

Lindström, Å. & Alerstam, T. (1992). Optimal fat loads in migrating birds: a test of time minimisation hypothesis. *Amer. Nat.* 140: 477–91.

Lindström, Å., Daan, S. & Visser, G. H. (1994). The conflict between moult and migratory fat deposition: a photoperiodic experiment with Bluethroats. *Anim. Behav.* 48: 1173–81.

Lindström, Å., Enemar, A., Andersson, G., von Proschwitz, T. & Nyholm, E. (2005). Density-independent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos* 110: 155–63.

Liu, J., Xiao, H., Lei, F., Zhu, Q., Qin, K., Zhang, X.-W., Zhang, X.-I., Zhao, D., Wang, G., Feng, Y., Ma, J., Liu, W., Wang, J. & Gao, G. F. (2005). Highly pathogenic H_5N_1 influenza virus infection in migratory birds. *Science* 309: 1206.

Liversidge, R. (1989). *Factors influencing migration of 'wintering' raptors in southern Africa.* In: *Raptors in the Modern World* (Eds Meyburg, B.-U. & Chancellor, R. D.). WWGBP, London, 151–8.

Lloyd, C. S. & Perrins, C. M. (1977). Survival and age at first breeding in the Razorbill *(Alca torda)*. *Bird Banding* 48: 239–52.

Löfgren, O., Hörnfeldt, B. & Carlsson, B.-G. (1986). Site tenacity and nomadism in Tengmalm's Owl *(Aegolius funereus* (L)) in relation to cyclic food production. *Oecologia* 69: 321–6.

Löhrl, H. (1959). Zur Frage des Zeitpunkts einer Prägung auf die Heimatregion beim Halbandschnapper *(Ficedula albicollis)*. *J. Orn.* 100: 132–40.

Lowen, J. (2007). Price of power. *Birdwatch* 2: 18–21.

Loxton, R. G. & Sparks, T. H. (1999). Arrival of spring migrants at Portland, Stokholm, Bardsey and Calf of Man. *Bardsey Observatory Report* 42: 105–43.

Lundberg, A. & Alatalo, R. (1992). *The Pied Flycatcher.* T. & A. D. Poyser, London.

Lundberg, A., Alatalo, R. V., Carlson, A. & Ulfstrand, S. (1981). Biometry, habitat distribution and breeding success in the Pied Flycatcher *Ficedula hypoleuca. Ornis Scand.* 12: 68–79.

MacCluskie, M. C. & Sedinger, J. S. (2000). Nutrient reserves and clutch-size regulation of Northern Shovelers in Alaska. *Auk* 117: 971–9.

Macdonald, M. A. (1977). Adult mortality and fidelity to mate and nest-site in a group of marked Fulmars. *Bird Study* 24: 165–8.

MacInnes, C. D. (1966). Population behaviour of eastern arctic Canada Geese. *J. Wildl. Manage.* 30: 536–55.

Maddock, M. & Geering, D. (1994). Range expansion and migration of the Cattle Egret. *Ostrich* 65: 191–203.

Madsen, J. (1995). Impacts of disturbance on migratory waterfowl. *Ibis* 137 (suppl.): 67–74.

Madsen, J. (2001). Spring migration strategies in Pinkfooted Geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. *Ardea* 89: 43–55.

Madsen, J., Cracknell, G. & Fox, T. (1999). *Goose Populations of the Western Palaearctic.* Natural Environment Research Institute, Rönde, Denmark. **Madsen, J. & Klaassen, M.** (2006). Assessing body condition and energy budget components by scoring

abdominal profiles in free-ranging Pink-footed Geese *Anser brachyrhynchus*. *J. Avian Biol.* 37: 283–7.

Magnin, G. (1991). Hunting and persecution of migratory birds in the Mediterranean region. In: *Conserving Migratory Birds* (Ed. Salathé, T.). International Council for Bird Preservation, Cambridge, 59–71.

Maher, W. J. (1970). The Pomarine Jaeger as a Brown Lemming predator in northern Alaska. *Wilson Bull.* 82: 130–57.

Main, I. G. (2000). Obligate and facultative partial migration in the Blackbird *(Turdus merula)* and the Greenfinch *(Carduelis chloris):* uses and limitations of ringing data. *Vogelwarte* 40: 286–91.

Main, I. G. (2002). Seasonal movements of Fennoscandian Blackbirds *Turdus merula*. *Ringing & Migration* 21: 65–74.

Mainguy, J., Bêty, J., Gauthier, G. & Giroux, J. F. (2002). Are body condition and reproductive effort of laying Greater Snow Geese affected by the spring hunt? *Condor* 104: 156–61.

Mainwood, A. R. (1976). The movements of Storm Petrels as shown by ringing. *Ringing & Migration* 1: 98–104.

Malkinson, M., Banet, C., Weisman, Y., Pokamunski, S., King, R., Drouet, M. T. & Deubel, V. (2002). Introduction of West Nile virus in the Middle East by migrating White Storks. *Emerg. Infect. Dis.* 8: 392–7.

Marchant, J. H. (1992). Recent trends in breeding populations of some common trans-Saharan migrant birds in northern Europe. *Ibis* 134: 113–19.

Marcström, V. & Mascher, J. W. (1979). Weights and fat in Lapwings *Vanellus vanellus* and Oystercatchers *Haematopus ostralegus* starved to death during a cold spell in spring. *Ornis Scand.* 10: 235–40.

Marion, L., Ulenaers, P. & van Vessen, J. (2000). *Herons in Europe.* In: *Heron Conservation* (Eds Kushlan, J. A. & Hafner, H.).

Academic Press, London, 1–32.

Marjakangas, A. & Kiviniemi, S. (2005). Dispersal and migration of female Black Grouse *Tetrao tetrix* in eastern central Finland. *Ornis Fenn.* 82: 107–16.

Marquenie, J. M. (2007). Green light to birds. Investigation into the effect of bird-friendly lighting. Nam Locatie L15-FA-1.

Marquiss, M., Hobson, K. A. & Newton, I. (2008). Stable isotope evidence for different regional source areas of Common Crossbill *Loxia curvirostra* irruptions into Britain. *J. Avian Biol.* 39: 30–4.

Marquiss, M. & Rae, R. (1994). Seasonal trends in abundance, diet and breeding of Common Crossbill *(Loxia curvirostra)* in an area of mixed species conifer plantation following the 1990 crossbill 'irruption'. *Forestry* 67: 31–47.

Marquiss, M. & Rae, R. (2002). Ecological differentiation in relation to bill size amongst sympatric, genetically undifferentiated crossbills *(Loxia* spp.). *Ibis* 144: 494–508.

Marra, P. P., Francis, C. M., Mulvihill, R. S. & Moore, F. R. (2005). The influence of climate on the timing and rate of bird migration. *Oecologia* 142: 307–15.

Marra, P. P., Hobson, K. A. & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable carbon isotopes. *Science* 282: 1884–6.

Marra, P. P. & Holmes, R. T. (2001). Consequence of dominance-related habitat segregation in a migrant passerine bird during the non-breeding season. *Auk* 118: 92–104.

Marsh, R. L. (1983). Adaptations of the Gray Catbird *Dumetella carolinensis* to long-distance migration: energy stores and substrate concentrations in plasma. *Auk* 100: 170–9.

Martin, G. R. (1990). *Birds by Night.* T. & A D. Poyser, London.

Martinez, M. M. (1983). Nidificación de *Hirundo rustica erythrogaster* (Boddaert) en la Argentina (Aves, Hirundinidae).

Neotrópica 29: 83–6.

Massa, B., Benvenuti, S., Ioalè, P., Lo Valvo, M. & Papi, F. (1991). Homing of Cory's Shearwaters *(Calonectris diomedea)* carrying magnets. *Boll. Zool.* 58: 245–7.

Matthews, G. V. T. (1953). Navigation in the Manx Shearwater. *J. Exp. Biol.* 30: 370–96.

Matthews, G. V. T. (1968). *Bird Navigation.* Second edition. Cambridge University Press, Cambridge. **Matthysen, E.** (1990). Behavioural and ecological correlates of territory quality in the Eurasian Nuthatch *(Sitta europaea)*. *Auk* 107: 86–95.

McClintock, C. P., Williams, T. C. & Teal, J. M. (1978). Autumnal bird migration observed from ships in the western North Atlantic Ocean. *Wilson Bull.* 49: 262–77.

McCulloch, M. N., Tucker, G. M. & Baillie, S. R. (1992). The hunting of migratory birds in Europe: a ringing recovery analysis. *Ibis* 134 (suppl. 1): 55–65.

McLandress, M. R. & Raveling, D. G. (1981). Changes in diet and body composition of Canada Geese before spring migration. *Auk* 98: 65–79.

McLandress, M. R. & Raveling, R. G. (1983). Hyperphagia and social behaviour of Giant Canada Geese prior to spring migration. *Wilson Bull.* 93: 310–24.

McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian Islands. *Auk* 98: 243–57.

McLaren, I. A., Lees, A. C., Field, C. & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: a statistical analysis. *Ibis* 148: 707–26.

McNeil, R., Diaz, M. T. & Villeneuve, A. (1994). The mystery of shorebird oversummering: a new hypothesis. *Ardea* 82: 143–52.

McWilliams, S. R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a

nutritional and physiological ecology perspective. *J. Avian Biol.* 35: 377–93.

McWilliams, S. R. & Karasov, W. H. (2005). *Migration takes guts.* In: *Birds of Two Worlds* (Eds Greenberg, R. & Marra, P. P.). Smithsonian Institution, Washington, DC, 67–8.

Mead, C. J. (1970). The winter quarters of British Swallows. *Bird Study* 17: 229–40.

Mead, C. J. & Harrison, J. D. (1979a). Colony fidelity and interchange in the Sand Martin. *Bird Study* 26: 99–106.

Mead, C. J. & Harrison, J. D. (1979b). Sand Martin movements within Britain and Ireland. *Bird Study* 26: 73–86.

Menu, S., Gauthier, G. & Reed, A. (2005). Survival of young Greater Snow Geese *(Chen caerulescens atlantica)* during fall migration. *Auk* 122: 479–96.

Merilä, J., Björkland, M. & Baker, A. J. (1997). Historical demography and present-day population structure of the Greenfinch *Carduelis chloris*— an analysis of mtDNA control-region sequences. *Evolution* 51: 946–56.

Mesquida, E. T., Villarán, A. & Pacual-Parra, J. (2007). Timing of autumn bird migration in central Spain in light of recent climate change. *Ardeola* 54: 251–9.

Metcalfe, N. B. & Furness, R. W. (1984). Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociobiol.* 15: 203–6.

Metcalfe, N. B. & Ure, S. E. (1995). Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc.. R. Soc. Lond. B* 261: 395–400.

Meyburg, B.-U., Ellis, D. H., Meyburg, C., Mendelsohn, J. M. & Scheller, W. (2001). Satellite tracking of two Lesser Spotted Eagles, *Aquila pomarina,* migrating from Namibia. *Ostrich* 72: 35–40.

Meyburg, B.-U. & Meyburg, C. (1999). The study of raptor migration in the Old World using satellite telemetry. *Proc.. Int. Orn. Congr.* 22: 2992–3006.

Meyburg, B.-U., Meyburg, C. & Barbraud, J.-C. (1998). Migration strategies of an adult Short-toed Eagle *Circaetus gallicus* tracked by satellite. *Alauda* 66: 39–48.

Meyburg, B.-U., Meyburg, C., Belka, T., Šreibr, O. & Vrana, J. (2004). Migration, wintering and breeding of a Lesser Spotted Eagle *(Aquila pomarina)* from Slovakia tracked by satellite. *J. Orn.* 145: 1–7.

Meyburg, B.-U., Scheller, W. & Meyburg, C. (1995b). Migration and wintering of the Lesser Spotted Eagle *(Aquila pomarina)*— a study by means of satellite telemetry. *J. Orn.* 136: 401–22.

Mihelsons, H. A., Mednis, A. A. & Blums, P. B. (1985). Regulatory mechanisms of numbers in breeding populations of migratory ducks. *Proc.. Int. Orn. Congr.* Moscow 18: 797–802.

Mikkonen, A. (1981). Factors influencing spring arrival of the Brambling *Fringilla montifringilla* in northern Finland. *Ornis Fenn.* 58: 78–82.

Mikkonen, A. V. (1983). Breeding site tenacity of the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in northern Finland. *Ornis Scand.* 14: 36–47.

Milá, B., Girman, D. J., Kimura, M. & Smith, T. B. (2000). Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proc.. R. Soc. Lond. B* 267: 1033–40.

Milwright, R. D. P. (2002). Redwing *Turdus iliacas* migration and wintering areas shown by recoveries of birds ringed in the breeding season in Fennoscandia, Poland, the Baltic Republics, Russia, Siberia and Iceland. *Ringing & Migration* 21: 5–15.

Møller, A. P. (1989a). Population dynamics of a declining Swallow *Hirundo rustica* population. *J. Anim. Ecol.* 58: 1051–63.

Møller, A. P. (1994). Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav. Ecol. Sociobiol.* 35: 115–22.

Møller, A. P. (2001). Heritability of arrival date in a migratory bird. *Proc.. R. Soc. Lond. B* 268: 203–6.

Møller, A. P. (2001). The effect of dairy farming on Barn Swallow *Hirundo rustica* abundance, distribution and reproduction. *J. Appl. Ecol.* 38: 378–89.

Møller, A. P. (2004). Protandry, sexual selection and climate change. *Global Change Biol.* 10: 2028–35.

Møller, A. P. & Hobson, K. A. (2004). Heterogeneity in stable isotope profiles predicts coexistence of populations of Barn Swallows *Hirundo rustica* differing in morphology and reproductive performance. *Proc.. R. Soc. Lond. B* 271: 1355–62.

Møller, A. P., Rubolini, D. & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc.. Natl. Acad. Sci. USA* 105: 16195–200.

Mönkkönen, M. (1992). Life history traits of Palaearctic and Nearctic migrant passerines. *Ornis Fenn.* 69: 161–72.

Moore, F. R. & Phillips, J. B. (1988). Sunset, skylight polarization and the migratory orientation of Yellow-rumped Warblers, *Dendroica coronata. Anim. Behav.* 36: 1770–78.

Moore, F. R. & Yong, W. (1991). Evidence of food-based competition among passerine migrants during stopover. *Behav. Ecol. Sociobiol.* 28: 85–90.

Moreau, R. E. (1928). Some further notes from the Egyptian deserts. *Ibis* 12, Ser.4: 453–75.

Moreau, R. E. (1951). The British status of the Quail and some problems of its biology. *Brit. Birds* 44: 257–76.

Moreau, R. E. (1961). Problems of Mediterranean Sahara migration. *Ibis* 103: 373–421, 580–623.

Moreau, R. E. (1972). *The Palaearctic–African Bird Migration System.* Academic Press, London. **Moreau, R. E. & Dolp, R. M.** (1970). Fat, water, weights and wing-lengths of autumn migrants in transit on the northwest coast of Egypt. *Ibis* 112: 209–28.

Morel, G. (1973). The Sahel zone as an environment for Palaearctic migration. *Ibis* 115: 413–17.

Morel, G. J. & Morel, M.-Y. (1992). Habitat use by Palaearctic migrant passerine birds in West Africa. *Ibis* 134 (suppl. 1): 83–8.

Morris, S., Richmond, M. E. & Holmes, D. W. (1994). Patterns of stopover by warblers during spring and fall migration on Appledore Island, Maine. *Wilson Bull.* 106: 703–18.

Morrison, R. I. G. (2006). Body transformations, condition, and survival in Red Knots *Calidris canutus* travelling to breed at Alert, Ellesmere Island, Canada. *Ardea* 94: 607–18.

Morrison, R. I. G. & Hobson, K. A. (2004). Use of body stores in shorebirds after arrival on High-Arctic breeding grounds. *Auk* 121: 333–44.

Morton, M. L. (2002). The Mountain White-crowned Sparrow: migration and reproduction at high altitude. *Studies in Avian Biol.* 24.

Morton, R. (1986). Rapid territory establishment by a Wood Warbler. *Ringing & Migration* 7: 56.

Moss, D. (1978). Song-bird populations in forestry plantations. *Quart. J. For.* 72: 5–14.

Mouritsen, H. (2001). Ringing recoveries contain hidden information about orientation mechanisms. *Ardea* 89: 31–42.

Mouritsen, H. & Larsen, O. N. (1998). Migrating young Pied Flycatchers *Ficedula hypoleuca* do not compensate for geographical displacements. *J. Exp. Biol.* 201: 2927–34.

Muheim, R., Åkesson, S. & Alerstam, T. (2003). Compass orientation and possible migration routes of passerine birds at high arctic latitudes. *Oikos* 103: 341–9.

Muheim, R., Moore, F. R. & Phillips, J. B. (2006a). Calibration of magnetic and celestial compass cues in migratory birds—a review of cue-conflict experiments. *J. Exp. Biol.* 209: 2004–2004.

Muheim, R., Phillips, J. B. & Akesson, S. (2006b). Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313: 837–9.

Mullié, W. C. & Keith, J. O. (1993). The effects of aerially applied fenithrothion and chlorpyrifos on birds in the savannah of northern Senegal. *J. Appl. Ecol.* 30: 536–50.

Munro, U., Munro, J. A., Phillips, J. B., Wiltschko, R. & Wiltschko, W. (1997a). Evidence for a magnetite-based navigational 'map' in birds. *Naturwissenschaften* 84: 26–8.

Munro, U., Munro, J. A., Phillips, J. B. & Wiltschko, W. (1997b). Effect of wavelength of light and pulse magnetisation on different magnetoreception systems in a migratory bird. *Austr. J. Zool.* 45: 189–98.

Murton, R. K. & Westwood, N. J. (1977). *Avian Breeding Cycles.* Clarendon Press, Oxford.

Myers, J. P. (1981). A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59: 1527–34.

Myers, P. J., Schick, C. T. & Castro, G. (1988). Structure in Sanderling *(Calidris alba)* populations: the magnitude of intra- and inter-year dispersal during the nonbreeding season. *Proc.. Int. Orn. Congr.* 19: 604–15.

Myres, M. T. (1964). Dawn ascent and reorientation of Scandinavian thrushes *(Turdus* spp.) migrating at night over the northeastern Atlantic Ocean in autumn. *Ibis* 106: 7–51.

Negro, J. J., Hiraldo, F. & Donázar, J. A. (1997). Causes of natal dispersal in the Lesser Kestrel: inbreeding avoidance or resource competition? *J. Anim. Ecol.* 66: 640–8.

Nelson, B. (1973). *Azraq: Desert Oasis.* Allen Lane, London.

Nelson, J. B. (1978). *The Gannet.* T. & A. D. Poyser, Berkhamsted, Herts.

Neto, J. M., Encarnação, V., Fearon, P. & Gosler, A. G. (2008). Autumn migration of Savi's Warblers *Locustella luscinioides* in Portugal: differences in timing, fuel deposition rate and non-stop flight range between the age classes. *Bird Study* 55: 78–85.

Newnham, J. A. (1984). Some aspects of the sea-bird movements observed from the Sussex coast during the spring 1983. *Sussex Bird Report* 36: 60–3.

Newton, I. (1972). *Finches.* Collins, London.

Newton, I. (1977). *Timing and success of breeding in tundra-nesting geese.* In: *Evolutionary Ecology* (Eds Stonehouse, B. & Perrins, C. M.). Macmillan, London, 113–26.

Newton, I. (1979). *Population Ecology of Raptors.* T. & A. D. Poyser, Berkhamsted, Herts.

Newton, I. (1992). Experiments on the limitation of bird numbers by territorial behaviour. *Biol. Rev.* 67: 129–73.

Newton, I. (1994). The role of nest-sites in limiting the numbers of hole-nesting birds: a review. *Biol. Conserv.* 70: 265–76.

Newton, I. (1995a). Relationship between breeding and wintering ranges in Palaearctic–African migrants. *Ibis* 137: 241–9.

Newton, I. (1995b). The contribution of some recent research on birds to ecological understanding. *J. Anim. Ecol.* 64: 675–96.

Newton, I. (1998a). *Migration patterns in West Palaearctic raptors.* In: *Holarctic Birds of Prey* (Eds Chancellor, R. D., Meyburg, B.-U. & Ferrero, J. J.). ADENEX-WWGBP, Calamonte, Spain, 603–12.

Newton, I. (1998b). *Population Limitation in Birds.* Academic Press, London. **Newton, I.** (2001). Causes and consequences of breeding dispersal in the Sparrowhawk. *Ardea* 89: 143–54.

Newton, I. (2000). Movements of Bullfinches within the breeding season. *Bird Study* 47: 372–6.

Newton, I. (2002). *Population limitation in Holarctic owls.* In: *Ecology and Conservation of Owls* (Eds Newton, I., Kavanagh, R., Olsen, J. & Taylor, I. R.). CSIRO Publishing, Collingwood, Victoria, Australia, 3–29.

Newton, I. (2003). *The Speciation and Biogeography of Birds.* Academic Press, London.

Newton, I. (2004). The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579–600.

Newton, I. (2006a). Advances in the study of irruptive migration. *Ardea* 94: 432–60.

Newton, I. (2006b). Can conditions experienced during migration limit the population levels of birds? *J. Orn.* 147: 146–66.

Newton, I. (2006c). Movement patterns of Common Crossbills *Loxia curvirostra* in Europe. *Ibis* 148: 782–8.

Newton, I. (2007). Weather-related mass-mortality events in migrants. *Ibis* 149: 453–67.

Newton, I. (2008). *The Migration Ecology of Birds.* Academic Press, London. **Newton, I. & Campbell, C. R. G.** (1970). Goose studies at Loch Leven in 1967/68. *Scott. Birds* 6: 5–18.

Newton, I. & Dale, L. (1996a). Relationship between migration and latitude among west European birds. *J. Anim. Ecol.* 65: 137–46.

Newton, I. & Dale, L. C. (1996b). Bird migration at different latitudes in eastern North America. *Auk* 113: 626–35.

Newton, I. & Dale, L. C. (1997). Effects of seasonal migration on the latitudinal distribution of west Palaearctic bird species. *J.*

Biogeog. 24: 781–9.

Newton, I., Ekner, A., Walker, D. & Sparks, T. H. (2010). The migration seasons of birds as recorded at Dungeness Bird Observatory in southeast England

Nice, M. M. (1933). Der Naturgeschichte des Singammers. *J. Orn.* 81: 552–95.

Nice, M. M. (1937). Studies in the life history of the Song Sparrow. Volume 1. *Trans. Linn. Soc. New York* 4: 1–247.

Nichols, J. D. & Hines, J. E. (1987). Population ecology of the Mallard. VIII. Winter distribution patterns and survival rates of winter-banded Mallards. Resource Publication 162. US Fish and Wildlife Service, Washington, DC.

Nichols, J. D., Reinecke, K. J. & Hines, J. E. (1983). Factors affecting the distribution of Mallards wintering in the Mississippi Alluvial Valley. *Auk* 100: 932–46.

Nicholson, E. M. (1977). Sir Landsborough Thomson, CB, OBE, DSc, Hon. LLD (1890–1977). *Brit. Birds* 70: 384–7.

Nilsson, L. (1979). Variation in the production of young of swans wintering in Sweden. *Wildfowl* 30: 129–34.

Nilsson, L. (2006). *Changes in migration patterns and wintering areas of south Swedish Greylag Geese* Anser anser. In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 514–16.

Nisbet, I. C. T. (1957). Wader migration at Cambridge sewage farm. *Bird Study* 4: 131–48.

Nisbet, I. C. T. (1959a). Calculation of flight directions of birds observed crossing the face of the moon. *Wilson Bull.* 71: 237–43.

Nisbet, I. C. T. (1959b). Wader migration in North America and its relation to transatlantic crossings. *Brit. Birds* 52: 205–15.

Nisbet, I. C. T. (1962). South-eastern rarities at Fair Isle. *Brit. Birds* 55: 74–85.

Nisbet, I. C. T. & Medway, L. (1972). Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114: 451–94.

Nolet, B. A. & Drent, R. H. (1998). Bewick's Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. *J. Avian Biol.* 29: 574–81.

Norman, S. C. & Norman, W. (1985). Autumn movements of Willow Warblers ringed in the British Isles. *Ringing & Migration* 6: 17–18.

Norris, C. A. (1947). Report on the distribution and status of the Corncrake. *Brit. Birds* 40: 226–44.

Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc.. R. Soc. Lond. B* 271: 59–64.

Noskov, G. A., Rezvyi, S. P., Rychkova, A. L. & Smirnov, O. P. (2005). *On migrations of the slender billed race of the Nutcracker* Nucifraga caryocatactes macrorhychos L. *in northwest Russia and adjacent areas.* In: *Ornithological Studies in the Ladoga Area* (Ed. Iovchenko, N. P.). St Petersburg University Press, St Petersburg, 61–80.

Nowakowski, J. K. & Chru ciel, J. (2004). Speed of autumn migration of the Blue Tit *(Parus caeruleus)* along the eastern and southern Baltic coast. *The Ring* 26: 3–12.

Oatley, T. B. (2000). Migrant European Swallows *Hirundo rustica* in southern Africa—a southern perspective. *Ostrich* 71: 205–9.

O'Briain, M. (1987). Families and other social groups of Brent Geese in winter. Unpub. report, University College, Dublin.

Olsen, B., Munster, V. J., Wallensten, A., Waldenstrom, J., Osterhaus, A. & Fouchier, R. A. M. (2006). Global patterns of influenza A virus in wild birds. *Science* 312: 384–8.

Olssen, O. (1958). Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus. Acta Vertebratica* 1: 91–189.

Orell, M. & Ojanen, M. (1979). Mortality rates of the Great Tit *Parus major* in a northern population. *Ardea* 67: 130–9.

Ormerod, S. J. (1989). The influence of weather on the body mass of migrating Swallows *Hirundo rustica* in South Wales. *Ringing & Migration* 10: 65–74.

Ormerod, S. J. (1991). Pre-migratory and migratory movements of Swallows *Hirundo rustica* in Britain and Ireland. *Bird Study* 38: 170–8.

Ottich, I. & Dierschke, V. (2003). Exploitation of resources modulates stopover behaviour of passerine migrants. *J. Orn.* 144: 307–16.

Ottosson, U., Waldenstrom, J., Hjort, C. & McGregor, R. (2005). Garden Warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes. *Ibis* 147: 750–7.

Owen, J. C. & Moore, F. R. (2006). Seasonal differences in immunological condition of three species of thrushes. *Condor* 108: 389–98.

Owen, J., Moore, F., Panella, N., Edwards, E., Bru, R., Hughes, M. & Komar, N. (2006). Migrating birds as dispersal vehicles for West Nile virus. *Ecohealth* 3: 79–85.

Owen, M. (1980). *Wild geese of the world.* B.T. Batsford Ltd, London.

Owen, M. & Black, J. M. (1991). *The importance of migration mortality in non-passerine birds.* In: *Bird Population Studies: Relevance to Conservation and Management*(Eds Perrins, C. M., Lebreton, J.-D. & Hirons, G. J. M.). Oxford University Press, Oxford, 360–72.

Palmer, W. L. (1962). Ruffed Grouse flight capability over water. *J. Wildl. Manage.* 26: 338–9.

Papi, F. (1989). Pigeons use olfactory cues to navigate. *Ethol. Ecol. Evol.* 1: 219–31.

Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* 67: 518–36.

Parr, R. (1992). The decline to extinction of a population of Golden Plover in north-east Scotland. *Ornis Scand.* 23: 152–8.

Partida, F. B. (2007). *Nomads of the Strait of Gibraltar.* Grafisur, Tarifa, Spain.

Patten, M. A. & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *Auk* 113: 911–23.

Patterson, I. J. (1982). *The Shelduck. A Study in Behavioural Ecology.* Cambridge University Press, Cambridge.

Payevsky, V. A. (1971). *Atlas of bird migrations according to banding data at the Courland Spit.* In: *Bird Migrations: Ecological and Physiological Factors* (Ed. Bykhovskii, B. E.). Leningrad, 1–124.

Payevsky, V. A. (1994). Age and sex structure, mortality and spatial winter distribution of Siskins *(Carduelis spinus)* migrating through eastern Baltic area. *Vogelwarte* 37: 190–8.

Peach, W. J., Baillie, S. R. & Underhill, L. (1991). Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to West Africa rainfall. *Ibis* 133: 300–5.

Peach, W. J., Crick, H. Q. P. & Marchant, J. H. (1995a). The demography of the decline in the British Willow Warbler population. *J. Appl. Stat.* 22: 905–22.

Peach, W. J., Thompson, P. S. & Coulson, J. C. (1994). Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus. J. Anim. Ecol.* 63: 60–70.

Pearson, D. (1972). The wintering and migration of Palaearctic passerines at Kampala, southern Uganda. *Ibis* 114: 43–60.

Pearson, D. J. (1973). Moult of some Palaearctic warblers wintering in Uganda. *Bird Study* 20: 24–36.

Pearson, D. J. (1990). *Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 44–59.

Pearson, D. J. & Backhurst, G. C. (1976). The southward migration of Palaearctic birds over Ngulia, Kenya. *Ibis* 118: 78–105.

Pearson, D. J., Backhurst, G. C. & Backhurst, D. E. G. (1979). Spring weights and passage of Sedge Warblers *Acrocephalus schoenobaenus* in central Kenya. *Ibis* 121: 8–19.

Pearson, D. J. & Lack, P. C. (1992). Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. *Ibis* 134 (suppl. 1): 89–98.

Peiponen, V. A. (1967). Südliche Fortpflanzung und Zug von *Carduelis flammea* (L.) in Jahre 1965. *Ann. Zool. Fenn.* 4: 547–9.

Pennycuick, C. J. (1969). The mechanics of bird migration. *Ibis* 111: 525–56.

Pennycuick, C. J. (1975). *Mechanics of flight.* In: *Avian Biology,* Volume 5 (Eds Farner, D. S. & King, J. R.). Academic Press, London, 1–75.

Pennycuick, C. J. (1989). *Bird Flight Performance: A Practical Calculation Manual.* Oxford University Press, Oxford.

Pennycuick, C. J. (2002). Gust soaring as a basis for the flight of petrels and albatrosses. *Avian Sci.* 2: 1–12.

Pennycuick, C. J. (2008). *Modelling the Flying Bird.* Academic Press, London.

Pennycuick, C. J., Bradbury, T. A. M., Einarsson, O. & Owen, M. (1999). Response to weather and light conditions of migrating

Whooper Swans *Cygnus cygnus* and flying height profiles, observed with the Argos satellite system. *Ibis* 141: 434–43.

Pennycuick, C. J., Einarsson, O., Bradbury, T. A. M. & Owen, M. (1996). Migrating Whooper Swans *Cygnus cygnus:* satellite tracks and flight performance calculations. *J. Avian Biol.* 27: 118–34.

Perdeck, A. C. (1958). Two types of orientation in migrating Starlings, *Sturnus vulgaris* L., and Chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea* 46: 1–37.

Perdeck, A. C. (1967). Orientation of Starlings after displacement to Spain. *Ardea* 55: 93–104.

Perrins, C. M., Harris, M. P. & Britton, C. K. (1973). Survival of Manx Shearwaters *Puffinus puffinus. Ibis* 115: 535–48.

Petersen, B. S. (1984). The origins of Herring Gulls *Larus argentatus* occurring in the Copenhagen area with special reference to recent changes. *Dansk. Orn. Foren. Tidskkr.* 78: 15–24.

Petersen, I. K., Hounisen, J. P., Kahlert, J., Christensen, T. K. & Desholm, M. (2006). *Final Results of Bird Studies at the Offshore Wind Farms at Nysted and Horns Rev, Denmark.* NERI, Rønde.

Pfeifer, R., Stadler, J. & Brandl, R. (2007). Birds from the Far East in Central Europe: a test of the reverse migration hypothesis. *J. Orn.* 148: 379–85.

Phillips, J. B. & Moore, F. R. (1992). Calibration of the sun compass by sunset polarized-light patterns in a migratory bird. *Behav. Ecol. Sociobiol.* 31: 189–93.

Phillips, R. A., Bearhop, S., Hamer, K. C. & Thompson, D. R. (1999). Rapid population growth of Great Skuas *Catharacta skua* at St Kilda: implications for management and conservation. *Bird Study* 46: 174–83.

Phillips, R. A., Silk, J. R. D., Croxall, J. P. & Afanasyev, V. (2006). Year-round distribution of White-chinned Petrels from

South Georgia: relationships with oceanography and fisheries. *Biol. Conserv.* 129: 336–47.

Pienaar, U. de V. (1969). Observations on the nesting habits and predators of breeding colonies of Red-billed Queleas *Quelea quelea lathami* (A. Smith) in the Kruger National Park. *Bokmakierie* 21 (suppl.): xi–xv.

Pienkowski, M. W. (1976). Recurrence of waders on autumn migration at sites in Morocco. *Vogelwarte* 28: 293–7.

Pierce, B. J. & McWilliams, S. R. (2005). Seasonal changes in composition of lipid stores in migratory birds: causes and consequences. *Condor* 107: 269–79.

Piersma, T. (1990). Climbing to high alt. Probably Piersma and Jukema 1990. Or other paper in same issue. *Ardea* 78: 315–338

Piersma, T. (1988). The annual moult cycle of Great Crested Grebes. *Ardea* 76: 82–5.

Piersma, T. (1997). Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* 80: 623–31.

Piersma, T. (1998). Phenotypic flexibility during migration: optimisation of organ size contingent on the risks and rewards of fueling and flight? *J. Avian Biol.* 29: 511–20.

Piersma, T. (2006). *Migration in the balance: tight ecological margins and the changing fortunes of shorebird populations.* In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 74–80.

Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Orn.* 148: S45–S59.

Piersma, T. & Davidson, N. C. (1992). The migrations and annual cycles of five subspecies of Knots in perspective. *Wader Study*

Group Bull. 64 (suppl.): 187–97.

Piersma, T. & Gill, R. E. (1998). Guts don't fly: small digestive organs in obese Bar-tailed Godwits. *Auk* 115: 196–203.

Piersma, T. & Jukema, J. (2002). Contrast in adaptive mass gains: Eurasian Golden Plovers store fat before midwinter and protein before prebreeding flight. Proc.. *R. Soc. Lond. B* 269: 1101–5.

Piersma, T. & Lindström, Å. (1997). Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* 12: 134–8.

Piersma, T., Rogers, D. I., Gonzalez, P. M., Zwarts, L., Niles, L. J., De Lima Serrano do Nascimento, I., Minton, C. D. T. & Baker, A. J. (2005). *Fuel storage rates before northward flights in Red Knots worldwide.* In: *Birds of Two Worlds* (Eds Greenberg, R. & Marra, P. P.). Smithsonian Institution, Washington, DC, 262–73.

Poole, A. & Agler, B. (1987). Recoveries of Ospreys banded in the United States 1914–84. *J. Wildl. Manage*.51: 148–55.

Popa-Lisseanu, A. G., Delgado-Huertas, A., Forero, M. G., Rodriguez, A., Arlettaz, R. & Ibanez, C. (2007). Bat's conquest of a formidable foraging niche: the myriads of nocturnally migrating songbirds. *PloS ONE* 2: e 205. (doi: 10.1371/journal/pone.0000205).

Porter, J. M. & Coulson, J. C. (1987). Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. *J. Anim. Ecol.* 56: 675–89.

Preston, F. W. (1966). The mathematical representation of migration. *Ecology* 47: 375–92.

Prop, J. (2004). Food finding. On the trail to successful reproduction in migrating geese. PhD thesis, University of Groningen, the Netherlands.

Prop, J. & Deerenberg, C. (1991). Spring staging in Brent Geese *Branta bernicla,* feeding constraints and the impact of diet on the

accumulation of body reserves. *Oecologia* 87: 19–28.

Prop, J., Black, J. M. & Shimmings, P. (2003). Travel schedules to the high arctic: Barnacle Geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103: 403–14.

Prop, J. & Deerenburg, C. (1991). Spring staging in Brent Geese *Branta bernicla,* feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19–28.

Pulido, F. (2007). Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Clim. Res.* 35: 5–23.

Pulido, F. & Berthold, P. (2003). *Quantitative genetic analyses of migratory behaviour.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 53–77.

Pulido, F. & Berthold, P. (2004). Microevolutionary response to climate change. In 'Birds and climate change'. *Adv. Ecol. Res.* 35: 151–83

Pulido, F., Berthold, P., Mohr, G. & Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird population. *Proc.. R. Soc. Lond. B* 268: 953–9.

Pulido, F., Berthold, P. & van Noordwijk, A. J. (1996). Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc.. *Natl. Acad. Sci. USA* 93: 14642–7.

Pützig, P. (1938). Über das Zug verhalten umgesiedelter englischer Stockenten. *Vogelzug* 9: 139–45.

Quay, W. B. (1989). Insemination of Tennessee Warblers during spring migration. *Condor* 91: 660–70.

Rabøl, J. (1969a). Orientation of autumn migrating Garden Warblers *Sylvia borin* after displacement from western Denmark (Blavand) to eastern Sweden (Ottenby). A preliminary experiment. *Dansk Orn. Foren. Tidsskr.* 63: 93–104.

Rabøl, J. (1969b). Reversed migration as the cause of westward vagrancy by four *Phylloscopus* warblers. *Brit. Birds* 62: 89–92.

Rabøl, J. (1976). The orientation of Pallas's Leaf Warbler *Phylloscopus proregulus* in Europe. *Dansk Orn. Foren. Tidsskr.* 70: 6–16.

Rabøl, J. (1987). Coexistence and competition between overwintering Willow Warblers *Phylloscopus trochilus* and local warblers at Lake Naivaska, Kenya. *Ornis Scand.* 18: 101–21.

Rabøl, J. (1992). Star-navigation in night-migrating passerines. *Dansk Orn. Foren. Tidsskr.* 86: 177–81.

Rabøl, J. (1993). The orientation system of long-distance passerine migrants displaced in autumn from Denmark to Kenya. *Ornis Scand.* 24: 183–96.

Rabøl, J. (1994). Compensatory orientation in Pied Flycatchers, *Ficedula hypoleuca,* following a geographical displacement. *Dansk Orn. Foren. Tidsskr.* 88: 171–82.

Rabøl, J. & Noer, H. (1973). Spring migration of the Skylark *(Alauda arvensis)* in Denmark. *Vogelwarte* 27: 50–65.

Rabøl, J. & Thorup, K. (2006). Migratory direction established in inexperienced bird migrants in the absence of magnetic field references in their pre-migratory period and testing. *Ethol. Ecol. Evol.* 18: 43–51.

Rainio, K., Tottrup, A. P., Lehikoinen, E. & Coppack, T. (2007). Effects of climate change on the degree of protandry in migratory songbirds. *Clim. Res.* 35: 107–14.

Ralph, C. J. & Mewaldt, L. (1975). Timing of site fixation upon the wintering grounds in sparrows. *Auk* 92: 698–705.

Rappole, J. H. (1995). *The Ecology of Migrant Birds. A Neotropical Perspective.* Smithsonian Institution Press, Washington, DC.

Rappole, J. H. & Warner, D. W. (1976). Relationships between behaviour, physiology, and weather in avian transients at a

migration stopover. *Oecologia* 26: 193–212.

Rappole, J. H., Derrickson, S. R. & Hubalek, Z. (2000). Migratory birds and spread of West Nile virus in the Western Hemisphere. *Emerg. Infect. Dis.* 6: 319–28.

Rayner, J. M. V. (1990). *The mechanics of flight and bird migration performance.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 283–99.

Redfern, C. P. F., Slough, A. E. J., Dean, B., Brice, J. L. & Hope Jones, P. (2000). Fat and body condition in migrating Redwings *Turdus iliacus. J. Avian Biol.* 31: 197–205.

Redfern, C. P. F., Topp, V. J. & Jones, P. (2004). Fat and pectoral muscle in migrating Sedge Warblers *Acrocephalus schoenobaenus. Ringing & Migration* 22: 24–34.

Rees, E. C. (1982). The effect of photoperiod on the timing of spring migration in the Bewick's Swan. *Wildfowl* 33: 119–32.

Rees, E. C. (1989). Consistency in the timing of migration for individual Bewick's Swans. *Anim. Behav.* 38: 384–93.

Rehfisch, M. M., Clark, N. A., Langston, R. H. W. & Greenwood, J. J. D. (1996). A guide to the provision of refuges for waders: an analysis of 30 years of ringing data from the Wash, England. *J. Appl. Ecol.* 33: 673–87.

Rehfisch, M. M., Holloway, S. J. & Austin, G. E. (2003). Population estimates of waders on the non-estuarine coasts of the UK and the Isle of Man during the winter of 1997–98. *Bird Study* 50: 22–32.

Reinikainen, A. (1937). The irregular migrations of the Crossbill, *Loxia c. curvirostra,* and their relation to the cone-crop of the conifers. *Ornis Fenn.* 14: 55–64.

Rheinwald, G. (1975). The pattern of settling distances of House Martins *Delichon urbica. Ardea* 63: 136–45.

Rheinwald, G. & Gutscher, H. (1969). Dispersion und Ortstreue der Mehlschwalbe *(Delichon urbica). Vogelwelt* 90: 121–40.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224–72.

Richardson, W. J. (1990). *Timing of bird migration in relation to weather: updated review.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 78–101.

Richdale, L. E. (1963). Biology of the Sooty Shearwater *Puffinus griseus. Proc.. Zool. Soc. Lond.* 141: 1–117.

Ridgill, S. C. & Fox, A. D. (1990). Cold weather movements of waterfowl in western Europe (spec. pub. 13). IWRB, Slimbridge, Glos.

Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. & Wiltschko, W. (2004). Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* 429: 177–80.

Robbins, C. S. (1980). Predictions of future Nearctic landbird vagrants to Europe. *Brit. Birds* 73: 448–57.

Roberts, T. S. (1907a). A Lapland Longspur tragedy. *Auk* 24: 369–77.

Roberts, T. (1907b). Supplemental note to 'A Lapland Longspur tragedy'. *Auk* 24: 449–50.

Robertson, D. (1980). *Rare Birds of the West Coast.* Woodcock Publications, Pacific Grove, CA.

Robertson, G. & Cooke, F. (1999). Winter philopatry in migratory waterfowl. *Auk* 116: 20–34.

Robinson, R. A., Balmer, D. E. & Marchant, J. H. (2008). Survival rates of hirundines in relation to British and African rainfall. *Ringing & Migration* 24: 1–6.

Rocke, T. E. (2006). *The global importance of avian botulism.* In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 422–6.

Rogers, D. T. (2006). Hidden costs: challenges faced by migratory shorebirds living on intertidal flats. PhD thesis, Charles Sturt University, Australia.

Rogers, M. J. & the Rarities Committee (2003). Report on rare birds in Great Britain in 2002. *Brit. Birds* 96: 542–609.

Rohwer, F. C. & Anderson, M. G. (1988). Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Orn.* 5: 187–221.

Rohwer, S., Hobson, K. & Rohwer, V. G. (2009). Migraotory double breeding in Neotropical migrant birds. *PNAS* 106: 19050–55.

Roos, G. (1991). Visible bird migration at Falsterbo in autumn 1989, with a summary of the occurrence of six *Carduelis* species in 1973–90. *Anser* 30: 229–53.

Rowan, W. (1926). On photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes. Proc. *Boston Soc. Nat. Hist.* 38: 147–89.

Rowan, W. & Batrawi, A. M. (1939). Comment on the gonads of some European migrants collected in East Africa immediately before their spring departure. *Ibis* 14: 58–65.

Rubolini, D., Møller, A. P., Rainio, K. & Lehikoinen, E. (2007). Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim. Res.* 35: 135–46.

Rubolini, D., Pastor, A. G., Pilastro, A. & Spina, F. (2002). Ecological barriers shaping fuel stores in Barn Swallows *Hirundo rustica* following the central and western Mediterranean flyways. *J. Avian Biol.* 33: 15–22.

Ruegg, K. C. & Smith, T. B. (2002). Not as the crow flies: a historical explanation for circuitous migration in Swainson's Thrush *(Catharus ustulus). Proc.. R. Soc. Lond. B* 269: 1375–81.

Rüppell, W. (1944). Versuche über Hamfinden ziehender Nebelkrähen nach Verfrachtung. *J. Orn.* 92: 106–33.

Rüppell, W. & Schüz, E. (1948). Ergebnis der Verfrachtung von Nebel-krähen *(Corvus corone cornix)* wahrend des Weg zuges. *Vogelwarte* 1: 30–36.

Russell, R. W., Carpenter, F. L., Hixon, M. A. & Paton, D. C. (1992). The impact of variation in stopover habitat quality on migrant Rufuous Hummingbirds. *Conserv. Biol.* 8: 483–90.

Rute, J.(1976). On the speed of migration as observed with the Tit (genus *Parus). Zool. Muz. Raksti* 15: 34–9.

Rutschke, E. (1990). Zur Etho-Okologie einer Wildpopulation der Graugans *(Anser Anser).* Proc.. Int. 100 DO-G meeting, Current Topics Avian Biol. *J. Orn. Sonderh.:* 365–71.

Saether, B. E., Grotan, V., Tryjanowski, P., Barbraud, C. & Fulin, M. (2006). Climate and spatio-temporal variation in the population dynamics of a longdistance migrant, the White Stork. *J. Anim. Ecol.* 75: 80–90.

Saino, N., Szép, T., Ambrosini, R., Romano, M. & Møller, A. P. (2004a). Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc.. R. Soc Lond. B* 271: 681–6.

Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F. & Møller, A. P. (2004b). Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol. Lett.* 7: 21–5.

Salewski, V. & Jones, P. (2006). Palaearctic passerines in Afrotropical environments: a review. *J. Orn.* 147: 192–201.

Salomonsen, F. (1951). The immigration and breeding of the Fieldfare *(Turdus pilaris* L.) in Greenland. *Proc.. Int. Orn. Congr.* 10: 515–25.

Salomonsen, F. (1955). The evolutionary significance of bird-migration. *Dan. Biol. Medd.* 22: 1062.

Salomonsen, F. (1968). The moult migration. *Wildfowl* 19: 5–24.

Sandberg, R. (1996). Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. *Ibis* 138: 514–24.

Sandberg, R. & Moore, F. R. (1996a). Migratory orientation of Red-eyed Vireos, *Vireo olivaceus,* in relation to energetic condition and ecological context. *Behav. Ecol. Sociobiol.* 39: 1–10.

Sandberg, R., Moore, F. R., Bäckman, J. & Lõhmus, M. (2002). Orientation of nocturnally migrating Swainson's Thrush at dawn and dusk: the importance of energetic condition and geomagnetic cues. *Auk* 119: 201–9.

Sandberg, R., Pettersson, J. & Persson, K. (1991). Migratory orientation of free-flying Robins *Erithacus rubecula*and Pied Flycatchers *Ficedula hypoleuca*-release experiments. *Ornis Scand.* 22: 1–11.

Sandberg, R., Bäckman, J. Ottoson, U. (1998). Orientation of Snow Buntings *(Plectrophenax nivalis)* close to the magnetic North Pole. *J. Exp. Biol.* 201: 1859–70.

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & van Bommel, F. P. J. (2006). Long-term population declines in Afro-Palaearctic migrant birds. *Biol. Conserv.* 131: 93–105.

Sappington, J. N. (1977). Breeding biology of House Sparrows in Mississippi. *Wilson Bull.* 89: 300–09.

Sauer, E. G. F. (1957). Die Sternenorientierung nachtlicht ziehender Grasmucken *(Sylvia atricapilla, borin* und *curruca). Z. Tierpsych.* 14: 29–70.

Sauer, E. G. F. & Sauer, E. M. (1955). Zur Frage der nächtlichen Zugorientierung von Grasmücken. *Rev. Suisse Zool.* 62: 250–59.

Sauer, E. G. F. & Sauer, E. M. (1960). Star navigation of nocturnal migrating birds. The 1958 planetarium experiment—Cold Spring

Harbour Symposium. *Quant. Biol.* 25: 463–73.

Saurola, P. (1981). Migration of the Sparrowhawk *Accipiter nisus* as revealed by Finnish ringing and migration data. *Lintumies* 16: 10–18.

Saurola, P. (1983). Movements of Short-eared Owl *(Asio flammeus)* and Long-eared Owl *(A. otus)* according to Finnish ring recoveries. *Lintumies* 18: 67–71.

Saurola, P. (1997). *Monitoring Finnish owls 1982–1996: methods and results.* In: *Biology and Conservation of Owls of the Northern Hemisphere* (Eds Duncan, J. R., Johnson, D. H. & Nicholls, T. H.). Second International Symposium, 5–9 February 1997. United States Department of Agriculture, Winnipeg, Manitoba, Canada, 363–80.

Saurola, P. (2002). *Natal dispersal distances of Finnish owls: results from ringing.* In: *Ecology and Conservation of Owls* (Eds Newton, I., Kavanagh, R., Olsen, J. & Taylor, I.) CSIRO Publishing, Collingwood, Victoria, Australia, 42–55.

Sauvage, A., Rumsey, S. & Rodwell, S. (1998). Recurrence of Palaearctic birds in the Lower Senegal River valley. *Malimbus* 20: 33–53.

Schaub, M. & Jenni, L. (2000). Body mass of six longdistance migrant passerine species along the autumn migration route. *J. Orn.* 141: 441–60.

Schaub, M. & Jenni, L. (2001). Variations in fuelling rates among sites, days and individuals in migrating passerine birds. *Funct. Ecol.* 15: 584–94.

Schaub, M., Kania, W. & Koppen, U. (2005). Variation of primary production during winter induces synchrony in survival rates in migratory White Storks *Ciconia ciconia. J. Anim. Ecol.* 74: 656–66.

Schaub, M., Jenni, L. & Bairlein, F. (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behav. Ecol.* 19: 657–66.

Schenk, J. (1934). Die Brutinvasionen des Rosenstares in Ungarn in den Jahren 1932 und 1933. *Aquila* 38–41: [136–53.]

Schifferli, A. (1967). Vom Zug Schweizerischer und Deutscher Schwarzer Milane nach Ringfunden. *Orn. Beob.* 64: 34–51.

Schloss, W. (1984). Ringfunde des Fichtenkreuzschnabels *(Loxia curvirostra)*. *Auspicium* 7: 257–84.

Schmaljohann, H. & Dierschke, V. (2005). Optimal bird migration and predation risk: a field experiment with Northern Wheatears *Oenanthe oenanthe*. *J. Anim. Ecol.* 74: 131–8.

Schmaljohann, H., Liechti, F., Bachler, E., Steuri, T. & Bruderer, B. (2008). Quantification of bird migration by radar—a detection probabliity problem. *Ibis* 150: 342–55.

Schneider, D. C. & Harrington, B. A. (1981). Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801–11.

Schüz E. (1938). Auflassung ostpreussischer Jungstörche in England 1936. *Vogelzug* 9: 65–70.

Schüz, E. (1949). Die Spät-Auflassung ostpreussischer Jungstörche in West-Deutschland durch die *Vogelwarte* Rossitten 1933. *Vogelwarte* 15: 63–78.

Schüz, E. (1950). Früh-Auflassung ostpreussischer Jungstörche in West-Deutschland durch die *Vogelwarte* Rossitten 1933–36. *Bonner Zool. Beitr.* 1: 239–53.

Schwabl, H. (1983). Ausprägung und Bedeutung des Teilzugverhaltens einer sudwestdeutschen Population der Amsel *Turdus merula*. *J. Orn.* 124: 101–15.

Schwilch, R., Grattarola, A., Spina, F. & Jenni, L. (2002a). Protein loss during long-distance migratory flights in passerine birds: adaptation or constraint. *J. Exp. Biol.* 205: 587–695.

Schwilch, R., Piersma, T., Holmgen, N. M. A. & Jenni, L. (2002b). Do migratory birds need a nap after a long non-stop flight? *Ardea* 90: 149–54.

Scott, D. K. (1980). The behaviour of Bewick's Swans at the Welney Wildfowl Refuge, Norfolk, and on surrounding fens: a comparison. *Wildfowl* 31: 5–18.

Scott, J. D., Fernando, K., Banerjee, S. N., Durden, L. A., Byrne, S. K., Banerjee, M., Mann, R. B. & Morshed, M. G. (2001). Birds disperse ixodid (Acari: Ixodidae) and *Borrelia* burgdorferi-infected ticks in Canada. *J. Med. Entomol.* 38: 493–500.

Senar, J. C., Borras, A., Cabrera, T. & Cabrera, J. (1993). Testing for the relationship between coniferous crop stability and Common Crossbill residence. *J. Field Orn.* 64: 464–9.

Senar, J. C., Burton, P. J. K. & Metcalfe, N. B. (1992). Variation in the nomadic tendency of a wintering finch *Carduelis spinus* and its relationship with body condition. *Ornis Scand.* 23: 63–72.

Senar, J. C., Copete, J. L. & Metcalfe, N. B. (1990). Dominance relationships between resident and transient wintering Siskins. *Ornis Scand.* 21: 129–32.

Sergio, F., Blas, J., Forrero, M. G., Donazur, J. A. & Hiraldo, F. (2007). Sequential settlement and site dependence in a migratory raptor. *Behav. Ecol.* 18: 811–21.

Serventy, D. L., Gunn, B. M., Skira, I. J., Bradley, J. S. & Wooller, R. D. (1989). Fledgling translocation and philopatry in a seabird. *Oecologia* 81: 428–9.

Shaffer, S. A., Tremblay, Y., Weimerskirsch, H., Scott, D., Thompson, D. R., Sagar, P. M., Moller, H., Taylor, G. A., Foley, D. G., Block, B. A. & Costa, D. P. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *PNAS* 1103: 2799–802.

Sharrock, J. T. R. (1973). *The Natural History of Cape Clear Island.* T. & A. D. Poyser, Berkhamsted, Herts.

Sharrock, J. T. R. & Fraser, P. (1997). How many rarities are we missing? *Brit. Birds* 90: 297.

Shaw, G. (1990). Timing and fidelity of breeding for Siskins *Carduelis spinus* in Scottish conifer plantations. *Bird Study* 37: 30–35.

Shields, W. M. (1984). Factors affecting nest and site fidelity in Adirondack Barn Swallows *(Hirundo rustica)*. *Auk* 101: 780–89.

Shirihai, H. (1996). *The Birds of Israel.* Academic Press, London.

Shirihai, H., Yosef, R., Aon, D., Kirwan, G. M. & Spaar, R. (2000). *Raptor Migration in Israel and the Middle East. A Summary of 30 Years of Field Research.* International Birding & Research Centre, Israel.

Shumakov, M. E. (2001). Development of orientation abilities and migratory direction in nocturnal migrants on the Courish Spit. *Avian Ecol. Behav.* 6: 76–7.

Sillett, T. S. & Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* 71: 296–308.

Sills, N.(2007). Lakenheath Fen—the first ten years. The 2006 Suffolk Bird Report. *Suffolk Birds* 56: 10–16.

Silvola, T. (1967). Changes in the bird populations in Utsjoki, Finnish Lapland in 1964–1966, caused by the mass-occurrence of the caterpillar *Oporinia autumnata. Ornis Fenn.* 44: 65–7.

Sinclair, A. R. E. (1978). Factors affecting the food-supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savanna. *Ibis* 120: 480–97.

Sinelschikova, A., Kosarev, V., Panov, I. & Baushev, A. N. (2007). The influence of wind conditions in Europe on the advance in timing of the spring migration of the Song Thrush *(Turdus philomelos)* in the south-east Baltic region. *Int. J. Biometeorol.* 51: 431–40.

Sladen, W. J. L., Lishman, W. A., Ellis, D. H., Shire, G. G. & Riniger, D. L. (2002). Teaching migration routes to Canada Geese

and Trumpeter Swans using ultralight aircraft, 1990–2001. *Waterbirds* 25 (spec. pub. 1) 132–7.

Slagsvold, T. (1976). Arrival of birds from spring migration in relation to vegetational development. *Norw.J. Zool.* 24: 161–73.

Smith, G. D. & McGrady, M. J. (2009). *Using passive integrated transponder (PIT) tags to better understand Peregrine Falcon population in South Scotland and Northeast England.* In: *Peregrine Falcon Populations—Status and Perspectives in the 21st Century* (Eds Sielicki, J. & Mizera, T.). European Peregrine Falcon Working Group, Turul, Warsaw, 399–414.

Smith, H. G. & Nilsson, J.- Å. (1987). Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit *(Parus caeruleus)* an evaluation of different hypotheses. *Auk* 104: 109–15.

Smith, R. D., Marquiss, M., Rae, R. & Metcalfe, N. B. (1993). Age and sex variation in choice of wintering site by Snow Buntings: the effect of altitude. *Ardea* 81: 47–52.

Smith, T. B., Clegg, S. M., Kimura, M., Ruegg, K., Milá, B. & Lovette, I. (2005). *Molecular genetic approaches to linking breeding and overwintering areas infive neotropical migrant passerines.* In: *Birds of Two Worlds* (Eds Greenberg, R. & Marra, P. P.). Smithsonian Institution, Washington, DC, 222–34.

Snow, D. W. (1978). Relationships between European and African avifaunas. *Bird Study* 25: 134–48.

Sokolov, L. V. (1997). Philopatry of migratory birds. *Phys. Gen. Biol. Rev.* 11: 1–58.

Sokolov, L. V. (2000a). Philopatry, dispersal and population structure of passerines on the Courish Spit of the Baltic Sea. *Vogelwarte* 40: 302–14.

Sokolov, L. V. (2001). Climate influence on year-to-year variations in timing of migration and breeding phenology in passerines on the Courish Spit. *The Ring* 231: 159–66.

Sokolov, L. V. (2006). Influence of global warming on the timing of migration and breeding of passerines in the 20th century. *Zool. Zhurnal* 85: 317–42.

Sokolov, L. V., Baumanis, J., Leivits, A., Poluda, A. M., Yefremov, V. D., Markovets, M. Y., Morozov, Y. G. & Shapoval, A. P. (2001). Comparative analysis of long-term monitoring data of numbers of passerines in nine European countries in the second half of the 20th century. *Avian Ecol. Behav.* 7: 41–74.

Sokolov, L. V., Markovets, M. Y. & Morozov, Y. G. (1999). Long-term dynamics of the mean date of autumn migration in passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 2: 1–18.

Sokolov, L. V., Markovets, M. Y., Shapoval, A. P. & Morozov, Y. G. (1998). Long-term trends in the timing of spring migration of passerines on the Courish Spit of the southern Baltic Sea. *Avian Ecol. Behav.* 1: 1–21.

Soloviev, M. Y., Minton, C. D. T. & Tomkovich, P. S. (2006). *Breeding performance of tundra waders in response to rodent abundance and weather from Taimyr to Chukotka, Siberia.* In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 131–7.

Sonerud, G. (1997). Hawk Owls in Fennoscandia: population fluctuations, effects of modern forestry, and recommendations on improving foraging habitats. *J. Raptor Res.* 31: 167–74.

Sonerud, G. A., Solheim, R. & Prestrud, K. (1988). Dispersal ofTengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. *Ornis Scand.* 19: 175–81.

Southern, H. N. (1938a). The spring migration of the Swallow over Europe. *Brit. Birds* 32: 4–7.

Southern, H. N. (1938b). The spring migration of the Willow Warbler over Europe. *Brit. Birds* 32: 202–6.

Southern, H. N. (1939). The spring migration of the Redstart over Europe. *Brit. Birds* 33: 34–8.

Southern, H. N. (1940). The spring migration of the Wood Warbler over Europe. *Brit. Birds* 34: 74–9.

Southern, H. N. (1941). The spring migration of the Redbacked Shrike over Europe. *Brit. Birds* 35: 114–19.

Spaans, A. L. (1977). Are Starlings faithful to their individual winter quarters? *Ardea* 64: 83–7.

Spaar, R. (1997). Flight strategies of migrating raptors: a comparative study of interspecific variation in flight characteristics. *Ibis* 139: 523–35.

Spaar, R. & Bruderer, B.(1996). Soaring migration of Steppe Eagles *Aquila nipalensis* in southern Israel: flight behaviour under various wind and thermal conditions. *J. Avian Biol.* 27: 289–301.

Sparks, T. H. (1999). Phenology and the changing pattern of bird migration in Britain. *Int. J. Biometeorol.*42: 134–8.

Sparks, T. (2000). *The long-term phenology of woodland species in Britain.* In: *Long-term Studies in British Woodlands* (Eds Kirby, K. S. & Morecroft, M. D.). *English Nature Science Series* 34, English Nature, Peterborough, 98–105.

Sparks, T., Heyen, H., Braslavska, O. & Lehikoinen, E. (1999). Are European birds migrating earlier? *BTO News* 223: 8–9.

Sparks, T. & Mason, C. F. (2001). *Dates of arrivals and departures of spring migrants taken from Essex Bird Reports 1950–1998.* In: *Essex Bird Report 1999* (Eds Mullins, A. & Vaughan, H.). Essex Birdwatching Society, Essex, 154–64.

Sparks, T. H., Bairlein, F., Bojarinova, J. G., Hüppop, O., Lehikoinen, E. A., Rainios, K., Sokolov, L. V. & Walker, D. (2005). Examining the total arrival distribution of migratory birds. *Global Change Biol.* 11: 22–30. **Sparks, T. & Tryjanowski,**

P. (2007). Patterns of spring arrival dates differ in two hirundines. *Clim. Res.* 35: 159–64.

Sparks, T. H., Huber, K., Bland, R. L., Crick, H. Q. P., Croxton, P. J., Flood, J., Loxton, R. G., Mason, C. F., Newnham, J. A. & Tryjanowski, P. (2007). How consistent are trends in arrival (and departure) dates of migrant birds in the UK? *J. Orn.* 148: 503–11.

Spendelow, P. (1985). Starvation of a flock of Chimney Swifts on a very small Caribbean island. *Auk* 102: 387–8.

Stenning, M. J., Harvey, P. H. & Campbell, B. (1988). Searching for density-dependent regulation in a population of Pied Flycatchers *Ficedula hypoleuca* Pallas. *J. Anim. Ecol.* 57: 307–17.

Sternberg, H. & Grinkov, V. G.(2006). The effect of hatching date on arrival time in spring, and the timing of breeding in male Pied Flycatchers. *J. Orn.* 147: 108–108.

Stervander, M., Lindström, N., Jonzén, N. & Andersson, A. (2005). Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *J. Avian Biol.* 36: 210–21.

Stevens, G. C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Amer. Nat.* 140: 893–911.

Steyn, P. (1982). *Birds of Prey of South Africa.* David Philip, Cape Town.

Stoate, C. & Moreby, S. J. (1995). Premigratory diet of trans-Saharan migrant passerines in the western Sahel. *Bird Study* 42: 101–6.

Stone, B. H., Sears, J., Cranswick, P. A., Gregory, R. D., Gibbons, D. W., Rehfisch, M. M., Aebischer, N. J. & Reid, J. B. (1997). Population estimates ofbirds in Britain and the United Kingdom. *Brit. Birds* 90: 1–22.

Storey, A. E. & Lien, J. (1985). Development of the first North American colony of Manx Shearwaters. *Auk* 102: 395–401.

Stowe, T. J., Newton, A. V., Green, R. E. & Mayes, E. (1993). The decline of the Corncrake *Crex crex* in Britain and Ireland in relation to habitat. *J. Appl. Ecol.* 30: 53–62.

Strandberg, R., Alerstam, T., Håke, M. & Kjellen, N. (2008). Migration performance in a short-distance migrant, the Common Buzzard *Buteo buteo,* recorded by satellite tracking. *Ibis* 151: 200–06.

Strandberg, R. (2008). Migration strategies of raptors. PhD thesis, University of Lund, Sweden.

Stresemann, E. & Stresemann, V.(1966) Die Mauser der Vögel. *J. Orn.* 107: 3–448.

Studds C. E. & Marra, P. P. (2005). Nonbreeding habitat occupancy and population Proc.ess: an upgrade experiment with a migratory bird. *Ecology* 86: 2380–5.

Studds, C. E. & Marra, P. P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a longdistance migratory bird, *Setophaga ruticilla. Clim. Res.* 35: 115–22.

Summers, R. W. & Underhill, L. (1987). Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii). *Bird Study* 34: 161–71.

Summers, R. W., Underhill, L. G. & Prys-Jones, R. P. (1995). Why do young waders in southern Africa delay their first return migration to the breeding grounds? *Ardea* 83: 351–7.

Svärdson, G. (1953). Visible migration within Fenno-Scandia. *Ibis* 95: 181–211.

Svärdson, G. (1957). The ‘invasion’ type of bird migration. *Brit. Birds* 50: 314–43.

Svazas, S. (2001). Recent changes of the wintering grounds of certain waterfowl populations in Europe determined by means of

the long-term census of wintering birds and ringing recoveries. *Avian Ecol. Behav.* 6: 53–4.

Swann, R. L. & Brockway, I. K. (2007). Site fidelity of Icelandic Greylag Geese between winters. *Ringing & Migration* 23: 238–42.

Swann, R. L. & Ramsay, A. D. K. (1983). Movements from, and age of return to, an expanding Scottish Guillemot colony. *Bird Study* 30: 207–14.

Swennen, C. (1990). Dispersal and migratory movements of Eiders *Somateria mollissima* breeding in the Netherlands. *Ornis Scand.* 21: 17–27.

Szép, T. (1995). Relationship between west African rainfall and the survival of central European Sand Martins *Riparia riparia. Ibis* 137: 162–8.

Szép, T., Møller, A. P., Vallner, J., Kovacs, B. & Norman, D. (2003). Use of trace elements in feathers of Sand Martins *Riparia riparia* for identifying moulting areas. *J. Avian Biol.* 34: 307–20.

Tamisier, A., Allouche, L., Aubry, F. & Dehorter, O. (1995). Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species. *Wildfowl* 46: 76–8.

Tamm, S. (1980). Bird orientation—single homing pigeons compared with small flocks. *Behav. Ecol. Sociobiol.* 7: 319–22.

Tavecchia, G., Baccetti, N. & Serra, L. (2005). Colony specific variation in the use of a moulting site in the migratory Little Tern *Sterna albifrons. J. Avian Biol.* 336: 501–9.

Terrill, S. B. (1987). Social dominance and migratory restlessness in the Dark-eyed Junco *(Junco hyemalis). Behav. Ecol. Sociobiol.* 21: 1–11.

Terrill, S. B. (1990). *Ecophysiological aspects of movements by migrants in the wintering quarters.* In: *Bird Migration: Physiology and Ecophysiology* (Ed. Gwinner, E.). Springer-Verlag, Berlin, 130–43.

Terrill, S. B. & Berthold, P. (1989). Experimental evidence for endogenously programmed differential migration in the Blackcap *Sylvia atricapilla*. *Experientia* 45: 207–9.

Terrill, S. B. & Ohmart, R. D. (1984). Facultative extension of fall migration by Yellow-rumped Warblers *(Dendroica coronata)*. *Auk* 101: 427–38.

Thies, H. (1991). Invasionen des Birkenzeisigs *(Carduelis flammea flammea)* nach Norddeutschland und ihre Ursachen—eine Literaturstudie. *Corax* 14: 73–86.

Thies, H. (1996) Zum Vorkommen des Fichtenkreuzschnabels *(Loxia curvirostra)* und anderer Loxia-Arten im Segeberger Forst 1970–1995 mit besonderer Erörterung der Zugphänologie. *Corax* 16: 305–34.

Thiollay, J. M. (1989). *Distribution and ecology of Palaearctic birds of prey wintering in West and Central Africa.* In: *Raptors in the Modern World* (Eds Meyburg, B.-U. & Chancellor, R. D.). WWGBP, London, 95–107.

Thiollay, J. M. (2006). The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis* 148: 240–54.

Thomas, D. K. (1979). Figs as a food source of migrating Garden Warblers in southern Portugal. *Bird Study* 26: 187–91.

Thompson, P. S., Baines, D., Coulson, J. C. & Longrigg, G. (1994). Age at first breeding, philopatry and breeding site fidelity in the Lapwing *Vanellus vanellus*. *Ibis* 136: 474–84.

Thomson, A. L. (1926). *Problems of Bird Migration.* Houghton Mifflin, London.

Thomson, A. L. (1936). *Bird Migration. A Short Account.* Witherby, London.

Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study* 51: 228–38.

Thorup, K., Alerstam, T., Håke, M. & Kjellen, N. (2003). Can vector summation describe the orientation system of juvenile Ospreys and Honey Buzzards?—An analysis of ring recoveries and satellite tracking. *Oikos* 103: 350–9.

Thorup, K. & Rabøl, J. (2001). The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *J. Avian Biol.* 32: 111–19.

Thorup, K., Ortvad, T. E. & Rabøl, J. (2006). Do Nearctic Northern Wheatears *(Oenanthe oenanthe leucorhoa)* migrate non-stop to Africa? *Condor* 108: 446–51.

Thorup, K., Rabøl, J. & Erni, B. (2007). Estimating variation among individuals in migration direction. *J. Avian Biol.* 38: 182–9.

Tomkovich, P. J. & Soloviev, M. Y. (1994). Site fidelity in high arctic breeding waders. *Ostrich* 65: 174–80.

Tøttrup, A. P. & Thorup, K. (2008). Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *J. Orn.* 149: 161–7.

Townsend, D. J. (1985). Decisions of a lifetime: establishment of spatial defence and movement pattern by juvenile Grey Plovers *(Pluvialis squatarola)*. *J. Anim. Ecol.* 54: 267–74.

Triplet, P. & Yésou, P. (2000). Controlling the flood in the Senegal delta: do waterfowl populations adapt to the new environment? *Ostrich* 71: 106–11.

Troillet, B. & Girard, O. (2006). *Anatidae numbers and distribution in West Africa in winter.* In: *Waterbirds around the World* (Eds Boere, G. C., Galbraith, C. A. & Stroud, D. A.). The Stationery Office, Edinburgh, 226–7.

Troy, D. M. (1983). Recaptures of Redpolls: movements of an irruptive species. *J. Field Orn.* 54: 146–51.

Tryjanowski, P., Kuzniak, S. & Sparks, T. (2002). Earlier arrival of some farmland migrants in western Poland. *Ibis* 144: 62–8.

Tryjanowski, P., Sparks, T. H., Ptaszyk, J. & Kosicki, J. (2004). Do White Storks *Ciconia ciconia* always profit from an early return to their breeding grounds? *Bird Study* 51: 222–7.

Tryjanowski, P. & Yosef, R. (2002). Differences between the spring and autumn migration of the Red-backed Shrike *Lanius collurio:* record from the Eilat stopover (Israel). *Acta. Orn.* 37: 84–90.

Tucker, G. & Heath, M. (1994). *Birds in Europe: Their Conservation Status.* Birdlife International, Cambridge.

Turner, A. (2006). *The Barn Swallow.* T. & A. D. Poyser, London.

Underhill, L. G. (2001). Four of our White Storks vanish into the clouds; one keeps going. *Promerops* 246: 12–14.

UNEP (United Nations Environment Programme). (2002). *Africa environment outlook: past, present and future perspectives.* Earthprint, Stevenage, England.

Vahatalo, A., Rainio, K., Lehikoinen, A. & Lehikoinen, E. (2004). Spring arrival ofbirds depends on the North Atlantic Oscillation. *J. Avian Biol.* 35: 210–16.

Väisänen, R. A. & Hildén, O. (1993). Siemensoyöjät runsastuvat talviruokinnan ansiosta. *Linnut* 28: 21–4 (in Finnish).

van Eerden, M. R., Zylstra, M. & Loonen, M. J. J. E. (1991). Individual patterns of staging during autumn migration in relation to body condition in Greylag Geese *Anser Anser* in the Netherlands. *Ardea* 79: 261–4.

van den Brink, B., Bijlsma, R. B. & van der Hawe, T. M. (2000). European Swallow *Hirundo rustica*in Botswana during three non-breeding seasons: the effects of rainfall on moult. *Ostrich* 71: 198–204.

van der Graaf, A. J., Stahl, J., Klimkowska, A., Bakker, J. P. & Drent, R. H.(2006). Surfing on a green wave—how plant growth

drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* 94: 567–77.

van der Wal, R. J. & Zomerdijk, P. J. (1979). The moulting ofTufted Duck and Pochard on the IJsselmeer in relation to moult concentrations in Europe. *Wildfowl* 30: 99–108.

van der Winden, J. (2002). The odyssey of the Black Tern *Chlidonias niger:* migration ecology in Europe and Africa. *Ardea* 90: 421–35.

van Dijk, A. J., de Roder, F. E., Marteijn, E. C. L. & Spickman, H. (1990). Summering waders on the Banc d Arguin, Mauritania: a census in June 1988. *Ardea* 78: 145–56.

van Gils, J. A., Munster, V. J., Radersma, R., Liefhebber, D., Fouchier, R. A. & Klaassen, M. (2007). Hampered foraging and migratory performance in swans infected with low-pathogenic avian influenza A virus. *PloS ONE* 2: e 184 (doi:10:10.1371/journal. Pone.0000184)

van Gils, J. A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C. (2006). Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biology* 4: 2399–404.

Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea* 85: 135–43.

Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *Auk* 117: 242–6.

Vepsäläinen, K. (1968). The effect of the cold spring 1966 upon the Lapwing *Vanellus vanellus* in Finland. *Ornis Fenn.* 45: 33–47.

Verheyen, R. (1955). Les Linottes, *Carduelis cannabina* (L.), nicheurs et visiteurs d'hiver en Belgique. *Gerfaut* 45: 5–25.

Village, A. (1987). Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. *Ornis Scand.* 18: 198–204.

Village, A. (1990). *The Kestrel.* T. & A. D. Poyser, Calton.

Virolainen, M. (1984). Breeding biology of the Pied Flycatcher *Ficedula hypoleuca* in relation to population density. *Ann. Zool. Fenn.* 21: 187–97.

Visser, M. E., Both, C. & Lambrechts, M. M. (2004). Global climate change leads to mis-timed avian reproduction. In: 'Birds and Climate Change'. *Adv. Ecol. Res.* 35: 89–110.

von Haartman, L. (1971). *Population dynamics.* In: *Avian Biology,* Volume 1 (Eds Farner, D. S. & King, J. R.). Academic Press, London, 391–459.

Votier, S. C., Bearhop, S., Newell, R. G., Orr, K., Furness, R. W. & Kennedy, M. (2004). The first record of Brown Shua *Catharacta antarctica* in Europe. *Ibis* 146: 95–102.

Wallin, K., Wallin, M., Levin, M., Järas, T. & Strandvik, P. (1987). Leap-frog migration in the Swedish Kestrel *Falco tinnunculus* population. *Acta Reg. Soc. Sci. Litt. Gotho. Zool.* 14: 213–22.

Wallraff, K. G. (2003). Zur olfakorischen Navigation der Vögel. *J. Orn.* 144: 1–31.

Walls, S. S. & Kenward, R. E. (1998). Movements of radiotagged Buzzards *Buteo buteo* in early life. *Ibis* 140: 561–8.

Walter, H. (1979). *Eleonora's Falcon. Adaptations to Prey and Habitat in a Social Raptor.* University of Chicago Press, Chicago.

Wanink, J. H. & Goudswaard, K. (2000). The impact of Lake Victoria's lakefly abundance on Palaearctic passerines. *Ostrich* 71: 194–7.

Wanless, S. & Okill, J. D. (1994). Body measurements and flight performance of adult and juvenile Gannets *Morus bassanus. Ringing & Migration* 15: 101–3.

Ward, P. (1963). Lipid levels in birds preparing to cross the Sahara. *Ibis* 105: 109–11.

Ward, D. H., Rexstad, E. S., Sedinger, J. S., Lindberg, M. S. & Dawe, N. K. (1997). Annual survival of Pacific Brant. *J. Wildl. Manage.* 61: 773–81.

Warham, J. (1990). *The Petrels. Their Ecology and Breeding Systems.* Academic Press, London.

Warren, S. M., Fox, A. D., Walsh, A. J., Merne, O. J. & Wilson, H. J. (1992). Wintering site interchange amongst Greenland White-Fronted Geese *Anser albifrons flavirostris* captured at Wexford Slobs, Ireland. *Bird Study* 39: 186–94.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993). Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110: 325–42.

Weindler, P., Wiltschko, R. & Wiltschko, W. (1996). Magnetic information affects the stellar orientation of young bird migrants. *Nature* 383: 158–60.

Welham, C. V. J. (1994). Flight speeds of migrating birds: a test of maximum range speed predictions from three aerodynamic equations. *Behav. Ecol.* 5: 1–8.

Wennerberg, L. (2001). Breeding origin and migratory pattern of Dunlin *(Calidris alpina)* revealed by mitochondrial DNA analysis. *Mol. Ecol.* 10: 1111–20.

Wenzel, B. M. (1991). Olfactory abilities of birds. *Proc.. Int. Orn. Congr.* 20: 1820–9.

Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M. & Baillie, S. R. (2002). *The Migration Atlas: Movements of the Birds of Britain and Ireland.* T. & A. D. Poyser, London.

Whitfield, D. P. (2003). Predation by Eurasian Sparrowhawks produces density dependent mortality of wintering Redshanks. *J. Anim. Ecol.* 72: 27–35.

Whittington, P. A., Dyer, B. M., Crawford, R. J. M. &

Williams, A. J. (1999). First recorded breeding of Leach's Storm Petrel *Oceanodroma leucorhoa* in the southern hemisphere, at Dyer Island, South Africa. *Ibis* 141: 327–30.

Widmer, M. & Biebach, H. (2001). Changes in body condition from spring migration to reproduction in the Garden Warbler *Sylvia borin:* a comparison of a lowland and a mountain population. *Ardea* 89: 57–68.

Wiggins, D. A., Part, T. & Gustaffson, L. (1994). Seasonal decline in Collared Flycatcher *Ficedula albicollis* reproductive success: an experimental approach. *Oikos* 70: 359–64.

Williams, G. C. (1950). Weather and spring migration. *Auk* 67: 52–65.

Williams, G. R. (1953). The dispersal from New Zealand and Australia of some introduced European passerines. *Ibis* 95: 676–92.

Williams, T. C. & Williams, J. M. (1990). *The orientation of transoceanic migrants.* In: *Bird Migration: Physiology and Ecophysiology*(Ed. Gwinner, E.). Springer-Verlag, Berlin, 7–21.

Williams, T. C., Williams, J. M., Ireland, L. C. & Teal, J. M. (1977). Bird migration over the western North Atlantic Ocean. *Amer. Birds* 31: 251–67.

Williamson, K. (1955). Migrational drift. *Proc.. Int. Orn. Congr.* 11: 179–86.

Wilson, G. E. (1976). Spotted Sandpipers nesting in Scotland. *Brit. Birds* 69: 288–92.

Wiltschko, R. (1992). Das Verhalten verfrachteter Vögel. *Vogelwarte* 36: 249–310.

Wiltschko, R. & Wiltschko, W. (1995). Magnetic orientation in animals. Springer-Verlag, Berlin.

Wiltschko, R. & Wiltschko, W. (1999). The orientation system of birds—III. Migratory orientation. *J. Orn.* 140: 273–308.

Wiltschko, R. & Wiltschko, W. (2003). *Mechanisms of orientation and navigation in migratory birds.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 433–56.

Wiltschko, W. (1968). Über den Einfluss statischer Magnetfelder auf die Zugorientierung der Rotkehlchen *(Erithacus rubecula)*. *Z. Tierpsychol.* 25: 537–58.

Wiltschko, W. & Gwinner, E. (1974). Evidence for an innate magnetic compass in Garden Warblers. *Naturwissenschaften* 61: 406.

Wiltschko, W. & Merkel, F. W. (1971). Zugorientierung von Dorngrasmucken *(Sylvia communis)*. *Vogelwarte* 26: 245–9.

Wiltschko, W., Daum-Benz, P., Fergenbauer-Kimmel, A. & Wiltschko, R. (1987). The development of the star compass in Garden Warblers *Sylvia borin*. *Ethology* 74: 285–92.

Wiltschko, W., Weindler, P. & Wiltschko, R.(1998). Interaction of magnetic and celestial cues in the migratory orientation of passerines. *J. Avian Biol.* 29: 606–17.

Wiltschko, W. & Wiltschko, R. (1972). Magnetic compass of European Robins. *Science* 176: 62–4.

Wiltschko, W. & Wiltschko, R.(1975a). The interaction of stars and magnetic field in the orientation system of night-migrating birds. I. Autumn experiments with European warblers (Gen. *Sylvia)*. *Z. Tierpsychol.* 37: 265–82.

Wiltschko, W. & Wiltschko, R. (1975b). The interaction of stars and magnetic field in the orientation system of night-migrating birds. II. Spring experiments with European Robins. *Z. Tierpsychol.* 37: 337–55.

Wiltschko, W. & Wiltschko, R. (1992). Migratory orientation: magnetic compass orientation of Garden Warblers *(Sylvia borin)* after a simulated crossing of the magnetic equator. *Ethology* 91: 70–9.

Wiltschko, W. & Wiltschko, R. (2007). Magnetoreception in birds: two receptors for two different tasks. *J. Orn.* 148: S61-S76.

Wingfield, J. C. (2003). *Avian migration regulation of facultative-type movements.* In: *Avian Migration* (Eds Berthold, P., Gwinner, E. & Sonnenschein, E.). Springer-Verlag, Berlin, 113–25.

Wingfield, J. C., Doak, D. & Hahn, T. P. (1993). *Integration of environmental cues regulating transitions of physiological state, morphology and behaviour.* In: *Avian Endocrinology* (Ed. Sharp, P. J.). Society for Endocrinology, Bristol, 111–22.

Winstanley, D. R., Spencer, R. & Williamson, K. (1974). Where have all the Whitethroats gone? *Bird Study* 21: *1–14.*

Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. (1994). Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris. Anim. Behav.* 48: 201–22.

Wojtusiak, R. J. (1949). Polish investigations on homing in birds and their orientation in space. Proc. *Linn. Soc. Lond.* 160: 99–108.

Wolff, W. J. (1970). Goal orientation versus one-direction orientation in Teal, *Anas c. crecca* during autumn migration. *Ardea* 58: 131–41.

Wolfson, A. (1959). *Ecologic and physiologic factors in the regulation of spring migration and reproductive cycles in birds.* In: *Comparative Endocrinology* (Ed. Gorbman, A.). Wiley, New York, 38–70.

Wood, B. (1992). Yellow Wagtail *Motacillaflava* migration from West Africa to Europe: pointers towards a conservation strategy for migrants on passage. *Ibis* 134 (suppl. 1): 66–76.

Wyllie, I. (1981). *The Cuckoo.* Batsford, London.

Yésou, P. (1995). Individual migration strategies in Cormorants *Phalacrocorax carbo* passing through or wintering in western France. *Ardea* 83: 267–74.

Yong, W. & Moore, F. R. (1993). Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. *Condor* 95: 934–43.

Yosef, R. & Chernetsov, N. (2005). Longer is fatter: body mass changes of migrant Reed Warblers *(Acrocephalus scirpaceus)* staging at Eilat, Israel. *Ostrich* 76: 142–7.

Zalakevicius, M., Bartkeviciene, G., Raudonikis, L. & Janultaitis, J. (2006). Spring arrival response to climate change in birds: a case study from eastern Europe. *J. Orn.* 147: 326–43.

Zalakevicius, M. & Zalakeviciute, R. (2001). Global climate warming and birds: a review of research in Lithuania. *Folia Zool.* 50: 1–17.

Zimin, V. B. (2001). Seasonal changes in the composition of marked population of Robins *Erithacus rubecula* in the Ladoga area. *Avian Ecol. Behav.* 6: 37–8.

Zink, G. (1981). *Der Zug Europäischer Singvögel.* Vogelzug-Verlag, Moggingen.

Zink, G. & Bairlein, F. (1995). *Der Zug Europäischer Singvögel.* AULA-Verlag, Wiesbaden.

Zonfrillo, B. (1983). Isle of May Bird Observatory and Field Station report for 1982. *Scott. Birds* 12: 218–24.

Zuckerbrot, Y. D., Safriel, U. N. & Paz, U. (1980). Autumn migration of Quail *Coturnix coturnix* at the north coast of the Sinai peninsula. *Ibis* 122: 1–14.

Zwarts, L., Blomert, A. M. & Hupkes, R. (1990). Increase of feeding time in waders preparing for spring migration from the Banc D Arguin, Mauritania. *Ardea* 78: 237–56

Glossary

Abmigration. The movement of a bird from one flyway to another, resulting in long breeding or wintering dispersal.

Accidental. A vagrant or stray species, not normally found in the region concerned.

Adaptation. Any feature of an organism that improves its ability to survive or reproduce compared with ancestral forms or with other coexisting individuals.

Adult plumage. The final breeding plumage of a bird; also called definitive or basic plumage.

Afrotropical region. Africa south of the Sahara desert, including Madagascar and other nearby islands.

Altitudinal migration. Seasonal return movement between higher and lower elevations in the same region.

Annual cycle. The yearly cycle of activities, including breeding, moult and migration, which in most bird species occur in regular sequence at about the same times each year.

Anti-trade winds. Upper winds at low latitudes that flow counter to the trade winds below them.

Aspect ratio. A measure of the shape of a bird's wing, calculated as wingspan squared divided by wing area.

Austral migration. Migration of southern hemisphere breeding birds.

Australasia. The biogeographical region embracing Australia, New Zealand, New Guinea, Tasmania, Timor, New Caledonia and

several smaller islands.

Azimuth. A compass bearing towards the sun in its present position (only the direction, not the vertical angle).

Barrier. Any physical feature that would usually prevent or restrict the movement of organisms from one side to the other.

Basal metabolic rate (BMR). The lowest rate at which an inactive bird consumes energy. See also **Metabolic rate.**

Beaconing. Goal-oriented movement based on following a stimulus emanating from the next goal.

Bergman's Rule. The tendency for individuals of a warm-blooded species to increase in body size towards the cooler parts of the range.

Bi-coordinate navigation. Navigation based on a virtual grid map involving gradients in two variables running in different directions from one another, enabling particular locations to be fixed. Indicates a 'map sense'.

Bird observatory. A field station manned for the purpose of observing, catching and marking migrant birds.

Bottleneck. In migration studies, a narrow corridor through which migrants must pass, such as a mountain pass or land bridge.

Botulism. A fatal paralysis caused by a neurotoxin produced by *Clostridium botulinum,* an anaerobic bacterium that thrives in rotting organic matter in shallow stagnant waters or mud during warm weather.

Breeding area/range. In migratory birds, the area in which a population reproduces.

Breeding dispersal. Movement between the breeding sites of an individual in different years. Measured as the distance between those breeding sites. See also **Natal dispersal, Non-breeding dispersal, Wintering dispersal.**

Broad-front migration. Migration across a region, with minimal streaming by topographic or other features.

Calendar effect. The tendency of birds to alter a physiological/behavioural Proc.ess with date; for example, moulting or migrating more rapidly, or at an earlier age, as the season advances.

Chain migration. The situation in which migratory populations that breed furthest north also winter furthest north, while populations that breed furthest south also winter furthest south, thus retaining the same latitudinal sequence summer and winter. Sometimes one population may occupy an area in summer, and another from a higher latitude in winter.

Circadian. From the Latin 'circa' meaning 'about', and 'dies' meaning 'day'. Literally 'about a day'. Usually applied to patterns of activity, such as sleep and wakefulness, which comprise the daily cycle of birds, and which deviate from a strictly diurnal schedule in individuals kept under constant light or darkness.

Circadian clock. An internal (body) clock that times physiological and behavioural Proc.esses during the diurnal cycle. Normally kept to 24 hours by the daily light–dark cycle.

Circadian cycle/rhythm. A regular cycle of bodily activities and functions which, in the absence of external cues, repeats with a periodicity of about 24 hours and is driven by the circadian clock (see above).

Circannual cycle/rhythm. From the Latin 'circa' meaning 'about', and 'annus' meaning 'year'. Literally 'about a year'. Applied to Proc.esses, such as breeding, moult and migration, which comprise the annual cycle of a bird, and are controlled partly by an endogenous rhythm (body clock).

Compass orientation. Orientation in a compass direction (either geographic or magnetic). Keeping a constant angle towards an external reference system to give a straight migration direction.

Competition. Any interaction that is detrimental to one or both participants, excluding parasitism and predation. It may involve *depletion,* where some individuals reduce the amount of a resource available to others, or *interference,* where some individuals, by aggression or other means, reduce access to a resource by other individuals.

Complete migrants. Obligate migrants, in which the entire population of a region migrates every year.

Connectivity. In migration studies, the link between breeding and non-breeding areas. Migratory connectivity can be weak (diffuse) or strong, depending on the degree to which individuals from different breeding areas mix in non-breeding areas or separate into different parts of a non-breeding area.

Crosswind. A wind blowing more or less perpendicular to the travel direction.

Cue conflict. The situation in which different environmental cues, which normally give the same message, give different messages. More specifically, when under experimental conditions, celestial and magnetic compasses indicate different directions.

Deferred maturity. Breeding for the first time, not in the first year, but in a later one.

Deferred migration. The situation in which young birds, having reached their non-breeding areas, remain there for one or more years before returning to the breeding range as they approach reproductive age. See also **Graded migration.**

Density dependent. Applied to a populationregulating factor which encourages numbers to increase when they are low, and to decrease when they are high, resulting in density-related changes in reproduction or mortality, immigration or emigration. Potential regulating factors include competition for food and other resources, parasitism (or infectious disease) and predation, all of which can affect greater proportions of individuals as their numbers rise.

Density independent. Applied to a population-limiting factor, such as severe weather or other natural disasters, which affects individuals in proportions that bear no consistent relationship to population size. Such factors tend to cause fluctuations in populations, rather than regulate them within restricted limits.

Differential migration. The situation in which some classes of individuals (ages, sexes) differ with respect to timing and distance of migration. See also **Partial migration.**

Digiscope. In ornithology, a digital camera attached to, or held against, a telescope.

Disorientation. Inability to follow a consistent direction on migration.

Dispersal. In ecology, the movement of an individual from its current place of residence, usually in no fixed direction or distance (see also **Natal dispersal, Breeding dispersal, Nonbreeding dispersal** and **Wintering dispersal).** In biogeography, range extension over a preexisting barrier.

Dispersion. The spatial distribution of individuals within a local population.

Displacement experiments. The capture of wild birds, their transport to a different site, release and follow-up. Commonly used to study orientation and homing behaviour.

Diurnal. Active during daylight hours.

Diurnal cycle. The daily cycle of activities, including feeding, rest, sleep and bodily functions.

DNA. Deoxyribonucleic acid, the double-stranded molecule that encodes and transmits genetic inheritance. It is present in the nucleus of every living cell. See also **Mitochondrial DNA.**

Doppler effect. An apparent change in the frequency of waves due to a relative motion between transmitter and receiver. It occurs when the transmitting source is moving towards or away from the

reception point, or whose source is fixed while the reception point is moving (as in satellite-based radio-tracking).

Drift. The extent to which a migrating bird is blown off course by wind.

Dry weight. Weight minus the water fraction.

Dynamic soaring. A form of soaring, mainly over water, dependent on a gradient of increasing wind speed upwards from the surface. Typically, a bird heads into the wind to gain height, then turns to glide with the wind, gradually losing height, and then repeats the Proc.ess, again and again, thereby travelling over long distances.

Eclipse plumage. Dull plumage worn by male ducks between successive bright plumages. Equivalent to 'winter plumage' in some other species, but worn for a shorter period postbreeding.

Emigration. Dispersal or migration away from an area.

Endogenous (rhythm). Internally generated and not dependent on (but may be modified by) an external stimulus. Usually applied to seasonal and diurnal Proc.esses, such as gonad growth and moult, which can occur autonomously in birds kept under a limited range of constant photoperiodic conditions.

Equinox. The twice-yearly date when, owing to the changing tilt of the earth, the sun appears to cross the equator, and when throughout the world, day and night are of equal length, usually about 21 March (spring equinox) and 21 September (autumn equinox).

Eruption. In migration studies, a massive emigration from a particular region. See also **Irruption.**

Escape movements. Mass movements from areas where conditions suddenly become hazardous for survival, as after deep snowfall. See also **Weather movements.**

Facultative. Applies to organisms that can adopt alternative modes of living. They are able, but not obliged, to behave in alternative

ways. Individual facultative migrants can choose whether to migrate or not, depending on prevailing conditions.

Fall. The sudden descent from sky to ground of large numbers of migrants, as they encounter adverse weather or seek refuge after a long flight.

Fat-free dry weight. The weight of a carcass, minus water and fat (lipid). The same as lean dry weight.

Fat-free weight. Weight minus fat (lipid) content. The same as lean weight.

Fidelity. Faithfulness, usually applied to a locality or mate; see **Mate-fidelity, Site-fidelity.**

Flight feathers. The large feathers of the wings, including primaries (attached to the bones of the 'hand') and secondaries (attached to the ulna, the inner bone of the 'forearm').

Flight muscles. The 'breast' muscles, including the pectoralis and supracoracoideus muscles of both sides, concerned respectively with downward and upward strokes of the wings.

Flight style. Two main styles involve flapping flight (powered by muscles) and soaring–gliding flight (powered by air currents). The former can be divided into continuous flapping, flap-gliding and bounding.

Flyway. An established route used year after year by large numbers of migrating birds.

Fresh weight. The weight of a carcass preserved without any evaporative water loss, equivalent to live weight.

Gene flow. The movement of genetic material within a population or between populations caused by the dispersal of individuals (or gametes in some animals, pollen or seeds in plants), or the hybridisation of individuals from different taxa.

Genotype. The totality of genetic factors that make up the genetic constitution of an individual. Alternatively, those components of

an individual's phenotype that result from genetic (as opposed to environmental) influences. See also **Phenotype.**

Gliding. Coasting with outstretched wings, usually with unfanned tail.

Goal orientation. Directed movement towards a known, desired destination.

Graded migration. The situation in which mainly young age classes, rather than returning to the breeding range in their first year, move progressively nearer the breeding range in successive years until they approach breeding age.

Great circle route. The shortest route between two points on the earth's surface. As the earth is a sphere, a great circle route requires progressive change in direction along the route, except on a north-south axis. Contrasts with **Rhumbline route.**

Heading. The direction of flight, as opposed to the track which results from the net effect of bird speed and direction and wind speed and direction.

Headwind. A wind aligned against the preferred direction of travel, slowing the bird.

Hirundine. Bird of the swallow family.

Holarctic region. The extra-tropical zone of the northern hemisphere, which includes both the Nearctic (North America) and Palaearctic (Eurasia) regions.

Home range. The area over which an individual habitually wanders during its day-to-day life, often centred on nest or roost sites.

Hyperphagia. The act of eating more per day than usual, in order to put on weight.

Immature. Non-specific term for 'pre-adult'. Often the stage, with distinct plumage(s), between juvenile and adult plumages.

Immigration. The arrival of new individuals from elsewhere; in biogeography, often to a previously unoccupied area.

Internal clock. An endogenous timekeeper (or body clock) which leads an animal to perform the same activities at approximately the same times of day or year. See **Circadian clock, Circannual cycle.**

Inter-Tropical Convergence Zone (ITCZ). A zone of low pressure circling the earth, where northwest trade winds meet southeast trade winds, and where rain falls. During the course of each year, the zone moves north then south of the equator, bringing distinct wet and dry seasons to large parts of the tropics, but six months out of step between the two hemispheres. Rain falls heaviest and longest on the equator, and declines in duration and amount with increasing distance to the north and south. In sea areas, the position of the zone is marked by almost windless conditions—the doldrums.

Invasion. In migration studies, the same as **Irruption.**

Irruption. In migration studies, a massive immigration to a particular region. More generally, a form of migration in which the proportion of individuals that participate, and the distances they travel, vary greatly from year to year. See also **Eruption.**

Isotherm. Contour line of equal temperature.

Isotope. A distinct form of an element distinguished by the nuclear mass of its atoms.

Jet stream. A stream of fast-flowing air at high altitude, usually travelling at more than 110 km per hour, and frequently at more than 180 km per hour.

Juvenile. Bird in its first complete feathered plumage, distinct from later plumages. Also used to describe birds in their first year of life.

Leading line. A topographical feature, such as a coastline, escarpment or river valley, along which migrating birds tend to fly.

Lean dry weight. Dry weight, minus the entire fat (lipid) and water contents.

Lean weight. Weight, minus fat (lipid) content.

Leapfrog migration. The situation in which higher-latitude breeding populations overfly lower-latitude breeding populations to winter beyond them, thus reversing their latitudinal sequence of distribution between summer and winter.

Limiting factor. In population ecology, the environmental parameter that most limits the size or distribution of a population.

Lipid weight. The weight of lipid (fat) in a carcass.

Live weight. The weight of a living bird.

Loop migration. The situation in which birds take markedly different routes on their outward and return journeys.

Loxodrome. Same as **Rhumbline route.**

Magnetic compass. A compass based on the earth's magnetic field.

Magnetic declination. The deviation of magnetic north from true north.

Magnetic inclination. The angle of the earth's magnetic force lines, which varies from horizontal at the magnetic equator to vertical at the magnetic poles.

Magnetic poles. The two points, on the north and south sides of the earth, between which compass needles line up.

Map-based navigation. Ability to determine spatial position with respect to home, or at least the direction toward home, based solely on information at the current distant position. Equivalent to map-and-compass navigation, or 'map sense'.

Mate-fidelity. Tendency to remain with, or re-pair with, the same breeding partner in different years.

Maximum range speed (Vmr). The speed at which the bird achieves the maximum flight range on the energy available.

Faster than **Minimum power speed (Vmp).**

Metabolic rate. The rate at which food and body reserves are converted to energy, including heat production, and usually expressed as kcal per bird per day. See also **Basal metabolic rate (BMR).**

Migrant. A bird that undertakes migration.

Migration. Applied to birds, a regular seasonal movement between separate breeding and non-breeding (wintering) areas. Applied to other animals, sometimes used more broadly for travel that occurs in a periodically and geographically predictable way, whether once or more times. In other branches of ecology, also used for range extension or shift, as in post-glacial times.

Migratory disposition. A state of readiness to migrate.

Migratory divide. An imaginary line on a map which separates breeding populations migrating in different directions. On one side of the line, birds migrate in one direction (say southwest), while on the other side, they migrate in another direction (say southeast). Also used for individuals from the same breeding area in which some migrate in one direction and others in another direction.

Migratory fat. The fat laid down as fuel (usually along with protein) in preparation for migration.

Migratory restlessness. A state of high activity in captive birds, thought to indicate their readiness to migrate. Usually occurs by day in diurnal migrants and by night in nocturnal migrants.

Migratory state/disposition. A state of readiness for migration, usually with appropriate body reserves, directional preferences and weather responses.

Migratory stream. A stream of migrants concentrated by topographic features, such as a coastline, escarpment or valley.

Minimum power speed (Vmp). The speed at which the bird consumes the least energy per unit time, and which therefore gives the maximum time airborne.

Mirror-image migration. Migration along the correct angle to the north–south axis, but on the wrong side of that axis; for example, southeast rather than southwest.

Misorientation. Taking the wrong migratory direction, but consistently.

Mitochondrial DNA (mtDNA). A small haploid DNA molecule housed in the mitochondria of cells. It does not recombine at fertilisation, but is clonally and maternally inherited, transmitted from mother to offspring of both sexes, and passed unchanged (except for mutation) down the generations.

Moult. Scheduled plumage renewal, or partial renewal, but excluding the unscheduled replacement of feathers lost accidentally.

Moult migration. Movement to a special place for moult. Typical participants include some ducks and other waterbirds which, after arrival at the moulting site, shed all their flight feathers simultaneously and become flightless for a few weeks until new ones are grown.

Mutation. An error in the replication of a nucleotide sequence or any other alteration in the genome that is not due to recombination, but which can sometimes change some characteristic of the organism.

Natal dispersal. Movement from birthplace to breeding place. Measured as the distance between natal and breeding sites of individuals. See also **Breeding dispersal, Wintering dispersal.**

Natural selection. The elimination from a population, through differential survival and reproduction, of those individuals less adapted to prevailing conditions.

Navigation. Following a specific course to a distant goal. Contrasts with **Orientation,** which is compass-directed only.

Niche. The specific habitat and food preferences of a species.

NOA. See **North Atlantic Oscillation.**

Nocturnal. Active during the hours of darkness. Nocturnal migrants include some normally diurnal species.

Nomadic. Having no fixed directional preferences, and often no fixed seasons of movement.

Nomadism. Movements that lead to irregular changes in distribution.

Non-breeding area. Area occupied between breeding seasons, or by immature birds at any season, usually after a migration. Also called **Wintering area.**

Non-breeding dispersal. Movement between nonbreeding sites of different years. Measured as the distances between the non-breeding sites of the same individuals in different years. See also **Wintering dispersal.**

Non-compass orientation. Oriented movement based on external stimuli, such as topographic features.

North Atlantic Oscillation (NAO). A large-scale climate phenomenon influencing weather in this region. Positive values indicate warmer and wetter winter-spring weather in northwest Europe, and the opposite conditions in southern Europe.

Obligate. Applies to organisms that have to behave in a particular way to survive and whose behaviour is innate. More specifically, individual obligate migrants migrate every year, and do not have the option of migrating or not, their behaviour being genetically fixed.

Orientation. The direction in which a migrant bird heads to a specific or non-specific goal. See also **Compass orientation.**

Orographic lift. Lift gained by soaring birds when they exploit the upward-directed air current caused by a horizontal wind striking a cliff or slope.

Orthodrome. Same as **Great circle route.**

Overshoot. Migration in the customary direction, but further than usual, leading to the appearance of birds in spring or autumn beyond the usual breeding or wintering areas.

Palaearctic region. The biogeographical region of extra-tropical climates in Eurasia and northernmost Africa.

Partial migration. A situation in which some birds from a given breeding area migrate away for the non-breeding season, while others remain in the breeding area year-round. See also **Differential migration.**

Passerine. Songbird.

Phenotype. The outward characteristics of an individual that result from a combination of genetic and environmental influences. See also **Genotype.**

Phenotypic flexibility/plasticity. The ability of a given genotype to produce different phenotypes or behaviours in response to different environmental conditions. The degree of flexibility is itself controlled genetically. See also **Facultative.**

Philopatry. The tendency of an individual to stay in, or return to, its home area (or birthplace).

Photoperiod. The light part of the 24-hour cycle, which can be adjusted experimentally.

Piloting. Goal-directed orientation based on following a sequence of familiar landmarks. See also **Beaconing** and **Navigation.**

Post-fledging dispersal. The movements in any direction from the natal site of newly independent young.

Pre-nuptial moult. A moult leading to the acquisition of breeding plumage.

Primaries. The outer large flight feathers, grown from the 'hand' of a bird. Along with the secondaries (grown from the 'forearm'), these feathers comprise the main 'flight feathers'.

Proximate factors. External stimuli (such as daylengths) which are used as cues by a bird to trigger preparation for breeding, migration or other events, or as timekeepers to set their endogenous time programmes at appropriate times of year.

Quiescent period. A part of the annual cycle when a bird is not breeding, moulting or migrating.

Radio-telemetry. The transfer of information collected from a remote source (such as a bird) to a receiver.

Radio-tracking. The location and tracking of a radio-marked individual from a signal emitted frequently by the radio.

Range. Large-scale geographical distribution.

Raptor. Bird of prey.

Refuge. In ecology, an area in which climate and vegetation type have remained relatively unchanged, while adjacent areas have changed markedly (as in glacial refuge). In wildlife management, a protected area of suitable habitat.

Resident. Remaining year-round in the same area; applied both to individuals and populations.

Reversed migration. Migration in a direction opposite to that expected for the time of year. Also known as reversed-direction migration, when applied to the whole journey.

Rhumbline route. A route between two points on the earth's surface that can be followed by maintaining a constant heading (direction) throughout. Longer than a **Great circle route,** except when directly north–south.

Satellite telemetry/tracking. A method of determining the location or other information from a bird attached with a small radio transmitter. The transmitter (known as a platform terminal

transmitter, PTT) emits a signal that is picked up by satellites orbiting the earth.

Seasonal. Applied to areas experiencing marked and regular changes in climate (and biological productivity) through the year, and to behaviours which occur only at certain times of year.

Sedentary. Remaining in the same limited area; non-migratory. See **Resident.**

Serial moult. A pattern of wing moult in which the bird has more than one locus of feather growth in the primaries or secondaries at once. Same as **Step moult.**

Short-stopping. Curtailment of an outward journey, usually in the presence of abundant food. If this situation persists, it can give rise to a change in wintering area.

Site-fidelity. The tendency to remain in, or return to, the same localities in different years.

Soaring. Gliding in circles with spread wings and tail, while gaining altitude in a rising air current.

Solstice. The dates each year when the tilt of the earth ensures that the sun reaches at each latitude its highest (summer solstice) and lowest (winter solstice) points in the sky, and when days reach their longest and shortest respectively, around 21 June and 21 December. The summer solstice in the northern hemisphere corresponds with the winter solstice in the southern hemisphere.

Split migration. A migration that is separated into two or more main parts by breaks of weeks or months, much longer than needed merely to replenish spent body reserves.

Split moult. A moult that is interrupted and separated into two or more main parts. Different feathers are replaced in each part.

Staging area. A place where large numbers of birds assemble before migration or break their journeys, usually to refuel but sometimes also to moult.

Star compass. A compass based on stellar cues, usually indicating geographical north or south.

Step moult. Same as **Serial moult.**

Stopover. A pause in a migratory journey.

Stopover site. A place where a bird stops on migration, including **Staging areas.**

Sun compass. A compass based on the position of the sun in the sky. As this position changes during the day, an animal must take account of this, by way of an internal clock.

Tailwind. Wind aligned more or less in the direction of travel, which therefore increases the bird's speed with respect to the ground.

Telescopic migration. The situation in which birds breeding in a wide span of latitude concentrate to spend the non-breeding season in a narrower span of latitude, giving no obvious chain or leapfrog patterns.

Territory. A defended area, from which other individuals of the same species (other than mate and dependent offspring) are normally excluded.

Territorial behaviour. The act of defending an area through advertisement and aggression.

Thermal. A column of rising air, within which birds circling on outstretched wings can gain height.

Thermal streets. Lines of thermals, along which birds can glide without losing height. The individual thermals are often topped with cumulus clouds, giving rise to 'cloud streets'.

Timekeeper. Usually applied to environmental cues, such as daylength, to which birds respond when preparing to migrate, breed or moult. See also **Proximate factors.**

Track. The course resulting from the net effect of the speed and flight direction of the bird and the speed and direction of the

wind.

Trade winds. An old maritime term for the prevailing tropical easterly winds which blow from subtropical high-pressure areas in latitudes 30–40°N and S, generally north from the northeast in the northern hemisphere and from the southeast in the southern hemisphere.

Ultimate factors. Factors that determine the value of a behaviour in the evolutionary sense, and lead birds to migrate, breed and moult, for example, at particular times of year.

Vagrancy. The appearance of birds outside their regular ranges, and off their usual migration routes.

Vagrant. A bird seen outside its regular range and migration route.

Vector navigation. Migration on an innate predetermined direction for a set period (equivalent to distance); also called clock-and-compass, time-and-direction or bearing-and-distance navigation. Usually pertains to young birds migrating to unfamiliar areas.

Vmp. See **Minimum power speed.**

Vmr. See **Maximum range speed.**

Weather movements. Any mass movements stimulated by extreme weather.

Wind drift. Applied to migrants blown off course, usually by crosswinds.

Wind tunnel. A tunnel, equipped with a powerful fan for driving through air at speed, facilitating the study of bird flight. The air speed can be adjusted so that the bird flies against it, thereby maintaining a constant position in a short section of the tunnel with a window, so that the bird can be kept under observation.

Wing area. The projected surface area of the wings, including the intervening part of the body, usually expressed in square metres.

Wing loading. Body weight divided by wing area, measured with the wings outstretched. The lower the wing loading of a species,

the more buoyant the flight.

Wingspan. The distance from wing-tip to wing-tip at full extent.

Wintering/non-breeding area/range. In migratory birds, the area where populations spend the non-breeding season, usually at lower latitudes.

Wintering dispersal. Movement between the wintering sites of different years. Measured as the distances between the wintering sites of the same individuals in different years. See also **Non-breeding dispersal.**

Index

The pagination of this electronic edition does not match the edition from which it was created. To locate a specific passage, please use the search feature of your e-book reader

SPECIES INDEX

Accentor, Hedge – *see* Dunnock
Accipiter brevipes – *see* Sparrowhawk, Levant
Accipiter gentilis – *see* Goshawk, Northern
Accipiter nisus – *see* Sparrowhawk, Eurasian
Acrocephalus arundinaceus – *see* Warbler, Great Reed
Acrocephalus paludicola – *see* Warbler, Aquatic
Acrocephalus palustris – *see* Warbler, Marsh
Acrocephalus scirpaceus – *see* Warbler, Reed
Acrocephalus schoenobaenus, see Warbler, Sedge,
Actitis hypoleucos – *see* Sandpiper, Common
Actitis macularia – *see* Sandpiper, Spotted
Aegithalos caudatus – *see* Tit, Longtailed
Aegolius funereus – *see* Owl, Tengmalm's (Boreal)
Alauda arvensis – *see* Skylark, Eurasian
Albatross, Black-browed, *Diomedia (Thalassarche) melanophris* 305
Albatross, Grey-headed, *Thalassarche chrystostoma* 10
Albatross, Laysan, *Diomedia immutabilis* 233, 250, 559, 565
Albatross, Wandering, *Diomedia exulans* 555, 579

Alca torda – *see* Razorbill
Alcedo atthis – *see* Kingfisher, Common
Alder, *Alnus* 394, 396, 402
Alle alle – *see* Auk, Little
Alnus – *see* Alder
Anas acuta – *see* Pintail, Northern
Anas americana – *see* Wigeon, American
Anas carolinensis – *see* Teal, Greenwinged
Anas clypeata – *see* Shoveler, Northern
Anas crecca – *see* Teal, Eurasian
Anas discors – *see* Teal, Blue-winged
Anas penelope – *see* Wigeon, Eurasian
Anas platyrhynchos – *see* Mallard
Anas strepera – *see* Gadwall
Anas querquedula – *see* Garganey
Anas rubripes – *see* Duck, American Black
Anser albifrons – *see* Goose, Greater White-fronted
Anser anser – *see* Goose, Greylag
Anser brachyrhynchus – *see* Goose, Pink-footed
Anser c. caerulescens – *see* Goose, Snow
Anser fabalis – *see* Goose, Bean
Anser indicus – *see* Goose, Barheaded
Anthropoides virgo – *see* Crane, Demoiselle
Anthus campestris – *see* Pipit, Tawny
Anthus cervinus – *see* Pipit, Redthroated
Anthus gustavi – *see* Pipit, Pechora
Anthus novaeseelandiae – *see* Pipit, Richard's
Anthus pratensis – *see* Pipit, Meadow
Anthus rubescens – *see* Pipit, American (Buff-bellied)

Anthus petrosus/spinoletta – *see* Pipit, Rock/Water
Anthus trivialis – *see* Pipit, Tree
Apus apus – *see* Swift, Common
Apus melba – *see* Swift, Alpine
Aquila chryaetos – *see* Eagle, Golden
Aquila nipalensis – *see* Eagle, Steppe
Aquila pomarina – *see* Eagle, Lesser Spotted
Ardea alba – *see* Egret, Great
Ardea cinerea – *see* Heron, Grey
Ardea purpurea – *see* Heron, Purple
Ardeola ralloides – *see* Heron, Squacco
Arenaria interpres – *see* Turnstone, Ruddy
Asio flammeus – *see* Owl, Shorteared
Asio otus – *see* Owl, Long-eared
Auk, Little, *Alle alle* 47, 63, 67, 80, 265, 297, 441, 508
Avocet, Pied, *Recurvirostra avosetta* 61, 216, 564
Aythya affinis – *see* Scaup, Lesser
Aythya collaris – *see* Duck, Ring-necked
Aythya ferina – *see* Pochard, Common
Aythya fuligula – *see* Duck, Tufted
Aythya marila – *see* Scaup, Greater
Bee-eater, European, *Merops apiaster* 80, 158, 174, 339, 340, 468
Beech, *Fagus sylvatica* 396, 399, 404, 419, 564
Betula – *see* Birch
Birch, *Betula* 196, 394–7, 401, 402, 407, 559, 564
Bittern, Great, *Botaurus stellaris* 60, 84
Blackbird, Eurasian, *Turdus merula* 314, 322, 335, 336
Blackbird, Yellow-headed, *Xanthocephalus xanthocephalus* 578

Blackcap, *Sylvia atricapilla* 39, 52–3, 64, 157, 165, 198, 275, 319–29, 339, 340, 342, 349, 364, 448, 497, 517–18, 553, 563, 577

Bluetail, Red-flanked, *Tarsiger cyanurus* 293, 294

Buethroat, *Lusinia svecica* 47, 50, 63, 98, 198, 199, 204, 307, 337, 448, 473, 480, 500, 558, 567

Bombycilla cedrorum – *see* Waxwing, Cedar

Bombycilla garrulus – *see* Waxwing, Bohemian

Botaurus stellaris – *see* Bittern, Great

Brambling, *Fringilla montifringilla* 35, 45, 55, 64, 85, 86, 192, 214, 215, 394, 396–7, 398, 399, 402, 404–5, 447, 457, 502, 512, 555, 564, 567, 568, 569

Branta bernicla – *see* Goose, Brent

Branta canadensis – *see* Goose, Canada

Branta leucopsis – *see* Goose, Barnacle

Bronze Cuckoo, Shining, *Chrysococcyx lucidus* 232

Bubo scandiaca – *see* Owl, Snowy

Bubulcus ibis – *see* Egret, Cattle

Bucephala clangula – *see* Goldeneye, Common

Bullfinch, Eurasian (Common), *Pyrrhula pyrrhula* 65, 396, 397, 399, 400, 405, 417, 419, 570

Bunting, Black-headed, *Emberiza melanocephala* 298

Bunting, Cirl, *Emberiza cirlus* 65

Bunting, Corn, *Miliaria calandra* 65

Bunting, Cretzschmar's, *Emberiza caesia* 303

Bunting, Indigo, *Passerina cyanea* 238, 559

Bunting, Lapland, *Calcarius lapponicus* 40, 65, 507

Bunting, Little, *Emberiza pusilla* 204, 293, 294

Bunting, Ortolan, *Emberiza hortulana* 50, 81, 291, 473, 519

Bunting, Reed, *Emberiza schoeniclus* 65, 330, 331

Bunting, Rustic, *Emberiza rustica* 97, 98, 293, 306

Bunting, Snow, *Plectrophenax nivalis* 40, 65, 195, 212, 366, 454, 574, 576
Burhinus oedicnemus – *see* Curlew, Stone
Bustard, Little, *Tetrax tetrax* 80, 295
Bustard, Great, *Otis tarda* 61, 80, 268, 552
Buteo buteo – *see* Buzzard, Common
Buteo b. vulpinus – *see* Buzzard, Steppe
Buteo lagopus – *see* Buzzard, Rough-legged
Buzzard, Common, *Buteo buteo* 26, 61, 71, 72, 167, 202, 442–3, 572
Buzzard, European Honey, *Pernis apivorus* 371, 461–2, 479, 533, 535
Buzzard, Rough-legged, *Buteo lagopus* 61, 423, 454
Buzzard, Steppe, *Buteo b. vulpinus* 75, 78, 561
Calandrella brachydactyla – *see* Lark, Greater Short-toed
Calcarius lapponicus – *see* Bunting, Lapland
Calidris alba – *see* Sanderling
Calidris alpina – *see* Dunlin
Calidris bairdii – *see* Sandpiper, Baird's
Calidris canutus – *see* Knot, Red
Calidris ferruginea – *see* Sandpiper, Curlew
Calidris fuscicollis – *see* Sandpiper, White-rumped
Calidris maritima – *see* Sandpiper, Purple
Calidris mauri – *see* Sandpiper, Western
Calidris melanotos – *see* Sandpiper, Pectoral
Calidris minuta – *see* Stint, Little
Calidris ruficollis – *see* Stint, Rufous-necked
Calidris temminckii – *see* Stint, Temminck's
Calonectris diomedea – *see* Shearwater, Cory's
Capercaillie, Western, *Tetrao urogallus* 61
Caprimulgus europaeus – *see* Nightjar

Carduelis (f.) cabaret – *see* Redpoll, Lesser
Carduelis cannabina – *see* Linnet, Eurasian
Carduelis carduelis – *see* Goldfinch, European
Carduelis chloris – *see* Greenfinch, European
Carduelis citrinella – *see* Finch, Citril
Carduelis flammea – *see* Redpoll, Common (Mealy)
Carduelis flavirostris – *see* Twite
Carduelis hornemanni – *see* Redpoll, Arctic (Hoary)
Carduelis spinus – *see* Siskin, Eurasian
Carpodacus erythrinus – *see* Rosefinch, Common
Carpodacus mexicanus – *see* Finch, House
Catbird, Gray, *Dumetella carolinensis* 568
Cepphus grille – *see* Guillemot, Black,
Certhia familiaris – *see* Tree-creeper, Eurasian
Ceryle alcyon, see Kingfisher, Belted
Cettia cetti – *see* Warbler, Cetti's
Chaffinch, Common, *Fringilla coelebs* 45, 64, 82, 85, 86, 140, 183, 195, 197, 229, 232, 283, 354, 355, 385, 386, 402, 442, 447, 457, 502, 512, 552, 558, 567, 569, 572
Charadrius alexandrinus – *see* Plover, Kentish
Charadrius dubius – *see* Plover, Little Ringed
Charadrius hiaticula – *see* Plover, Common Ringed
Charadrius morinellus – *see* Dotterel
Chen caerulescens – *see* Goose, Snow
Chen rossii – *see* Goose, Ross's
Chiffchaff, Common (Eurasian), *Phylloscopus collybita* 38, 51–3, 64, 81, 181, 218, 335, 342, 480, 517, 518, 535, 556
Chiffchaff, Siberian, *Phylloscopus c. tristis* 289
Chlidonias leucopterus – *see* Tern, White-winged Black

Chlidonias niger – *see* Tern, Black
Chrysococcyx lucidus – *see* Cuckoo, Shining Bronze
Cinclus cinclus – *see* Dipper, White-throated
Ciconia ciconia – *see* Stork, White
Ciconia nigra – *see* Stork, Black
Circaetus gallicus – *see* Eagle, Short-toed
Circus aeruginosus – *see* Harrier, Marsh
Circus cyaneus – *see* Harrier, Hen
Circus macrourus – *see* Harrier Pallid
Circus pygargus – *see* Harrier Montagu's
Clangula clangula – *see* Duck, Long-tailed
Coccothraustes coccothraustes – *see* Hawfinch
Columba livia – *see* Pigeon, Rock
Columba oenas – *see* Dove, Stock
Columba palumbus – *see* Woodpigeon
Coot, Common (Eurasian) – *Fulica atra* 41, 55, 61, 80, 81, 432, 441
Cormorant, Great, *Phalacrocorax carbo* 38, 60, 70, 80, 81, 104, 151, 216, 277, 278, 279, 442, 455, 459, 469, 471, 513, 555, 556, 580
Corncrake, *Crex crex* 39, 61, 493, 516, 523, 524, 532, 535, 552, 561, 570, 577
Corvus corax – *see* Raven, Common
Corvus c. corone/cornix – *see* Crow, Carrion/Hooded
Corvus frugilegus – *see* Rook
Corvus monedula – *see* Jackdaw, Eurasian
Corylus avellana – *see* Hazel
Coturnix coturnix – *see* Quail, Common
Coturnix japonica – *see* Quail, Japanese
Cowbird, Brown-headed, *Molothrus ater* 299
Crake, Spotted, *Porzana porzana*, 61, 516

Crane, Common, *Grus grus* 61, 140, 552
Crane, Demoiselle, *Grus virgo* 167
Crane, Sandhill, *Grus canadensis* 303, 566
Crane, Whooping, *Grus americana* 232, 258, 566
Creatophora cinerea – *see* Starling, Wattled
Crex crex – *see* Corncrake
Crossbill, Common, *Loxia curvirostra* 396, 400, 408–14, 417–19, 558, 560, 563, 568, 570, 575
Crossbill, Parrot, *Loxia pytyopsittacus* 396, 408, 414, 415, 417
Crossbill, Scottish, *Loxia scoticus* 64, 408, 413
Crossbill, Two-barred, *Loxia leucoptera* 396, 408, 409, 414, 417, 419, 562
Crow, Carrion/Hooded, *Corvus c. corone/cornix* 64, 364, 534, 574
Cuckoo, Common, *Cuculus canorus* 1, 2, 31, 63, 158, 210, 451, 473, 474, 517–19, 535
Cuckoo, Shining Bronze, *Chrysococcyx lucidus* 232
Cuculus canorus – *see* Cuckoo, Common
Curlew, Eurasian, *Numenius arquata* 42, 43, 47, 59, 62, 174, 187, 273, 274, 275, 279, 450, 471, 490, 552, 559
Curlew, Stone, *Burhinus oedicnemus* 38, 62, 494, 523, 535
Cygnus buccinator – *see* Swan, Trumpeter
Cygnus columbianus – *see* Swan, Bewick's/Tundra/Whistling
Cygnus cygnus – *see* Swan, Whooper
Cygnus olor – *see* Swan, Mute
Delichon urbica – *see* Martin, Northern House
Dendrocopos major – *see* Woodpecker, Great Spotted
Dendrocopus minor – *see* Woodpecker, Lesser spotted
Dendroica coronata – *see* Warbler, Yellow-rumped
Dendoica striata – *see* Warbler, Blackpoll

Diomedia chrysostoma – *see* Albatross, Grey-headed
Diomedia exulans – *see* Albatross, Wandering
Diomedea immutabilis – *see* Albatross, Laysan
Diomedea melanophris – *see* Albatross, Black-browed
Dipper, White-throated, *Cinclus cinclus* 59, 63, 378
Diver, Black-throated, *Gavia arctica* 58, 60
Diver, Great Northern, *Gavia immer* 40, 60
Diver, Red-throated, *Gavia stellata* 41, 46, 60
Dotterel, *Charadrius (Eudromias) morinellus* 39, 62, 271, 434–5, 448
Dove, European Collared, *Streptopelia decaocto* 63, 264, 563
Dove, European Turtle, *Streptopelia turtur* 63, 81, 379, 472, 473, 474, 482, 516, 517-19, 523
Dove, Stock, *Columba oenas* 63, 330
Duck, American Black, *Anas rubripes* 305
Duck, Ferruginous, *Aythya nyroca* 470
Duck, Harlequin, *Histrionicus histrionicus* 174, 269
Duck, Long-tailed, *Clangula hyemalis* 61, 209
Duck, Mandarin, *Aix galericulata* 37
Duck, Ring-necked, *Aythya collaris* 306, 309
Duck, Tufted, *Aythya fuligula* 61, 277, 301, 388, 429, 470, 578
Dumetela carolinensis, see Catbird, Gray
Dunlin, *Calidris alpina* 42, 59, 62, 269, 274, 275, 285, 471, 579
Dunnock, *Prunella modularis* 63, 346
Eagle, Bald, *Haliaeetus leucocephalus* 128
Eagle, Golden, *Aquila chrysaetus* 38, 61, 382
Eagle, Lesser Spotted, *Aquila pomarina* 75, 445, 568
Eagle, Short-toed, *Circaetus gallicus* 473, 531, 568
Eagle, Steppe, *Aquila nipalensis* 75, 445
Eagle, White-tailed, *Haliaeetus albicilla* 61

Egret, Cattle, *Bubulcus ibis* 352, 567
Egret (Heron), Great White, *Egretta alba* 289, 293
Egret, Little, *Egretta garzetta* 60, 529
Egretta alba, see Egret, Great White
Egretta garzetta – see Egret, Little
Eider, Common, *Somateria mollissima* 61, 104, 123, 273, 441
Eider, King, *Somateria spectabilis* 305, 441
Eider, Steller's, *Polysticta stelleri* 306
Emberiza caesia – see Bunting, Cretzschmar's
Emberiza cirlus – see Bunting, Cirl
Emberiza citrinella – see Yellowhammer
Emberiza hortulana – see Bunting, Ortolan
Emberiza melanocephala – see Bunting, Black-headed
Emberiza pusilla – see Bunting, Little
Emberiza rustica – see Bunting, Rustic
Emberiza schoeniclus – see Bunting, Reed
Eremophila alpestris – see Lark, Shore/Horned
Erithacus rubecula – see Robin, European
Eudromias morinellus – see Dotterel
Fagus sylvatica – see Beech
Falco amurensis – see Falcon, Amur
Falco biarmicus – see Falcon, Lanner
Falco columbarius – see Merlin
Falco eleonarae – see Falcon Eleanora's
Falco naumanni – see Kestrel, Lesser
Falco peregrinus – see Falcon, Peregrine
Falco rusticolus – see Gyrfalcon
Falco subbuteo – see Hobby, Eurasian
Falco tinnunculus – see Kestrel, Common

Falco vespertinus – *see* Falcon, Red-footed
Falcon, Amur, *Falco amurensis* 464
Falcon, Eleonora's, *Falco eleonorae* 533–34, 578
Falcon, Lanner, *Falco biarmicus* 533
Falcon, Peregrine, *Falco peregrinus* 21, 61, 309, 504–5, 533, 556, 576
Falcon, Red-footed, *Falco vespertinus* 49, 98, 473, 483
Ficedula albicollis – *see* Flycatcher, Collared
Ficedula hypoleuca – *see* Flycatcher, European Pied
Ficedula parva – *see* Flycatcher, Red-breasted
Fieldfare, *Turdus pilaris* 1, 45, 63, 174, 305, 396, 403, 406, 574
Finch, Citril, *Carduelis citrinella* 382
Finch, House, *Carpodacus mexicanus* 355, 551
Firecrest, *Regulus ignicapillus* 64
Flycatcher, Collared, *Ficedula albicollis* 218, 283, 303, 362, 371, 473, 479, 562, 579
Flycatcher, European Pied, *Ficedula hypoleuca* 52, 64, 115, 158, 204, 213, 217, 222, 232, 244, 268, 269, 349, 362, 369, 371, 448, 479, 483, 488–9, 498, 517, 518–19, 523, 525, 553, 561, 562, 567, 578
Flycatcher, Red-breasted, *Ficedula parva* 64, 302, 303, 306, 360
Flycatcher, Spotted, *Muscicapa striata* 52, 64, 211, 347, 360, 473, 475, 476, 517–19, 524, 525, 535, 560, 564
Fratercula arctica – *see* Puffin, Atlantic
Fringilla coelebs – *see* Chaffinch
Fringilla montifringilla – *see* Brambling
Fulica atra – *see* Coot, Common
Fulmar, Northern, *Fulmarus glacialis* 9, 60, 277, 390
Fulmarus glacialis – *see* Fulmar, Northern
Gallinago gallinago – *see* Snipe, Common
Gallinula chloropus – *see* Moorhen, Common

Gadwall, *Anas strepera* 61, 223, 427
Gannet, Northern, *Morus bassanus* 10, 38, 60, 305, 455, 570
Garganey, *Anas querquedula* 61, 469, 516
Garrulus glandarius – see Jay, Eurasian
Gavia arctica – see Diver, Black-throated
Gavia immer – see Diver, Great Northern
Gavia stellata – see Diver, Red-throated,
Glareola pratincola, see Pratincole, Collared
Godwit, Bar-tailed, *Limosa lapponica* 62, 149, 203, 275, 471
Godwit, Black-tailed, *Limosa limosa* 21, 59, 62, 202, 203, 450, 473
Goldcrest, *Regulus regulus* 16, 64, 77, 198, 554
Goldeneye, Common, *Bucephala clangula* 61, 273, 558
Goldfinch, European, *Carduelis carduelis* 38, 52, 64, 341, 388
Goosander, *Mergus merganser* 61, 439
Goose, Bar-headed, *Anser indicus* 167, 506
Goose, Barnacle, *Branta leucopsis* 40, 61, 79, 92, 117, 136, 219, 269, 337–8, 385, 387, 496, 498, 514, 556–7, 564, 566, 572, 578
Goose, Bean, *Anser fabalis* 60
Goose, Brent, *Branta bernicla* 1, 40, 61, 69, 79, 92, 101, 102, 122, 136, 141, 142, 168, 253, 254, 360, 490–1, 495, 514, 557, 558, 561–2, 571–2, 577
Goose, Canada, *Branta canadensis* 122, 123, 142, 258, 386, 437, 555, 567, 568, 576
Goose, Greylag, *Anser anser* 61, 85, 194, 274, 336, 437, 570, 577, 578
Goose, Snow/Blue, *Chen caerulescens* 122, 123, 203, 496, 504, 514, 552, 554, 556, 557, 560, 564, 567, 568
Goose, Pink-footed, *Anser brachyrhynchus* 61, 69, 79, 123, 387, 504, 567
Goose, Ross's, *Chen rossii,* 122

Goose, White-fronted, *Anser albifrons* 40, 41, 61, 123, 168, 269, 279, 280, 336, 555, 560, 579
Goshawk, Northern, *Accipiter gentilis* 61, 451, 454
Grebe, Black-necked, *Podiceps nigricollis* 60, 441
Grebe, Great Crested, *Podiceps cristatus* 60, 177, 335, 441, 551, 572
Grebe, Little, *Tachybaptus ruficollis* 60, 305
Grebe, Pied-billed, *Podilymbus podiceps* 305
Grebe, Red-necked, *Podiceps grisegena* 60
Grebe, Slavonian, *Podiceps auritus* 60
Greenshank, Common *Tringa nebularia* 62, 337
Grosbeak, Pine, *Pinicola enucleator* 396, 403, 418
Grus americana – *see* Crane, Whooping
Grus canadensis – *see* Crane, Sandhill
Grus grus – *see* Crane, Common
Grus virgo – *see* Crane, Demoiselle
Grouse, Black, *Tetrao tetrix* 37, 61, 443, 567
Grouse, Red, *Lagopus lagopus* 37, 38, 61
Guillemot, Black, *Cepphus grille* 38, 63
Guillemot, Brünnich's *Uria lomvia* 390
Guillemot, Common, *Uria aalge* 62, 277, 278, 442, 444, 455, 459, 554, 577
Gull, Common, *Larus canus* 43, 53, 55, 388
Gull, Common Black-headed, *Larus ridibundus* 19, 38, 43, 53, 62, 266, 309, 311, 455
Gull, Glaucous, *Larus hyperboreus* 44, 62, 377
Gull, Great Black-backed, *Larus marinus* 44, 62, 279, 442, 455, 556
Gull, Herring, *Larus argentatus* 44, 62, 235, 257, 277, 335, 442, 455, 556, 558, 572
Gull, Iceland, *Larus glaucoides* 44, 62

Gull, Lesser Black-backed, *Larus fuscus* 44, 62, 257, 307, 335, 339, 455, 472, 563
Gull, Little, *Larus minutus* 44, 62
Gull, Mediterranean, *Larus melanocephalus* 62, 340
Gull, Ring-billed, *Larus delawarensis* 293, 305, 307, 309, 310
Gull, Sabine's, *Larus sabini* 47, 62, 297, 381
Gull, Yellow-legged, *Larus michahellis* 48, 62
Gyps fulvus – *see* Vulture, Eurasian Griffon
Gyrfalcon, *Falco rusticolus* 19, 377
Haematopus ostralegus – *see* Oystercatcher, Eurasian
Haliaeetus albicilla – *see* Eagle, White-tailed
Haliaeetus leucocephalus – *see* Eagle, Bald
Harrier, Hen, *Circus cyaneus* 61, 454
Harrier, Marsh, *Circus aeruginosus* 38, 61
Harrier, Montagu's, *Circus pygargus* 61, 451, 524, 531, 552
Harrier, Pallid, *Circus macrourus* 424, 531
Hawfinch, *Coccothraustes coccothraustes* 65
Hazel, *Corylus avellana* 396, 415
Heron, Black-crowned Night, *Nyctycorax nycticorax* 293, 337, 528–29
Heron, Great White – *see* Egret, Great White
Heron, Grey, *Ardea cinerea* 45, 46, 60, 277, 442
Heron, Purple, *Ardea purpurea*528–29, 556, 557
Heron, Squacco, *Ardeola ralloides* 293
Himantopus himantopus – *see* Stilt, Black-winged
Hippolais caligata – *see* Warbler, Booted
Hippolais icterina – *see* Warbler, Icterine
Hippolais olivetorum – *see* Warbler, Olive-tree
Hippolais pallida – *see* Warbler, Olivaceous

Hippolais polyglotta – *see* Warbler, Melodious
Hirundo rustica – *see* Swallow, Barn
Histrionicus histrionicus – *see* Duck, Harlequin
Hobby, Eurasian, *Falco subbuteo* 39, 52, 61, 451, 473, 534–35
Hoopoe, Eurasian, *Upupa epops* 63, 291, 298
Hydrobates pelagicus – *see* Petrel, European Storm
Irania gutturalis – *see* Robin, White-throated
Jackdaw, Eurasian, *Corvus monedula* 64
Jay, Eurasian, *Garrulus glandarius* 64, 396, 397, 399, 400, 402, 417, 564
Jynx torquilla – *see* Wryneck, Eurasian
Kestrel, Common, *Falco tinnunculus* 38, 61, 268, 269, 451, 551, 558, 578
Kestrel, Lesser, *Falco naumanni* 264, 265, 268, 445, 524, 558, 569
Kingfisher, Common, *Alcedo atthis* 63
Kite, Black, *Milvus migrans* 75, 218, 269, 277, 445
Kite, Red, *Milvus milvus* 21, 61, 442, 451
Kittiwake, Black-legged, *Rissa tridactyla* 9, 37, 38, 56, 62, 266, 390, 444, 445, 572
Knot, Red, *Calidris canutus* 42, 62, 168, 200, 275, 385, 386, 471, 500-2, 552
Lagopus lagopus – *see* Grouse, Red
Lagopus mutus – *see* Ptarmigan, Rock
Lanius collurio – *see* Shrike, Red-backed
Lanius excubitor – *see* Shrike, Great Grey (Northern)
Lanius minor – *see* Shrike, Lesser Grey
Lanius nubicus – *see* Shrike, Masked
Lanius senator – *see* Shrike, Woodchat
Lapwing, Northern, *Vanellus vanellus* 42, 54, 62, 174, 269, 309, 339, 450, 577, 578

Lark, Greater Short-toed, *Calandrella brachydactyla* 473, 482
Lark, Shore/Horned, *Eremophila alpestris* 63
Lark, Wood, *Lullula arborea* 63
Larus argentatus – *see* Gull, Herring
Larus canus – *see* Gull, Common
Larus delawarensis – *see* Gull, Ring-billed
Larus fuscus – *see* Gull, Lesser Black-backed
Larus glaucoides – *see* Gull, Iceland
Larus hyperboreus – *see* Gull, Glaucous
Larus marinus – *see* Gull, Great Black-backed
Larus melanocephalus – *see* Gull, Mediterranean
Larus michahellis – *see* Gull, Yellow-legged
Larus minutus – *see* Gull, Little
Larus ridibundus – *see* Gull, Black-headed
Larus sabini – *see* Gull, Sabine's
Lemming, as food 423, 490, 491, 554, 567
Leptoptulos crumeniferus – *see* Stork, Maribou
Limosa lapponica – *see* Godwit, Bartailed
Limosa limosa – *see* Godwit, Black-tailed
Linnet, Eurasian, *Carduelis cannabina* 52, 64, 176, 232, 388, 402
Locustella fluviatilis – *see* Warbler, Eurasian River
Locustella lanceolata – *see* Warbler, Lanceolated
Locustella luscinioides – *see* Warbler, Savi's
Locustella naevia – *see* Warbler, Grasshopper
Loxia curvirostra – *see* Crossbill, Common
Loxia leucoptera – *see* Crossbill, Two-barred
Loxia pytyopsittacus – *see* Crossbill, Parrot
Loxia scotica – *see* Crossbill, Scottish
Lullula arborea – *see* Lark, Wood

Luscinia luscinia – *see* Nightingale, Thrush
Luscinia megarhynchos – *see* Nightingale, Common
Luscinia svecica – *see* Bluethroat
Lymnocryptes minimus – *see* Snipe, Jack,
Magpie, Black-billed, *Pica pica* 64
Mallard, *Anas platyrhynchos* 61, 123, 201, 257, 305, 427, 457, 498, 566, 570
Martin, Northern House, *Delichon urbica* 18, 20, 63, 264, 518
Martin, Sand, *Riparia riparia* 52, 63, 156, 265, 347, 361, 369, 473, 492, 496, 517, 518, 528, 557, 568
Melanitta fusca – *see* Scoter, Velvet
Melanitta nigra – *see* Scoter, Common
Melospiza melodia – *see* Sparrow, Song
Merganser, Red-breasted, *Merganser serrator* 61
Mergus albellus – *see* Smew
Mergus merganser – *see* Goosander
Mergus serrator – *see* Merganser, Red-breasted
Merlin, *Falco columbarius* 40, 61, 361, 505
Merops apiaster – *see* Bee-eater, European
Miliaria calandra – *see* Bunting, Corn
Milvus migrans – *see* Kite, Black
Milvus milvus – *see* Kite, Red
Molothrus ater – *see* Cowbird, Brown-headed
Moorhen, Common, *Gallinula chloropus* 12, 61
Morus bassanus – *see* Gannet, Northern
Motacilla alba – *see* Wagtail, Pied/White
Motacilla cinerea – *see* Wagtail, Grey
Motacilla citreola – *see* Wagtail, Citrine
Motacilla flava – *see* Wagtail, Yellow

Murrelet, Ancient, *Synthliborhamphus antiquus* 305
Muscicapa striata – *see* Flycatcher, Spotted
Neophron percnopterus – *see* Vulture, Egyptian
Nightingale, Common, *Luscinia megarhynchos* 63, 364, 473, 494, 517, 518, 519, 520, 554, 563, 564
Nightingale, Thrush, *Luscinia luscinia* 157, 174, 364, 473, 475, 476, 565
Nightjar, Eurasian, *Caprimulgus europaeus* 3, 63, 174, 516, 518, 522, 566
Nucifraga caryocatactes – *see* Nutcracker, Spotted
Nucifraga columbiana – *see* Nutcracker, Clark's
Numenius arquata – *see* Curlew, Eurasian
Numenius phaeopus – *see* Whimbrel
Nutcracker, Clark's, *Nucifraga columbiana* 415
Nutcracker, Spotted (Thick-billed, Slender-billed), *Nucifraga caryocatactes* 369, 396, 400, 415–417, 418, 560, 570
Nuthatch, Wood, *Sitta europaea* 64, 396, 397, 568
Nyctea scandiaca – *see* Owl, Snowy
Nycticorax nycticorax – *see* Heron, Black-crowned Night
Oak – *Quercus* 396
Oceanodroma leucorhoa – *see* Petrel, Leach's Storm
Oenanthe hispanica – *see* Wheatear, Black-eared
Oenanthe oenanthe – *see* Wheatear, Northern
Oriole, Golden, *Oriolus oriolus* 64, 162, 371, 473, 476, 479
Oriolus oriolus – *see* Oriole, Golden
Osprey, *Pandion haliaetus* 19, 61, 137, 139, 357, 361, 451, 457, 535
Otis tarda – *see* Bustard, Great
Otus scops – *see* Owl, Scops
Ouzel, Ring, *Turdus torquatus* 39, 52, 53, 63

Owl, Barn, *Tyto alba* 59, 63, 423
Owl, Great Grey, *Strix nebulosa* 423
Owl, Long-eared, *Asio otus* 47, 63, 82, 422, 423, 562, 565, 574
Owl, Northern Hawk, *Surnia ulula* 423, 424, 454
Owl, Scops, *Otus scops* 174, 480
Owl, Short-eared, *Asio flammeus* 47, 63, 82, 420, 421–3, 445, 565, 574, 578
Owl, Snowy, *Nyctya scandiaca* 47, 371, 420, 422–4, 454, 560
Owl, Tawny, *Strix aluco* 63, 423
Owl, Tengmalm's (Boreal), *Aegolius funereus* 268, 421, 422, 565, 567, 576
Oystercatcher, Eurasian, *Haematopus ostralegus* 43, 61, 224, 273, 275, 277
Pandion haliaetus – *see* Osprey
Panurus biarmicus – *see* Tit, Bearded
Parakeet, Ring-necked, *Psittacula krameri* 36
Parrotbill, Bearded – *see* Tit, Bearded
Partridge, Grey, *Perdix perdix* 11, 12, 61
Parus ater – *see* Tit, Coal
Parus caeruleus – *see* Tit, Blue
Parus cristatus – *see* Tit, Crested
Parus major – *see* Tit, Great
Parus montanus – *see* Tit, Willow
Parus palustris – *see* Tit, Marsh
Passer domesticus – *see* Sparrow, House
Passer montanus – *see* Sparrow, Tree
Passerina cyanea – *see* Bunting, Indigo
Pelecanus onocrotalus – *see* Pelican, Great White
Pelican, Great White, *Pelecanus onocrotalus* 75

Perdix perdix – *see* Partridge, Grey
Peregrine – *see* Falcon, Peregrine
Pernis apivorus – *see* Buzzard, European Honey
Petrel, European Storm, *Hydrobates pelagicus* 60, 308, 436
Petrel, Leach's Storm – *Oceanodroma leucorhoa* 60, 579
Petrochelidon pyrrhonata – *see* Swallow, Cliff
Phalacrocorax aristotelis – *see* Shag, European
Phalacrocorax carbo – *see* Cormorant, Great
Phalaenoptilus nuttallii – *see* Poorwill, Common
Phalarope, Grey, *Phalaropus fulicarius* 47, 48, 62, 254, 297, 457
Phalarope, Red-necked, *Phalaropus lobatus* 62, 449
Phalarope, Wilson's, *Phalaropus tricolor* 174
Phalaropus fulicarius – *see* Phalarope, Grey
Phalaropus lobatus – *see* Phalarope, Red-necked
Phalaropus tricolor – *see* Phalarope, Wilson's
Philomachus pugnax – *see* Ruff
Phoebastria immutabilis – *see* Albatross, Laysan
Phoenicurus ochruros – *see* Redstart, Black
Phoenicurus phoenicurus – *see* Redstart, Common
Phylloscopus bonelli – *see* Warbler, Bonelli's
Phylloscopus borealis – *see* Warbler, Arctic
Phylloscopus collybita – *see* Chiffchaff, Common (Eurasian)
Phylloscopus c. tristis – *see* Chiffchaff, Siberian
Phylloscopus inornatus – *see* Warbler, Yellow-browed (Inornate)
Phylloscopus proregulus – *see* Warbler, Pallas's (Lemon-rumped)
Phylloscopus schwarzi – *see* Warbler, Radde's
Phylloscopus sibilatrix – *see* Warbler, Wood
Phylloscopus trochiloides – *see* Warbler, Greenish
Phylloscopus trochilus – *see* Warbler, Willow

Picea abies – *see* Spruce, Norway
Picus viridis – *see* Woodpecker, Green
Pigeon, Rock, *Columba livia* 63
Pigeon, Stock, *Columba oenas* 63, 330
Pigeon,Wood, *Columba palumbus* 38, 63
Pine, Scots, *Pinus sylvestris* 394, 396, 408, 410, 562
Pine, Siberian Stone, *Pinus sibirica* 396, 415
Pinicola enucleator – *see* Grosbeak, Pine
Pintail, Northern, *Anas acuta* 61, 272, 309, 427, 428, 429, 470
Pipit, American (Buff-bellied), *Anthus rubescens* 539
Pipit, Meadow, *Anthus pratensis* 35, 40, 52, 63, 520
Pipit, Pechora, *Anthus gustavi* 301
Pipit, Red-throated, *Anthus cervinus* 98, 473
Pipit, Richard's, *Anthus novaeseelandiae* 47, 63, 390
Pipit, Rock/Water, *Anthus petrosus/spinoletta* 63, 382
Pipit, Tawny, *Anthus campestris* 293, 473
Pipit, Tree, *Anthus trivialis* 52, 63, 473, 517, 518, 519, 520
Platalea leucorodia – *see* Spoonbill, Eurasian
Plectrophenax nivalis – *see* Bunting, Snow
Plover, European Golden, *Pluvialis apricaria* 42, 62, 108, 177, 571
Plover, Grey, *Pluvialis squatarola* 62, 274, 450, 458
Plover, Kentish, *Charadrius alexandrina* 174, 271
Plover, Little Ringed, *Charadrius dubius* 62, 480
Plover, Ringed, *Charadrius hiaticula* 59, 62, 168, 178, 275, 360, 389, 459, 471
Pluvialis apricaria – *see* Plover, European Golden
Pluvialis squatarola – *see* Plover, Grey
Pochard, Common, *Aythya ferina* 9, 61, 277, 429, 454, 470, 556, 578

Podiceps cristatus – *see* Grebe, Great Crested
Podiceps grisegena – *see* Grebe, Red-necked
Podiceps nigricollis – *see* Grebe, Black-necked
Podilymbus podiceps, see Grebe, Pied-billed
Polysticta stelleri – *see* Eider, Steller's
Porzana porzana – *see* Crake, Spotted
Poorwill, Common, *Phalaenoptilus nuttallii* 3
Pratincole, Collared, *Glareola pratincola* 174, 473
Prunella modularis – *see* Dunnock
Ptarmigan, Rock, *Lagopus mutus* 61, 177, 377, 382
Puffin, Atlantic, *Fratercula arctica* 8, 38, 63, 267, 455, 562
Puffinus gravis – *see* Shearwater, Great
Puffinus griseus – *see* Shearwater, Sooty
Puffinus mauritanicus – *see* Shearwater, Balearic
Puffinus puffinus – *see* Shearwater, Manx
Pyrrhula pyrrhula – *see* Bullfinch, Eurasian
Quail, Common, *Coturnix coturnix* 61, 80, 164, 174, 271, 321, 433, 434, 472, 473, 482, 508, 516, 532, 551, 557, 569, 580
Quail, Japanese, *Coturnix japonica* 321, 557
Quelea quelea – *see* Quelea, Red-billed
Quelea, Red-billed, *Quelea quelea* 445, 481, 565
Quercus – *see* Oak
Rail, Water, *Rallus aquaticus* 61
Rallus aquaticus – *see* Rail, Water
Raven, Common, *Corvus corax* 64, 377, 382
Razorbill, *Alca torda* 62, 455, 567
Recurvirostra avosetta – *see* Avocet, Pied
Redpoll, Common (Mealy), *Carduelis flammea* 40, 45, 174, 395, 396, 400, 402, 403, 406–7, 417, 418, 419, 434, 445, 461

Redpoll, Hoary (Arctic), *Carduelis hornemanni* 396
Redpoll, Lesser, *Carduelis f. cabaret* 399
Redshank, Common, *Tringa totanus* 4, 42, 59, 62, 79, 275, 498, 555
Redshank, Spotted, *Tringa erythropus* 62, 174, 450
Redstart, Common, *Phoenicurus phoenicurus* 52, 63, 164, 209, 210, 222, 321, 322, 448, 473, 498, 517, 518, 519, 576
Redstart, Black, *Phoenicurus ochrurus* 52, 321, 322
Redwing, *Turdus iliacus* 40, 45, 63, 406, 569
Regulus ignicapillus – *see* Firecrest
Regulus regulus – *see* Goldcrest
Remiz pendulinus – *see Tit, Penduline*
Riparia riparia – *see* Martin, Sand
Rissa tridactyla – *see* Kittiwake, Black-legged
Robin, European, *Erithacus rubecula* 63, 322, 381, 456, 457, 551, 554
Robin, White-throated, *Irania gutturalis* 303
Rook, *Corvus frugilegus* 12, 64
Rosefinch, Common, *Carpodacus erythrinus* 39, 65, 174, 293, 360, 464
Rowan, *Sorbus aucuparia* 393, 396, 397
Ruff, *Philomachus pugnax* 53, 62, 450, 453, 561
Sanderling, *Calidris alba* 62, 68, 234, 273, 274, 279, 457, 490, 569
Sandgrouse, Pallas', *Syrrhaptes paradoxus* 426
Sandpiper, Baird's, *Calidris bairdii* 360, 539
Sandpiper, Common, *Actitis hypoleuca* 38,, 53, 62, 273, 480, 510–11, 517, 518, 539
Sandpiper, Curlew, *Calidris ferruginea* 62, 174, 273, 279, 450, 471, 490, 559
Sandpiper, Green, *Tringa ochropus* 53, 62, 174, 269, 480
Sandpiper, Marsh, *Tringa stagnatilis* 174

Sandpiper, Pectoral, *Calidris pectoralis* 234, 295, 296
Sandpiper, Purple, *Calidris maritima* 62, 168, 269, 275
Sandpiper, Spotted, *Actitis macularia* 174
Sandpiper, White-rumped, *Calidris fuscicollis* 295, 297
Sandpiper, Wood, *Tringa glareola* 62, 470, 480
Saxicola rubetra – *see* Whinchat
Saxicola torquata – *see* Stonechat, Common
Scaup, Greater, *Aythya marila* 42, 209
Scaup, Lesser, *Aythya affinis* 62
Scoter, Common (Black), *Melanitta nigra* 38, 61
Scoter, Velvet, *Melanitta fusca* 61
Scolopax rusticola – *see* Woodcock, Eurasian
Serin, European, *Serinus serinus* 336, 352, 353
Serinus citrinella – *see* Finch, Citril
Serinus serinus – *see* Serin, European
Shag, European, *Phalacrocorax aristotelis* 38, 60, 442, 443, 455
Shearwater, Balearic *Puffinus mauritanicus* 60
Shearwater, Cory's, *Calonectris diomedia* 47, 60, 251, 293, 557, 568
Shearwater, Great, *Puffinus gravis* 47, 60
Shearwater, Manx, *Puffinus puffinus* 12, 28, 37, 39, 60, 125, 126, 136, 233, 250, 341, 436, 459, 555, 562, 568, 572, 577
Shearwater, Sooty, *Puffinus griseus* 47, 60, 136, 151, 573
Shelduck, Common, *Tadorna tadorna* 61, 438, 470, 571
Shoveler, Northern, *Anas clypeata* 61, 123, 272, 305, 427, 470, 498
Shrike, Lesser Grey, *Lanius minor* 383, 475, 476, 534
Shrike, Masked, *Lanius nubicus* 298, 303
Shrike, Great Grey (Northern), *Lanius excubitor* 46, 47, 64
Shrike, Red-backed, *Lanius collurio* 39, 50, 64, 157, 209, 361, 369, 448, 475–6, 519, 564, 578

Shrike, Woodchat, *Lanius senator* 298, 299, 473, 480, 534
Siskin, Eurasian, *Carduelis spinus* 45, 64, 191, 276, 316, 395, 396, 398, 399, 401, 402, 405, 417, 434, 445, 457
Sitta europaea – *see* Nuthatch, Wood
Skua, Brown, *Stercararius antarctica* 308
Skua, Great, *Stercorarius skua* 62, 308, 381, 572
Skua, Long-tailed, *Stercorarius longicaudus* 424, 552
Skua, Parasitic (Arctic), *Stercorarius parasiticus* 214
Skua, Pomarine, *Stercoraris pomarinus* 62
Skylark, Eurasian, *Alauda arvensis* 52, 63, 271, 390, 432, 573
Smew, *Mergus albellus* 61
Snipe, Common, *Gallinago gallinago* 42, 43, 62, 80, 512
Snipe, Jack, *Lymnocryptes minimus* 42, 174, 512, 539
Somateria mollissima – *see* Eider, Common
Somateria spectabilis – *see* Eider, King
Sorbus aucuparia – *see* Rowan
Sparrow, House, *Passer domesticus* 12, 64
Sparrow, Song, *Melospiza melodia* 265, 308, 570
Sparrow, Tree, *Passer montanus* 64, 232
Sparrow, White-crowned, *Zonotrichia leucophrys* 64, 232, 252, 310, 551, 556, 565, 569
Sparrow, White-throated, *Zonotrichia albicollis* 299, 308
Sparrowhawk, Eurasian, *Accipiter nisus* 64, 122, 264, 265, 451, 503, 504, 570, 574
Sparrowhawk, Levant, *Accipiter brevipes* 75
Spoonbill, Eurasian, *Platalea leucorodia* 60
Spruce, Norway, *Picea abies* 214, 215, 394, 396, 397, 398, 400, 407, 408, 409–11, 412, 413, 414, 460, 462, 464
Starling, Common, *Sturnus vulgaris* 15, 35, 45, 55, 64, 80, 85, 228–9, 236, 237, 271, 273–4, 325, 335, 336, 355, 378, 425, 432, 452, 559,

572, 576, 580
Starling, Rose-coloured, *Pastor roseus* 425, 426
Starling, Wattled, *Creatophora cinerea* 455, 482
Stercorarius antarctica – *see* Skua, Brown
Stercorarius longicaudus – *see* Skua, Long-tailed
Stercorarius parasiticus – *see* Skua, Arctic
Stercorarius pomarinus – *see* Skua, Pomarine
Stercorarius skua – *see* Skua, Great
Sterna albifrons – *see* Tern, Little
Sterna bengalensis – *see* Tern, Lesser Crested
Sterna caspia – *see* Tern, Caspian
Sterna dougallii – *see* Tern, Roseate
Sterna hirundo – *see* Tern, Common
Sterna paradisaea – *see* Tern, Arctic
Sterna sandvicensis – *see* Tern, Sandwich
Stilt, Black-winged, *Himantopus himantopus* 273, 338
Stint, Little, *Calidris minuta* 47, 62, 175, 273, 480
Stint, Temminck's, *Calidris temminckii* 62, 198, 563
Stonechat, Common, *Saxicola torquata* 52, 63, 180, 181, 183, 185, 197, 289, 326, 520, 563
Stork, Black, *Ciconia nigra* 75
Stork, Maribou, *Leptoptulos crumeniferus* 482
Stork, White, *Ciconia ciconia* 23, 27, 71, 75, 76, 80, 112, 139, 140, 144, 145, 186, 201, 202, 203, 229, 230, 231, 256, 276, 279, 329, 337, 340, 341, 364, 445, 492, 508, 529, 530, 533, 553, 554, 557, 565, 567, 574, 575, 578
Streptopelia decaocto – *see* Dove, Eurasian Collared
Streptopelia turtur – *see* Dove, European Turtle
Strix aluco – *see* Owl, Tawny

Strix nebulosa – *see* Owl, Great Grey

Sturnus (Pastor) roseus – *see* Starling, Rose-coloured

Sturnus vulgaris – *see* Starling, Common

Surnia ulula – *see* Owl, Northern Hawk

Swallow, Barn, *Hirundo rustica* 1, 4, 17, 20, 21, 23, 37, 39, 52, 63, 82, 104, 111, 120, 132, 133, 134, 143, 164, 174, 178, 201, 203, 209, 210–11, 214, 216, 217, 219, 221, 224, 271, 273, 274, 281, 330, 340, 343, 345, 361, 369, 457, 473, 474, 489, 490, 496, 508, 509, 517, 518, 522, 528, 535, 563, 569, 574, 575, 578

Swallow, Cliff, *Petrochelidon pyrrhonata* 329, 555

Swan, Bewick's/Tundra/Whistling, *Cygnus columbianus* 92, 135, 196, 347, 498, 506, 553, 570, 573, 575

Swan, Mute, *Cygnus olor* 16, 19, 60, 335, 442

Swan, Trumpeter, *Cygnus buccinator* 258, 576

Swan, Whooper, *Cygnus cygnus* 40, 60, 143, 249, 279, 338, 495, 554, 571

Swift, Alpine, *Apus melba* 174, 298

Swift, Common, *Apus apus* 20, 63, 78, 80, 103, 112, 113, 116, 126, 158, 174, 204, 211, 222, 297, 304, 436, 490, 509, 517, 518, 523, 565, 566, 576

Sylvia atricapilla – *see* Blackcap

Sylvia borin – *see* Warbler, Garden

Sylvia cantillans – *see* Warbler, Subalpine

Sylvia communis – *see* Whitethroat, Common

Sylvia curruca – *see* Whitethroat, Lesser

Sylvia hortensis – *see* Warbler, Orphean

Sylvia nisoria – *see* Warbler, Barred

Sylvia r¼ppellii – *see* Warbler, R¼ppell's

Sylvia undata – *see* Warbler, Dartford

Synthliboramphus antiquus – *see* Murrlet, Ancient

Syrrhaptes paradoxus – *see* Sandgrouse, Pallas'
Tachybaptus ruficollis – *see* Grebe, Little
Tadorna tadorna – *see* Shelduck, Common
Tarsiger cyanurus – *see* Bluetail, Red-flanked
Teal, Blue-winged, *Anas discors* 305, 309
Teal, Eurasian, *Anas crecca* 61, 223, 428, 429, 470, 496, 580
Teal, Green-winged, *Anas carolinensis* 309
Tern, Arctic, *Sterna paradisaea* 37, 39, 62, 78, 150, 151, 224, 383
Tern, Black, *Chlidonias nigra* 47, 48, 62, 150, 273, 441, 578
Tern, Caspian, *Sterna caspia* 309
Tern, Common, *Sterna hirundo* 29, 62, 150, 389, 458, 530, 558, 559
Tern, Lesser Crested, *Sterna bengalensis* 305
Tern, Little, *Sterna albifrons* 62, 441, 530, 556, 577
Tern, Roseate, *Sterna dougallii* 62, 530
Tern, Sandwich, *Sterna sandvicensis* 62, 305
Tern, White-winged, *Chlidonias leucopterus* 273
Tetrao tetrix – *see* Grouse, Black
Tetrax tetra – *see* Bustard, Little
Tetrao urogallus – *see* Capercaillie, Western
Thalassarche melanophris – *see* Albatross, Black-browed
Thrush, Grey-cheeked, *Catharus minimus* 254, 556
Thrush, Mistle, *Turdus viscivorus* 63
Thrush, Song, *Turdus philomelos* 15, 35, 45, 55, 63, 80, 81, 99, 232, 247, 378, 379, 433, 442, 575, 580
Tit (Parrotbill), Bearded, *Panurus biarmicus* 64, 268, 419, 420
Tit, Blue, *Parus caeruleus* 64, 132, 133, 396, 399, 419, 420, 442, 455, 456, 571, 576
Tit, Coal, *Parus ater* 64, 133, 396, 419–20
Tit, Crested, *Parus cristatus* 64

Tit, Great, *Parus major* 64, 133, 336, 396, 399, 419, 420, 442, 561, 571
Tit, Long-tailed, *Aegithalos caudatus* 64
Tit, Marsh, *Parus palustris* 64
Tit, Penduline, *Remiz pendulinus* 306, 560
Tit, Willow, *Parus montanus* 64
Tree-creeper, Eurasian, *Certhia familiaris*, 64, 80, 379
Trichodroma muraria – *see* Wallcreeper
Tringa erythropus, see Redshank, Spotted
Tringa glareola – *see* Sandpiper, Wood
Tringa nebularia – *see* Greenshank, Common
Tringa ochropus – *see* Sandpiper, Green
Tringa stagnatilis – *see* Sandpiper, Marsh
Tringa totanus – *see* Redshank, Common
Troglodytes troglodytes – *see* Wren, Winter
Turdus iliacus – *see* Redwing
Turdus merula – *see* Blackbird, Eurasian
Turdus philomelos – *see* Thrush, Song
Turdus pilaris – *see* Fieldfare
Turdus torquatus – *see* Ouzel, Ring
Turdus viscivorus – *see* Thrush, Mistle
Turnstone, Ruddy, *Arenaria interpres*, 62, 124, 168, 187, 223, 269, 274, 275, 385, 386, 501, 555, 556, 562
Twite, *Carduelis flavirostris* 64, 382
Tyto alba – *see* Owl, Barn
Upupa epops – *see* Hoopoe, Eurasian
Uria aalge – *see* Guillemot, Common
Uria lomvia – *see* Guillemot, Brunnich's
Vanellus vanellus – *see* Lapwing, Northern

Vireo, Red-eyed, *Vireo olivaceus* 293, 295, 574
Vireo olivaceus – *see* Vireo, Red-eyed
Vulture, Egyptian, *Neophron percnopterus* 473, 475
Vulture, Eurasian Griffon, *Gyps fulvus* 73, 77, 176, 508
Wagtail, Citrine, *Motacilla citreola* 339
Wagtail, Grey, *Motacilla cinerea* 63
Wagtail, Pied/White, *Motacilla alba* 63, 281, 282, 388, 480, 558
Wagtail, Yellow, *Motacilla flava* 52, 63, 114, 115, 156, 158, 183, 184, 213, 271, 337, 360, 369, 454, 480, 517–19, 523, 557, 560, 580
Wallcreeper, *Tichodroma muraria* 305
Warbler, Aquatic, *Acrocephalus paludicola* 47, 64, 362
Warbler, Arctic, *Phylloscopus borealis* 204, 291, 301, 360, 464
Warbler, Barred, *Sylvia nisoria* 48, 64, 157, 174, 302, 306, 473, 475
Warbler, Blackpoll, *Dendroica striata* 295, 301
Warbler, Bonelli's, *Phylloscopus bonelli* 303, 473
Warbler, Booted, *Hippolais caligata* 306
Warbler, Cetti's, *Cettia cetti* 63, 317, 553
Warbler, Dartford, *Sylvia undata* 64
Warbler, Garden, *Sylvia borin* 52, 64, 107,116, 119, 120, 159, 164, 174, 179, 222, 238, 369, 473, 476, 480, 494, 517, 518, 519, 552, 562, 571, 579
Warbler, Grasshopper, *Locustella naevia* 64, 518, 522
Warbler, Great Reed, *Acrocephalus arundinaceus* 174, 218, 219, 269, 361, 364, 473, 476, 480, 553
Warbler, Greenish, *Phylloscopus trochiloides* 269, 293, 301, 364–5
Warbler, Icterine, *Hippolais icterina* 64, 98, 174, 473, 474, 519
Warbler, Lanceolated, *Locustella lanceolata* 174, 295
Warbler, Marsh, *Acrocepalus palustris* 39, 64, 131, 132, 134, 174, 269, 361, 473, 475, 476, 517, 518, 519, 565
Warbler, Melodious, *Hippolais polyglotta* 174, 292, 293, 473

Warbler, Olivaceous, *Hippolais pallida* 303, 473, 480

Warbler, Olive-tree, *Hippolais olivetorum* 303, 475, 562

Warbler, Orphean, *Sylvia hortensis* 473

Warbler, Pallas' (Leaf), *Phylloscopus proregulus* 289, 291, 301, 302

Warbler, Radde's, *Phylloscopus schwarzi* 295

Warbler, Reed, *Acrocepalus scirpaceus* 52, 53, 64, 154, 156, 204, 222, 317, 361, 473, 476, 517, 518, 560

Warbler, River, *Locustella fluviatilis* 174, 293, 475, 519

Warbler, R¼ppell's, *Sylvia r¼ppellii*, 473

Warbler, Savi's, *Locustella luscinioides* 198, 218, 460, 480, 517, 518, 519, 551, 570

Warbler, Sedge, *Acrocephalus schoenobaenus* 52, 64, 108, 116, 154–5, 158, 164, 174, 194, 203, 204, 473, 476, 480, 488, 497, 500, 517, 518, 522, 526, 527, 535, 553, 554, 571, 573

Warbler, Subalpine, *Sylvia cantillans* 298, 473, 480

Warbler, Willow, *Phylloscopus trochilus* 10, 52, 64, 78, 114, 132, 159, 164, 172, 174, 175, 190, 204, 209, 269, 360, 363, 369, 464, 473, 476, 483, 497, 517, 518, 519, 571, 576

Warbler, Wood, *Phylloscopus sibilatrix* 64, 174, 209, 218, 369, 371, 473, 479, 483, 517, 518, 519, 524, 569, 576

Warbler, Yellow-browed (Inornate), *Phylloscopus inornatus* 64, 295, 301, 307

Warbler, Yellow-rumped (Myrtle), *Dendroica coronata* 559, 577

Waxwing, Bohemian, *Bombycilla garrulus* 45, 63, 190, 191, 393, 395, 396, 400, 402, 403, 406, 407, 417, 418

Waxwing, Cedar, *Bombycilla cedrorum* 299

Wheatear, Northern, *Oenanthe oenanthe* 35, 40, 52, 63, 78, 110, 111, 148, 164, 168, 174, 218, 358–60, 464, 473, 503, 517, 518, 519, 557

Wheatear, Black-eared, *Oenanthe hispanica* 473

Whimbrel, *Numenius phaeopus* 48, 62, 174, 269

Whinchat, *Saxicola rubetra* 52, 63, 483, 517, 518, 519–21

White-eye (Silvereye), Tasmanian, *Zosterops lateralis* 245
Whitethroat, Common (Greater), *Sylvia communis* 52, 64, 156, 198, 369, 473, 475, 478, 517, 518, 527
Whitethroat, Lesser, *Sylvia curruca* 39, 52, 64, 114, 156, 159, 165, 198, 238, 361, 473, 517, 518
Wigeon, American, *Anas americana* 289, 309
Wigeon, Eurasian, *Anas penelope* 42, 61, 223, 301, 307, 429, 470
Woodcock, Eurasian, *Scolopax rusticola* 42, 59, 62, 80
Woodpecker, Great Spotted, *Dendrocopus major* 63, 396, 400, 417
Woodpecker, Green, *Picus viridis* 63
Woodpecker, Lesser Spotted, *Dendrocopus minor* 63
Wren (Winter), *Troglodytes trogrodytes* 16, 38, 63
Wryneck, Eurasian, *Jynx torquilla* 47, 50, 63, 80, 96, 516, 519
Xanthocephalus xanthocephalus – *see* Blackbird, Yellow-headed
Xema sabini – *see* Gull, Sabine's
Yellowhammer, *Emberiza citrinella* 65
Zonotrichia albicollis – *see* Sparrow, White-throated
Zonotrichia leucophrys – *see* Sparrow, White-crowned

SUBJECT INDEX

Adaptations, for flight/migration 2–3, 69–70, 83, 106–10, 114–21, 124–7,169, 316–18
Adipose tissue 107, 127
Africa, as wintering area 37, 39, 463–85, 526–31
  birds that migrate to 39, 463–4, 516
  ecology of migrants 477–84, 526–531
 wetlands 468–72, 531
 movements within 472–477, 479–480
 rainfall and habitat 464–8, 485, 526–31

seas around 472, 530
Age, and autumn arrival/departure 450–2
and directional spread 300
and dispersal 270, 277–9, *see* Dispersal, natal, breeding
and dominance/size 192–3, 453
and homing 228–34
and migration 7–8, 145–6, 192–3, 202, 230, 231–2, 277–9, 447–62
and migratory fattening 460–1
and response to displacement 228–31, 233–4
and site fidelity 277–9
and spring arrival/departure 448–9, 460–2
and vagrancy 287, 300, 311
Agriculture, effects on migrants 493, 519–23, 531
Alps, and migration 156, 166–7, 368
Altitude, of flight 98–105, 161–2, 166–8
Altitudinal migration, *see* Migration, altitudinal
Annual cycles 143–5, 170–88
Ascent, on migration 91, 99
Assortative mating 329, 332, 366
Auditory sense, *see* Sense, of hearing
Autumn migration 51–5, 195–9, 205, 220–3, 225, 228–31, 346, 399–404, 449–52, 498
annual variation in dates 346
comparison with spring 205
in relation to spring arrival 204
Avian influenza 506
Barometric pressure, perception of 227, 248
Barrier, crossing 2, 10–11, 98, 101, 142–143, 147–169, 366–368
Desert 10–11, 152–165

evolution of 366–8
ice 101, 167–8
mountain 98, 166–7, 368
sea 142–3, 147–51, 367–8
Basal metabolic rate (BMR) 68, 115, 118
Bat, predation on migrants by 534
Baxter, E. V. 539
Bearing-and-distance, *see* Navigation, vector
Benguela current 472
Bergmann's Rule 389
Bird Observatories 22–4, 539
Bird strikes, *see* Collisions
BMR, *see* Basal metabolic rate
Body clock, *see* Annual cycles; Diurnal rhythms; Endogenous rhythms
Body, composition/reserves 3, 32–4, 68–9, 106–27, 148–9, 150, 154–6, 161–3, 188
and breeding/survival 121–125, 495–7, 500, 515
seasonal changes in 118–25, 127
effects on predation risk 111–12, 502–3
Body size/weight, and flight/migration 66–70, 73, 76–8, 455–6
and fuelling rates 117–18
and vagrancy 292
Bosphorus 72, 75
Botulism 506
Breeding success, effect on numbers 489
Breeding and wintering ranges, relationships 382–5
British Trust for Ornithology 15, 211, 516
Cage birds, escaped 287

Calendar effects 199, 203
Camera, infrared 14
Cannon net 18, 19
Capital and income models 121–5
Captive breeding 34, 319
Capture methods 16–19
Carbohydrate, as energy source 109, 161
Carcass analyses 32–3, 110–11
Cardio-vascular system 3, 127
Carrying capacity, of habitat 487
Carry-over effects 495–8, 515
Ceilometer 14
Celestial cues 235–9, 246–8
Chain migration 356 388–90
Changes in migration 57–8, 307–8, 327–32, 333–50, 372
  breeding in wintering range 340–1
  directions 307–8, 327–9, 339–40, 341
  lengthening of routes 338–9, 346
  migratory to sedentary 335–6
  sedentary to migratory 336
  shortening of routes 336–8, 346
  timing 341–6, 347
Circadian rhythms, *see* Diurnal rhythms
Circannual rhythms 179–85; *see also* Annual cycles; Endogenous rhythms
Clarke, W. E. 22, 538–9
Climate change effects 333–5, 341–3, 525; *see also* Glaciation
Clock, internal, *see* Annual
  cycles; Diurnal rhythms; Endogenous rhythms

Clock-and-compass, *see*
Navigation, vector
Cloud, effects on migration, *see*
Weather, cloud effects
Col de Bretolet 166
Collisions, with lighthouses, masts etc. 15, 249, 511–13, 537, 538
Colour marking 21
Compass orientation 227–32, 260
Auditory 227, 248
Calibration 246, 249
Celestial 235–9
Defective 300–4
Infrasound 227, 248
Magnetic 239–48, 258, 260, 513
Olfactory 227, 248
polarised light 227,237, 247, 248, 258, 260
star/stellar 235, 238–9, 246–7, 255, 258, 260
Compass orientation *cont.*
sun (azimuth) 235–7, 239, 247, 254–5, 258, 260
Competition
and dispersal 268
and distribution/range 356–8
and food 268, 497, 498–9
and habitat/territory 216–18, 223–4
and mates 219
and nest-sites 268, 493, 497
and migration 193, 313–314, 390, 391
and migratory fattening 460
and territories 217–218, 268, 488, 497

and winter habitat 223–224
Conservation 493, 522–4, 535
Cordeaux, J. 537–8
Corticosterone 193
Cross-breeding, *see* Hybrids
Cues, of direction 235–48, 260;
see also Compass orientation
Cue conflicts, in orientation 246–8
Dawn ascent 100
Daylength, response to 145, 173, 181–6, 193–4, 199, 200, 206, 349
Death, *see* Mortality
Deferred breeding/return to breeding areas 186–8, 458–60
Dehydration, in migrants 102–3, 152, 159, 161–3
Density, dependence 268, 497–8, 515
Descent from migration 105; *see also* Falls
Desert, crossing 10–11, 152–65, 366–7
Asian 164–5
Sahara 119–20, 139, 152–64, 366–7, 371–2, 463–4
Detour 165, 358, 368
Diet, and migration 115–17, 127, 379–80, 390
Digestive capacity 115, 117, 127
Direction, *see* Migration, directions; Compass orientation
Disease, in migrants, *see* Botulism; Parasitism
Disorientation 91, 248–9, 297, 300
Dispersal 5, 261–86
and age/sex 267–8, 277–9
and density/competition 268
and food-supply 276; *see also* Irruption
Dispersal *cont.*

and genetic structure 285–6
and habitat 263, 271–3, 277
and inbreeding avoidance 263
and range expansion 285, 352;
see also Range, expansion
and vagrancy 288, 292–3
benefits and costs 262–3
breeding 5, 261–2, 269–71, 279, 398–9, 412–13, 428–9
long-distance 271–3
natal 5, 261, 263–8, 413, 428
within breeding season 271
non-breeding/wintering 5, 262, 273–7, 279, 404–7, 429
northward of wetland birds 293
post-fledging 5, 6, 281–2, 292
Displacement experiments
228–35, 250–1
Dispersive migration, *see*
Migration, dispersive
Distribution of migrants 31
among age/sex groups 453–7
among migrants in Africa
477–8
wintering 37, 38
Disturbance effects on migrants
433, 503–5
Diurnal rhythms 193, 235–6, 252, 258, 260
DNA, and migration studies 30, 308, 362–4, 365, 373
Dominance, and movements
192–3, 268, 460, 455–7, 462

Drift, by wind 93–8
and vagrancy 288, 295–7
compensation for 94–7, 231, 249–50, 259
Drought, *see* Weather, drought effects; Rainfall
Dungeness 23, 50–4
Dynamic soaring 74
Eastwood, E. 25
Eclipse plumage, of ducks 175–6
Emigration, *see* Dispersal; Irruptions; Autumn migration
Emlen cage 32
Endogenous rhythms 179–85, 192, 193, 200, 206; *see also* Annual cycles; Diurnal rhythms
Energy, consumption/expenditure 106–9, 114–18, 161–3
Eruption, *see* Irruptions
Escape movements 432–3
EURING 16
Eurasian-African migration system 370–2, 463–4
Evolution/modification of migration 313–32, 348–50
from higher or lower latitudes 352–8
of directions 323–9, 350
of inclination 320–1, 350
of migration patterns 356–8
of morphology 326
of timing 321–6, 348–50

of routes 305–8, 327–9, 350, 358–70
Facultative, migration, *see* Migration, facultative
Fair Isle 22, 23, 50, 288, 289–90
Falls, of migrants 97–8, 105
Falsterbo Bird Observatory 399–400, 401
Fat/fattening 3, 106–27,161–3,166,193–5, 197–9, 200, 206, 498–502
costs of 111–12
in adults 110–11, 114–18, 193–5, 498–502
in nestlings 125–6
see also Body composition/reserves
Feathers 2, 171, 172, 176, 199; *see also* Moult
Abrasion 176
use in chemical analyses 30
Feeding on the wing 112–13
Flight 66–87
altitudes, *see* Altitude, of flight
and body weight 66–70, 76–8
bounding 69–70
calls 14, 84–5
cost-saving 69–74
energy/power needs 68
flapping 2, 69–71
formation 70, 84
gliding-soaring, *see* Soaring- gliding
low level 103–4
non-stop 77–8, 142–3, 147–51, 158–9
range 77, 142–143, 147–51, 158–9
speed 66–7, 141

maximum range 67–9
minimum power 67–9
Flight: stopover ratios 140–2
Flock, migratory 84–6, 255–8
Flyway 74–6, 385–7
Fog, *see* Weather, fog effects
Food, and annual cycles 170–3
and competition, *see*
Competition, and food
and dispersal 268, 271–2, 276, 398–9, 404–7, 423, 426, 427–9, 450
and fuelling rates 114–18, 194, 206, 498–500
and irruptions 392–430
and migration 5–6, 212, 214–15, 223, 313, 336, 348–9, 392–430
limitation by 492, 493, 500–2, 521–3, 526–31
Fruit-eating by migrants 115–17
Fruiting patterns, of trees 393–4
Fuelling strategies 154–8, 160
Gas flares, effects on migrants 513
Gätke, H. 15, 538
Genetic, basis/control of
migration 34, 185, 191, 194, 228–32, 255, 260, 318–32, 335, 348, 350, 370, 372
Geographical gradients/patterns 356–8, 374–91, 458–60
age/sex ratios 453–5
latitudinal 356–8, 374–8, 380–1, 385–90
longitudinal 385–7
Geolocation device (GLS) 27, 28, 134, 136
Gibraltar 71, 72, 74, 148, 153

Glaciation, effects on migration
patterns 351–73
Gliding, *see* Soaring-gliding
Global positioning device (GPS) 27
Global warming, *see* Climate, change
Glycogen 67, 109
Goal navigation/orientation, *see*
Navigation, bicoordinate
Gonad growth/regression 181, 200–1, 205
Graded return migration 458–9
Great Circle route 252–5, 302
Greenland ice-cap, migration
over 101, 168
Guiding 258
Gut structure, and diet 115
Habitat, destruction/loss 494, 521–5, 531
effects on migration 201–2, 203
occupancy/settlement 216–18, 223
of migrants in Africa 479
Harvie-Brown, A. J. 537
Hearing, *see* Sense, of hearing
Heligoland 105, 288, 291
Trap 16–17, 24
Heritability studies 329
Hibernation 3–4
Himalayas 164, 166–7, 444
Hippocampus, in migratory birds 318
Homing, after displacement 232–5, 305–7
to breeding sites 227–33, 261

to wintering sites 233–4
see also Site-fidelity
Hormones, and migration 193, 205
Hybrid/hybridisation 319, 326–30, 364–5
Hyperphagia 114–15
Hypoxia 167
Human, disturbance, *see* Disturbance
Hunting of migrants 20, 339, 491, 504, 532–3
Hurricanes, *see* Weather, hurricanes
Ice-age, *see* Glaciation
Ice-crossing 101, 167–8
Immigration, *see* Dispersal, Irruptions
Inbreeding avoidance 263
Infections, *see* Parasitism
Infra-sound 227, 248
Inter-tropical convergence zone (ITCZ) 464–5
Internal clock/time keeper, *see*
Annual cycles; Diurnal
rhythms; Endogenous
rhythms
Invasions, *see* Irruptions
Irruptions 6, 191, 392–430
into Britain 417–19
of crossbills 408–15
of desert species 425–6
of finches and fruit-eaters 392–420, 429–30
of nutcrackers 415–17
of owls and raptors 392, 420–24
of waterfowl 392, 427–9

Irruptive migrants
breeding distributions 407, 445, 426, 427–8
fluctuations in breeding densities 397–8, 409, 420–1, 426, 427–8
autumn emigration 196, 399–401
Irruptive migrants *cont.*
breeding dispersal 398–9, 412–13, 421–4, 426, 427–8
breeding in migration and wintering areas 407, 424
timing and directions 401–4
wintering dispersal 404–7, 429
wintering densities 404
Isle of May 22, 50
Isotope analyses 29–30, 123, 163, 363
Itinerant breeding 433–5
Laboratory research 31–4
Lack, David 25, 541
Landmarks, and migration/homing 235, 249, 258, 259, 260
Latitude, and annual cycles 178–9, 182–3
and migration 183–4, 186, 207–16, 220–2, 356–8, 374–8, 380–9
Leap-frog migration 357, 388–90
Learning, of natal/breeding sites 282–4
of migration routes 256–8
of orientation cues 235, 238, 241, 246, 260
of wintering sites 284
Lighthouse, and bird strikes 15, 249, 511–12, 537, 538
Listening, for migrants 14
Locality responses 242–5
Loop migration 76, 369–70
Loxodrome, *see* Rhumbline route
Lyme disease 506

Magnetic, compass, *see* Compass, magnetic
Map-and-compass, *see* Navigation, bicoordinate
Map-sense, *see* Navigation, bicoordinate
Mass, *see* Weight
Mate, competition for 219
Mate-fidelity 263, 271, 273
Mating/parental systems, and migration 448–50
Maximum range speed 67–9
Messina Strait, migration site 76
Metabolism, *see* Basal metabolic rate
Methodology 13–34
Migration, altitude of, *see* Altitude, of flight
  Altitudinal 5, 381–2
Migration *cont.*
  annual calendar 50–5, 170–9
  autumn, *see* Autumn migration
  axes 56–7, 402, 405
  chain, *see* Chain migration
  changes in, *see* Changes in migration
  comparison between autumn and spring 205
  control 179–88, 189–206, 207–16, 220–3, 224–5, 430, 431–6
  corridor 72, 73–6, 385–7
  costs/benefits 10–11, 314–16
  definition 1, 5–6, 7
  descent from 105; *see also* Falls
  development from higher or lower latitudes 352–6
  differential, *see* Age, Sex
  direction, *see* Migratory, direction
  dispersive 5, 282, 442–5

distance 6, 321–3, 453–9
diurnal/nocturnal 13–14, 80–3, 87, 131, 193
duration 128–46, 321–3
facultative 189–93, 204, 222–3, 315–16, 333, 350, 392, 430, 431, 456
flexibility 430, 446
irruptive, *see* Irruptions
leap-frog, *see* Leap frog migration
long distance 7, 77, 130–4, 144–5, 147–51, 155, 158–60, 164–5, 168
loop, *see* Loop migration
mirror-image 288, 300–1, 311
nocturnal, *see* Migration, diurnal/nocturnal
obligate 189–92, 222, 315, 330, 430, 431
parallel, *see* Geographic patterns, partial 1, 35, 38–9, 60–5, 130, 314–16, 320, 330, 335–6, 462
patterns 356–8; *see also* Geographical patterns
position in annual cycle 173–9
reverse 86–87, 195
reversed-direction 288, 301–4, 311–12
routes 358–70, 385–7
seasonality 1, 6, 7, 8, 12, 50–5
short distance 7
speed 128–46
from individual ring
recoveries 129–32
from population ring
recoveries 133–4
Migration, speed *cont.*

from radio-tracking 134–40
methods of assessing 128–9
split 173–5, 431–4, 473–4
spring, *see* Spring migration
telescopic, *see* Telescopic migration
timing 2, 7, 50–5, 130, 173–5, 189–206, 208–16, 220–3, 321–3, 390, 401; *see also* Autumn migration; Spring migration
weather-induced 431–3
within breeding season 433–7
within non-breeding season 403–4, 431–3, 473–7
Migratory, directions 6, 8–10, 32, 56–7, 194–5, 288, 300–4, 311–12, 323–9, 341, 401–3, 440, 441; *see also* Compass orientation
Divide 144, 323–6, 364–6
Fattening 32–3, 68–9, 106–27
Inclination 320–1
Restlessness 32, 192, 1935, 319–23
State 88, 193–4
status of British and Irish birds 35–65
Minimum power speed 67–9
Mirror image migration, *see* Migration, mirror image
Misorientation 300
Mist net 17–19
Moon watching 14
Moreau, R. E. 541–2
Mortensen, H. 15
Mortality, in breeding areas 509–11
in flight 504–9

migration-related 164, 507–11, 514–15
weather-induced 507–11
Moult 173–9, 195–9, 201, 206, 431, 437–42, 484
Migration 431, 437–42
Mountain-crossing 98, 166–7, 368, 370
Movements, different types 4–6;
see also Dispersal; Irruption;
Migration; Nomadism
Muscle, breast/flight 2–3
Nature Reserves, and migrants 493
Navigation, ability 226–60
Bicoordinate 227–31, 258, 259, 260
Vector 227, 258; *see also*
Compass orientation
Nest sites, limiting breeding numbers 488, 490, 493, 523
Newton, A. 537, 538
Nocturnal migration, *see* Migration, diurnal/nocturnal
Nomadism 6, 392, 445–6
North Atlantic Oscillation (NAO) 296–7, 344
Numbers of species, in British Isles 35
migrating to Africa 39, 463–4
Obligate migration, *see* Migration, obligate
Observation of migration, by eye 13–15, 89
Ocean, *see* Sea-crossings
Olfaction, *see* Sense, of smell
Organs, changes in 118–21
see also Body composition/reserves
Orientation, *see* Compass orientation
Orientation cage 32–3, 231, 300, 319

Orthodrome, *see* Great Circle Route
Ottenby Bird Observatory 401
Overshooting 288, 297–9
Palaearctic-African migration system 370–2, 463–4
Parasitism 313–14, 505–6
Partial migration, *see* Migration, partial
Passage migrants 1, 35, 47–50, 60–5
Passage times, spring 212–13
  autumn-spring comparison 54, 220
Pathogen, *see* Parasitism
Pectoralis muscle, *see* Muscle, breast
Pelagic birds, *see* Seabirds
Pesticide effects 493
Philopatry 261; *see also* Site- fidelity, to birthplace
Photoperiod, *see* Daylength
Piloting 259
PIT tags 29, 458
Population, limitation 486–515, 516–36
  in breeding/wintering areas 487–94, 516–31
  on migration 498–506
  trends in migrants 516–36
  size, effect on vagrancy 288, 293–5
Post-breeding retreat from breeding range 220–3, 225
Post-fledging dispersal, *see* Dispersal, post-fledging
Power lines, collisions 512
Predation, and migrants 101, 111–12, 194, 313–14, 433, 491, 493, 502–5, 533–4
Pre-laying exodus 436–7
Protein, as migratory fuel 106–9, 161–3

Proximate factors 172–3, 193, 206; *see also* Endogenous rhythms
PTTs 26–7
Pyrenees 166
Radar, use of 13–14, 24–5, 83, 89, 91, 94, 95–6, 98–100, 166, 248–9, 250, 541
Radio-tracking 13, 25–9, 92, 99, 101, 134–43, 186, 249, 250–1, 422, 443–4, 514
Rainfall, effects on habitats/food 464–8, 479, 485, 492–3, 494, 497, 526–31
Range, expansion 285, 293, 305–8, 339–40, 352
  relation between breeding and wintering 382–5
Raptor migrations 45–7, 71–6, 97, 100, 137–40, 142, 167, 451
Recolonisation of northern continents in spring 207–13
Refuge, glacial, *see* Glaciation
Re-occupation of breeding area 216–18
  of wintering area 222–3
Reorientation, after displacement 94–7, 228–35, 249–50, 259
Residency 1, 11–12, 35, 37–9, 60–5, 330
Respiratory system 3
Rest 78–80
Return migration, *see* Spring migration
Reversed-direction migration, *see* Migration, reversed direction
Rhumbline route 252–5
Ringing, methods/results 13, 15–16, 20–2, 58–9, 113, 128–34, 143–5, 156–8, 227–35, 257, 261–84, 305–7, 309–11, 339, 340, 346–7, 398, 399, 404–7, 428, 441
Rintoul, L. J. 539
Rocket net 19
Rodents, population cycles 420, 491
Roosts, communal 20–1, 273–4

Rossitten, *see* Rybachy
Rowan, W. 31
Rybachy 23, 386, 457
Sahara Desert, *see* Desert, Sahara
Sahel zone, and migrants 153, 159–60, 467, 472–5, 477, 526–31
Sandstorms 163
Satellite-based tracking 13, 25–9 186, 250; *see also* Radiotracking
Scilly Isles 50, 288, 289–90
Sea crossings, by landbirds 7, 142–3, 147–51, 158, 295–7, 309–10
Seabird, movements 5, 7, 9–10, 12, 37, 38, 39, 43–4, 47–8, 59, 73–4, 136, 150–1, 250–1, 290–1, 297
  Navigation 250–1
  site fidelity/dispersal 265–7, 284
  vagrancy 290–1, 308, 309
  wrecks 297, 508–9
Sedentariness, *see* Residency
Seed crops 393–4, 400
Sense, of direction; *see*
  Navigation, bicoordinate;
  Compass orientation
  of hearing 227, 248
  of magneto-detection 227, 243
  of pressure detection 227, 248
  of smell 227, 251
Sex, and autumn departure 449–50
  and body size 453
  and migration 192–3, 196, 202–3, 447–62
  and dispersal/site fidelity 267–8
  and spring arrival/departure 448–9, 460

migratory fattening 460
Ships, and migrants 4, 287, 308–10
Site, attachment 282–5
Site-fidelity 261–8
age differences in 277–9
and predictability of
habitat/food supply 266, 275–7, 398–9, 404–8, 421–3, 426, 427–9, 430, 408
lack of 271–3, 275–7, 279, 398–9, 404–7
sex differences in 267–8, 270
Site-fidelity *cont.*
to birth place 261–8
to breeding place 261, 263, 269–73, 279
to mate 263, 271, 273
to non-breeding/wintering
place 273–7, 279, 305–7
to stopover site 280–1, 307
see also Dispersal
Skokholm 22, 23
Sleep 78–9, 83
Snow, *see* Weather, snow effects
Soaring-gliding 2, 70–4, 77, 97, 112, 136–40, 141–2
Social, bonds in migration 84–6, 255–8
organisation/systems 483–4
Speed, of flight, *see* Flight, speed
of migration, *see* Migration, speed
Spring migration 51–5, 199–205, 207–16, 343–7, 448–9
annual variation in dates 214–16
arrival, in breeding area 214–19, 343–50

changes in dates 343–7, 349–50
date and breeding success 219, 349
relationship with autumn
departure 52–3, 204
species differences in dates 50–5, 208–13
Staging area, *see* Stopover area
Star compass, *see* Compass, star
Starvation, of migrants 509–10
Stopover areas 156–60
and moult 173–4
and performance 498–502
and population impact 500–2
departure from site 86
fidelity to 280–1, 307
mortality during 502–6
periods on 113–14, 135–6, 139, 140–2, 460
Summer visitors 1, 39, 60–4
Sun, azimuth, *see* Compass
orientation, sun
Sunset cues, *see* Compass
orientation, sun
Swimming 2
Telescopic migration 358, 388–90
Temperature, body 161
and spring arrival 90, 207–16, 341–6, 347
changes with altitude 102
Territories, competition for, *see* Competition, and territories
Testes, *see* Gonad growth/regression
Thermals, and migration 70–3, 97

Thomson, A. L. 15, 540–1
Time shifts 236–9, 251–2
Timing mismatches 348–9, 489, 525
Topographic influence, on
migration 368; *see also*
Mountain-crossing
Torpidity 3–4
Trace element analyses 30
Translocation experiments 227–35, 282–4
Transponder, *see* PIT tag
Trapping methods 16–19
Ultimate factors 172–3
Updrafts 70, 71; *see also* Thermals
Vagrancy 50, 287–312
and body size 292
and dispersal 292–3
and drift 295–7
and escaped cage birds 287
and population size 293–5
and range expansion 305–8
and ring recoveries 308–11
and site fidelity 305–7
and weather/wind 288, 295–7, 299
causes of 288
Vagrancy *cont.*
observer bias 287, 289–91
probability of arrival 291–2
shadow 302, 303
ship-assisted 287, 308–10

Vagrant 36, 50, 287–312
North American in Europe 295–7, 311–12
Siberian in western Europe 295, 311–12
Vector migration, *see* Navigation, vector
Walking 2
Water, budget/needs 152, 159, 161–3
Waterfowl migration 9, 40, 41, 121–4, 135–6, 141, 142–3, 212–13, 272–3, 277, 280, 427–9, 454, 469–70, 498–9, 514
Weather, and in-flight mortality 507–9
and migration 81–2, 88–105, 149–50, 195, 238, 248–9, 486, 507–9
and vagrancy 295–7, 311
cloud effects 89, 91, 97, 100–1, 248–9
cold/snow effects 329, 509–11
drought effects 425–8, 526–531
fog/mist effects 89, 238, 297, 511
hurricane effects 297, 304
movements 431–3
rain effects 6, 89, 90, 91; *see also* Rainfall
Weather, and in-flight mortality *cont.*
temperature effects 347–8, 482–3, 495–6
wind effects, *see* Wind
Weight, gain 107–8, 117–18
loss during migration 119–21
see also Body composition/reserves
West Nile Virus 506
Whoosh net 19
Williamson, K. 539–40
Wind, effects on direction; *see* Drift

effects on flight altitude 98–105
effects on migration 91–101, 105, 249, 295–7, 311–12, 347–8
effects on vagrancy 288
turbines, effects on birds 513
Wind-farms, and birds 513
Winter/non-breeding
distributions, *see*
Distributions, wintering
Movements 403–4, 431–3
Visitors 1, 35, 39–47, 60–5
Withdrawal from breeding
range, *see* Post-breeding, retreat from breeding range
Withdrawal from wintering
range 186, 199–203
Witherby, H. F., 288, 540
Zugunruhe, see Migratory, restlessness

The New Naturalist Library

1. Butterflies — E. B. Ford
2. British Game — B. Vesey-Fitzgerald
3. London's Natural History — R. S. R. Fitter
4. Britain's Structure and Scenery — L. Dudley Stamp
5. Wild Flowers — J. Gilmour & M. Walters
6. The Highlands & Islands — F. Fraser Darling & J. M. Boyd
7. Mushrooms & Toadstools — J. Ramsbottom
8. Insect Natural History — A. D. Imms
9. A Country Parish — A. W. Boyd
10. British Plant Life — W. B. Turrill
11. Mountains & Moorlands — W. H. Pearsall
12. The Sea Shore — C. M. Yonge
13. Snowdonia — F. J. North, B. Campbell & R.Scott
14. The Art of Botanical Illustration — W. Blunt
15. Life in Lakes & Rivers — T. T. Macan & E. B. Worthington
16. Wild Flowers of Chalk & Limestone — J. E. Lousley
17. Birds & Men — E. M. Nicholson
18. A Natural History of Man in Britain —
H. J. Fleure & M. Davies
19. Wild Orchids of Britain — V. S. Summerhayes

20. The British Amphibians & Reptiles — M. Smith
21. British Mammals — L. Harrison Matthews
22. Climate and the British Scene — G. Manley
23. An Angler's Entomology — J. R. Harris
24. Flowers of the Coast — I. Hepburn
25. The Sea Coast — J. A. Steers
26. The Weald — S. W. Wooldridge & F. Goldring
27. Dartmoor — L. A. Harvey & D. St. Leger Gordon
28. Sea Birds — J. Fisher & R. M. Lockley
29. The World of the Honeybee — C. G. Butler
30. Moths — E. B. Ford
31. Man and the Land — L. Dudley Stamp
32. Trees, Woods and Man — H. L. Edlin
33. Mountain Flowers — J. Raven & M. Walters
34. The Open Sea: I. The World of Plankton — A. Hardy
35. The World of the Soil — E. J. Russell
36. Insect Migration — C. B. Williams
37. The Open Sea: II. Fish & Fisheries — A. Hardy
38. The World of Spiders — W. S. Bristowe
39. The Folklore of Birds — E. A. Armstrong
40. Bumblebees — J. B. Free & C. G. Butler
41. Dragonflies — P. S. Corbet, C. Longfield & N. W. Moore
42. Fossils — H. H. Swinnerton
43. Weeds & Aliens — E. Salisbury
44. The Peak District — K. C. Edwards

45. The Common Lands of England & Wales — L. Dudley Stamp & W. G. Hoskins
46. The Broads — E. A. Ellis
47. The Snowdonia National Park — W. M. Condry
48. Grass and Grasslands — I. Moore
49. Nature Conservation in Britain — L. Dudley Stamp
50. Pesticides and Pollution — K. Mellanby
51. Man & Birds — R. K. Murton
52. Woodland Birds — E. Simms
53. The Lake District — W. H. Pearsall & W. Pennington
54. The Pollination of Flowers — M. Proctor & P. Yeo
55. Finches — I. Newton
56. Pedigree: Words from Nature — S. Potter & L. Sargent
57. British Seals — H. R. Hewer
58. Hedges — E. Pollard, M. D. Hooper & N. W. Moore
59. Ants — M. V. Brian
60. British Birds of Prey — L. Brown
61. Inheritance and Natural History — R. J. Berry
62. British Tits — C. Perrins
63. British Thrushes — E. Simms
64. The Natural History of Shetland — R. J. Berry & J. L. Johnston
65. Waders — W. G. Hale
66. The Natural History of Wales — W. M. Condry
67. Farming and Wildlife — K. Mellanby
68. Mammals in the British Isles — L. Harrison Matthews
69. Reptiles and Amphibians in Britain — D. Frazer

70. The Natural History of Orkney — R. J. Berry
71. British Warblers — E. Simms
72. Heathlands — N. R. Webb
73. The New Forest — C. R. Tubbs
74. Ferns — C. N. Page
75. Freshwater Fish — P. S. Maitland & R. N. Campbell
76. The Hebrides — J. M. Boyd & I. L. Boyd
77. The Soil — B. Davis, N. Walker, D. Ball & A. Fitter
78. British Larks, Pipits & Wagtails — E. Simms
79. Caves & Cave Life — P. Chapman
80. Wild & Garden Plants — M. Walters
81. Ladybirds — M. E. N. Majerus
82. The New Naturalists — P. Marren
83. The Natural History of Pollination — M. Proctor, P. Yeo & A. Lack
84. Ireland: A Natural History — D. Cabot
85. Plant Disease — D. Ingram & N. Robertson
86. Lichens — Oliver Gilbert
87. Amphibians and Reptiles — T. Beebee & R. Griffiths
88. Loch Lomondside — J. Mitchell
89. The Broads — B. Moss
90. Moths — M. Majerus
91. Nature Conservation — P. Marren
92. Lakeland — D. Ratcliffe
93. British Bats — John Altringham
94. Seashore — Peter Hayward

95. Northumberland — Angus Lunn
96. Fungi — Brian Spooner & Peter Roberts
97. Mosses & Liverworts — Nick Hodgetts & Ron Porley
98. Bumblebees — Ted Benton
99. Gower — Jonathan Mullard
100. Woodlands — Oliver Rackham
101. Galloway and the Borders — Derek Ratcliffe
102. Garden Natural History — Stefan Buczacki
103. The Isles of Scilly — Rosemary Parslow
104. A History of Ornithology — Peter Bircham
105. Wye Valley — George Peterken
106. Dragonflies — Philip Corbet & Stephen Brooks
107. Grouse — Adam Watson & Robert Moss
108. Southern England — Peter Friend
109. Islands — R. J. Berry
110. Wildfowl — David Cabot
111. Dartmoor — Ian Mercer
112. Books and Naturalists — David E. Allen

EDITORS

SARAH A. CORBET, ScD

Prof. RICHARD WEST, ScD, FRS, FGS

DAVID STREETER, MBE, FIBiol

JIM FLEGG, OBE, FIHort

Prof. JONATHAN SILVERTOWN

*

The aim of this series is to interest the general reader in the wildlife of Britain by recapturing the enquiring spirit of the old naturalists. The editors believe that the natural pride of the British public in the native flora and fauna, to which must be added concern for their conservation, is best fostered by maintaining a high standard of accuracy combined with clarity of exposition in presenting the results of modern scientific research.

Author's Foreword and Acknowledgements

THE PHENOMENON OF BIRD migration has fascinated people from the earliest times. The arrivals and departures of different species marked the seasons, heralding spring and autumn, and providing a reliable calendar long before anything better became available. Migration has repeatedly prompted familiar questions, such as where do birds go or come from, why do they do it, how do they know when and where to travel, and how do they find their way?

For more than a century, biologists have attempted to answer these questions, using increasingly sophisticated methodology, and research has blossomed in recent years. In the last few decades, hardly a year has passed without the publication of a new book or symposium volume dealing with some aspect of bird migration, and each year dozens of papers have appeared in the scientific journals, reporting new research findings. Some of this material is summarised in this book, as it relates to the birds of the British Isles. But it is impossible to write about bird migration without also drawing heavily on the enormous contribution to the subject made by amateur naturalists. Most of what we know about bird movements is derived from ring recoveries, and most of the bird-ringing in the British Isles and elsewhere is performed by volunteers, as is the majority of observational work.

Unlike professionals, who are largely bound by scientific fashion, amateurs can afford to take whatever direction their curiosity dictates. Anyone can study birds, wherever they live, and the wide distribution of skilled bird-watchers enables questions to be addressed countrywide, as illustrated by the many national surveys organised by the British Trust for Ornithology. Without these skilled

volunteers, we would have practically no long-term data from which to assess the changing numbers, distributions and migration dates of birds.

This is not the first book I have written on bird migration. Much of the published information on the subject was summarised in an earlier work, *The Ecology of Bird Migration* (Newton, 2008). That book was aimed primarily at professionals, including research students, and dealt in detail with most aspects of the subject, and with bird movements worldwide. The present book provides a briefer account of this information, and updates it with new findings, but concentrates on migration as it relates to the birds of Britain and Ireland. It is organised into four main sections: the first is introductory, describing the different types of bird movements, methods of study and the main migration patterns seen around the British Isles; the second part is concerned mainly with the process of migration—with timing, energy needs, weather effects and navigation; the third with evolution and change in migratory behaviour; and the fourth with the geographical and ecological aspects of bird movements. Although all these chapters relate mainly to the birds of the Britain and Ireland, I have sometimes drawn on examples from other parts of the world, where they better illustrate a point.

It will be clear in the following pages how much I owe to the generosity of bird photographers who have allowed me to use some of their best work as illustrations. More than 200 images enliven the text, provided by Tim Appleton (1 image), Franz Bairlein (2), Kurt Burnham (2), Nigel Clark (1), Larry Dalziel (1), Edmund Fellowes (54), Dick Forsman (6), Sean Gray (20), Paul Hackett (2), Brian Irving (34), Alan Martin (2), Rebecca Nason (12), David Norman (1), James Packer (1), Jill Pakenham (3), Cal Sandfort (2), Bobby Smith (11), Frank Snijkers (18), Jack Stevens (5), Colin Turvey (8), John Willsher (10), John Wright (14), and the Royal Society for the Protection of Birds (3). I would also like to thank Harry Scott for helpful advice on the use of photographic images, Rob Davies for

help with the land-cover maps, and Keith Brockie for providing the drawings.

During the writing of this book, I have benefited greatly from the comments of David Jenkins, who has read and criticised the draft manuscript (some parts more than once), and offered many constructive suggestions. Richard Carden also commented helpfully on four of the chapters, and David Parkin on Chapter 3. In his role as editor, Jim Flegg read the entire penultimate draft and offered many helpful suggestions. Last but not least, I thank my wife, Halina, for commenting constructively on the draft manuscript, and for her encouragement and support during the writing process.

About the Author

Ian Newton OBE, FRS, FRSE is an ornithologist and applied scientist, and a leading expert on bird ecology and biogeography, specialising in finches, waterfowl and birds of prey, especially the sparrowhawk.He graduated from Bristol University and gained his doctorate in finch behaviour at Oxford, followed by research on bullfinch damage in orchards.He joined the Natural Environment Research Council in 1967, initially studying population ecology of ducks and geese, followed by the impact of pesticides on birds of prey. Among other books, he has written a previous New Naturalist volume, Finches (1972).

Visit www.AuthorTracker.com for exclusive information on your favorite HarperCollins author.

Photographic Inserts



FIG 1. Cuckoo *Cuculus canorus* a summer visitor to the British Isles which spends the winter in tropical Africa. (Edmund Fellowes)



FIG 2. Common Redshanks *Tringa totanus* whose wintering population consists of local breeders and winter visitors mainly from Iceland. (Brian Irving © HELM-Images)



FIG 3. Puffin *Fratercula árctica* which nests on offshore islands around the British Isles, and winters widely over the West Atlantic, usually far from land. (Edmund Fellowes)



FIG 4. Pochard *Aythya ferina* (drake), a scarce breeder but common winter visitor to the British Isles, coming from as far east as central Siberia. (Edmund Fellowes)





FIGS 5 & 6.Gannet Moms *bassanus* a large seabird in which some individuals (mainly immatures) from British and Irish colonies migrate as far as West Africa for the winter (Sean Gray/Grayimages); Willow Warbler *Phylloscopus trochilus* which, despite its small size, performs some of the longest and most arduous migrations found among landbirds. (Frank Snijkers)



FIG 7. Grey Partridge *Perdix perdix* a once-common resident in much of Britain and Ireland, now much declined. Most individuals disperse to breed less than one kilometre from where they were hatched. (Bobby Smith)



FIG 8. Attaching a ring to the leg of a Wren *Troglodytes troglodytes*. Note the special pliers for dealing with different sized rings. (John Willsher)



FIG 9. Brood of Barn Swallows *Hirundo rustica.* In the early years of bird ringing, before effective methods were developed for catching adults, most birds were ringed as nestlings. (Bobby Smith)

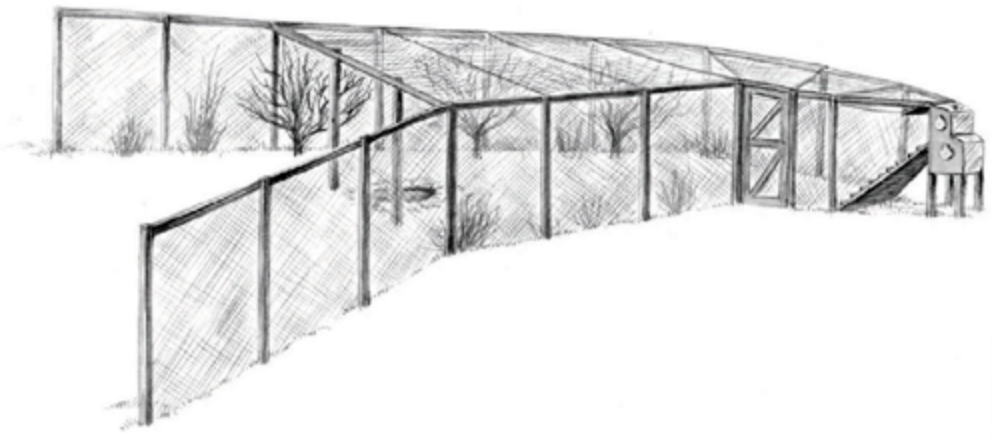


FIG 10. A Heligoland bird trap, a large wire-netting funnel through which birds can be driven and caught in a glass-fronted box at the end. (Drawn by Keith Brockie.)



FIG 11. Driving swans and other waterfowl into a specially constructed funnel trap at Caerlavarock in southwest Scotland. (Edmund Fellowes)



FIG 12. Catching House Martins *Delichon urbica* in mist nets. (JohnWillsher)



FIG 13. Cannon net being fired over shorebirds. (Nigel Clark)



FIG 9. Gyr Falcon *Falco rusticolus* caught using a baited clap-net. (Cal Sandfort)



FIG 15. House Martin *Delichon urbica* a summer visitor to the British Isles which has been ringed here in large numbers but has provided hardly any ring recoveries from its African wintering areas. (Sean Gray/Grayimages)



FIG 16. Markers visible at a distance: Peregrine Falcon *Falco peregrinus* showing colour ring for reading through a telescope, and a normal metal ring carrying an address through which its recovery can be reported. (Kurt Burnham); Red Kite *Milvus mihus* with numbered/lettered wing tags. (Edmund Fellowes)

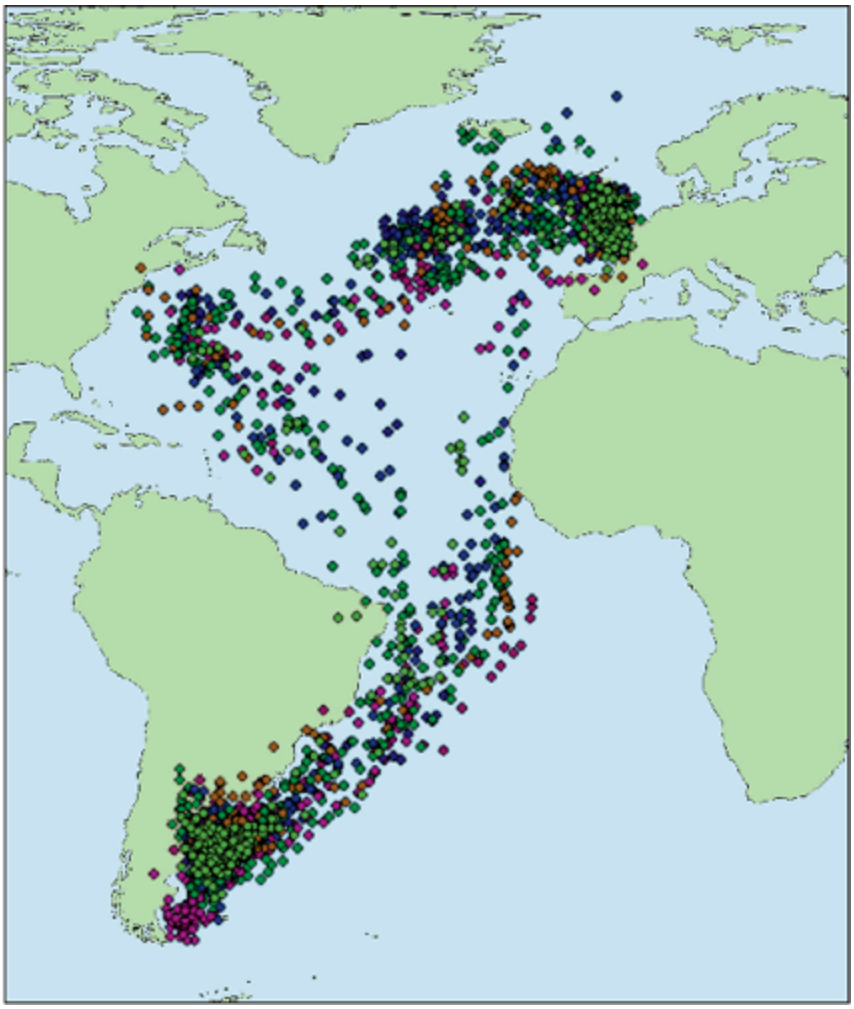


FIG 17. Map of Bird Observatories around the British Isles. In the past, other observatories operated for a time elsewhere. Map provided by Peter HowlettoftheBird Observatories Council.



FIG 18. Common Buzzard *Buteo buteo* with radio-transmitter attached. (John Willsher)

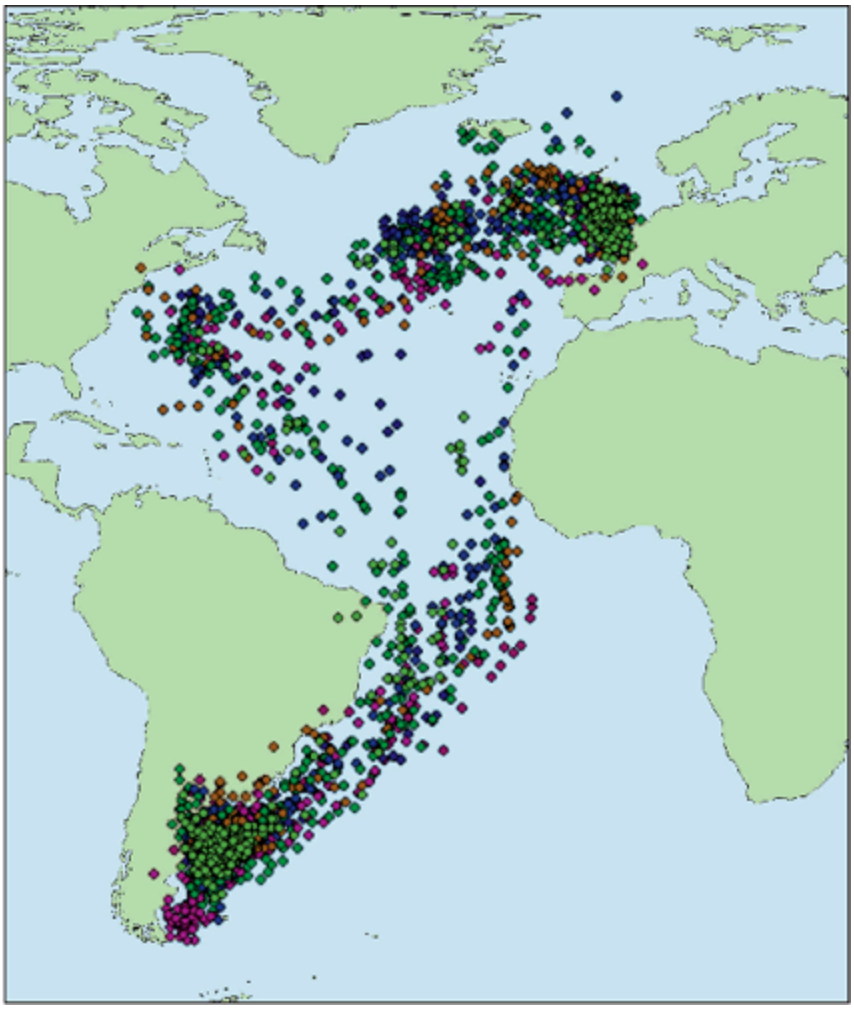


FIG 19. Migrations of Manx Shearwaters *Puffinus puffinus* nesting on Skomer Island, Wales, based on eleven birds tracked using geolocation devices. These devices bear light sensors which can be used to estimate the locations of each bird at intervals from prevailing light-dark cycles. The apparent appearance of these pelagic birds overland is attributable to imprecision in some of the location estimates given by this method. Nevertheless, the records indicate that these shearwaters winter off eastern South America (confirming ring recoveries), and cross the Atlantic at different latitudes on their outward and return journeys (previously unknown from ringing). In effect, they fly a 'loop migration'. (Modified from Guilford *et al.* 2009.)

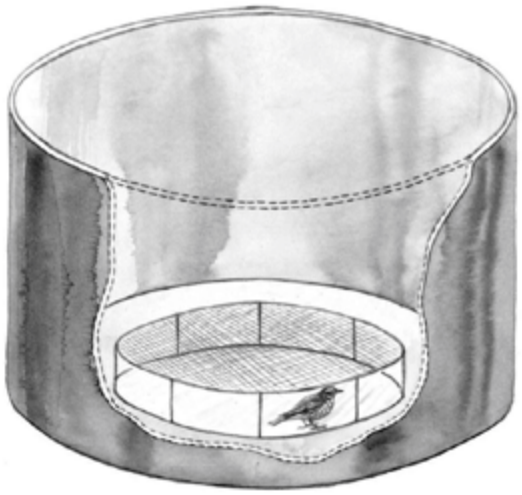


FIG 20. Equipment for measuring the directional preferences of birds in field conditions: protective non-transparent wall around and test cage within. The cage is shaped like a round cake. It is made of two circles of wire, connected by eight vertical wires. The top is covered with wire netting through which the test bird can see the sky. The side wall is covered by transparent foil (kitchen wrap or cling film) on which pecks and scratches are made by the bird in its attempts to escape (mostly in the direction of migration). The cage is placed within a circular fence of uniformly-coloured solid plastic that prevents the bird from seeing any landmarks, leaving only the sky visible. After a standard time (say ten minutes) in the cage, the bird is removed, as is the transparent foil, and the pecks and scratches are counted in each sector of the foil, each equivalent to a different compass direction. A new piece of foil is then attached in preparation for the next bird. With two cages available, up to six birds can be tested each hour by a single observer. More sophisticated orientation cages are used to test birds in laboratory conditions. (From Busse, 2000, drawn by Keith Brockie.)



FIG 21. Meadow Pipit *Anthus pratensis* a partial and short-distance migrant in the British Isles, and a passage migrant and winter visitor from further north. (Edmund Fellowes)

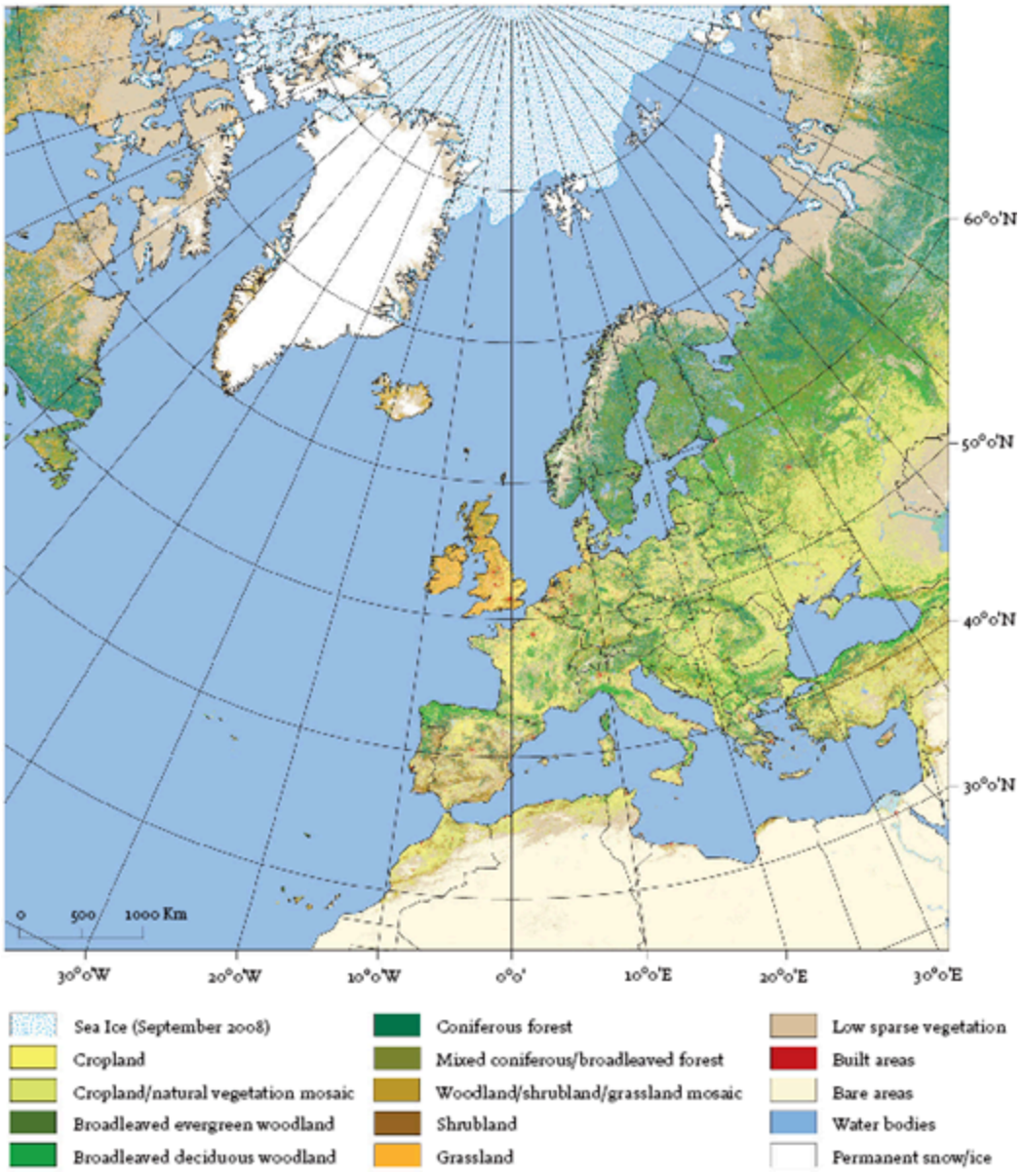


FIG 22. The British Isles in geographical context. The map shows the entire longitudinal span from which birds from arctic regions are drawn to winter in Britain and Ireland. (Courtesy of Globcover Land Cover v2 database. European Space Agency/Globcover Project, led by MEDIAS-France, 2008.)



FIG 23. Two game-birds that are wholly resident within the British Isles, and usually disperse to breed no more than a few kilometres from their hatch sites: Red Grouse *Lagopus lagopus* and Black Grouse *Tetrao tetrix* both males. (Edmund Fellowes)



FIG 24. Black Guillemot *Cepphus giylle* a non-migratory inshore species, which breeds along the rocky coasts of northwest Britain and Ireland. (Jack Stephens)



FIG 25. Winter-plumaged Great Northern Divers *Gavia immer* which are visitors to inshore waters around the British Isles, most commonly seen in the north and west. (Sean Gray/Grayimages)



FIG 26. White-fronted Geese *Anser albifrons* of which two populations winter in the British Isles, from Greenland and northern Eurasia respectively. The ones shown are European birds (race *A. a. albifrons)* distinguished by their orange, as opposed to pink, bills. (Frank Snijkers)



FIG 27. Wigeon *Anas penelope* (drakes), uncommon breeders but abundant winter visitors to the British Isles drawn from Iceland and as far east as central Siberia. (Brian Irving © HELM-Images)



FIG 28. Scaup *Aythya mania* common winter visitors mainly to the shallow seas around the British Isles. (Brian Irving © HELM-Images)



FIG 29. Common Snipe *Gallinago gallinago* a breeder and widespread winter visitor in the British Isles. (Brian Irving © HELM-Images)



FIG 30. Curlews *Numenius arquata* and Oystercatchers *Ostralegus haematopus* on a winter shoreline. (Brian Irving © HELM-Images)



FIG 31. Immature Glaucous Gull *Larus hyperboreus* an uncommon winter visitor from the arctic to the British Isles. (Rebecca Nason)



FIG 32. Little Gull larus *minutus* an uncommon but regular winter visitor to coastal districts and a passage migrant through Britain each autumn and spring. This bird, photographed on spring passage is in full breeding plummage (John Wright)



FIG 33. Two common winter visitors to the British Isles: Redwing *Turdus iliacus* and Fieldfare Turdus *pilaris*. (Brian Irving © HELM-Images)



FIG 34. Grey Heron *Ardea dnerea* a partial migrant and winter visitor in the British Isles. (Edmund Fellowes)



FIG 35. Great Grey Shrike *Lanius excubitor* a rare winter visitor to the British Isles. (Paul Hackett)



FIG 36. Red-throated Diver *Gavia stellata* in summer plumage, a regional breeder and winter visitor to inshore waters around the British Isles. (Jack Stephens)



FIG 37. Grey Phalarope *Phalaropusfulicarius* in winter plumage, a scarce passage migrant in the British Isles. (Sean Gray/Grayimages)



FIG 38. Yellow-legged Gull *Lams michahellis* which breeds mainly to the south, and appears in southern England mainly in late summer. (Sean Gray/Grayimages)



FIG 39. Flock of wintering Knots *Calidris canutus* Solway estuary, southwest Scotland. (Brian Irving © HELM-Images)

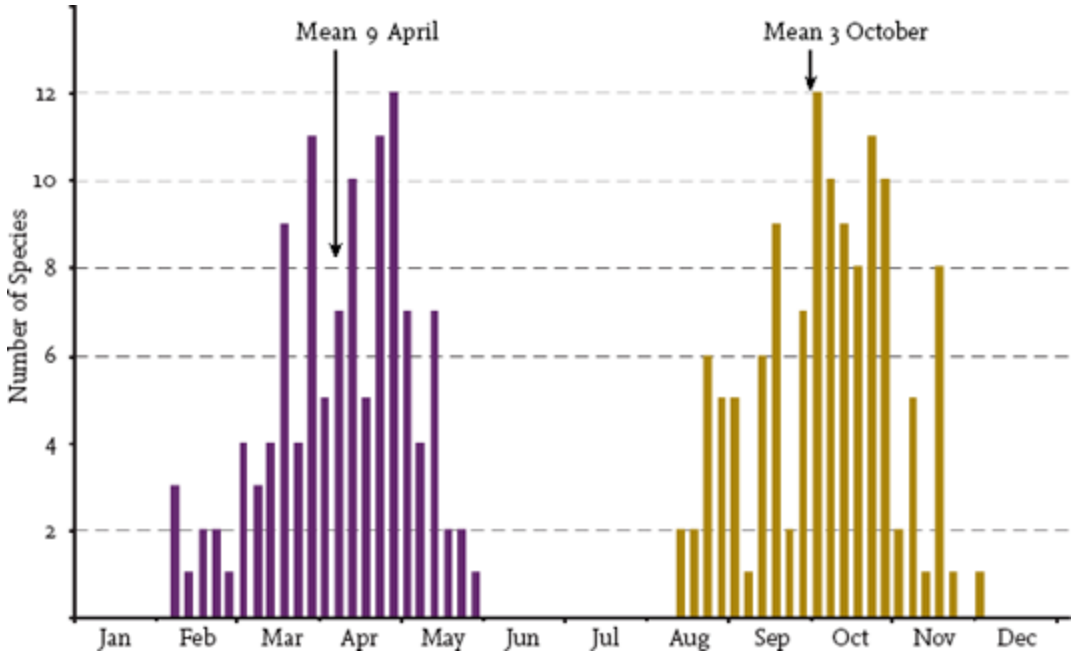


FIG 40. Mean spring and autumn passage dates of different bird species in southeast England, as measured at Dungeness Bird Observatory, 1990–2007. Species are grouped into 5-day periods through the year. The overall average spring passage date of all species at this location was 9 April and the overall average autumn date was 3 October, but while some of these birds were British breeders, others at the same season were associated with breeding areas further north or northeast. (From Newton *et al.* 2010.)

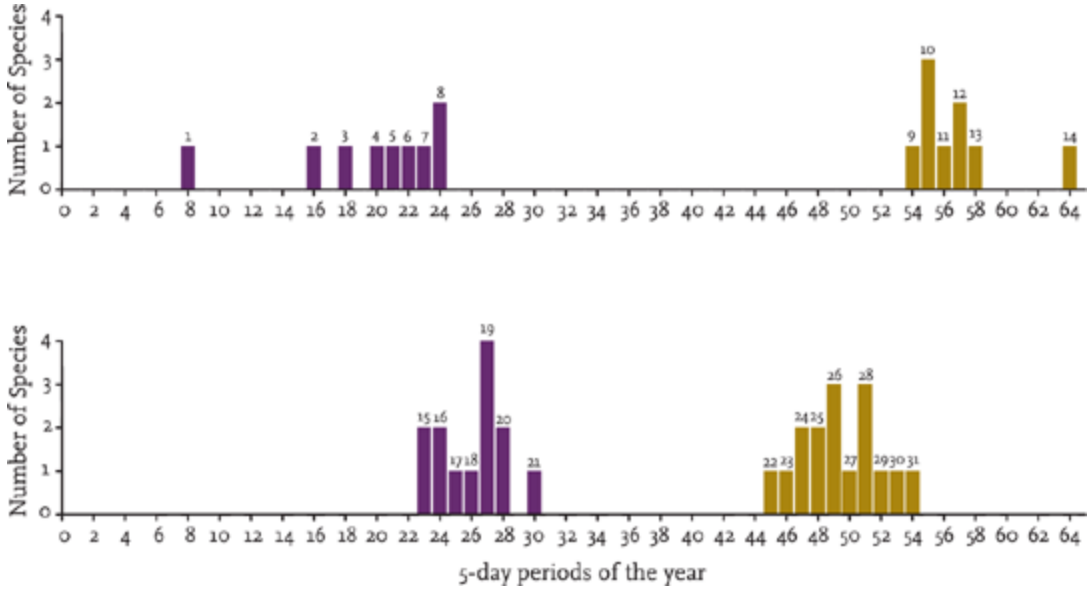


FIG 41. Mean spring and autumn dates of various passerines at Dungeness Bird Observatory shown separately for short-distance migrants wintering within Europe (top), and long distance migrants wintering in Africa south of the Sahara (bottom). In general., long-distance migrants arrived later and left earlier than short-distance ones, spending shorter periods in their breeding areas. These birds are likely to have included not only British breeders, but also others breeding further north in Europe. Columns represent the following species: I - Greenfinch; 2—Stonechat; 3—Meadow Pipit; 4—Skylark; 5—Chiffchaff; 6—Black Redstart; 7—Linnet; 8—Blackcap, Goldfinch; 9—Linnet; 10—Meadow Pipit, Black Redstart, Blackcap; II - Chiffchaff; 12—Stonechat, Skylark; 13—Goldfinch; 14—Greenfinch; 15—Willow Warbler, Common Redstart; 16—Tree Pipit, Northern Wheatear; 17—Yellow Wagtail; 18—Sand Martin; 19—Whitethroat, Garden Warbler, Barn Swallow, Lesser Whitethroat; 20—House Martin, Spotted flycatcher; 21—Reed Warbler; 22—Reed Warbler; 23—Whitethroat; 24—Sedge Warbler, Willow Warbler; 25—Sand Martin, Yellow Wagtail; 26—Northern Wheatear, Pied Flycatcher; 26—Garden Warbler; 27—Lesser Whitethroat; 28—Whinchat, Spotted Flycatcher, Tree Pipit; 29—Common Redstart; 30—House Martin; 31—Barn Swallow. (From Newton *et al.* 2010.)



FIG 41. Ring Ouzel *Turdus torquatus* which breeds in upland areas of the British Isles and winters in southern Spain and North Africa. It is one of the earliest summer visitors to arrive in Britain each spring. (Sean Gray/Grayimages)

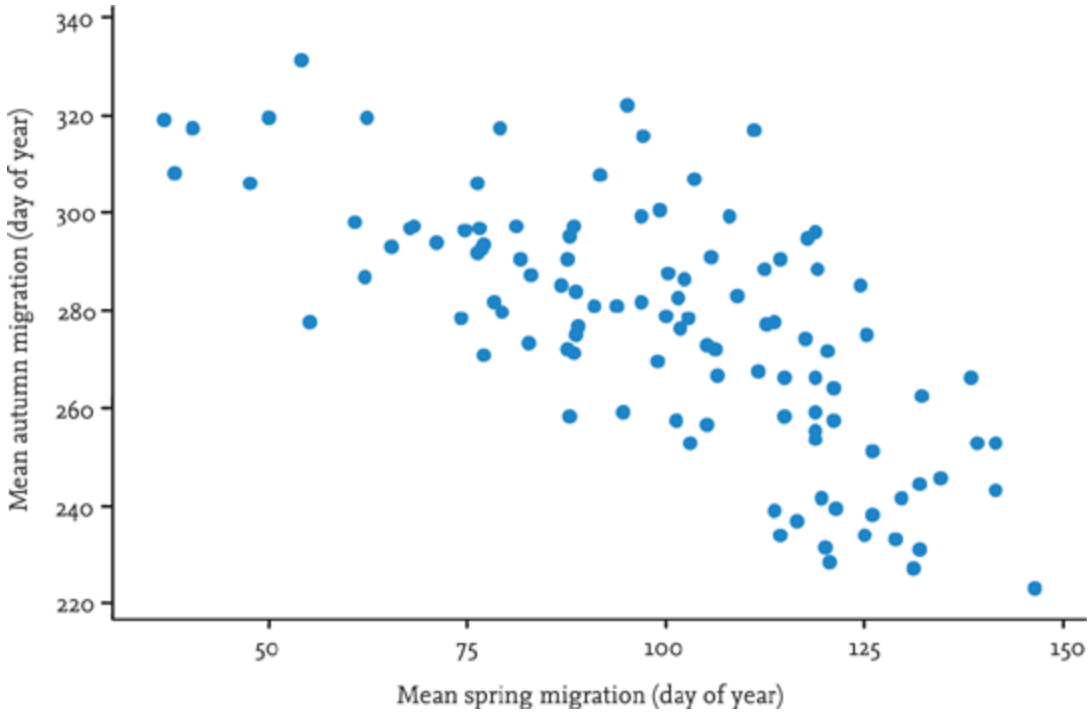


FIG 43. Relationship between mean arrival dates and mean departure dates of different bird species in southeast England, as measured at Dungeness Bird Observatory, 1990–2007. In general., species that passed through early in spring tended also to pass through later in autumn, and vice versa. Regression relationship, r = -0.713, P > 0.001. (From Newton *et al.* 2010.)



FIG 44. Lapwings *Vanellus vanellus* are some of the first winter visitors to arrive in Britain each year, with massive immigration beginning from late June,

augmenting the local residents. (Brian Irving © HELM-Images)



FIG 45. Common Gull larus *canus* a local breeding species, whose numbers in the British Isles are greatly increased in winter through the immigration of continental birds. (Edmund Fellowes)



FIG 46. Black-legged Kittiwake *Rissa tridactyla* a pelagic species which breeds on coastal cliffs around the British Isles, and ranges widely over the North Atlantic in winter. (Edmund Fellowes)



FIG 47. Winter-plumaged Black-throated Diver *Gavia árctica* an uncommon breeding species and winter visitor to the inshore waters of the British Isles, mainly in the north and east. One of several species for which no useful ring recoveries are yet available from British breeding or wintering birds. (Frank Snijkers)



FIG 48. Pink-footed Geese *Anser brachyrhynchus* flying in energy-saving V-formation. (Edmund Fellowes)

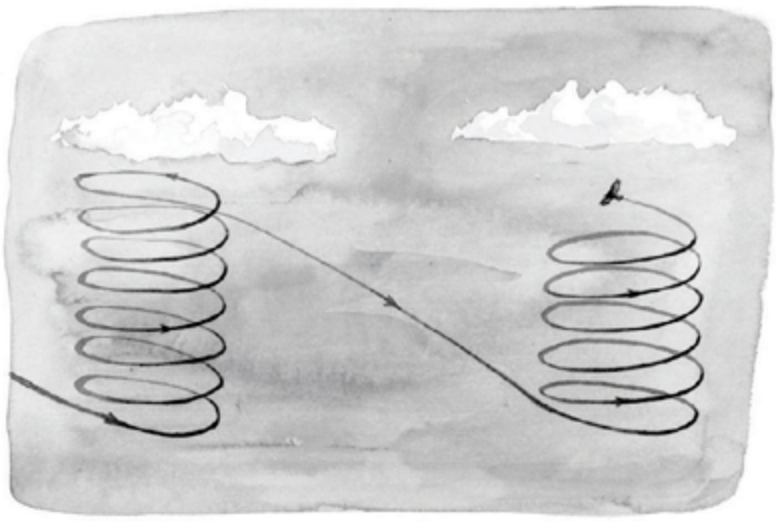


FIG 49. Soaring-gliding bird migration, indicating soaring within thermals, gaining height, and gliding between thermals, losing height. Thermals are often topped with cumulus clouds. (Drawn by Keith Brockie.)



FIG 50. Common Buzzard *Buteo buteo* in soaring flight, with wings and tail spread to catch rising air currents. (John Wright)

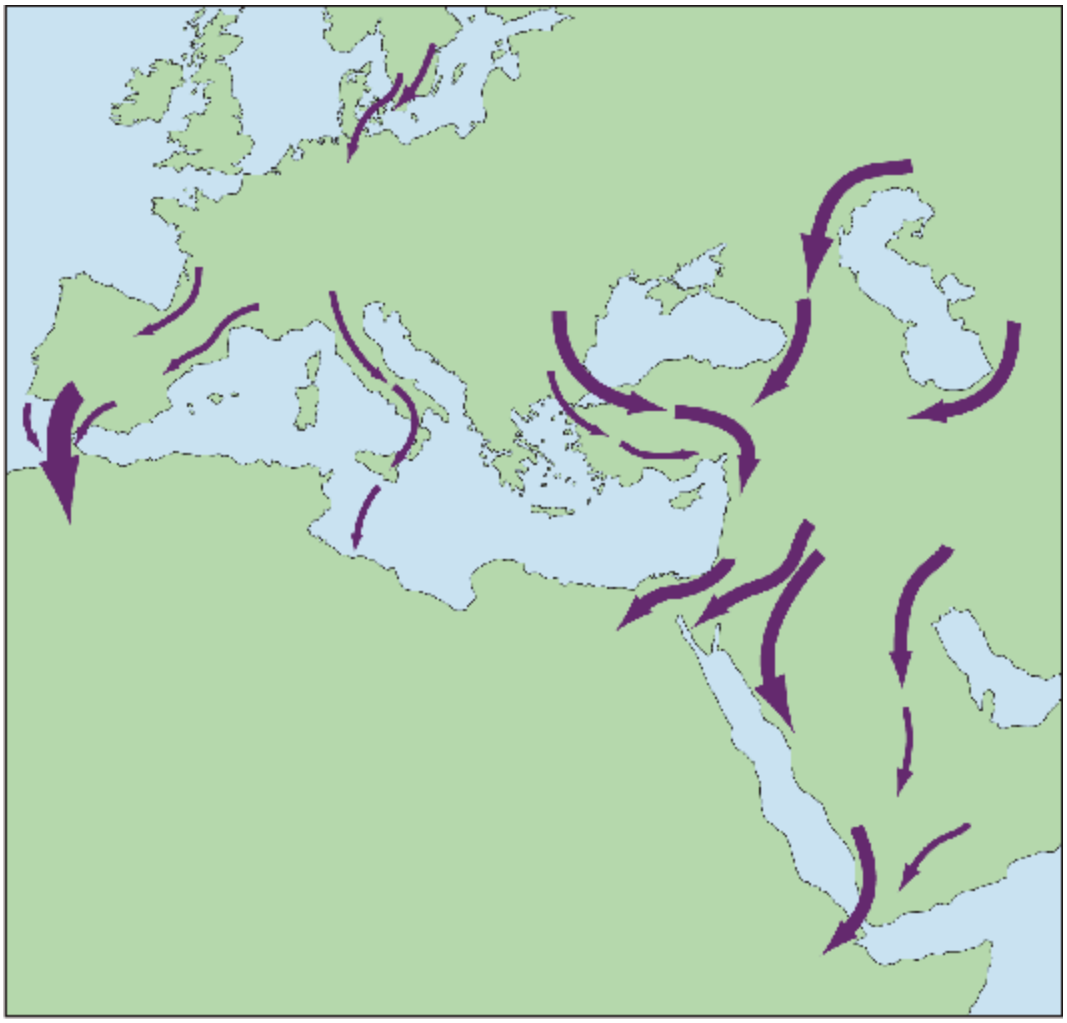


FIG 51. Main flyways used by soaring birds travelling from Europe to Africa.



FIG 52. White Storks *Ciconia ciconia* soaring on migration over Egypt. (Dick Forsman)



FIG 53. Goldcrest *Regulus regulus* the smallest (5 g) of European birds, which is a partial migrant and winter visitor in the British Isles. It migrates at night, from some northern regions covering distances exceeding 1,000 km. (Sean Gray/Grayimages)



FIG 54. Young Swifts *Apus apus* at their nest in a building. These birds are almost ready to leave the nest, after which they are likely to remain on the wing continuously for at least a year, when they seek their own nest sites. (Bobby Smith)



FIG 55. Sleeping Redshanks *Tringa totanus* Leighton Moss, Lancashire. Many shorebirds, on arrival from migration, quickly fall asleep. (Brian Irving © HELM-Images)



FIG 56. Ortolan Bunting *Emberiza hortulana* one of the few seed-eating species to migrate across the Sahara desert to winter in the northern tropics of Africa. Unlike other European buntings, which are residents or short-distance migrants, Ortolans migrate largely at night. This individual appeared as a vagrant on Fair Isle. (Rebecca Nason)

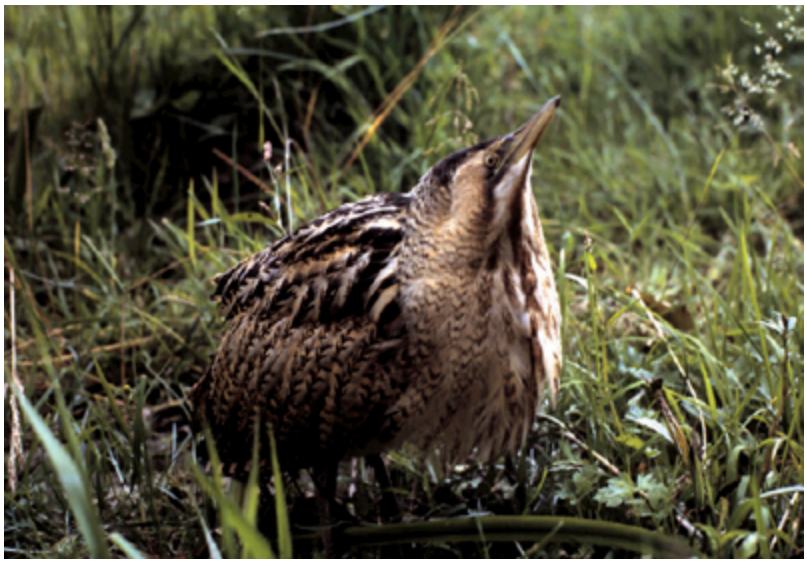


FIG 57. Bittern *Botaurus stellaris* a normally solitary species which has been seen to assemble into small groups before setting off on migration (see text). The species is a scarce partial migrant and winter visitor in the British Isles. (Bobby Smith)



FIG 58. Greylag Geese *Anser anser* residents and winter visitors to the British Isles. Like other geese, Greylag migrate in family parties within the flocks, allowing the young to learn the route from their parents. (Brian Irving © HELM-Images)



FIG 59. Barnacle Geese *Bmnta leucopsis* in fields near the Solway Estuary, winter visitors to this area from Svalbard. (Edmund Fellowes)

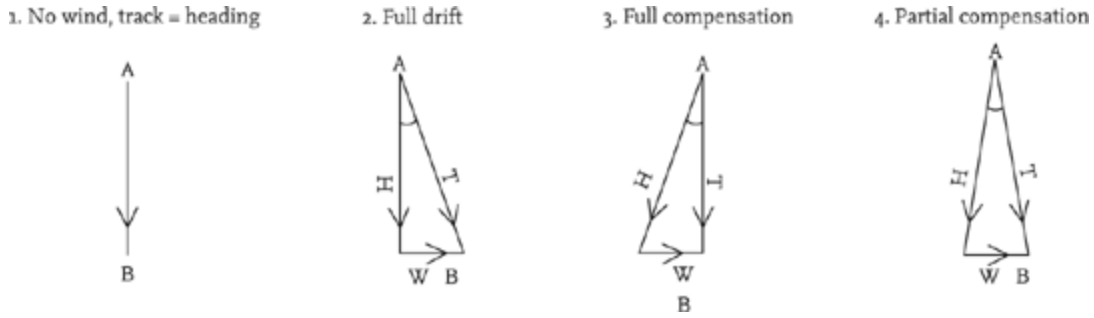


FIG 60. Effects of side-winds (W) on the migratory tracks (T) of birds, depending on adjustments of heading (H). When there is no side-wind, heading and track are the same (1): but under a strong side wind there can be either full drift (no compensation, 2); no drift (full compensation, 3); or partial drift (partial compensation, 4). (Modified from Kerlinger, 1989.)

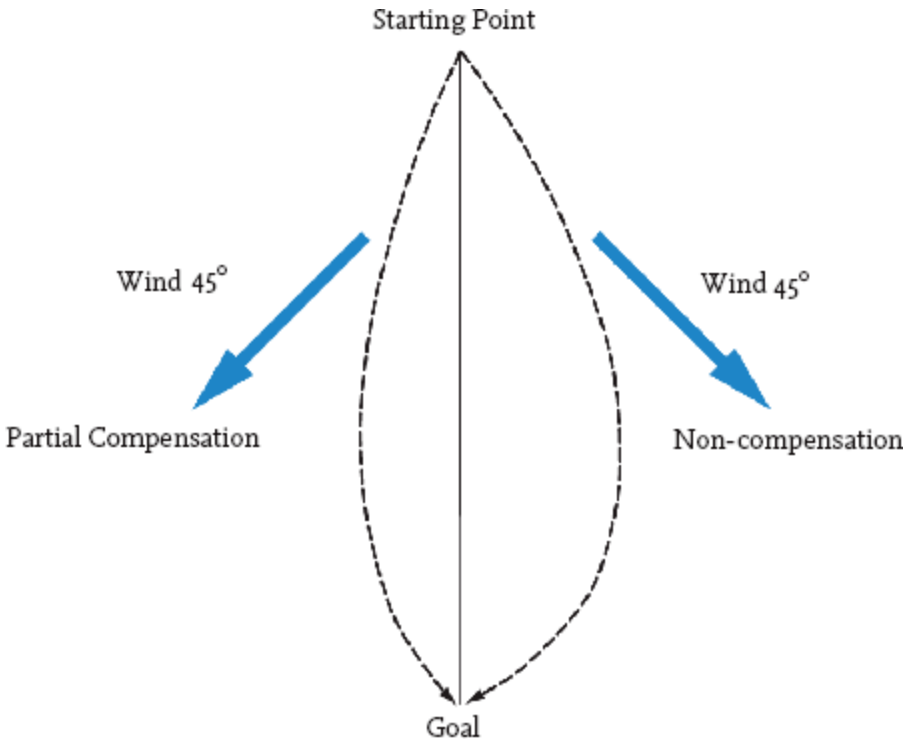


FIG 61. Optimal use of a crosswind by a migrant. The bird is drifted by the wind during the initial stage of migration and later over-compensates to reach its goal. (From Alerstam, 1979.)



FIG 62. Wryneck Jynx *torquilla* a former breeder, but now mainly a passage migrant which appears in eastern Britain mainly in easterly winds. (Sean

Gray/Grayimages)



FIG 63. Rustic Bunting *Emberiza rustica* a rare vagrant which occurs in eastern coastal Britain mainly at times of easterly winds during migration seasons. (John Wright)

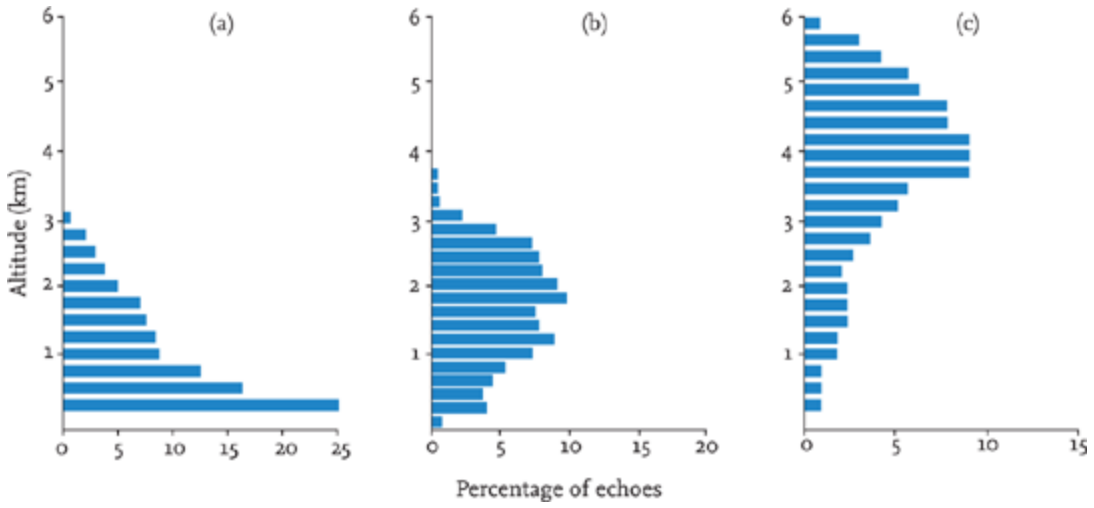


FIG 64. Altitudinal distribution of migrants as registered by radar studies in: (a) Lowlands of central Europe, spring (Bruderer, 1971); (b) South Sweden, spring, mainly waterfowl and shorebirds (Green, 2004); (c) Antigua, Caribbean, autumn (Williams *et al.* 1977).

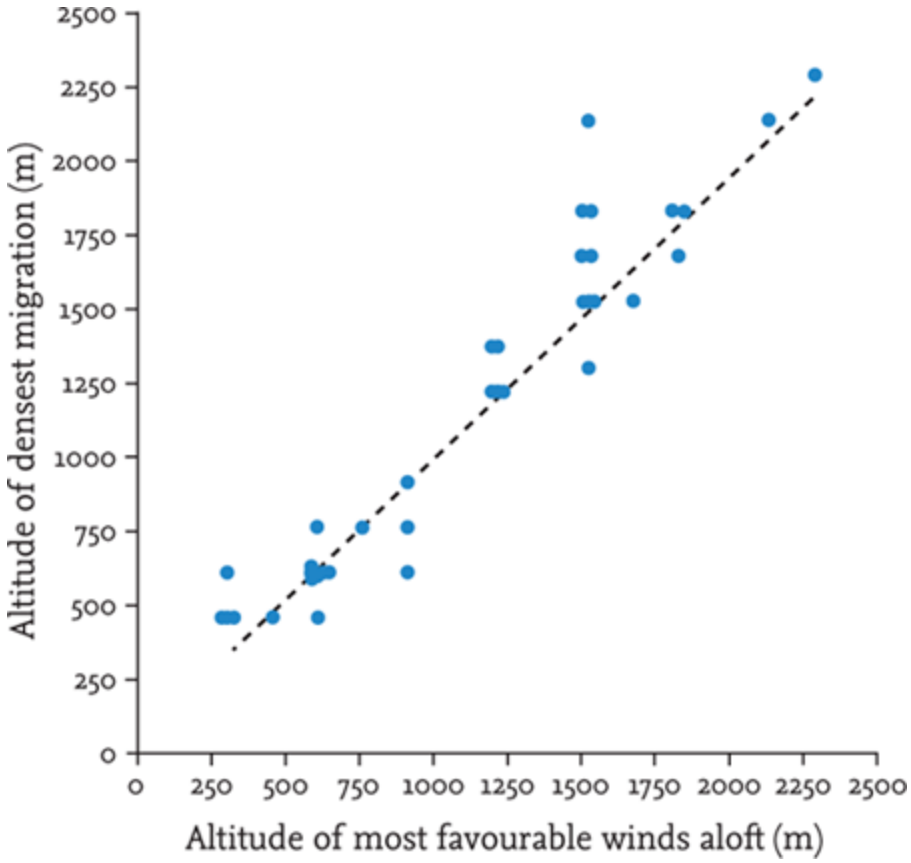


FIG 65. Correlation between the altitude of densest nocturnal bird migration and the altitude of the most favourable wind, as measured by radar in the southeastern USA. Many birds adjusted the height of their migration each night in order to take advantage of the most favourable wind (defined as a wind blowing toward the north-northeast in spring or south-southwest in autumn and occurring at the lowest possible altitude). Regression relationship: $y = 58.6 + o.987(x)$, $r = 0.96$, $t = 22.9$, $P > 0.01$, $N = 38$. (From Gauthreaux, 1991.)



FIG 66. Light-breasted Brent Geese *Branta bemicla hrota* which cross the Greenland Ice cap on their journeys between Ireland and their breeding areas in north-eastern Canada. (Sean Gray/Grayimages)



FIG 67. Eider Ducks *Somateria mollissima* which normally migrate low over the sea. (Brian Irving © HELM Images)

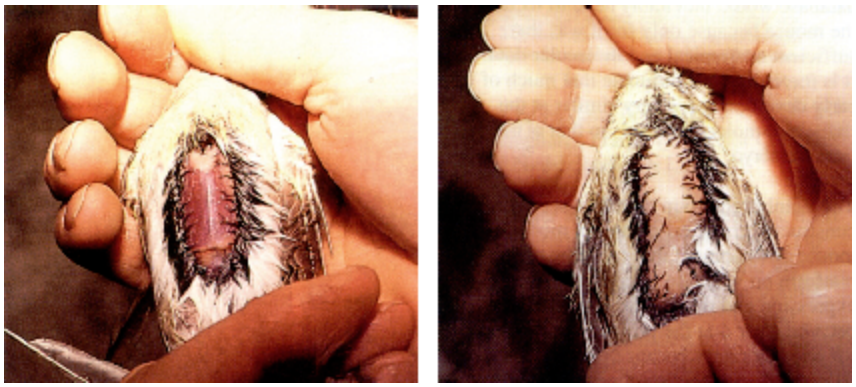


FIG 68. Breasts of Garden Warblers *Sylvia borin* with feathers dampened and moved aside to show (above left) a lean bird and (above right) a fat one just prior to migration. (Franz Bairlein)



FIG 69. Golden Plover Píuwíaíis aprícaría, whose body composition varies greatly between the autumn and spring migrations, with much more protein accumulated prior to spring migration, in preparation for breeding. (Edmund Fellowes)

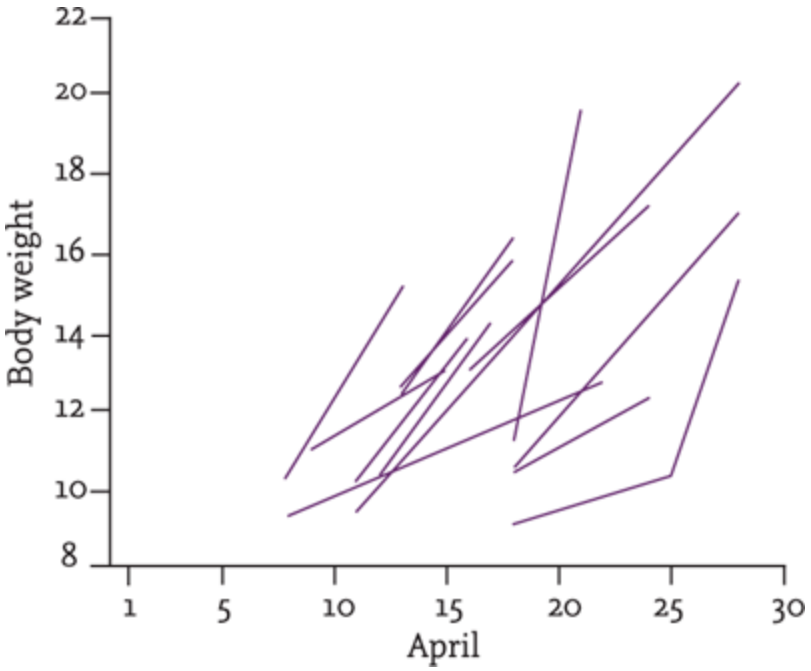


FIG 70. Body mass changes, reflecting pre-migratory fuel deposition, in Sedge Warblers *Acrocephalus schoenobaenus* caught repeatedly in spring 1971 near Nairobi in Kenya. The maximum rate recorded was for a bird which went from 11.2 g to 19.6 g in three days, a 75 per cent increase. Another bird more than doubled its weight in 17 days. For most individuals this site may have provided their last feed before crossing the Sahara desert. (From Pearson *et al.* 1979.)

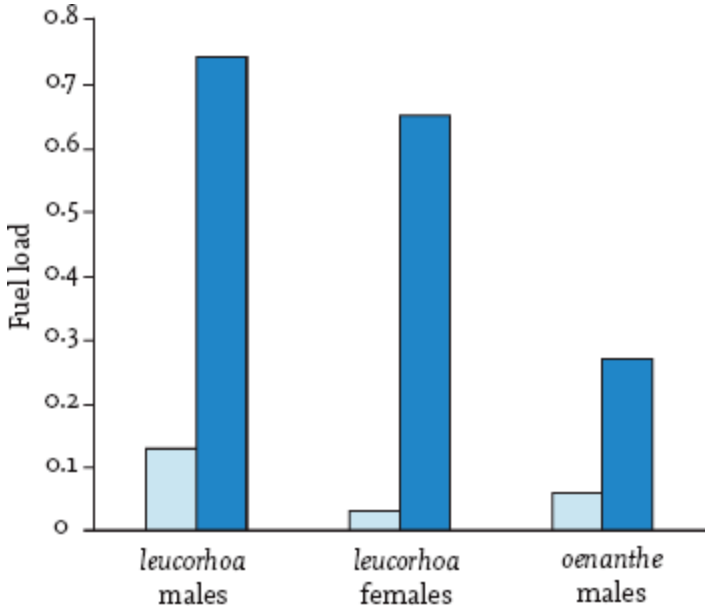


FIG 71. Mean fuel loads at arrival (light blue) and departure (dark blue) in two races of Northern Wheatears *Oenanthe oenanthe* calculated for individuals that stayed at least two days on Heligoland Island in spring. The race O. *o. leucorhoa* migrates mainly over water to Greenland, while the smaller race O. *o. oenanthe* migrates mainly overland within Europe. Fuel load is a relative measure: a value of 0.5 is equivalent to a body mass 50% above lean body mass. (From Dierschke *et al.* 2005.)



FIG 72. Northern Wheatear *Oenanthe oenanthe* (juvenile) caught on migration. (John Willsher)

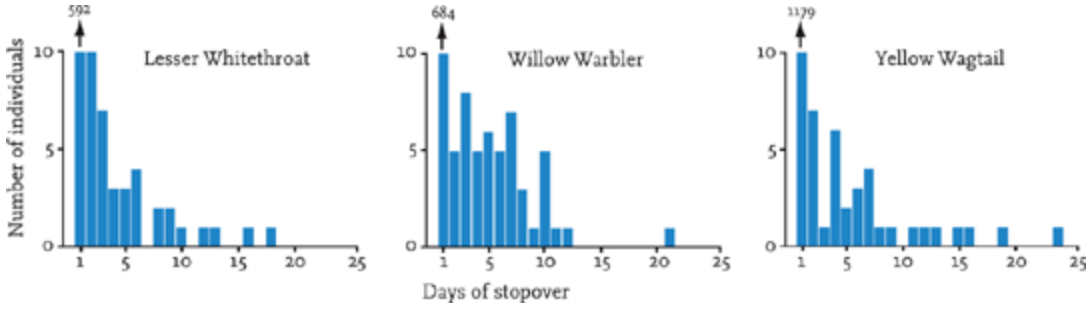


FIG 73. Minimum stopover periods in spring of birds at the oasis of Sadat Farm, in the Libyan Desert of Egypt. Sample sizes for birds trapped and ringed on one day only are shown above the columns. The remaining records are based on retraps of ringed birds. Most of the visiting birds were recorded on only one day, and may

have passed through without feeding, while others stayed for more than ten days, replenishing their body reserves. (From Biebach *et al.* 1986.)



FIG 74. Garden Warbler *Sylvia borin* (juvenile), which like some other warblers, feeds mainly on berries in late summer when fattening for migration. (JohnWillsher)

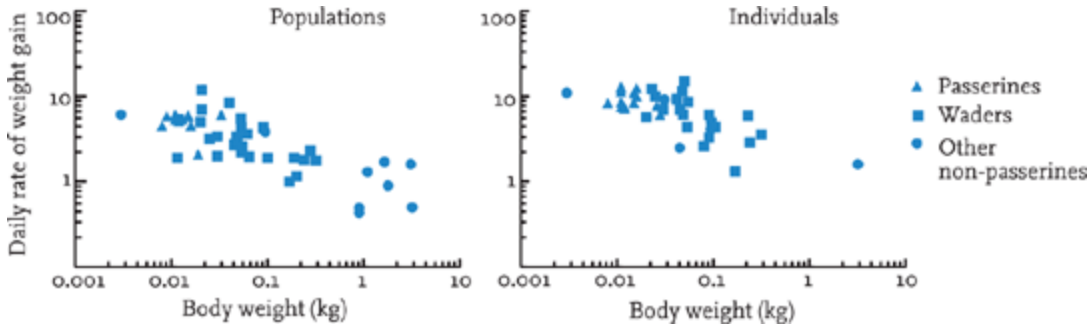


FIG 75. Maximum daily rates of pre-migratory weight increase in relation to lean body mass recorded in different bird species. Data are based on changes in body weights over time (minimum two days). Maximum rates decreased with increase in body mass, both for individuals and for mean values from populations. Allowing for body mass, the three main groups of birds examined (passerines, shorebirds and other non-passerines) showed no significant differences in rates of daily fuel deposition. Overall, the relationship between maximum daily weight gain and body mass (BM) for populations was $1.16\ BM^{0.35}$ ($r^2 = 0.66$, $P > 0.001$) and for individuals $2.17\ BM^{0.34}$ ($r^2 = 0.54$, $P > 0.001$). (From Lindström, 2003, in which the original reference sources may be found.)

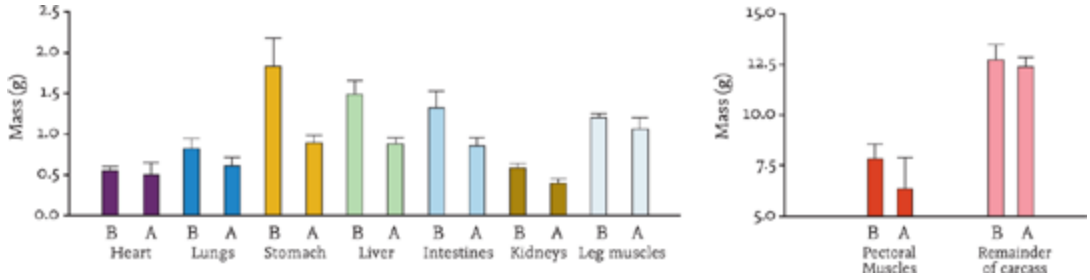


FIG 76. Comparison of the weights of different organs of Garden Warblers *Sylvia borin* before (B—Ethiopia) and after (A—Egypt) crossing the Sahara Desert in spring. Columns show mean values of lean dry mass and lines 95% confidence limits. (From Biebach & Bauchinger, 2003.)



FIG 77. Common Swift *Apus apus* a fast-flying species in which the pre-fattened young migrate long distances soon after leaving the nest. (Brian Irving © HELM Images)

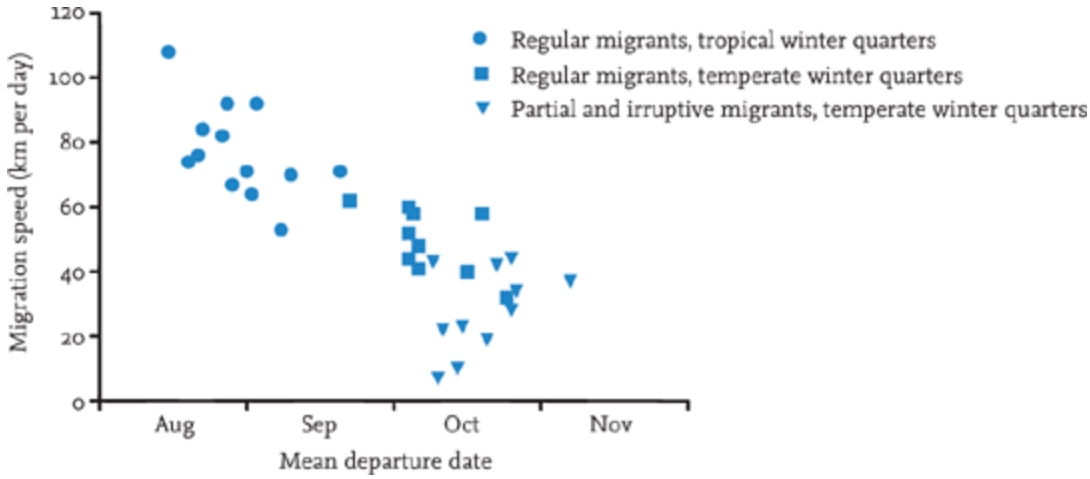


FIG 78. Migration speeds recorded for passerines ringed in Finland in relation to the seasonal timing of migration as recorded at Ottenby in Sweden. The trend highlights the reduction of migration speed with advance in mean departure date, and the differences between different categories of migrants. (From Alerstam & Lindström, 1990, based on data in Hildén & Saurola, 1982)



FIG 79. Marsh Warbler *Acrocephalus palustris* a long distance migrant that travels via eastern Europe to South Africa. (Frank Snijkers)

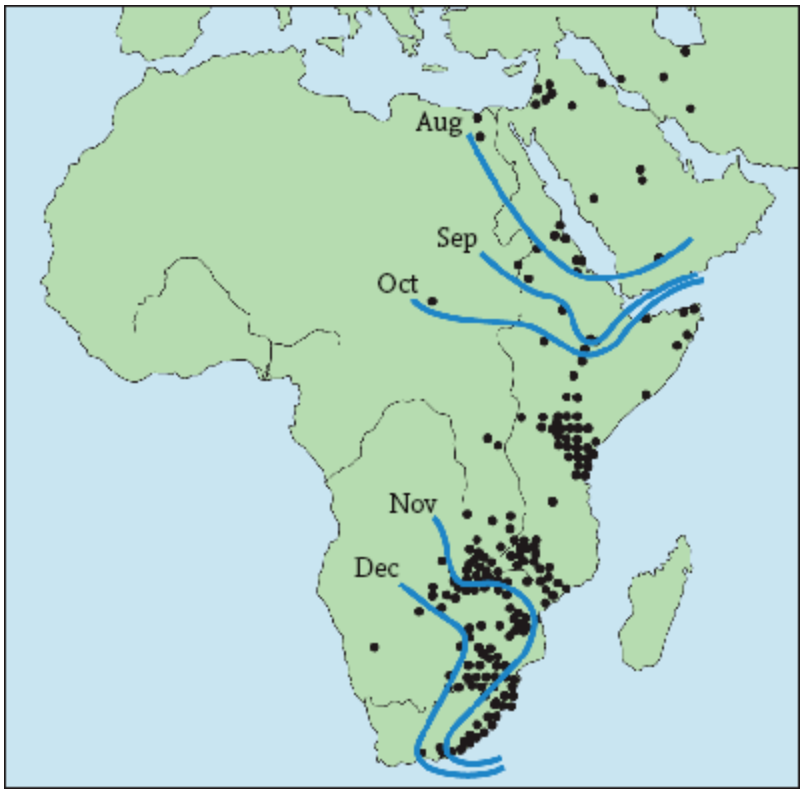


FIG 80. The course of migration of European Marsh Warblers *Acrocephalus palustris* to South African wintering areas. The whole southward journey takes at least five months, and lines show progress, as revealed by ring recoveries (Dowsett-Lemaire &, Dowsett, 1987). The return journey is faster, taking less than three months. This species therefore spends nearly two-thirds of each year on migration.



FIG 81. Tundra (Bewick's) Swan *Cygnus columbianus* a species tracked on migration between western Europe and arctic Siberia. (Jill Pakenham)

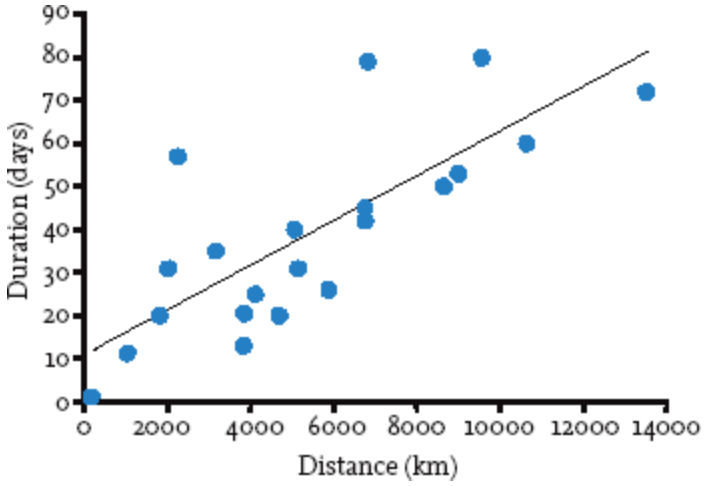


FIG 82. Relationships between duration and distance in the autumn migrations of different raptor species, based on the mean values from different studies. Birds travelling longer distances took longer over their journeys. Regression relationship: Duration (days) = $11.8 + 0.00493^{x}$ distance (km), $r = o.75$, $P > 0.001$. No relationship was apparent between migration speed and distance: speed (km per day) $= 116 + 0.0057^{x}$ distance (km), $r = 0.31$, $P = 0.162$. (Details from Newton, 2008.)



FIG 83. Osprey *Pandion haliaetus* tracked on migration between various parts of Europe and the northern tropics of Africa. (John Wright)

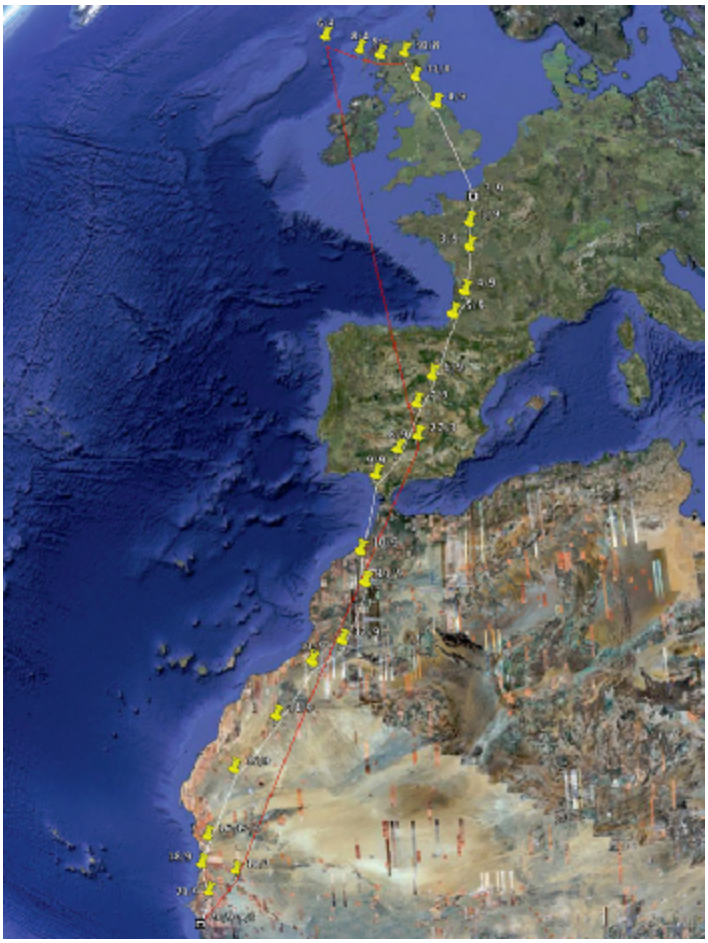


FIG 84. Migrations of a satellite-tracked radio-tagged Osprey *Pandion haliaetus* between Senegal and Scotland (visualised on Google Earth), showing the daily flights and the nightly stopping places. On its spring migration, this bird was drifted off course and overshot it nesting site before returning there. (With permission from the website of the Highland Wildlife Foundation.)

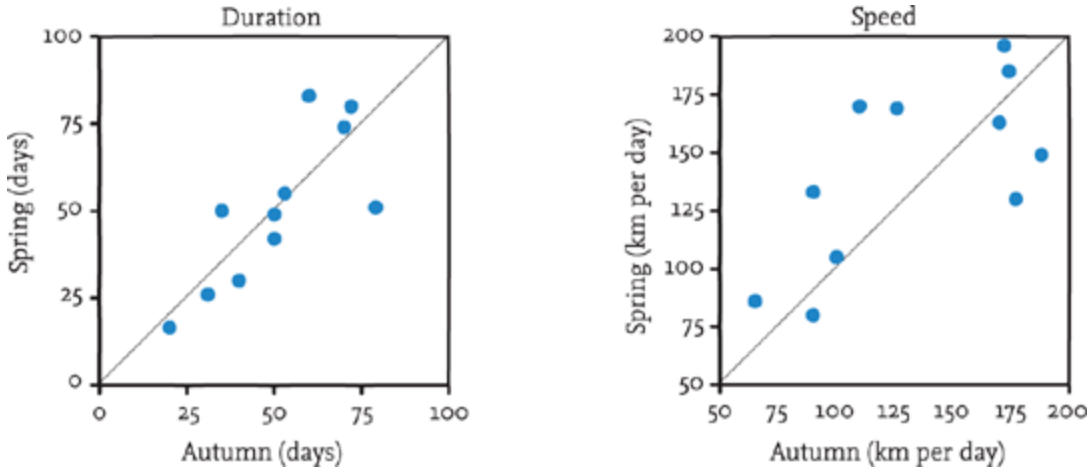


FIG 85. Relationship between the durations and speeds of the autumn and spring migrations of different raptor populations, based on the mean values from different studies listed in Newton, 2008. The line on each graph shows the relationship expected if the two migrations were of equal duration and speed. Overall, no significant difference was apparent in the duration or speed between seasons (on a paired t-test for duration, t = 0.08, P = o.94; for speed, t = -o.93, P = o.37).



FIG 86. Whooper Swans *Cygnus (ygnus* tracked on migration between Iceland and the British Isles. (Edmund Fellowes)

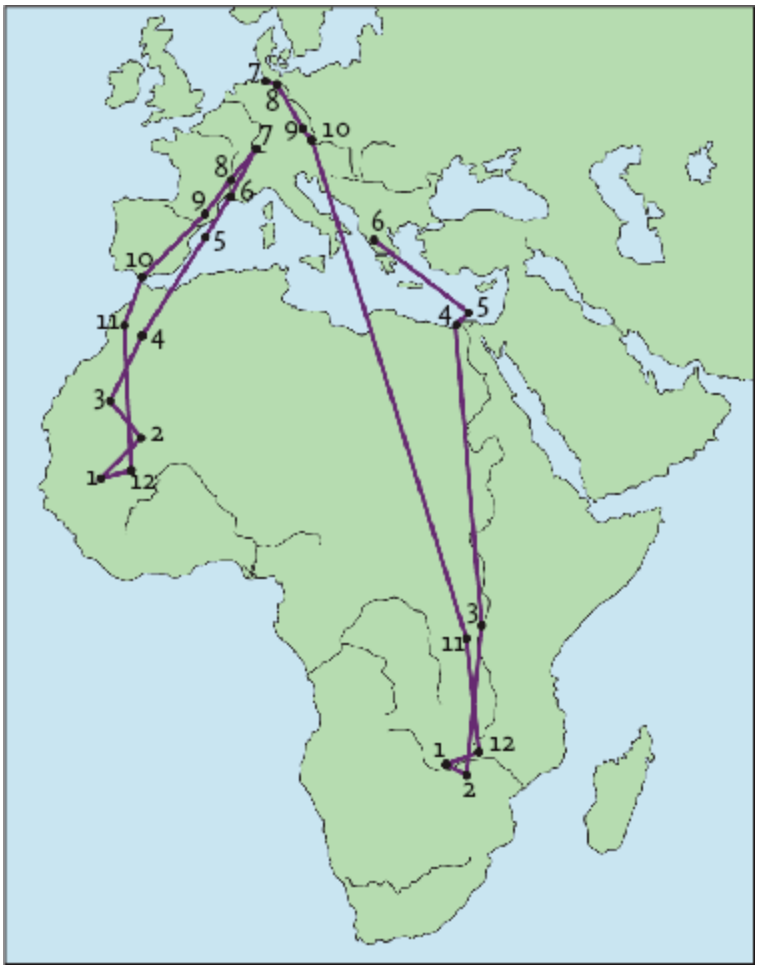


FIG 87. Course of first-year migration in White Storks *Ciconia ciconia* from southwestern Germany (westerly route) and northwestern Germany (easterly route), showing the migratory divide. Dots show the average monthly location of ringed birds. The lines join the dots of successive months, but do not necessarily reflect the exact routes followed. First-year storks are on the move for much of the year, and most do not reach the breeding areas until it is too late to nest that year. Birds taking the eastern route cover twice the distance but in the same time as the western birds. (From Bairlein, 2001.)



FIG 88. Bar-tailed Godwit *Limosa lapponica* in early June, freshly arrived on tundra breeding grounds. (Edmund Fellowes)



FIG 89. Arctic Tern *Sterna paradisaea* which winters in the seas around Antarctica, and performs some of the longest migrations known among birds. (Edmund Fellowes)



FIG 90. Sedge Warbler *Acrocephalus schoenobaenus* which almost doubles its weight through migratory fuel deposition in autumn, and may then migrate non-stop from southern Britain to the northern tropics. Reed Warbler *Acrocephalus scirpaceus* which accumulates less fat than the Sedge Warbler, and migrates through western Europe in short flights, with frequent stops. (Frank Snijkers)



FIG 91. Lesser Whitethroat *Sylvia curruca* which is thought to travel from British breeding areas to African wintering areas by two long flights, with a major autumn stopover in Italy. (John Willsher)

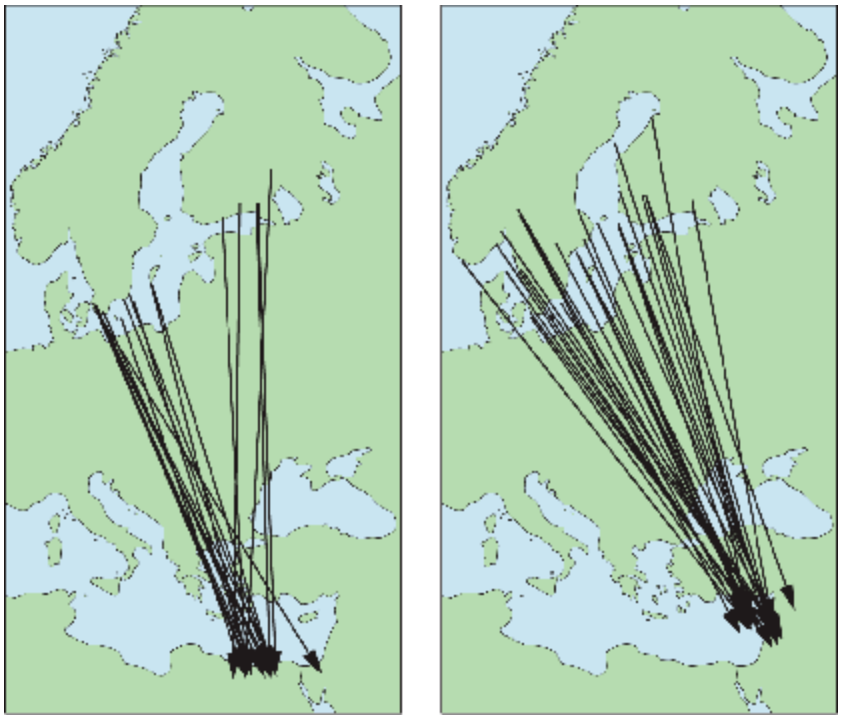


FIG 92. Birds ringed in northern Europe and recovered in the eastern Mediterranean region. Lines connect the ringing site with the recovery site for each individual. Above left: Thrush Nightingale Insania *lusania*. Above right: Blackcap *Sylvia atricapilla*. These are two out of seven passerines species which migrate from northern Europe round the eastern Mediterranean in autumn for which there are sufficient ring recoveries for analysis. (From Fransson *et al.* 2005.)



FIG 93. Yellow Wagtail *Motacilla flava* (race *flavissima* from Britain), a regular trans-Saharan migrant, thought to often cross the Mediterranean and Sahara in a single non-stop flight. (Rebecca Nason)



FIG 94. Golden Oriole *Oriolus oriolus* a regular trans-Saharan migrant, which winters in forest and woodland. (John Willsher)



FIG 95. The Greenland ice-cap seen from the air. (Kurt Burnham)



FIG 96. Moult in a Willow Warbler *Phylloscopus trochilus* which begins at the innermost primary feather and progresses outwards. Note the contrast between the new feathers and the old faded and worn ones from the previous moult. This species undergoes two moults per year, and this individual was photographed in late summer in Britain, the old feathers having been grown during the previous winter in Africa. (David Norman)

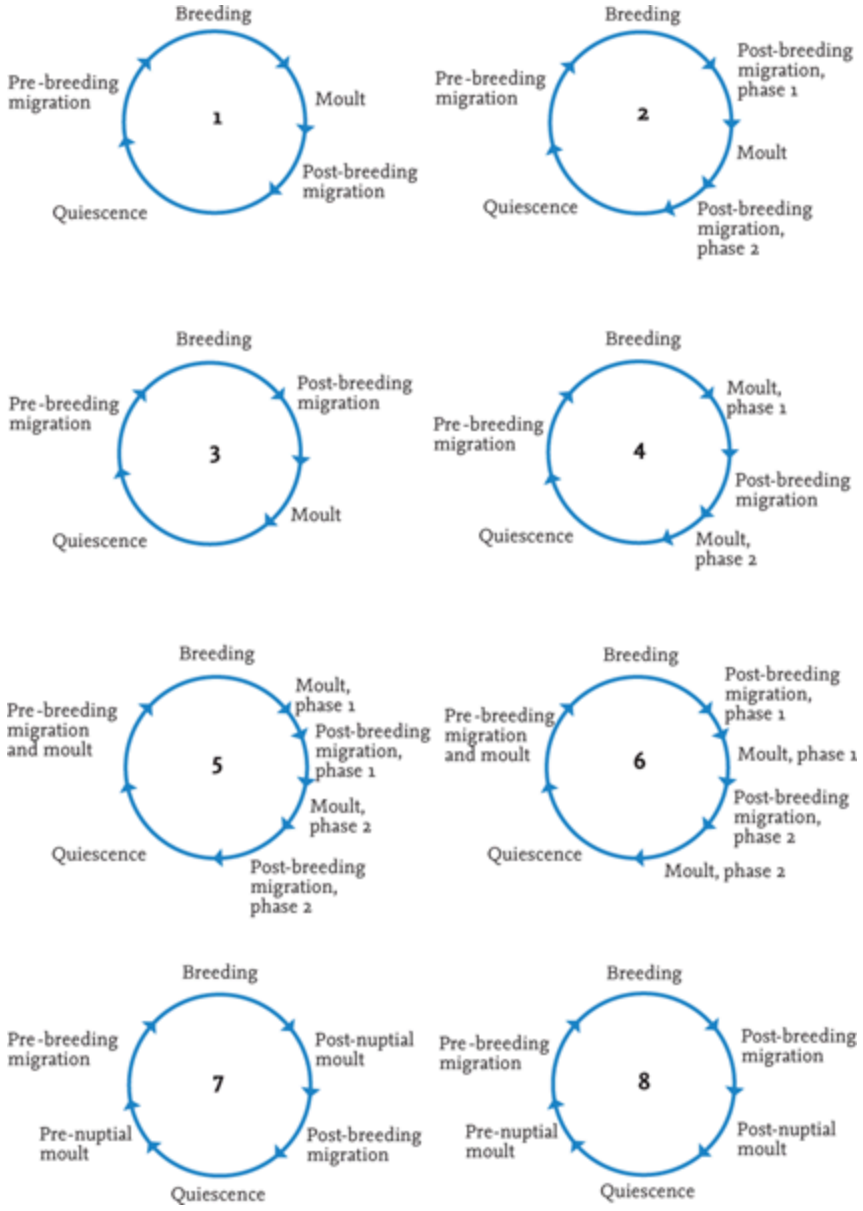


FIG 97. Eight common sequences of annual cycle events described among European migratory birds. Events are listed beginning with breeding. The term 'quiescence' denotes a period when the bird is not breeding, moulting or migrating.

1 Examples: Common Redpoll *Carduelis flammea,* Thrush-Nightingale Luscinia *luscinia,* Fieldfare *Turdus pilaris,* Jack Snipe *Lymnocryptes minimus.*

2 Examples: Great Reed Warbler *Acrocephalus arundinaceus,* River Warbler *Locustella fluviatilis,* Northern Lapwing *Vanellus vanellus,* some populations of Green Sandpiper *Tringa ochropus,* various ducks. **3.** Examples: Common Rosefinch

Carpodacus erythrinus, Common Swift *Apus apus, Whimbrel Numenius phaeopus,* Harlequin Duck *Histrionicus histrionicus,* together with some shearwaters, terns and skuas that breed and winter in opposite hemispheres. In some of these species, the moult is prolonged and the quiescent period short or non-existent (as in Barn Swallows *Hirundo rustica* wintering in South Africa). **4.** Examples: Barred Warbler *Sylvia nisoria,* Alpine Swift *Apus melba,* Scops Owl *Otus scops,* Bee-eater *Merops apiaster,* Red-necked Nightjar *Caprimulgus ruficollis,* Collared Pratincole *Clareola pratincola,* Marsh Sandpiper *Tringa stagnatilis,* juveniles of Common Quail *Coturnix coturnix*. **5.** Examples: Kentish Plover *Charadrius alexandrinus,* Spotted Redshank *Tringa erythropus,* some individuals of Curlew Sandpiper *Calidris ferruginea.* **6.** Examples: Wilson's Phalarope *Phalaropus tricolor,* Spotted Sandpiper *Actitis macularia,* and other populations of shorebirds. **7.** Example with two complete moults per year: Willow Warbler *Phylloscopus trochilus;* examples with one complete and one partial moult per year: Melodious Warbler *Hippolais polyglotta* and many shorebirds. **8.** Examples: Lanceolated Warbler *Locustella lanceolata* and some other *Locustella* warblers, Curlew Sandpiper *Calidris ferruginea.*



FIG 98. Little Stint *Calidris minuta* an uncommon passage migrant in the British Isles. This individual., photographed in early May, was on migration, and replacing its greyish winter plumage by darker breeding plumage. (Colin Turvey)



FIG 99. Linnet *Carduelis cannabina* a common partial migrant in the British Isles. The red in the breeding plumage of the male results from abrasion, when the dull brown tips of the feathers wear off to expose the colour below. The species thus acquires a special breeding plumage without the need to moult. (Frank Snijkers)



FIG 100. Great-crested Grebes *Podiceps cristatus* showing (above left) distinct winter and (above right) summer plumages. (Frank Snijkers)



FIG 101. Rock Ptarmigan *Lagopus mutus* showing (above left) distinct winter and (above right) summer plumages. Both are still in moult, and the summer bird shows remnants of the preceding white winter plumage. (Cal Sandfort, left; Edmund Fellowes, right.)



FIG 102. Ringed Plover *Charadrius hiaticula* in which most European populations moult rapidly in their breeding areas in late summer before migrating within Europe, while arctic-nesting birds leave their nesting areas soon after breeding and moult in their southern African winter quarters. (Edmund Fellowes)



FIG 103. Garden Warbler *Sylvia borin* subject of experiments on the circannual rhythm—the 'body clock' which underlies breeding, moult and migration. (Bobby Smith)



FIG 104. Stonechat *Saxícola torquata* (female), another subject of experiments on the circannual rhythm. (Brian Irving © HELM-Images)

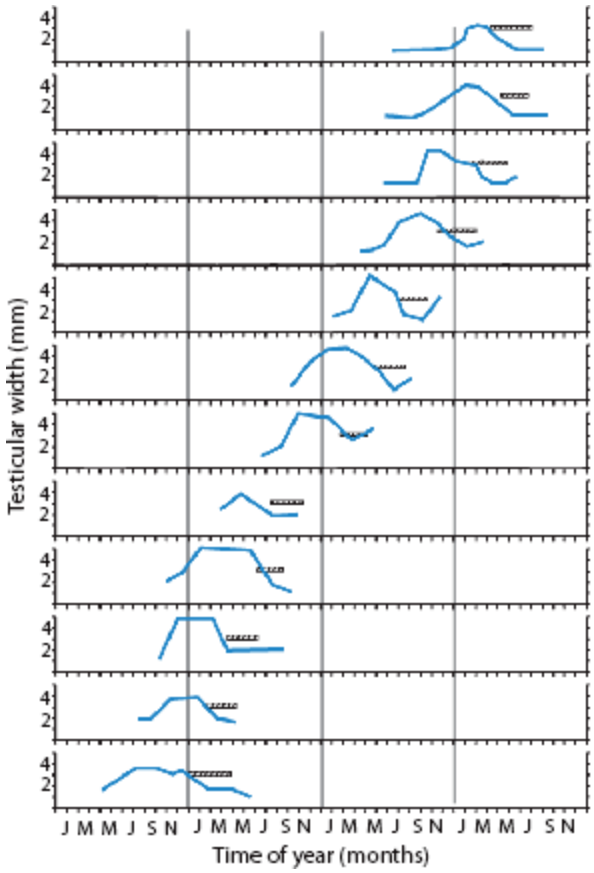


FIG 105. The breeding and moulting periods of an African Stonechat *Saxícola torquata axillaris* kept on artificial constant daylengths (11.75 ^{nr} light alternating with 12.25 hr dark) over ten years. Lines show testis sizes measured by laparotomy, and bars show moulting periods. Data for successive calendar years are plotted from top to bottom on the extreme right, and from each year the three preceding years are also shown. This is done to show how, under constant daylengths, the circannual cycle (of about 9 months) gets progressively earlier (bird year 3 occurs in calendar year 2 and so on). In contrast to the pattern shown, under natural daylengths the cycle keeps in step with the calendar years. (Modified from Gwinner, 1996.)



FIG 106. A ‘t/iunbergí-type’Yellow Wagtail *Motacillaflava* from arctic Norway, the latest subspecies to leave tropical Africa in spring for breeding areas in northernmost Europe. For British race, see Figure 93. (Edmund Fellowes)



FIG 107. Turnstone *Arenaria interpres* in which many individuals spend their first-summer in their ‘wintering’ areas, and do not return to the breeding range until they are two or more years old. (Edmund Fellowes)



FIG 108. Waxwings *Bombycilla ganulus* irruptive migrants from northern Europe. (Brian Irving © HELM-Images)

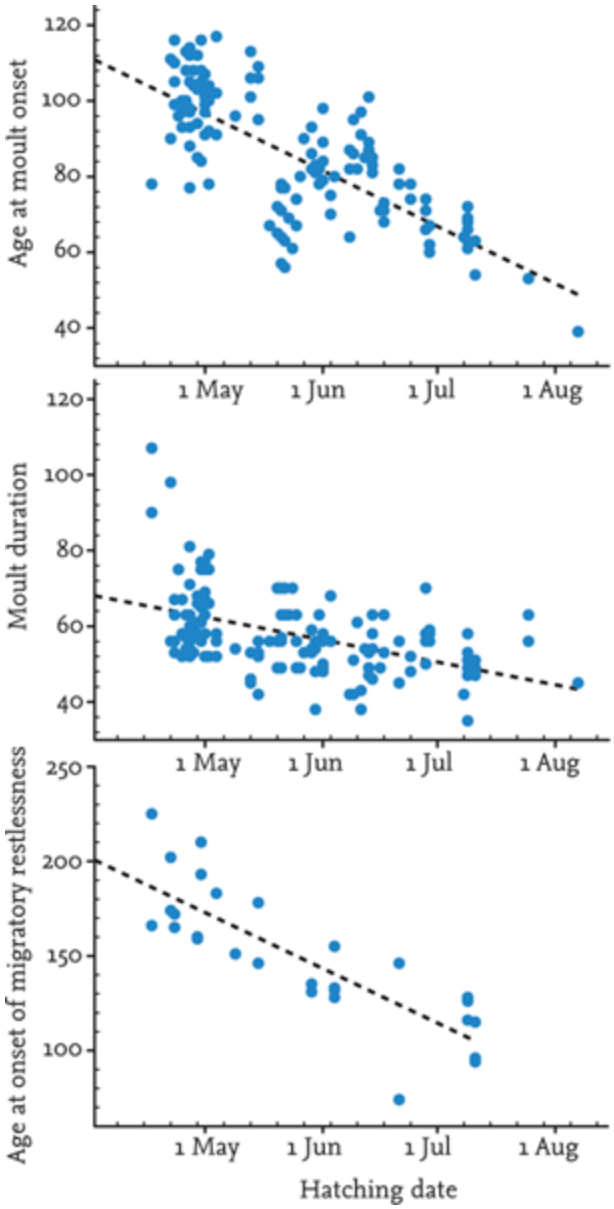


FIG 109. The relationship between hatching date and age of onset of moult (top), moult duration (middle) and age of onset of migratory restlessness (bottom) in captive European Stonechats *Saxícola torquata* kept on natural daylengths. Later hatching individuals start moult and migratory fattening at a later date, but an earlier age than early-hatched ones, and also moult more rapidly. (Modified from Helm *et al.* 2005.)



FIG 110. Red-spotted Bluethroat Insania *svecica* a passage migrant in the British Isles which is regularly blown into eastern Britain at migration times. As in many other passerines, late-bred young moult and fatten more rapidly than earlier ones, thus reducing the delay in their autumn migration. (Edmund Fellowes)



FIG 111. Spring flock of Knots *Calidris canutus* at Snettisham, Norfolk, showing mixed plumages, with some birds still in grey winter plumage and others largely in red breeding plumage. Dunlins *Calidris alpina* in the foreground, some also in breeding plumage. (Chris Gomersall/RSPB-Images)



FIG 112. Black-tailed Godwit *Limosa limosa* in which breeding partners, although migrating independently of one another, show synchrony in their arrival dates in nesting areas. (Frank Snijkers)

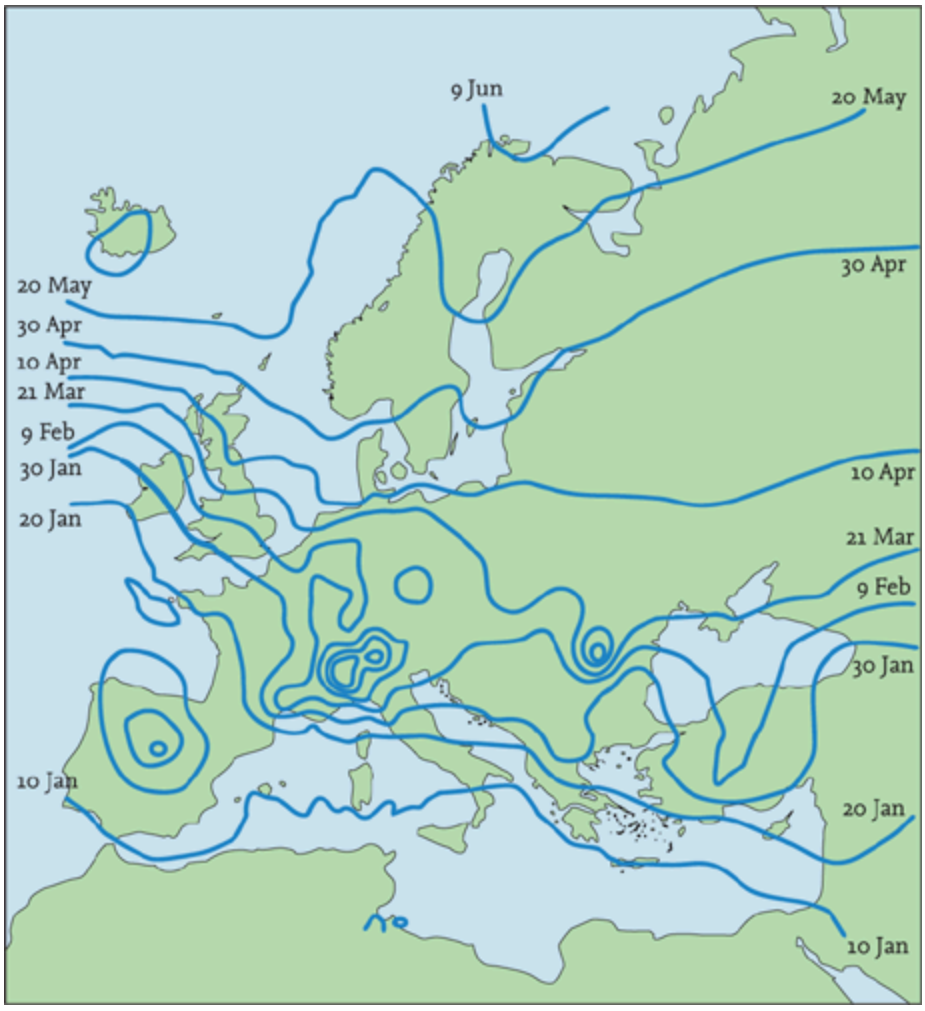


FIG 113. The advance of spring, as shown by the dates that the rising io°C isotherm reached different parts of Europe, based on average values for 1971–2000. (Adapted from T. H. Sparks, unpublished.)

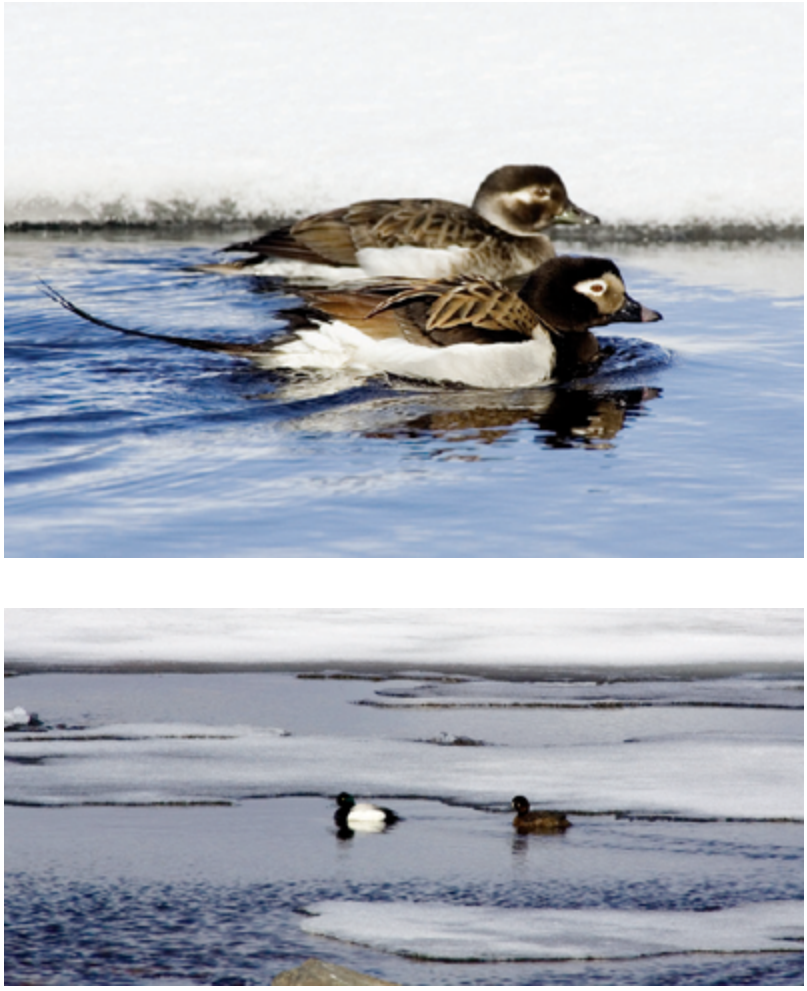


FIG 114. Long-tailed Ducks *Clangula hyemalis* and Scaups *Aythya mania*, which winter on the seas around the British Isles, arrive in their arctic nesting areas in early June, as soon as open water becomes available there. (Edmund Fellowes)

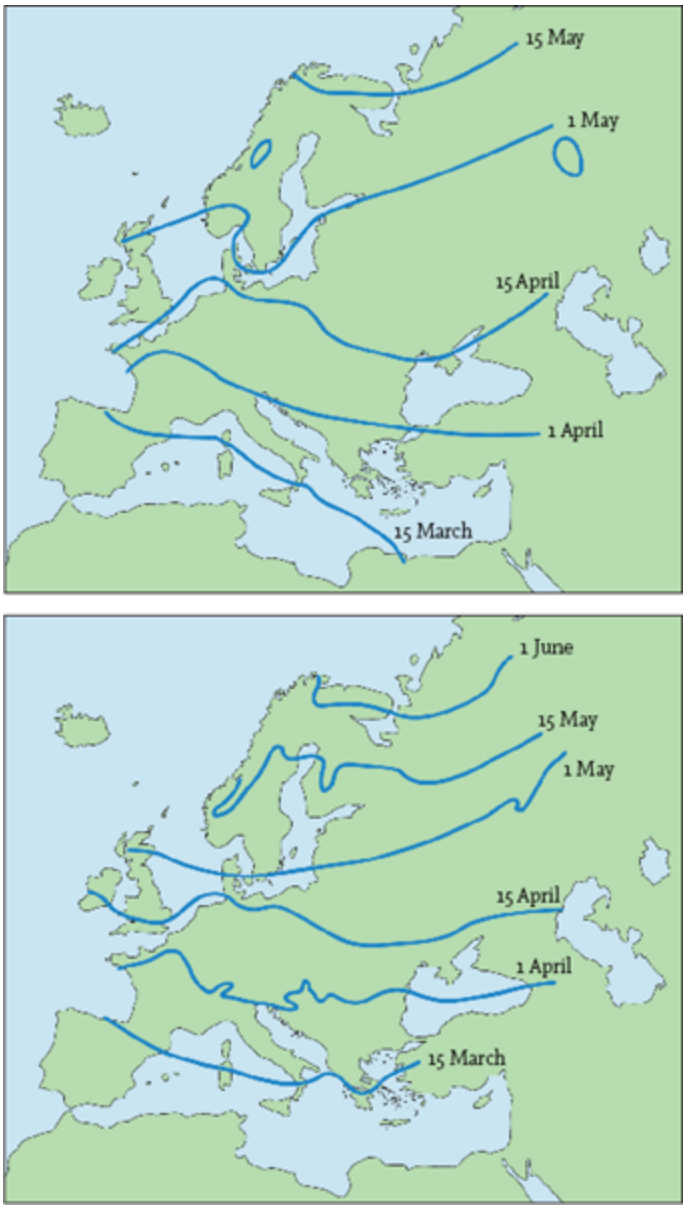


FIG 115. The northward advance of (left) the Common Redstart *Phoenicurus phoenicurus* and (below left) the Barn Swallow *Hirundo rustica* through Europe in spring. (From Southern, 1938a, 1939.)



FIG 116. Barn Swallow *Hirundo rustica* whose spring arrival dates in the British Isles correlate with spring temperatures. (Edmund Fellowes)



FIG 117. Snow Bunting *Plectrophenax nivalis* (adult male in breeding plumage), which ideally arrives in arctic breeding areas as the snow is retreating, leaving cleared areas and exposing seeds and insects trapped since the previous summer. (Jack Stephens)

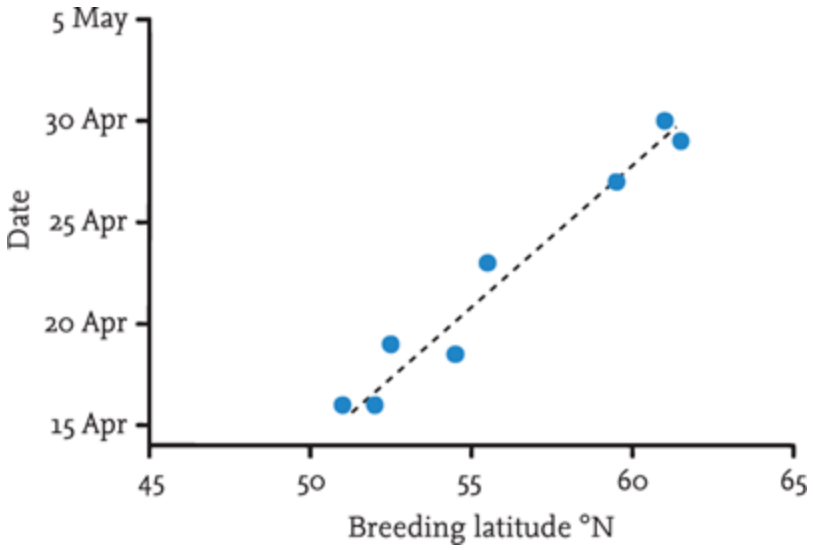


FIG 118. Median passage dates through North Africa of Pied Flycatchers *Ficedula hypoleuca* breeding at different latitudes in Europe, based on information from ring recoveries. Populations passed through North Africa in order of their breeding latitude, south to north. (From Both % te Marvelde 2007.)



FIG 119. Arctic Skua *Stercorarius parasiticus* breeder and passage migrant in the British Isles, which often migrates at the same times as the tern species that it robs for food. In spring, dark-phase birds, like the one in this photograph, nest mainly in the southern parts of their breeding range, and tend to pass northward earlier than pale-phase birds which predominate in the northern parts of the breeding range. (Rebecca Nason)

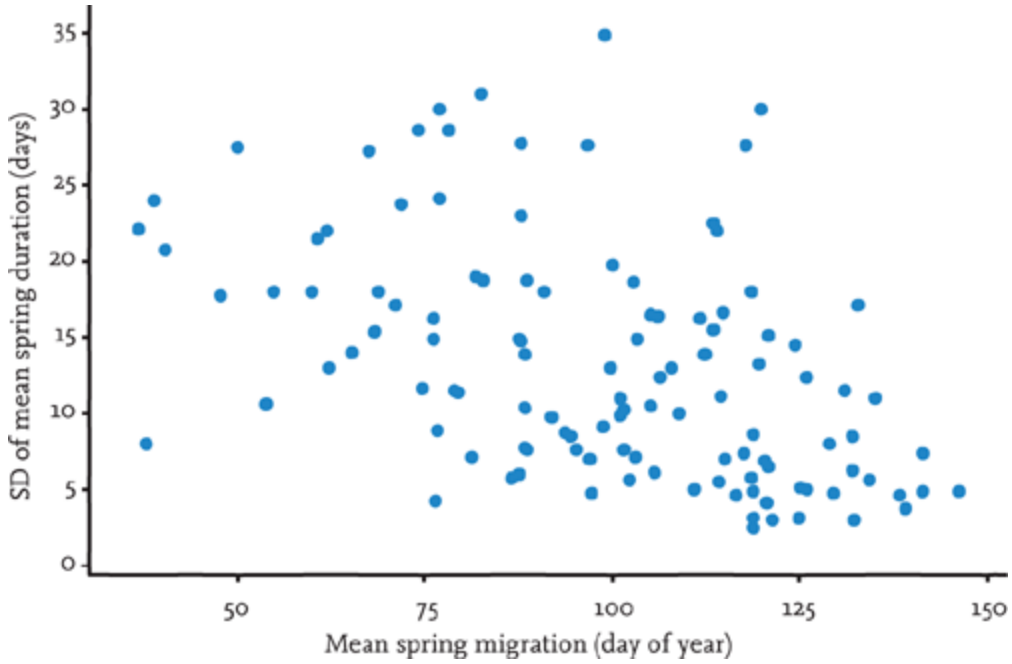


FIG 120. Annual variations (as reflected in standard deviations, SD) in the mean passage dates of migratory species in relation to their mean arrival dates over many years, based on records from Dungeness Bird Observatory, 1990–2007. Earlier migrating species had more variable mean passage dates from year to year than did later arriving species. Earlier ones were mainly short-distance migrants that wintered within Europe, while later ones were mainly long-distance migrants that wintered in Africa south of the Sahara. Regression relationship: r = -0.468, $P > 0.001$. (From Newton *et al.* 2010.)



FIG 121. Avocet *Recurvirostra avosetta* in which individuals that winter furthest away are latest to return to the nesting area in spring. (Brian Irving © HELM-Images)

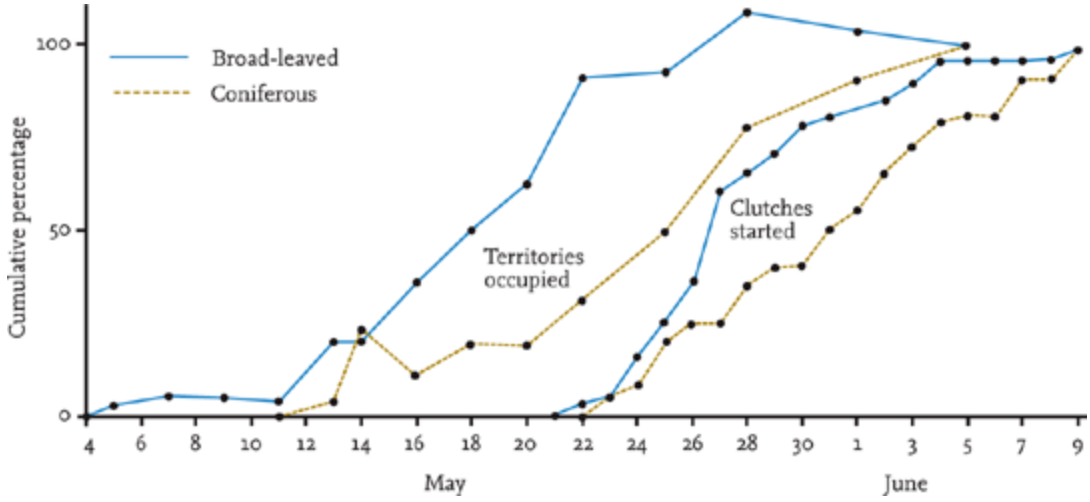


FIG 122. Settling and egg-laying dates of Pied Flycatchers *Ficedula hypoleuca* in broad-leaved and coniferous forests in central Sweden. In the preferred broad-leaved areas, food supplies increased earlier in spring, the birds settled earlier and at greater density, and annual breeding success (in terms of young per female) was higher than in coniferous areas. (Redrawn from Lundberg *et al.* 1981.)

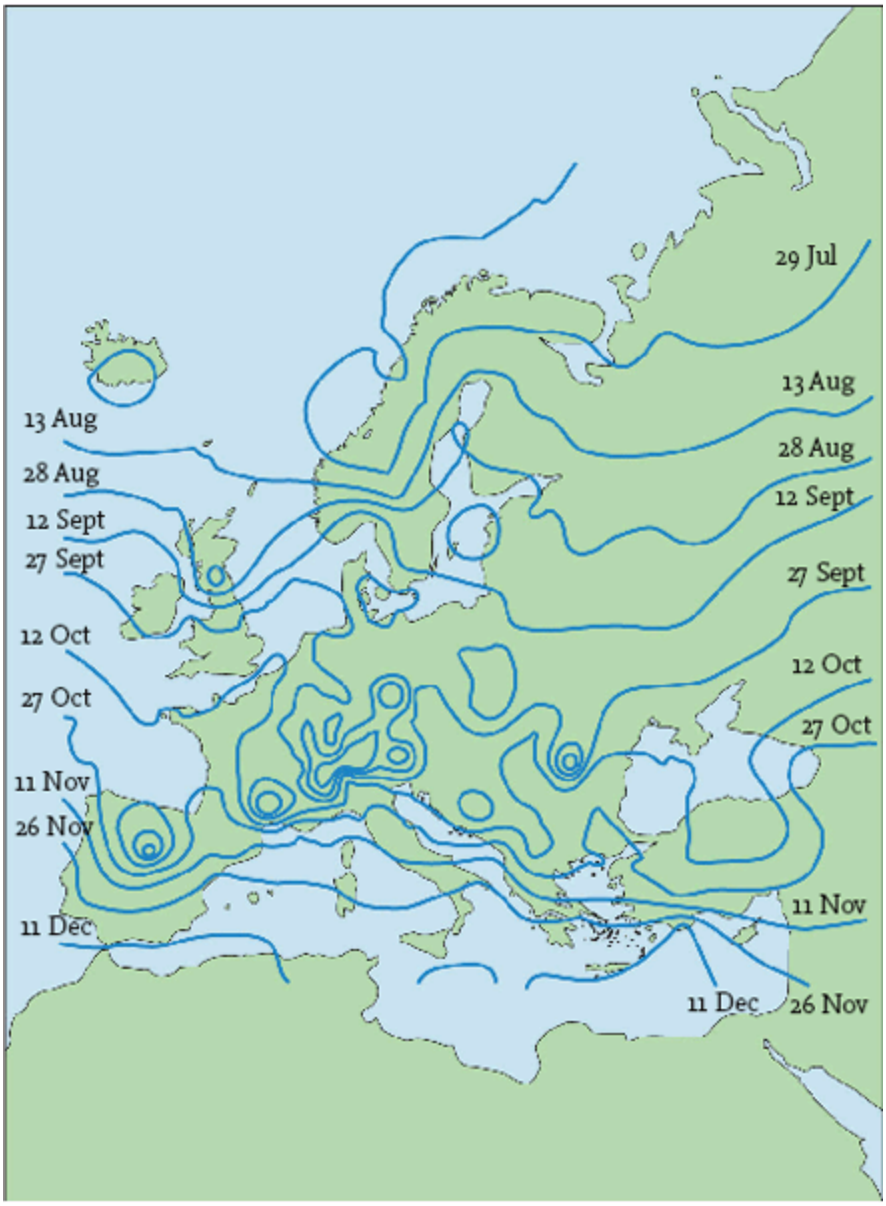


FIG 123. The advance of autumn, as shown by the dates of return of the falling 10°C isotherm to various parts of Europe, based on average values for 1971–2000. (Redrawn from T. H. Sparks, unpublished.)



FIG 124. Oystercatcher *Haematopus ostralegus* which, on arrival in winter quarters, competes for a place in a good feeding area. (Brian Irving © HELM-Images)



FIG 125. The difference in response to displacement off the migratory route between adult birds (which homed to a familiar wintering area) and juvenile birds (which flew in an appropriate direction for an appropriate distance, but without correcting for their off-course displacement).

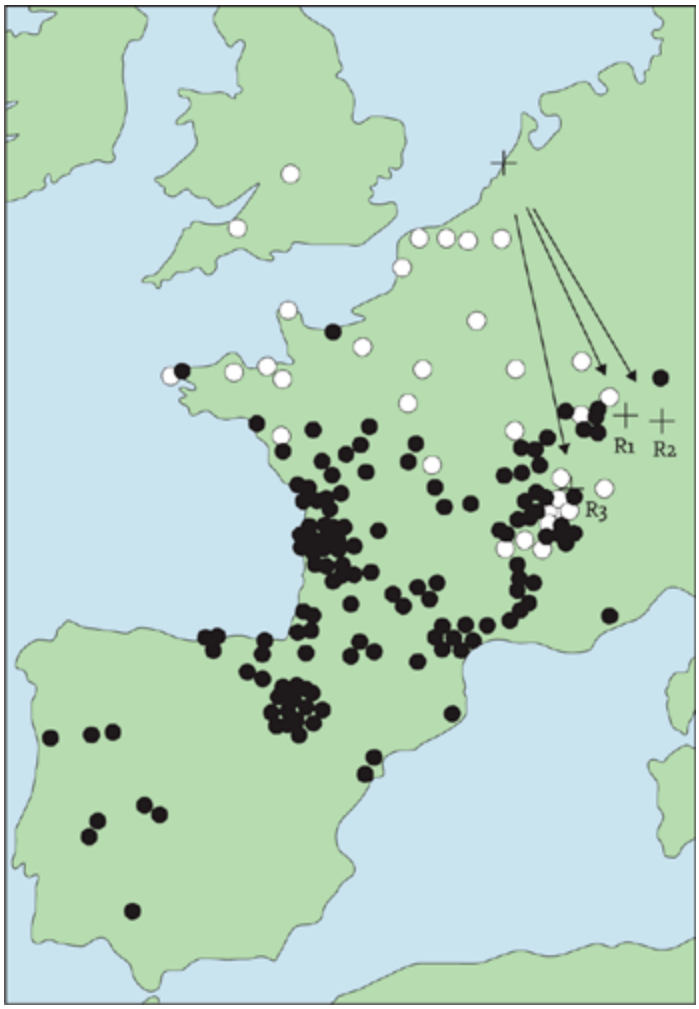


FIG 126. Difference in recovery patterns of adult and juvenile Common Starlings *Stumus vulgaris* that were displaced about 500 km south-southeast (Netherlands to Switzerland) off their normal west-southwest migration route through the Netherlands. Birds were caught on migration at site +, transported and released at Basel (Ri), Zürich (R2) and Genf (R3). Filled circles show recoveries of juveniles and open circles of adults during the ensuing autumn-winter. (From Perdeck, 1958.)



FIG 127. White Storks *Ciconia acordó* subjects of early displacement experiments to study the role of inheritance and social factors in migratory behaviour. (Frank Snijkers)



FIG 128. Manx Shearwater *Puffinus puffinus* a long distance migrant, subject to early experiments on homing behaviour. (John Wright)



FIG 129. Sanderling *Calidris alba* a common winter visitor to the soft coasts of the British Isles, elsewhere subject to experiments on site fidelity. (Frank Snijkers)



FIG 130. Common Starling *Stumus vulgaris* subject of several early experiments on navigation and homing behaviour. (Brian Irving © HELM-Images)

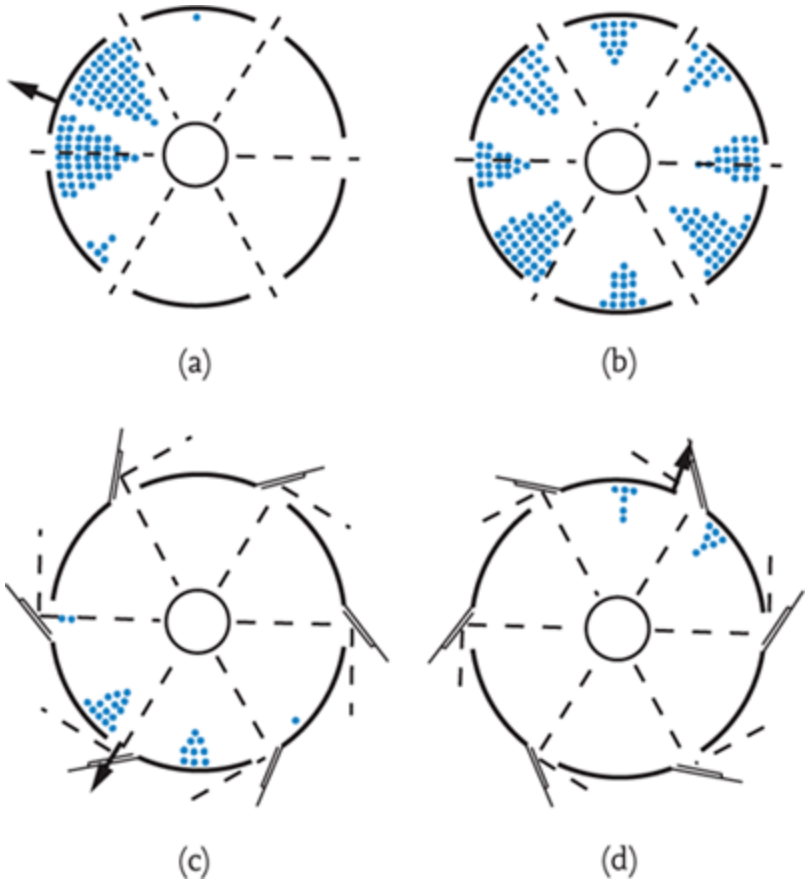


FIG 131. Orientation of spontaneous diurnal migratory activity in a captive Starling *Stumus vulgaris* under various conditions of sun exposure. The bird was tested in a pavilion with six windows during the spring migration season, (a) Behaviour under clear skies, (b) Behaviour under total overcast, when the sun was not visible, (c) Behaviour when the image of the sun was deflected 90° anti-clockwise by means of mirrors, (d) Behaviour when the sun was deflected 90° clockwise by means of mirrors. Each dot represents 10 seconds of fluttering activity. Dotted lines show incidence of light from the sky, arrows denote mean direction of activity. (Redrawn from Kramer, 1951.)

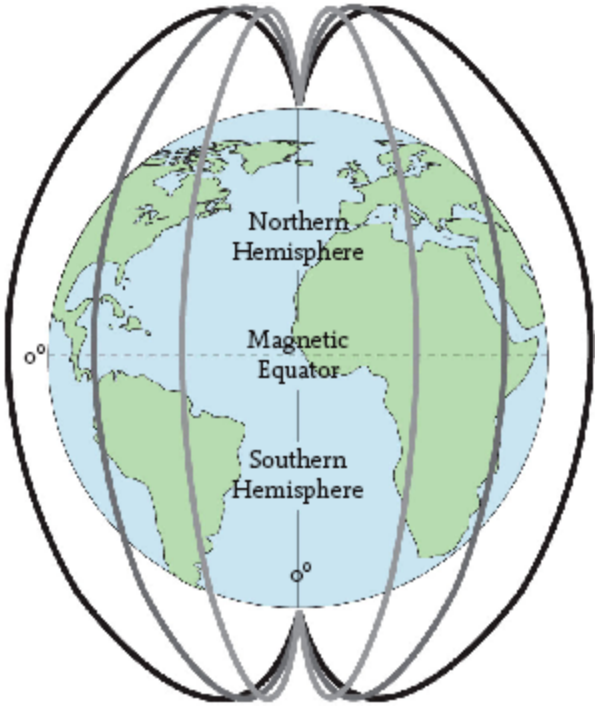


FIG 132. Diagram depicting force lines in the earth's magnetic field.



FIG 133. Pied Flycatcher *Ficedula hypoleuca* subject of experiments on navigation. (Edmund Fellowes)



FIG 134. Cory's Shearwater *Calonectris diomedia* a late summer visitor to the seas around the southern British Isles, and subject of experiments on homing behaviour. (Colin Turvey)

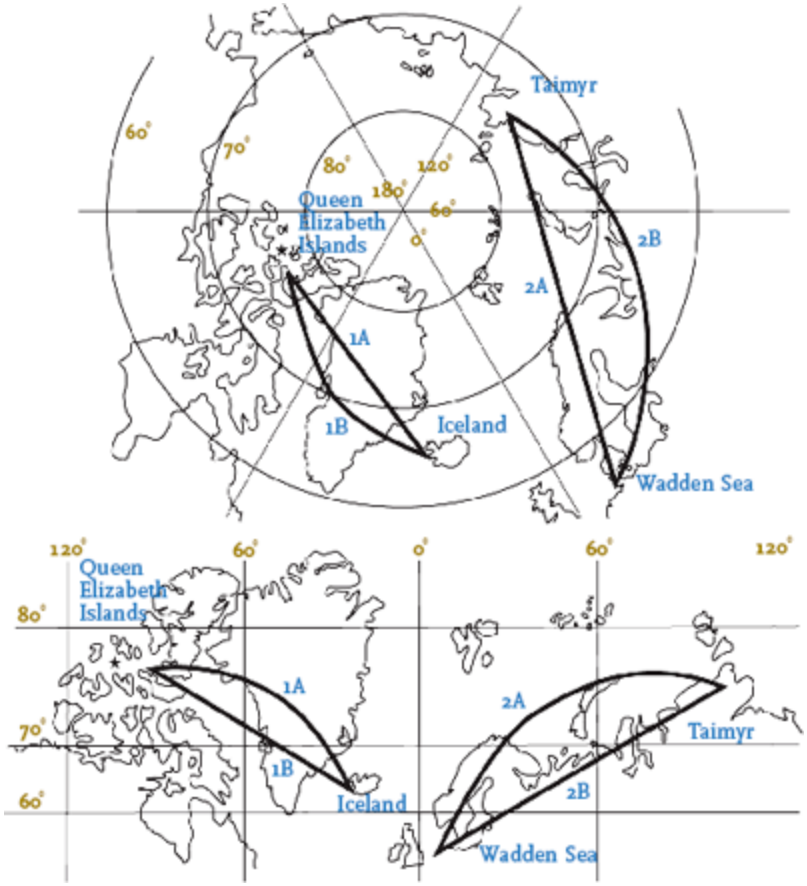


FIG 135. Great circle (orthodrome) and rhumbline (loxodrome) routes between points of departure and destination for migratory flights by certain high arctic shorebirds and Brent Geese *Branta bernicla* drawn on an azimuthal stereographic map projection (top, depicting great circle routes as straight lines) and on a Mercator map projection (above, depicting rhumbline routes as straight lines). Between Iceland and the Queen Elizabeth Islands, great circle (1A) distance and courses are 2,535 km and 328°/265° (initial/final course). Rhumbline (1B) distance and course are 2,665 km and 300° throughout. Between the Wadden Sea and Taimyr Peninsula, great circle (2A) distance and courses are 4,234 km and 23°/110° (initial/final course). Rhumbline (2B) distance and course are 4,634 km and 59° throughout. Spring flight routes by the high arctic migrants are in agreement with rhumbline but not with great circle routes. The position of the magnetic North Pole is indicated by a star. (From Alerstam, 1990b)



FIG 136. Herring Gull *Lams argentatus* subject of experiments on the role of social influence on migratory behaviour. (Edmund Fellowes)

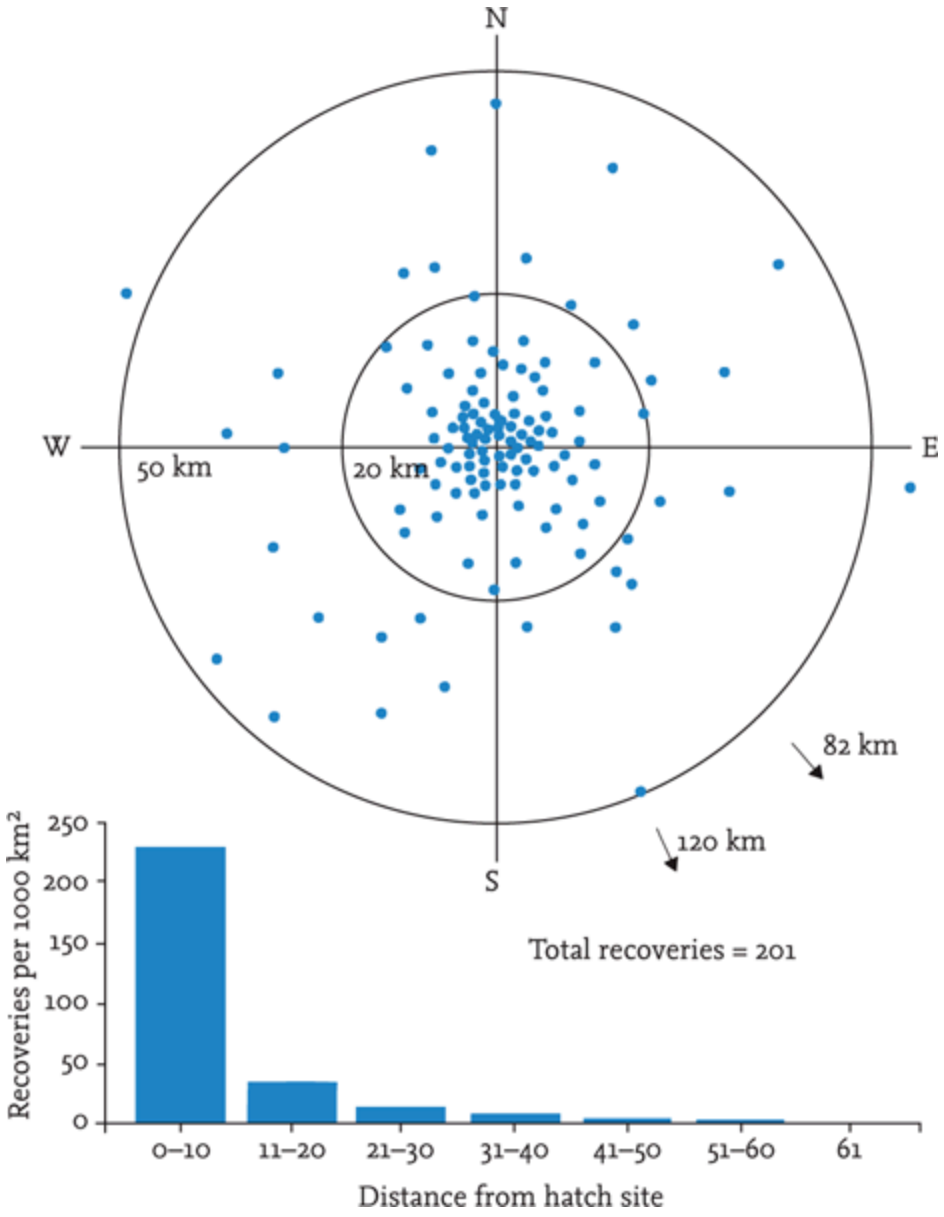


FIG 137. Locations of Sparrowhawks *Accipiter nisus* ringed as chicks and recovered in a later breeding season, shown in relation to hatching site (centre). Recoveries came from all sectors of the compass and declined in density with increasing distance from the hatching site. The histogram shows the density of recoveries in concentric areas moving out from the hatch site. Based on recoveries from the British ringing scheme (Newton, 1979).

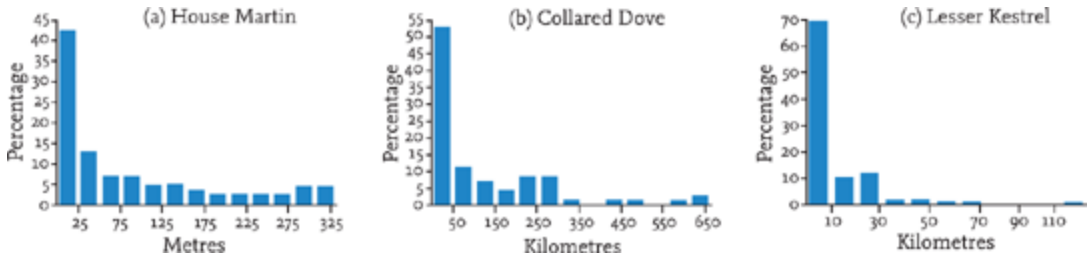


FIG 138. Natal dispersal patterns of three European species ringed as chicks and recovered in a later breeding season. In all three species recoveries declined in numbers with increasing distance from the natal site, but the distances differed between species. (a) Northern House Martin *Delichon urbica* (Rheinwald, 1975); (b) Eurasian Collared Dove *Streptopelia decaocto* (Hengeveld, 1993); and (c) Lesser Kestrel *Falco naumanni* (Negro *et al.* 1997).



FIG 139. Kittiwake *Risset tridactyla* a colonial seabird, in which many individuals return to the colony of their birth, while others move to other colonies further afield. (Brian Irving © HELM-Images)



FIG 140. Atlantic Puffins *Fratercula árctica* in which individuals visit several colonies in their pre-breeding years before settling to nest. (Jack Stephens)

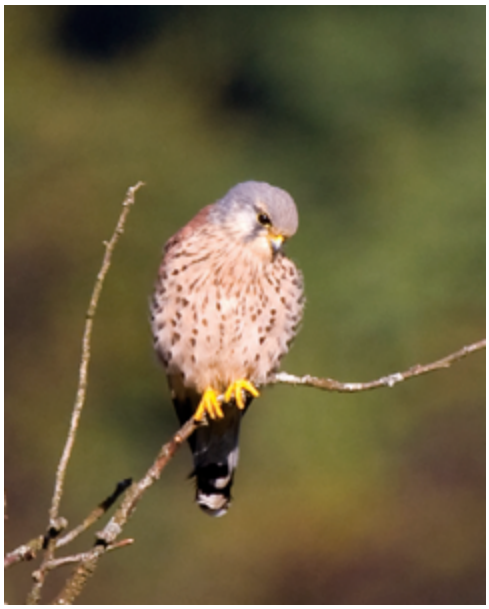


FIG 141. Kestrel *Falco tinnunculus* (male), a partial migrant in the British Isles. The young disperse further between their hatch sites and subsequent breeding sites in years when food (voles) is scarce, and later-hatched young disperse generally further than early-hatched ones. (Brian Irving © HELM-Images)

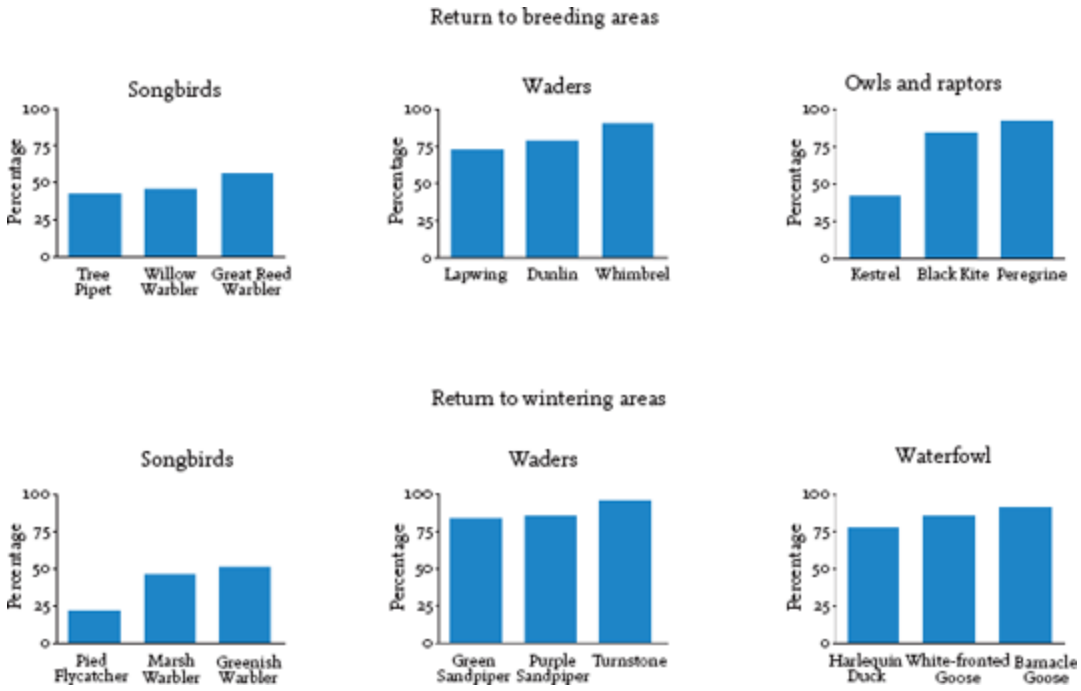


FIG 142. Proportions of adults in migratory bird populations that returned to the same breeding sites (upper) or wintering sites (lower) in successive years. Allowing for mortality, the species depicted reveal some of the most extreme examples of site-fidelity found among birds, in which all (or almost all) surviving individuals may be inferred to have returned to the same site in successive years. Some of the species shown bred in one continent and wintered in another. (From Newton, 2008.)

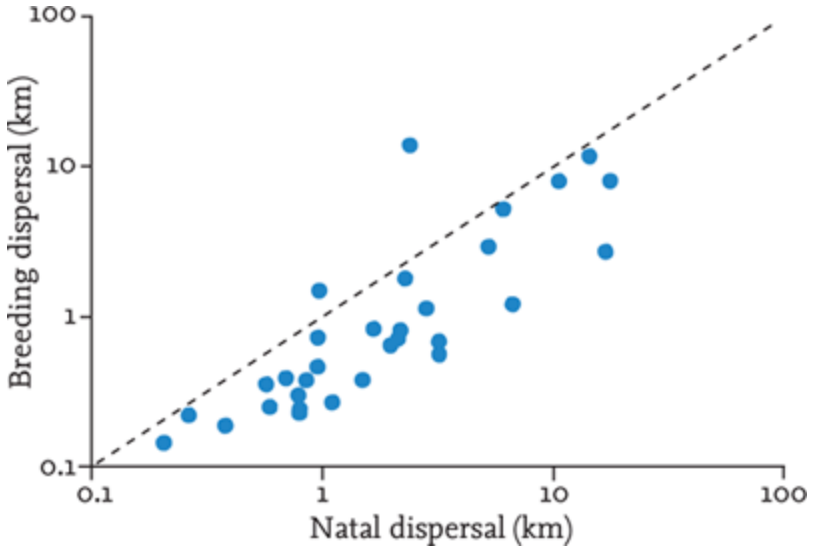


FIG 143. Relationship between the geometric means of the natal and breeding dispersal distances of 31 different bird species, based on recoveries from the British ringing scheme. In most species individuals dispersed greater distances between their natal and breeding sites than between the breeding sites of different years. Note log scales. (From Paradis *et al.* 1998.)

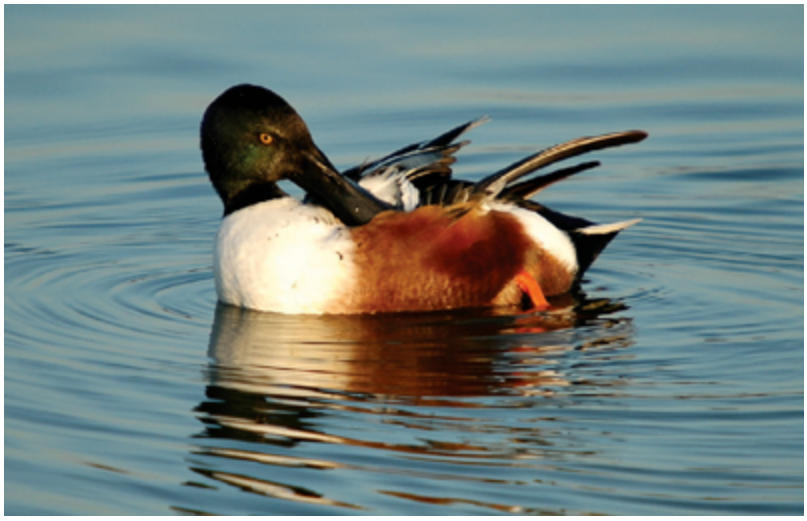


FIG 144. Shoveler *Anas clypeata* (drake), a bird of shallow (often ephemeral) waters that often moves long distances between the nesting sites of successive years. (Brian Irving © HELM-Images)



FIG 145. Common Starlings *Stumus vulgaris* assembled at a winter roost near Gretna in south Scotland. (Edmund Fellowes)



FIG 146. Purple Sandpiper *Calidris maritima* a wintering shorebird of rocky coasts, in which individuals often return to the same wintering sites year after year. (Brian Irving © HELM-Images)



FIG 147. Eurasian Siskin *Carduelis spinus* (adult male), an irruptive seed-eater in which individual wintering areas vary in location from year to year. (Alan Martin)



FIG 148. Tufted Duck *Aythyafuligula* (drake), in which individuals can winter in widely separated areas in different years. (Edmund Fellowes)



FIG 149. Common Guillemots *Uria aalge* in which individuals winter nearer to their nesting colonies as they age, and return to the same crowded nest ledges year after year. The flock includes two Razorbills *Alca torda.* (Edmund Fellowes)



FIG 150. Great Cormorants *Phalacrocorax carbo* which show strong fidelity to their nesting sites, but in winter young birds migrate further than older ones. Adults show increasing fidelity to wintering sites with advancing age. The birds shown are of continental-type (race P. *c. sinensis)* which colonised Britain from the 1980s, nesting in trees at inland lakes and reservoirs, rather than on coastal cliffs, like the earlier-established subspecies (P. *c. carbo)*. (John Wright)



FIG 151. Pied Wagtail *Motacilla alba* in which juveniles disperse in various directions in late summer before moving generally southward on migration. A pattern seen in many other species. (Edmund Fellowes)



FIG 152. Collared Flycatcher *Ficedula albicollis* a rare visitor to the British Isles, but elsewhere subject of experiments on site attachment. (Dick Forsman)



FIG 153. Dunlin *Calidris alpina* the most abundant wintering wader in coastal areas of the British Isles, and elsewhere subject of experiments on winter site attachment. (Sue Tranter/RSPB images)

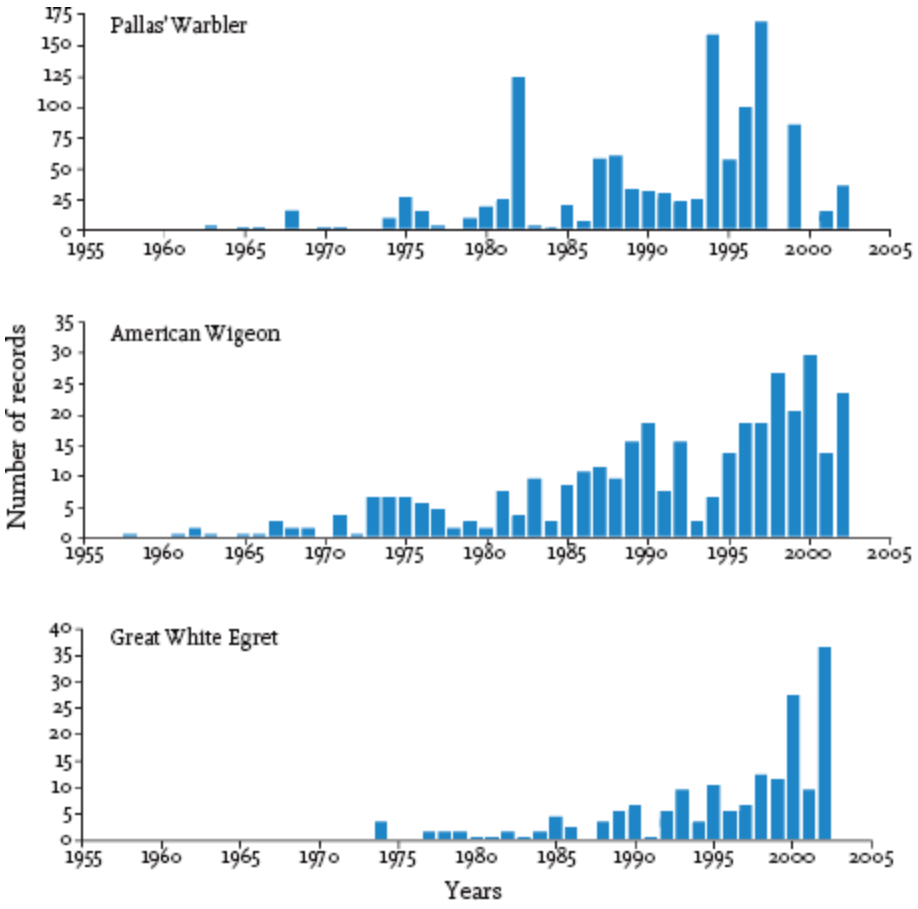


FIG 154. Numbers of some vagrant species recorded in Britain, 1955–2002. Pallas' Warbler *Phylloscopus proregulus* (from Fraser et al., 1999, and subsequent reports); American Wigeon *Anas americana* (from Fraser *Sa* Rogers, 2005); Great White Egret *Egretta alba* (from Rogers and the Rarities Committee, 2003).

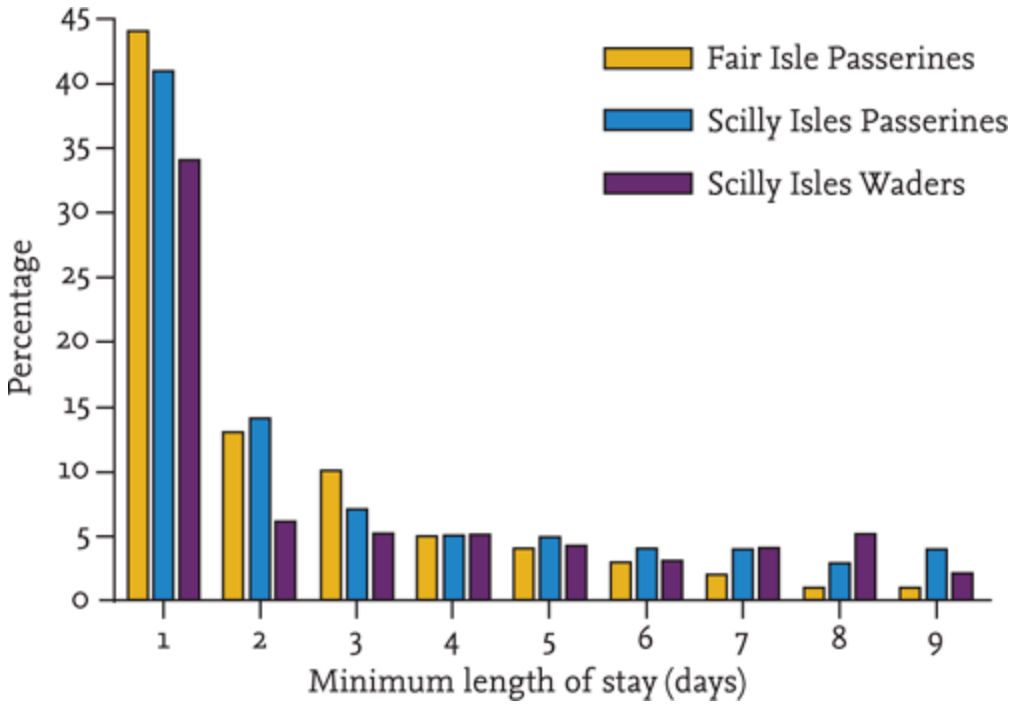


FIG 155. Apparent length of stay of individual vagrants at two localities. Based on data from passerines on Fair Isle and from passerines and waders on the Scilly Isles, 1958–93. (From Fraser, 1997.)

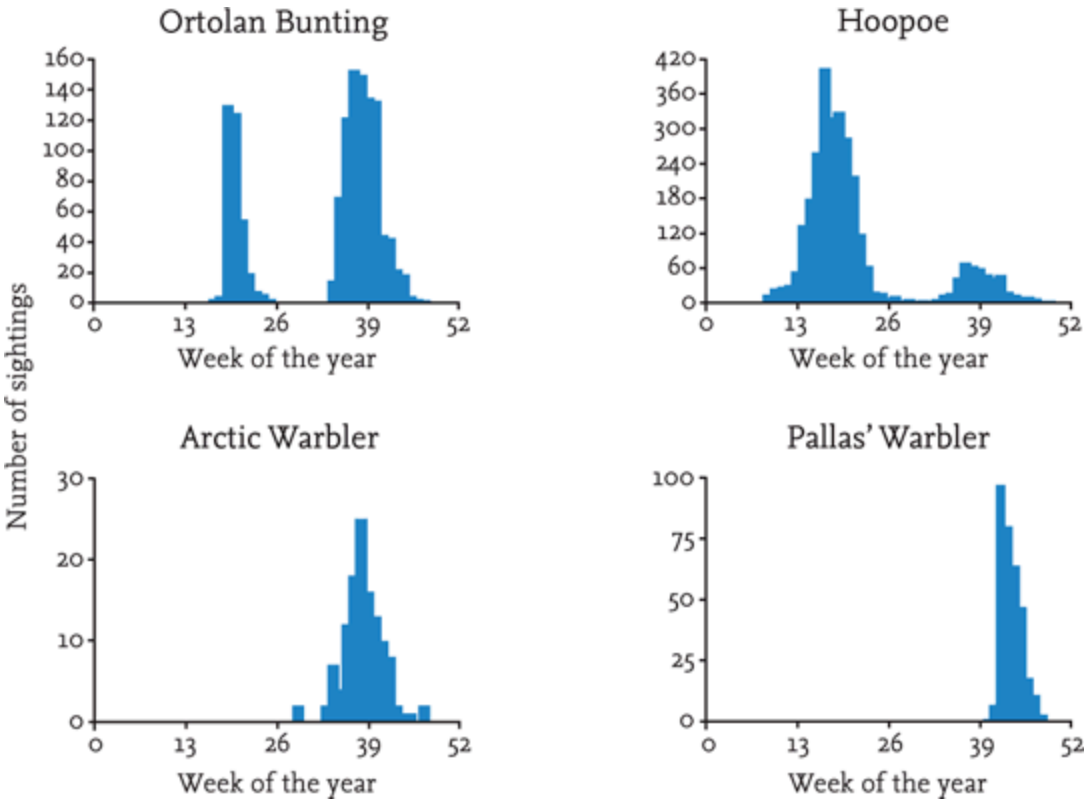


FIG 156. Seasonal appearance of four rarities to Britain, as determined from the number of records in different weeks of the year. All four are more or less restricted to migration seasons, and the two warblers only to autumn. (From records published in British *Birds)*



FIG 157. Melodious Warbler *Hippolais polyglotta* a vagrant from nearby Europe with appears in the British Isles mainly in late summer. (Bobby Smith)



FIG 158. Red-flanked Bluetail *Tarsiger cyanurus* which during the 20th century spread westward across Eurasia into Finland, and now occurs as a rare vagrant to Britain, seen mainly in eastern districts in autumn. (John Wright)



FIG 159. Little Bunting *Emberiza pusilla* a rare drift vagrant to the British Isles, which appears mainly under strong easterly winds. This one appeared on Fair Isle. (Rebecca Nason)



FIG 160. Pectoral Sandpiper *Calidris melanotos* which appears as a vagrant in the British Isles, mainly from North America but perhaps also from Siberia. (Edmund Fellowes)



FIG 161. Hoopoe *Upopa epops* which has bred in Britain, but appears mainly in spring (as an overshoot migrant), but also in autumn. This one was photographed in south Scotland in September 2008. (Edmund Fellowes)



FIG 162. Woodchat Shrike *Lanius senator* which appears in the British Isles mainly in spring, as a supposed 'overshoot' migrant. (Sean Gray/Grayimages)



FIG 163. Pallas' Warbler *Phylloscopus proregulus* (left) and Yellow-browed Warbler *Phylloscopus inornatus* (right), two species which breed in Asia, and have appeared in increasing numbers each autumn in the British Isles. These individuals were photographed on Fair Isle. (Rebecca Nason)

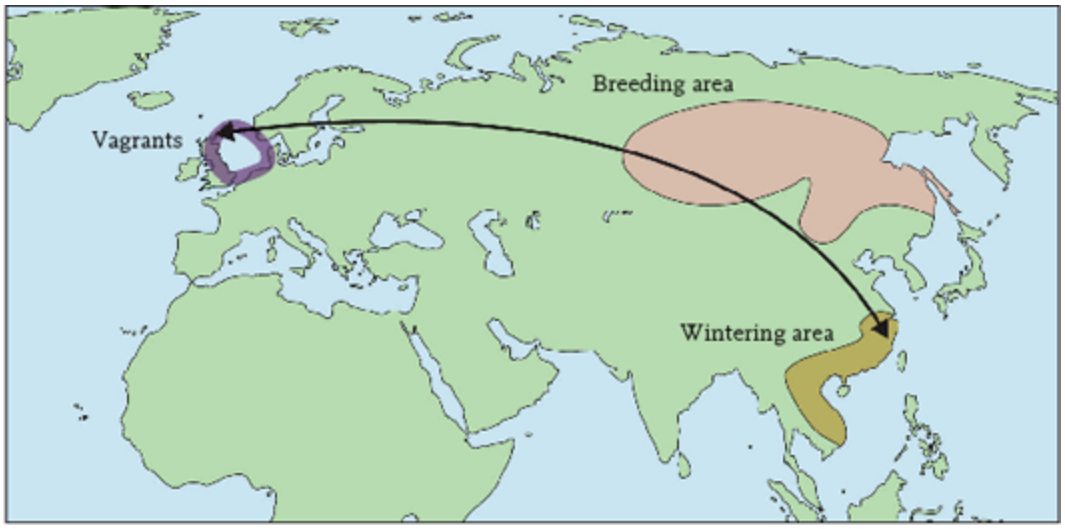


FIG 164. Hypothetical reversed 'great circle' migration route of Pallas' Warbler *Phylloscopus proregulus*. (From Rabøl, 1969b)



FIG 165. Red-breasted Flycatcher *Ficedula parva* which appears in the British Isles mainly at migration time in late summer. (Rebecca Nason)



FIG 166. White-crowned Sparrow *Zonotrichia leucophrys* a rare spring vagrant from North America. This one, providing the seventh record for Britain, was photographed at Cley in Norfolk, where its presence during January-March 2008 attracted so many bird watchers that £6,400 was raised for the village church restoration fund. (Rebecca Nason)



FIG 167. Blackbird *Turdus merula* (adult male), a partial migrant and winter visitor in the British Isles, but across the geographical range the species can vary from resident, to partial migrant and complete migrant in different regions. (Brian Irving © HELM-Images)



FIG 168. Wings of two Old World wetland warblers clearly fall into two groups, as illustrated by the rounded wings of (above right) the comparatively sedentary Cetti's Warbler *Cettia cetti* and (above left) the pointed wings of the highly migratory Reed Warbler *Acrocephalus scirpaceus*. Note the relative lengths of the outer flight feathers, which give greater 'aspect ratios' in the migrants. (Drawn by Keith Brockie.)



FIG 169. Blackcap *Sylvia atricapilla* (female), which varies in migratory behaviour across Europe, and has been subject to extensive experimental work on the inheritance of migratory behaviour. (Bobby Smith)

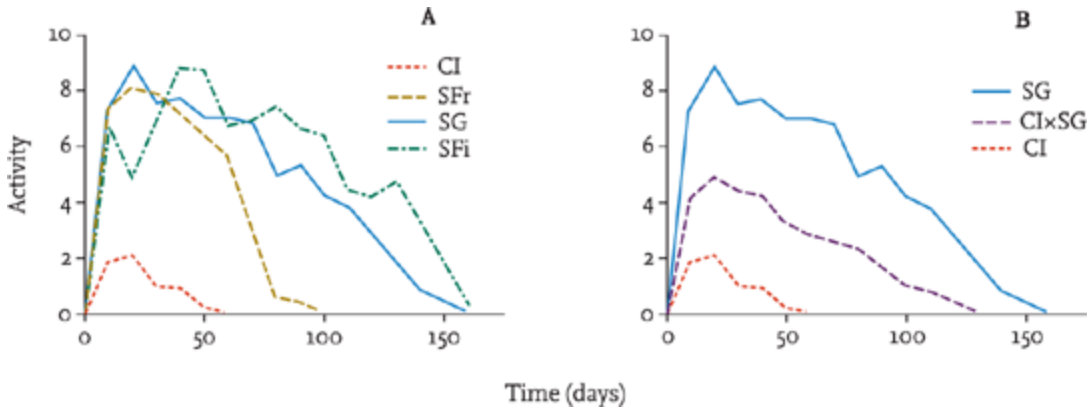


FIG 170. Patterns of migratory activity *(zugunruhe)* of Blackcaps *Sylvia atricapilla.* (A) Activity of birds from four different populations. (B) Activity of birds from two of these populations and their hybrids. SFi—birds from southern Finland; SG—southern Germany; SFr—southern France; CI—Canary Islands. (From Berthold & Querner, 1981.)



FIG 171. (Above left) Common Redstart *Phoenicians phoenicurus* (male), a long-distance migrant which winters in tropical Africa. (Above right) Black Redstart *Phoenicurus ochrurus* (male), a short-distance migrant which winters within Europe. (John Willsher and Colin Turvey)

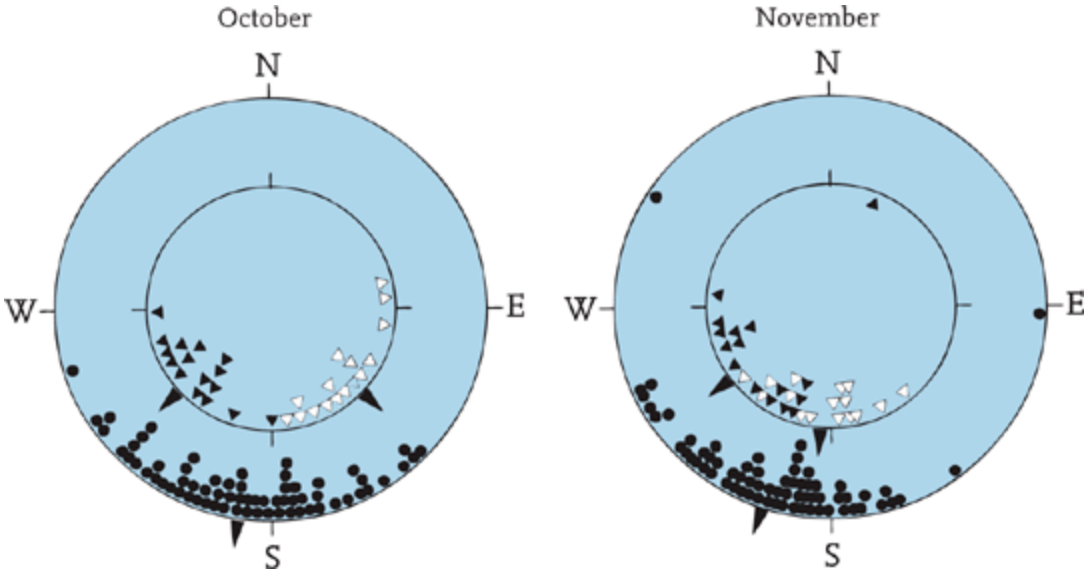


FIG 172. Orientation directions of Blackcaps *Sylvia atricapilla* from two populations breeding east and west of a migratory divide in Europe, and from hybrids between these two populations. Within the inner circle, triangles indicate the parental population from southwest Germany (filled) and eastern Austria (open), while in the outer circle, dots show first-generation offspring of mixed pairs bred in aviaries. Arrowheads indicate group mean directions. The hybrids took mean directions intermediate between the two parental forms. Note the seasonal shift in direction shown in November by the southeastward migrating parents and the intermediate mean orientation of the hybrid offspring. (From Helbig, 1991b, 1996)

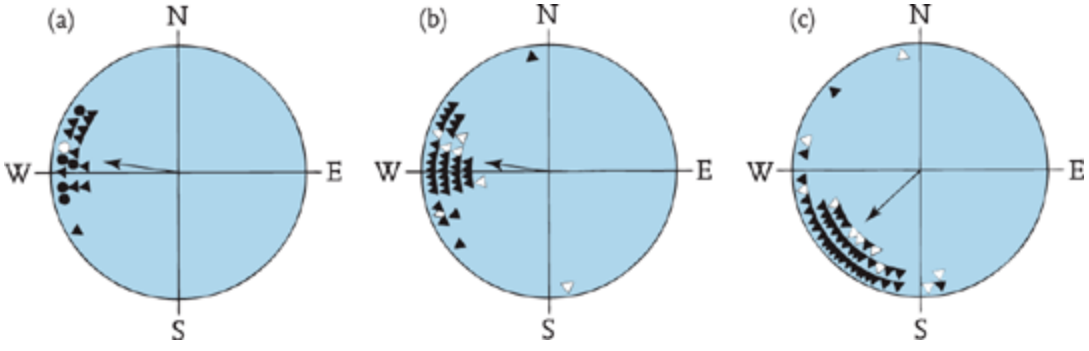


FIG 173. Autumn orientation of Blackcaps *Sylvia atricapilla* caught in winter in Britain (a), their captive-bred first-generation offspring (b), and a control group from southwest Germany (c). Each symbol shows the direction of the mean vector of one individual during 15–20 tests. The findings indicate that British wintering

Blackcaps have different inherent directional preferences from Blackcaps that breed in the same region of central Europe but winter to the southwest in Iberia. (Modified from Helbig, 1996.)



FIG 174. Reed Bunting *Emberiza schoeniclus* a mainly resident species in the British Isles, in which a small proportion of individuals may migrate several hundred kilometres to winter further south. (Brian Irving © HELM-Images)



FIG 175. Chiffchaff *Phylloscopus collybita,* a short-distance partial migrant that winters in Europe and Africa. In recent decades it has begun to winter in increasing numbers in southern Britain. (Frank Snijkers)



FIG 176. Greenshank *Tringa nebularia,* which has a wide wintering range from Europe to Africa, but in recent decades has begun to winter in increasing numbers in Europe. (Brian Irving © HELM-Images)



FIG 177. Barnacle Goose *Branta leucopsis,* once restricted to arctic latitudes for breeding, but has recently established nesting colonies at various sites around the Baltic and in the Netherlands, and (a different population) also in Iceland. (Brian Irving © HELM-Images)



FIG 178. Lesser Black-backed Gull *Larus fuscus,* which became increasingly resident in the British Isles during the latter half of the twentieth century, although many immatures still migrate as far as West Africa. Birds presumably from Iceland are also wintering increasingly on the coasts of eastern North America. (Brian Irving © HELM-Images)



FIG 179. Mediterranean Gull *Larus melanocephalus* (winter plumage), a recent colonist from continental Europe which is now rapidly expanding its numbers and

range in southern Britain. Large numbers of continental birds also appear in Britain outside the breeding season. (Sean Gray/Grayimages)

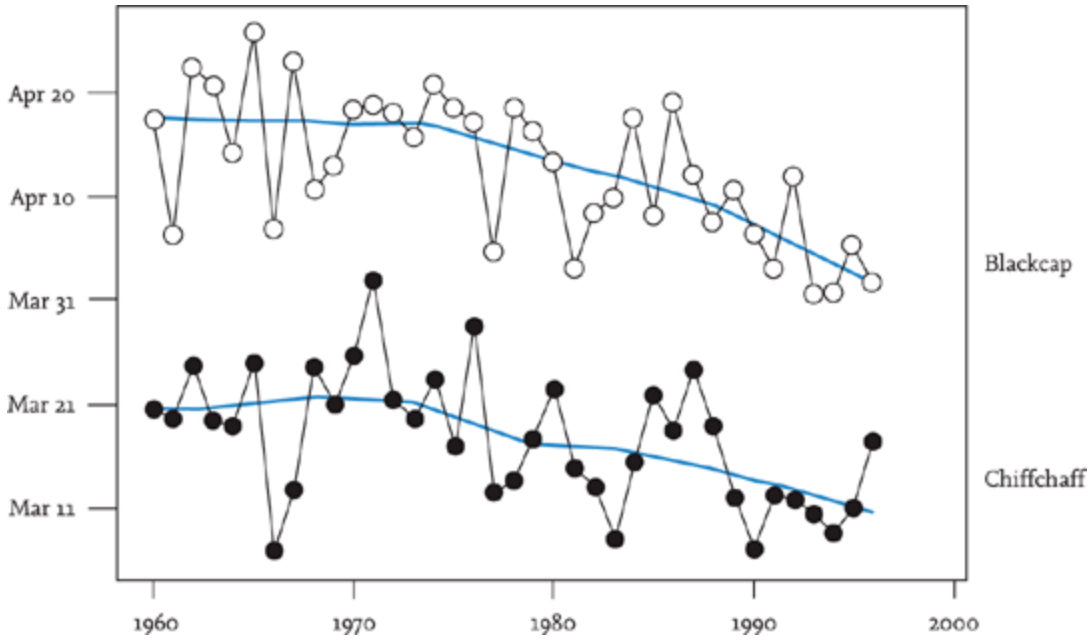


FIG 180. Mean first arrival dates of Common Chiffchaffs *Phylloscopus collybita* and Blackcaps *Sylvia atricapilla* at eight coastal Bird Observatories in Britain during 1960–96. In both species the response to temperature is in the order of 2–3 days earlier per 1°C rise in mean spring temperature. (From Sparks, 2000.)

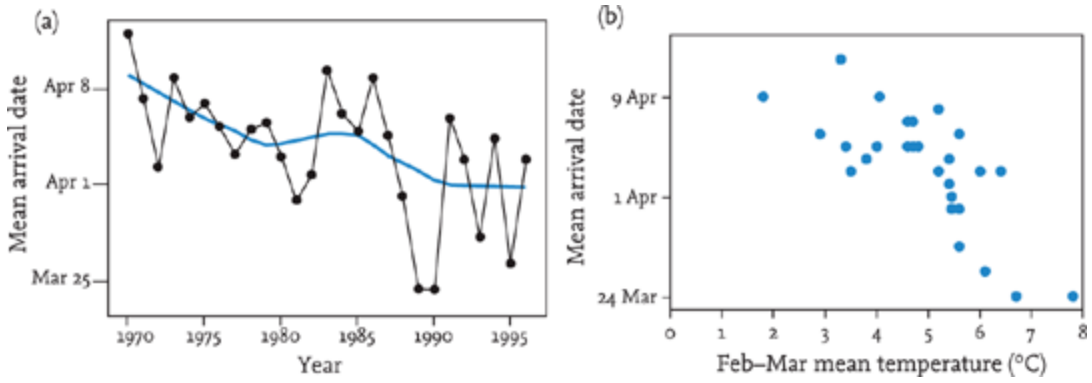


FIG 181. (a) Mean first arrival dates of Barn Swallows *Hirundo rustica* averaged for seven Bird Observatories in Britain, 1970–97, during which time mean arrival dates advanced by about one week in association with gradual spring warming, (b) Relationship between mean first arrival date and the mean temperature for February-March in the breeding areas. (From Sparks *et al.,* 1999.)



FIG 182. Blackcap *Sylvia atricapilla,* which has developed new migratory habits in recent decades, migrating from central Europe to winter in the British Isles, while local British-breeding Blackcaps continue to winter in southern Spain and Africa. (Frank Snijkers)



FIG 183. Serin *Serinus serinus,* which during the 20th century spread north through central Europe and became migratory in the most northern of the areas colonised. The species is a rare visitor to Britain which has occasionally bred. (Sean Gray/Grayimages)



FIG 184. Chaffinch *Fringilla coelebs* (male) which, on genetic evidence, probably survived the last glaciation in North Africa and southern Europe, and spread further north through Europe as forest developed following the return of milder conditions. (Edmund Fellowes)



FIG 185. Northern Wheatear *Oenanthe ornanthe* (male), whose migration routes are thought to reflect patterns of post-glacial range expansion. (Frank Snijkers)

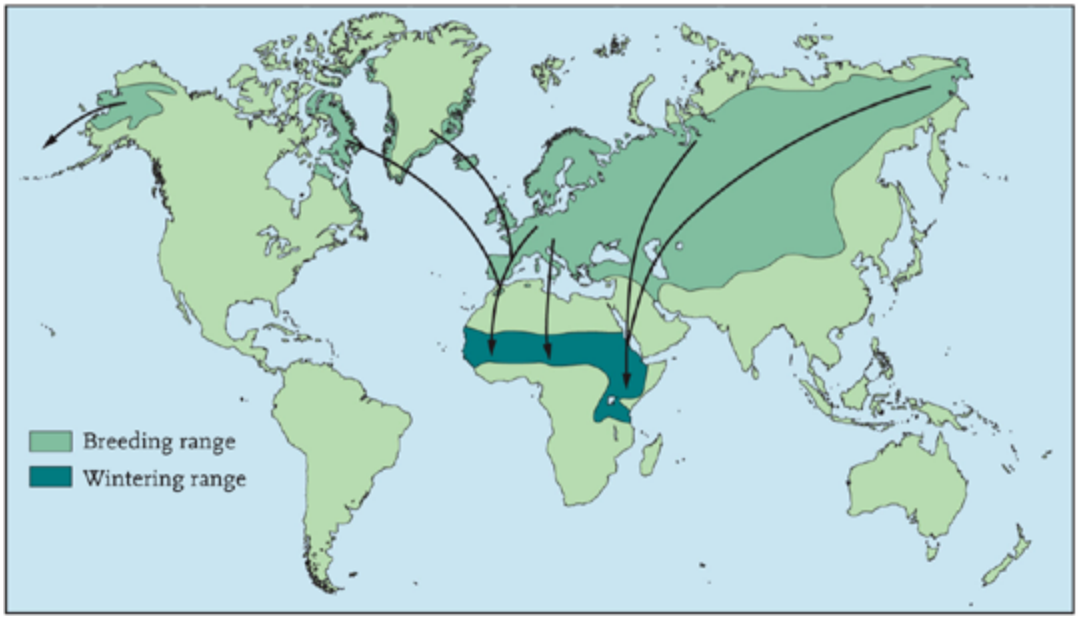


FIG 186. Northern Wheatears *Oenanthe oenanthe* from the entire breeding range (light shading) converge on Africa for the winter (dark shading).



FIG 187. Red-backed Shrike *Lanius collurio,* one of several species whose west European breeding populations migrate via the east end of the Mediterranean to reach their African wintering areas. (Paul Hackett)



FIG 188. Aquatic Warbler *Acrocephalus paludicola* (juvenile), which occurs in Britain only in small numbers on autumn migration. (JohnWillsher)

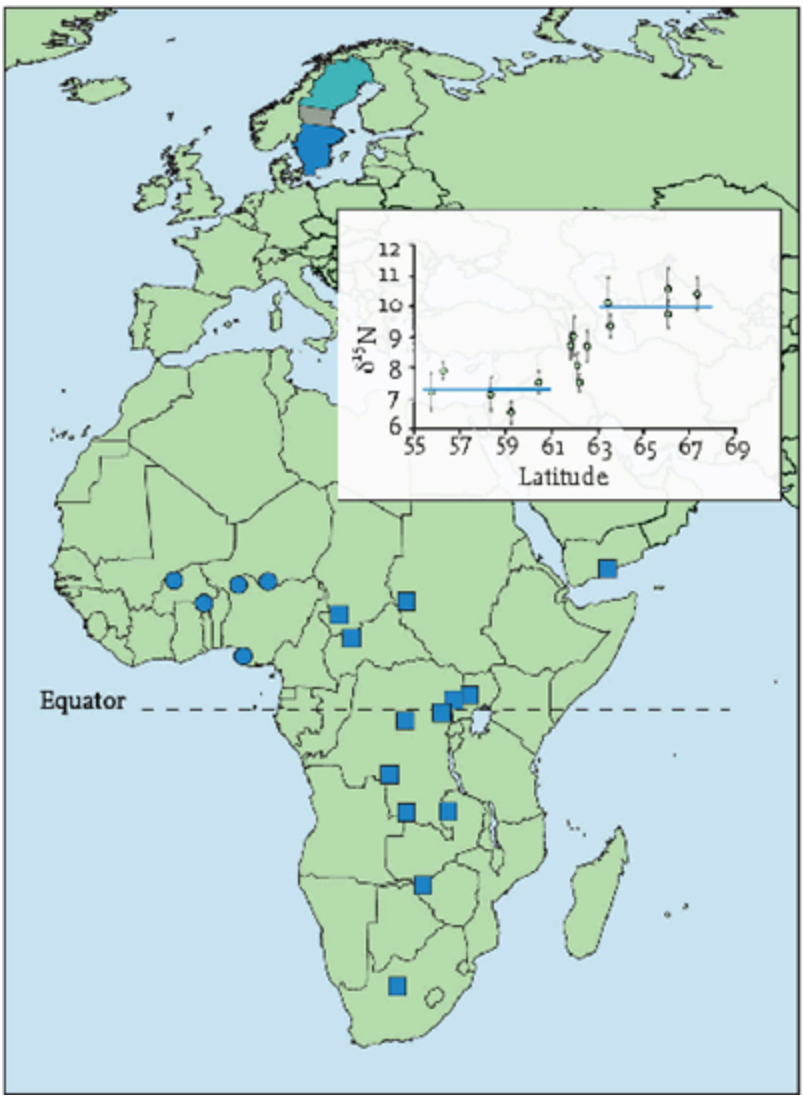


FIG 189. Recoveries of Willow Warblers *Phylloscopus trochilus* ringed in Sweden. Those from birds ringed in southern Sweden are shown as filled circles and those from northern Sweden as squares. The breeding distribution shows the approximate location of the hybrid zone between two subspecies (P. *t. aaedula* in the north and P. *t. trochilus* in the south) where there is a migratory divide. The diagram shows the nitrogen isotope (^{15} N) signature in birds from southern Sweden, the hybrid zone, and northern Sweden. These isotope data reflect the location of the winter moult in Africa, and hence the differing wintering areas of the two populations. (Based on Chamberlain *et al.,* 2000.)



FIG 190. Greenish Warbler *Phylloscopus trochiloides,* a rare vagrant to the British Isles, which occurs as a 'ring species' around the Tibetan Plateau. (Rebecca Nason)

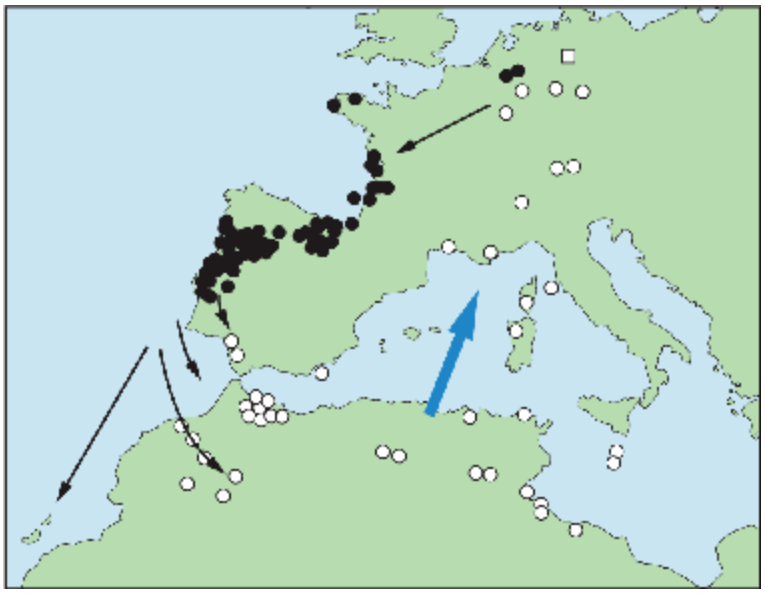


FIG 191. 'Loop migration' of European Pied Flycatchers *Ficedula hypoleuca* ringed near Brunswick in northern Germany (open square). Black dots: recoveries during autumn migration (n = 71); circles: recoveries during spring migration (n = 40); arrows: main migration directions in autumn (black) and spring (blue). Autumn migration follows a fairly narrow westerly route, whereas spring migration follows a much broader and more easterly route. The recoveries suggest that birds stop mainly in southwest Europe on their autumn journey to west tropical Africa and mainly in North Africa on their return spring journey. (From Bairlein, 2001.)



FIG 192. Wood Warbler *Phylloscopus sibilatrix,* a declining summer visitor to Britain which winters primarily in the humid tropical forests of Africa. (Sue Tranter-RSPB Images)

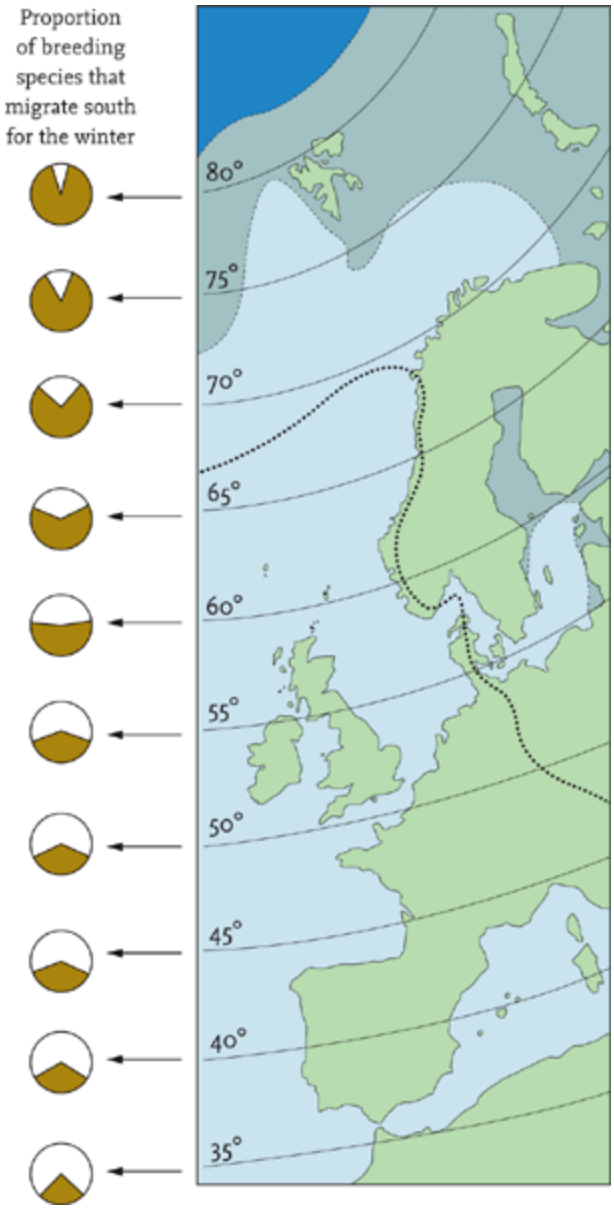


FIG 193. Map of western Europe showing the proportions of breeding bird species at different latitudes that migrate south for the winter. Legend: dark blue—permanent ice; grey blue—winter ice; dotted line—o°C mean January isotherm. (From Newton & Dale, 1996a.)

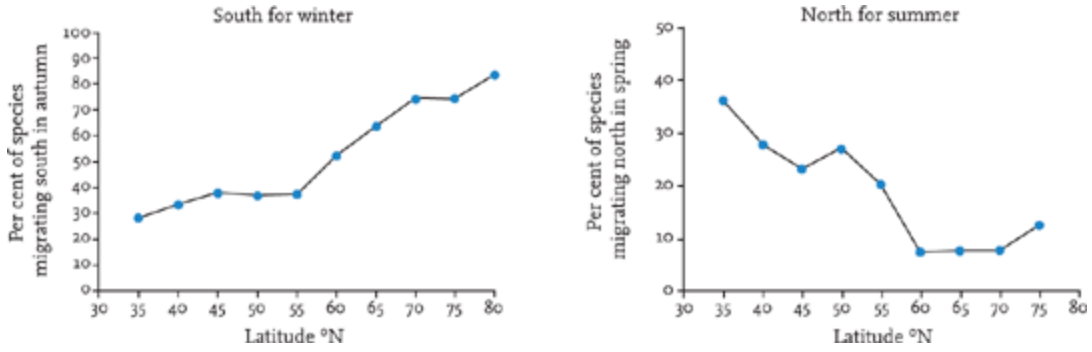


FIG 194. Proportions of breeding bird species (y-axis) at different latitudes (x-axis) in western Europe that (a) migrate south for the winter or (b) north for the summer. For southward migration, on regression analysis for western Europe: $y = 41.49–1.03 + 0.02x2$, $r^2 = 0.97$. For northward migration, on regression analysis for western Europe: $y = 55.65–0.66x$, $r^2 = 0.81$. For the first of these relationships, a quadratic equation gave a significantly better fit than a linear one. Because 23 species leave Europe altogether in winter, spending their non-breeding period in Africa, the figures for the southward and northward migrations do not exactly match. (From Newton & Dale, 1996a.)



FIG 195. Gyrfalcon *Falco rusticolus* (immature), one of the few bird species in which most individuals remain in the arctic year-round. It is a rare winter visitor to the British Isles: white-phase birds, like the one shown, are likely to derive from

Greenland or eastern North America, and dark-phase ones from Iceland or northern Europe. (Cal Sandfort)



FIG 196. Dipper *Cinclus anchis,* an inhabitant of fast-flowing streams which can therefore remain in wintering areas while neighbouring still waters are frozen, forcing their occupants out. (Jill Pakenham)

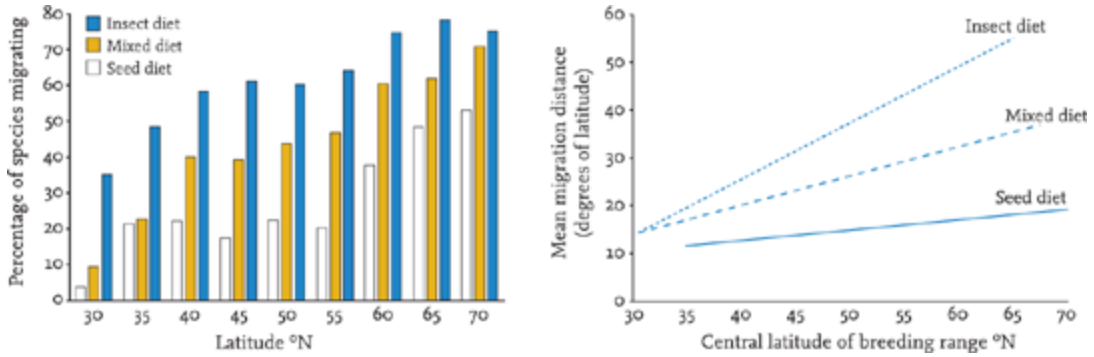


FIG 197. Migration in relation to diet in west European songbirds. (Above left) Proportion of species breeding at different latitudes which migrate south for the winter. (Above right) Distances moved by migrants as measured by the difference between the central latitudes of the breeding and wintering ranges. Lines calculated by regression analyses. (From Newton, 1995b.)

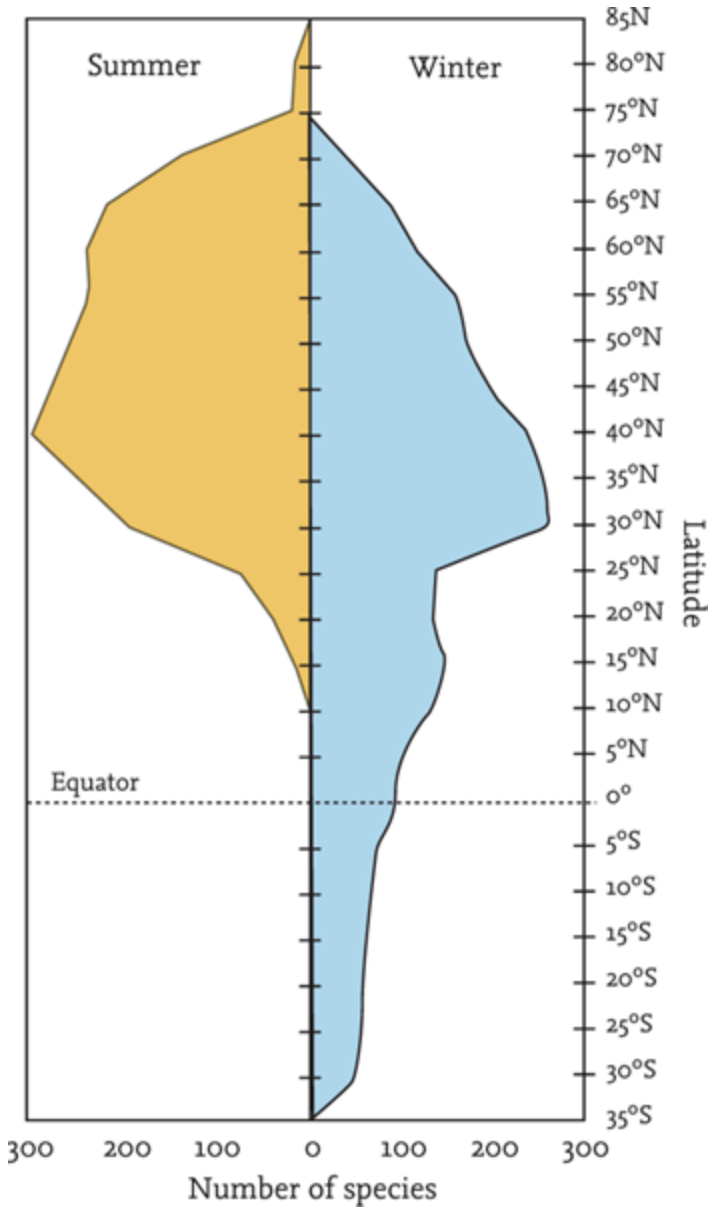


FIG 198. Latitudinal shift between summer and winter distributions of bird species that breed in Europe. Includes wintering areas in Europe and Africa. (From Newton, 1995b.)



FIG 199. Twite *Carduelis flavirostris,* a short distance migrant within the British Isles which largely abandons its upland breeding areas for the winter, moving to lower ground, and especially coastal areas. (Edmund Fellowes)

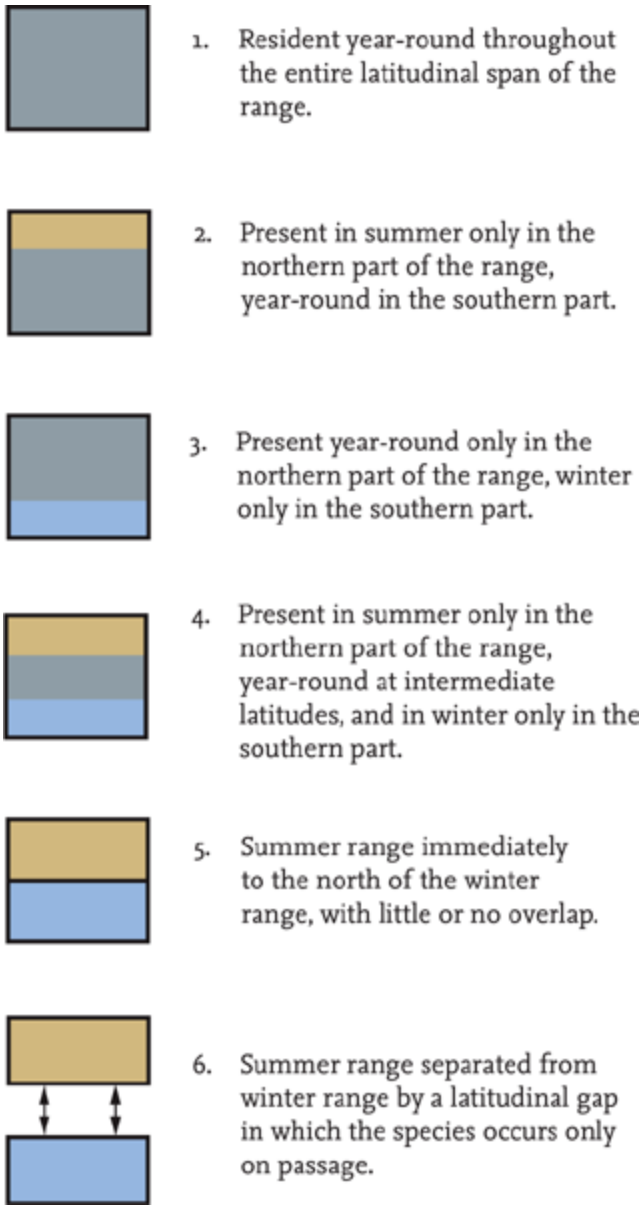


FIG 200. Main migration patterns found in European birds, based on the degree of separation between breeding and wintering ranges.

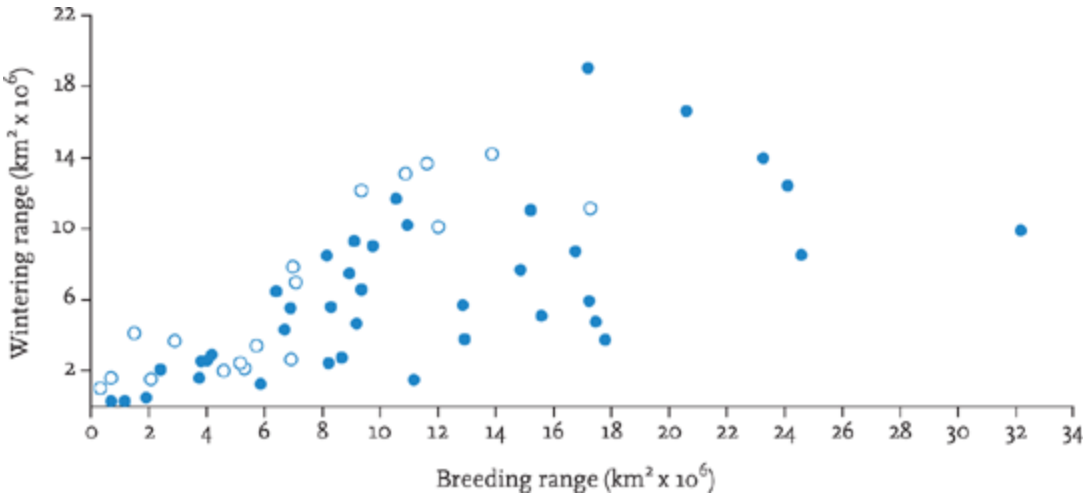


FIG 201. Relationship between sizes of breeding and wintering ranges of 57 landbird species which breed entirely in Eurasia and winter entirely in Africa. Warblers are shown separately as open circles. (From Newton, 1995a)

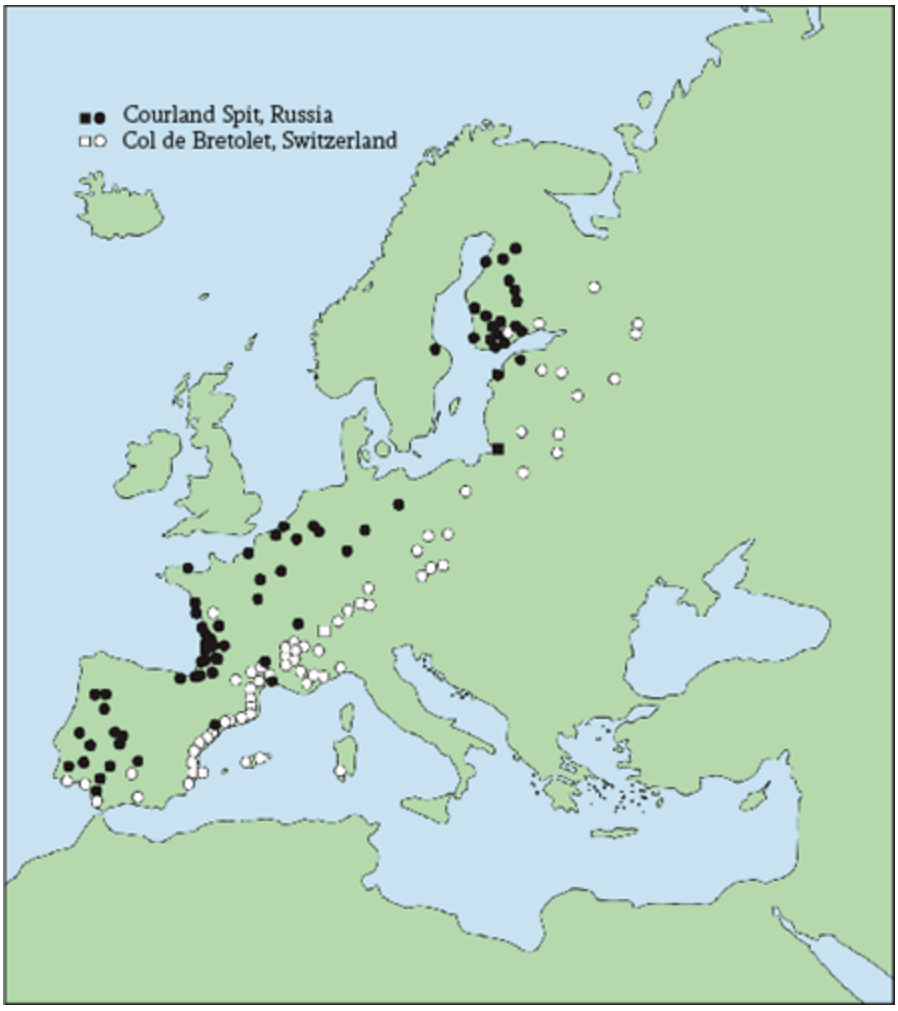


FIG 202. Parallel migration as shown by ring recoveries of Chaffinches *Fringilla coelebs* caught while migrating through the Courland Spit (Rybachy), Russia (filled square, filled circles) and the Col de Bretolet, Switzerland (open square, open circles). (From Bairlein, 2001.)

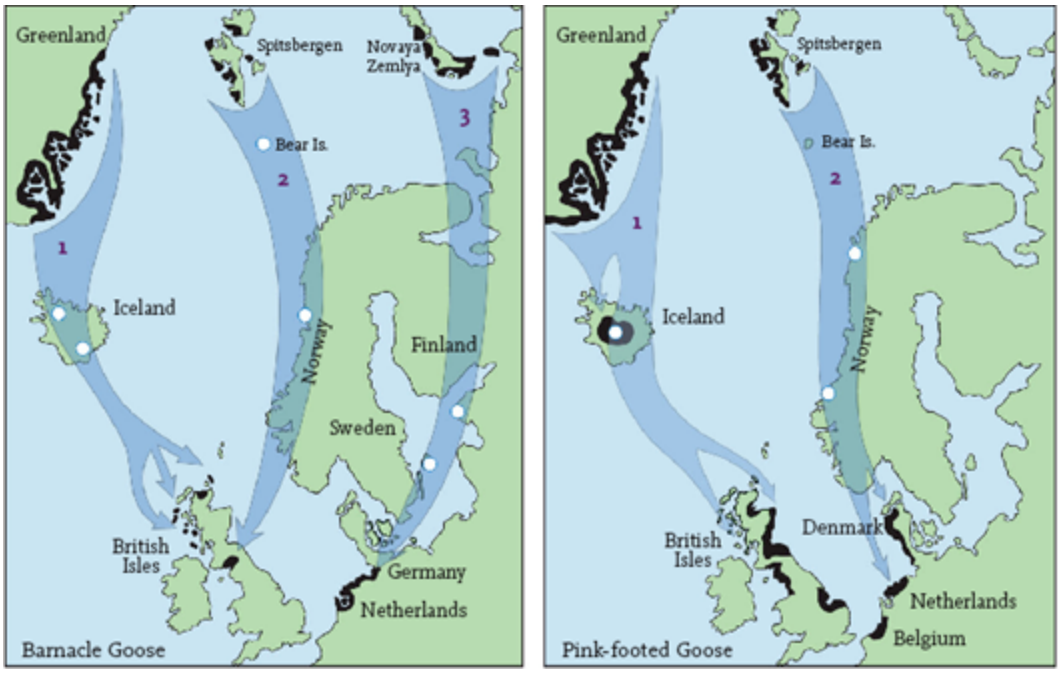


FIG 203. Breeding areas, migration routes and wintering areas of three populations of Barnacle Geese *Branta leucopsis* and two populations of Pink-footed Geese *Anser brachyrhynchus.* Black shading depicts the separate breeding and wintering areas, darker blue the migration routes, and white spots the main stopover sites. (From Madsen *et al.,* 1999.)



FIG 204. Pink-footed Geese *Anser brachyrhynchus,* in which populations from different breeding areas also have discrete wintering areas. Those wintering in Britain derive from Iceland and east Greenland. (Edmund Fellowes)

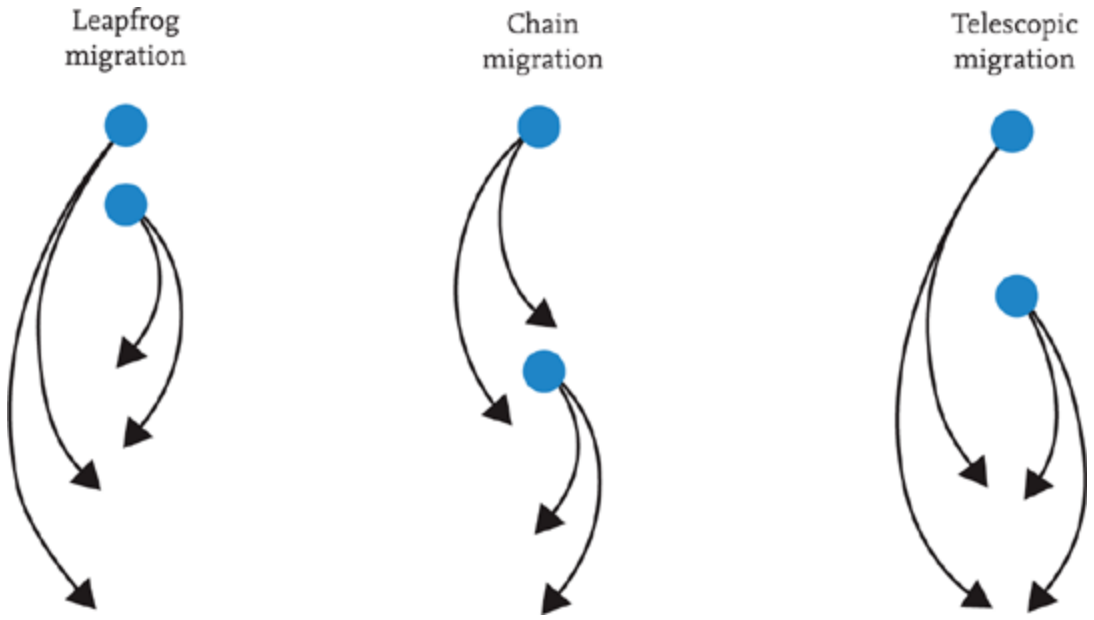


FIG 205. Three common latitudinal patterns in the migrations of different bird species. In leapfrog migration, populations occur in wintering areas in reverse latitudinal sequence as they occur in their breeding areas, the most northerly breeding population wintering furthest south. In chain migration, populations occur in wintering areas in the same latitudinal sequence as they occur in their breeding areas, each population replacing the other southwards. In telescopic migration, populations breeding in different latitudes all occur together in the same wintering latitudes. In the first two patterns, populations breeding in different latitudes tend to remain separate in breeding and wintering areas despite migration, whereas in the third pattern they separate only in the breeding season. (Partly from Salomonsen, 1955.)



FIG 206. Common Tern *Sterna hirundo,* a leap-frog migrant which winters mainly off the west coast of Africa, the British birds chiefly north of the equator, and the Scandinavian ones chiefly south of the equator. (John Wright)



FIG 207. Waxwings *Bombycilla garrulus,* irruptive migrants which specialise on fleshy fruits, such as rowan, hawthorn and rose hips. (Brian Irving © HELM-Images)

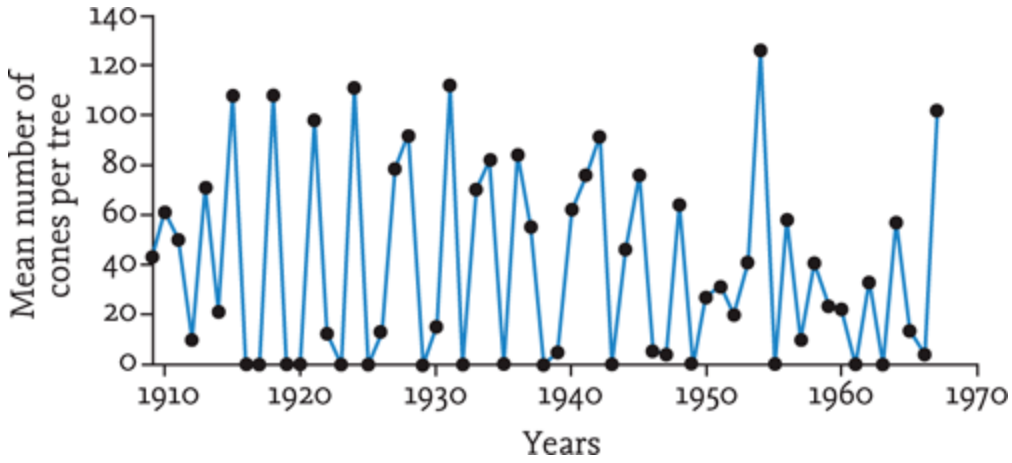


FIG 208. The mean number of Norway Spruce *Picea abies* cones per tree each year in southern Sweden, 1909–67. (From Hagner, 1965 and Götmark, 1982.)



FIG 209. Bullfinch *Pyrrhula pyrrhula* (male) which is resident in parts of its range, such as the British Isles, and an irruptive migrant in the boreal forests of northern Europe, where it is affected mainly by the abundance of rowan fruits. This individual., feeding on seeds from withered blackberries, belongs to the resident British race. (Sean Gray/Gray-Images)

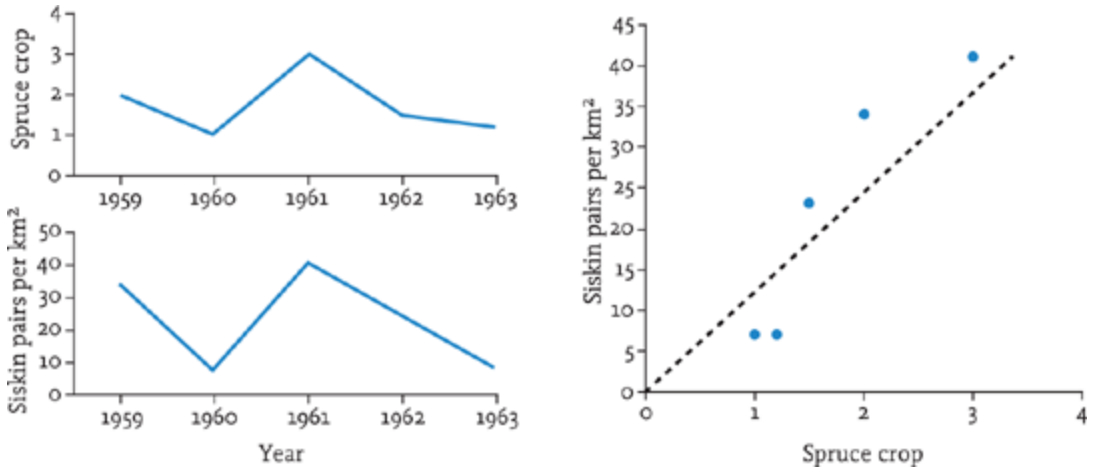


FIG 210. Numbers of breeding Eurasian Siskins *Carduelis spinus* in relation to the spruce crop in Finland. Siskins shown in pairs per km^2 and cone crops classified in four categories (from Haapanen, 1966). For similar patterns for Siskins in other areas see Hogstad, 1967; Shaw, 1990; and Förschler *et al.,* 2006.

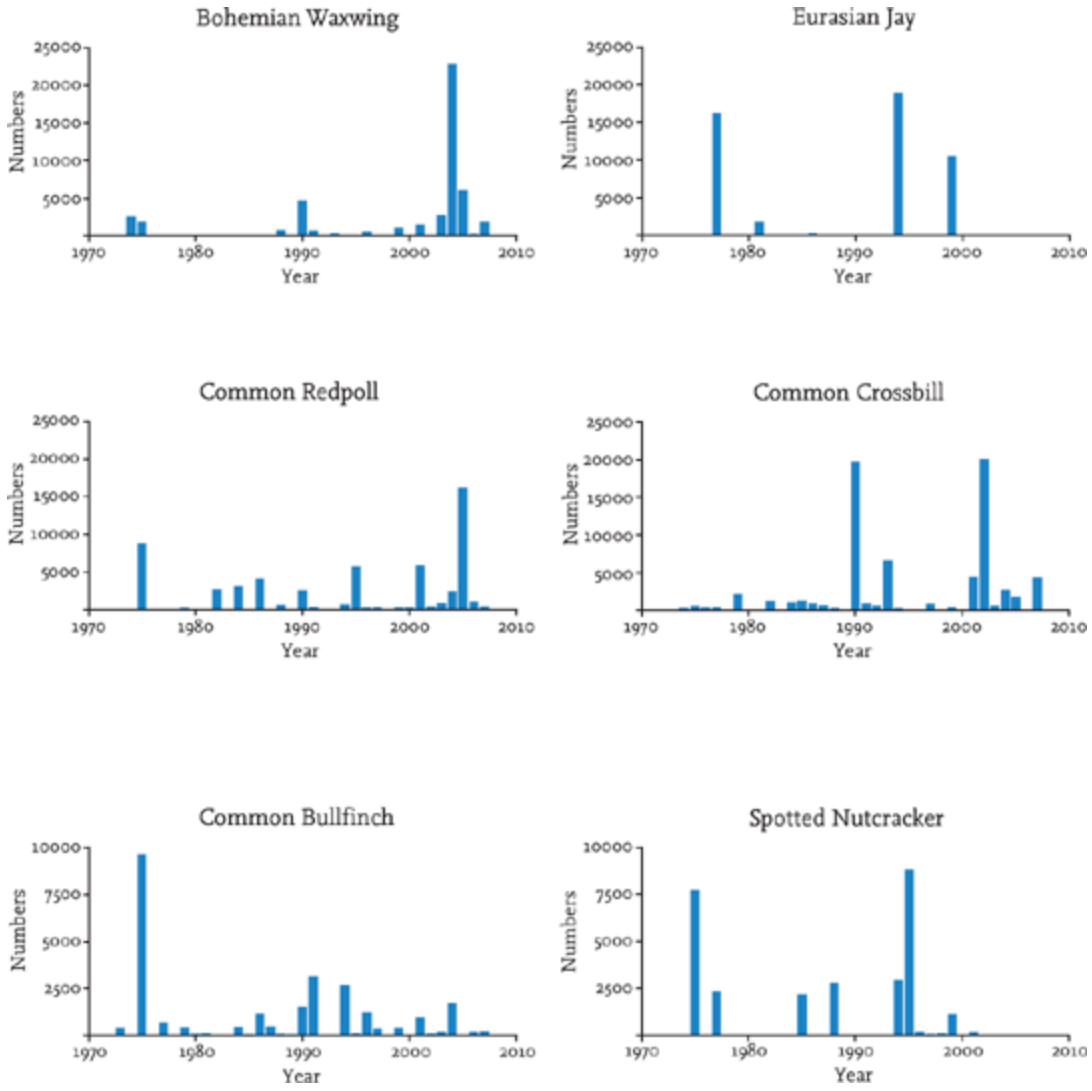


FIG 211. Annual fluctuations in the numbers of six irruptive species (all diurnal migrants) counted during August-November while migrating over Falsterbö in southern Sweden, 1973–2008. Compiled from data on the Falsterbö website. (Kjellén, 2008.)



FIG 212. Eurasian Siskins *Carduelis spinus,* in which the timing and extent of migration varies greatly from year to year. These individuals were attracted by niger seed in a garden feeder. (Edmund Fellowes)



FIG 213. Common (Mealy) Redpoll *Carduelis flammea* which specialises on seeds of birch and alder, but also takes many conifer seeds in spring when the cones open. (Edmund Fellowes)

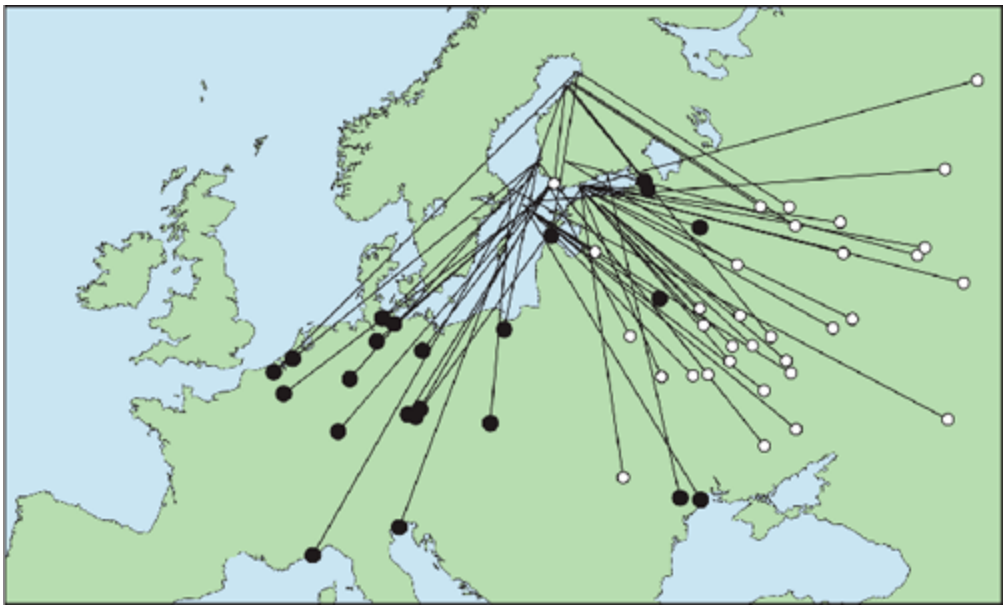


FIG 214. Winter recoveries of Common Redpolls *Carduelis flammea* ringed in Finland. Circles—winter 1965/66, dots—winter 1972/73 (after Zink & Bairlein, 1995). For other information on Redpoll wintering areas in different years, see Lensink *et al.,* 1986 and Thies, 1991.



FIG 215. Brambling *Fringiia montifringiia* (male) which in summer feeds mainly on insects and in winter on beechmast, but occasionally visits garden feeders for sunflower and other seeds. (Edmund Fellowes)



FIG 216. Common Crossbill *Loxia curvirostra,* an irruptive migrant specialising on conifers, being able to extract the seeds from closed cones. (Sean Gray/Grayimages)

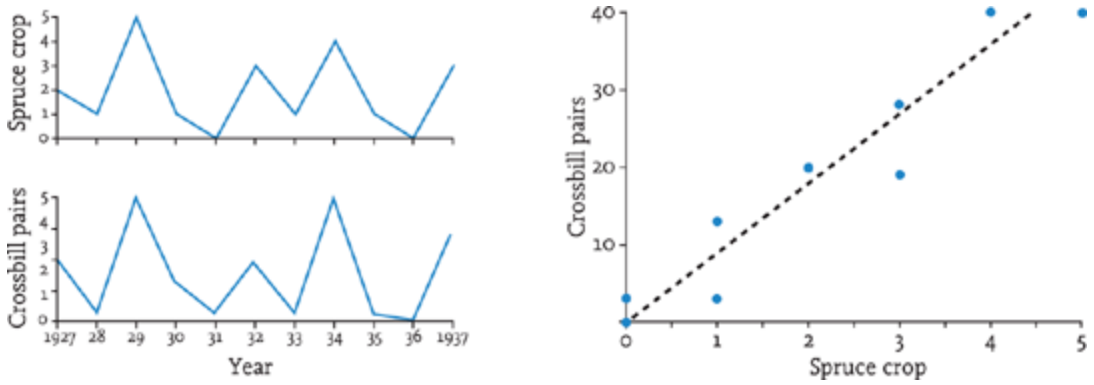


FIG 217. Relationship between the population density of the Common Crossbill *Loxia cwvirostra* and the cone crop of Norway Spruce *Picea abies* in Finland (n = 7, r_S = 0.826, P = 0.028). Crossbills in number of pairs per 120 km transect; spruce crop ranked in five categories (from Reinikainen, 1937). For similar patterns in other areas, see Thies, 1996; Förschler *et al.,* 2006.

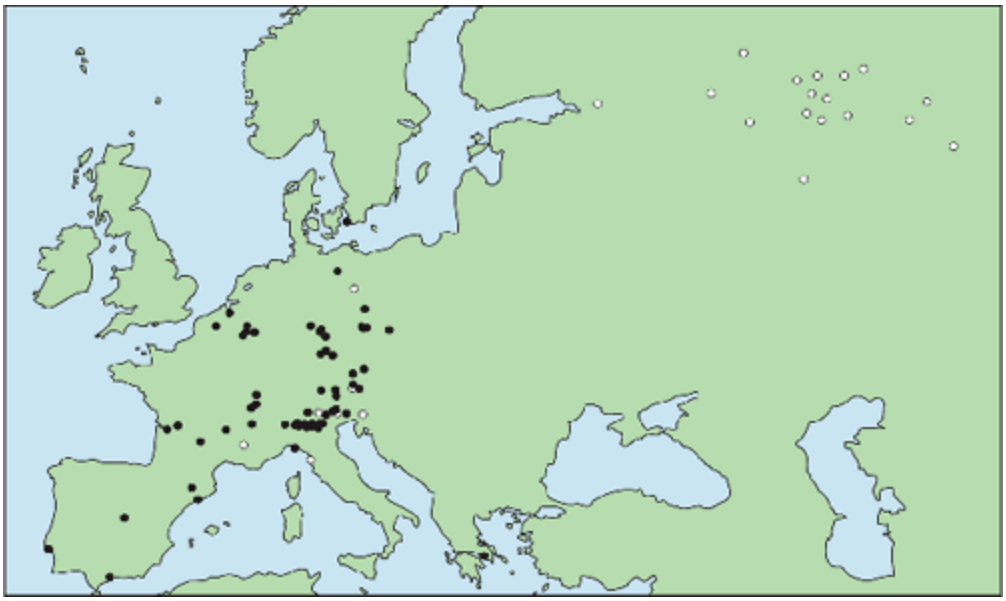


FIG 218. Recoveries of Common Crossbills *Loxia curvirostra* ringed at migration time in June–October of invasion years in Germany, and recovered in the following year (filled circles) and later years (open circles) respectively. All the 83 birds recovered in the following year (to 31 May) were in the invasion areas of western Europe, whereas 22 out of 44 birds recovered in later years were far to the northeast, in the boreal zone of northern Russia (significance of difference in distribution, $\chi^2 = 34.2$, < 0.001). Only movements more than 50 km are included. These recoveries indicate that some irrupting Crossbills return to their region of origin in a later year. Map compiled from the recoveries listed in Schloss, 1984, which include recoveries from the invasions of 1930, 1935, 1953, 1956, 1959, 1962, 1963, 1972, 1977 and 1979, although two-thirds of all recoveries in Russia probably stem from the invasion of 1963. Schloss, 1984, lists nine other recoveries in northern Russia of birds ringed in Germany in non-invasion years or outside the migration season, some of which are in Figure 219. In addition to the records shown, another Common Crossbill ringed at Falsterbo in Sweden on 12 August 1963 was recovered in a later year in northern Russia at 60°18′N, 54°18′E, and one ringed in Northamptonshire in England on 2 June 1991 was recovered 1,958 km east-northeast on 14 April 1998 in northern Russia (58°16′N, 28°54′E). For other similar recoveries of birds ringed in Switzerland, see Newton, 1972.

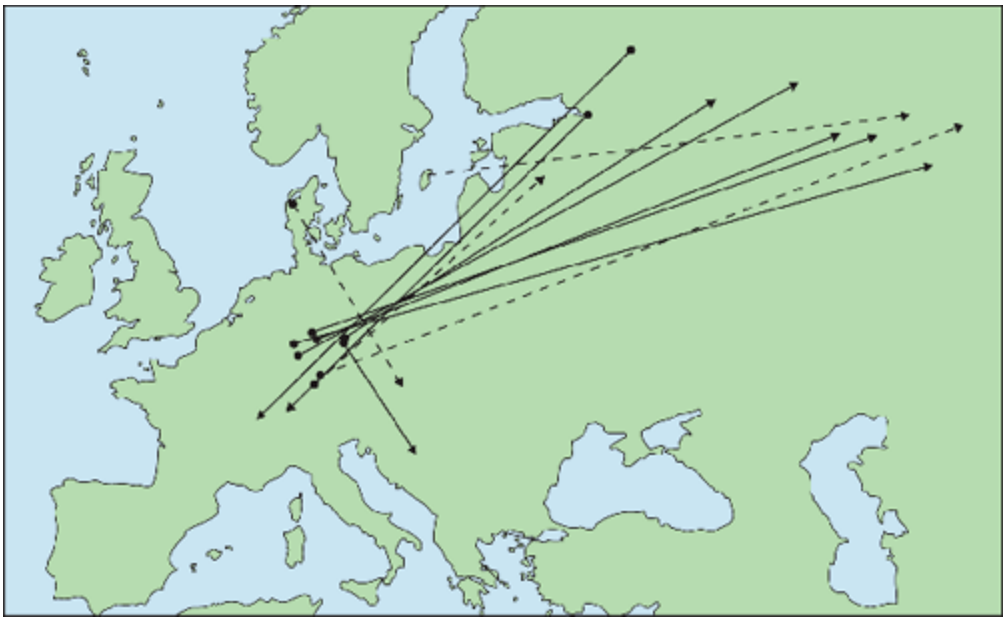


FIG 219. Ringing and recovery sites of Common Crossbills loxia *curvirostra* that were both ringed and recovered in different breeding seasons (taken as January–April in areas of Norway Spruce *Picea abies)*. Spots represent ringing sites and arrow heads recovery sites. Continuous lines—ringed as adults (representing breeding dispersal); dashed lines—ringed as juveniles (representing natal dispersal). Compiled mainly from information in Schloss, 1984; also from Danish Ringing Report (1931–34), Swedish Ringing Report (1965), Swiss Ring recoveries provided by Lukas Jenni, and Russian ring recoveries provided by Konstantin Litvin. (Details listed in Newton, 2006c.)



FIG 220. Two-barred Crossbill *Loxia leucoptera* a rare irruptive migrant to Britain, which in its Eurasian range feeds mainly from the soft-scaled cones of larch. One of the biggest recorded irruptions into the British Isles occured in 2008, evident chiefly in Shatland (Dick Forsman)



FIG 221. Slender-billed Nutcracker *Nucifraga caryocatactes* on the move. This irruptive migrant only rarely reaches the British Isles from northern Russia and Siberia. (Dick Forsman)



FIG 222. Coal Tit *Parus ater,* a resident in the British Isles, but a common irruptive migrant in northern Europe, from which region birds occasionally reach the British Isles. (Edmund Fellowes)



FIG 223. Bearded Tit *Panurus biarmicus,* a reed-bed species which is known for eruptive dispersive movements in years of high numbers. (John Willsher)

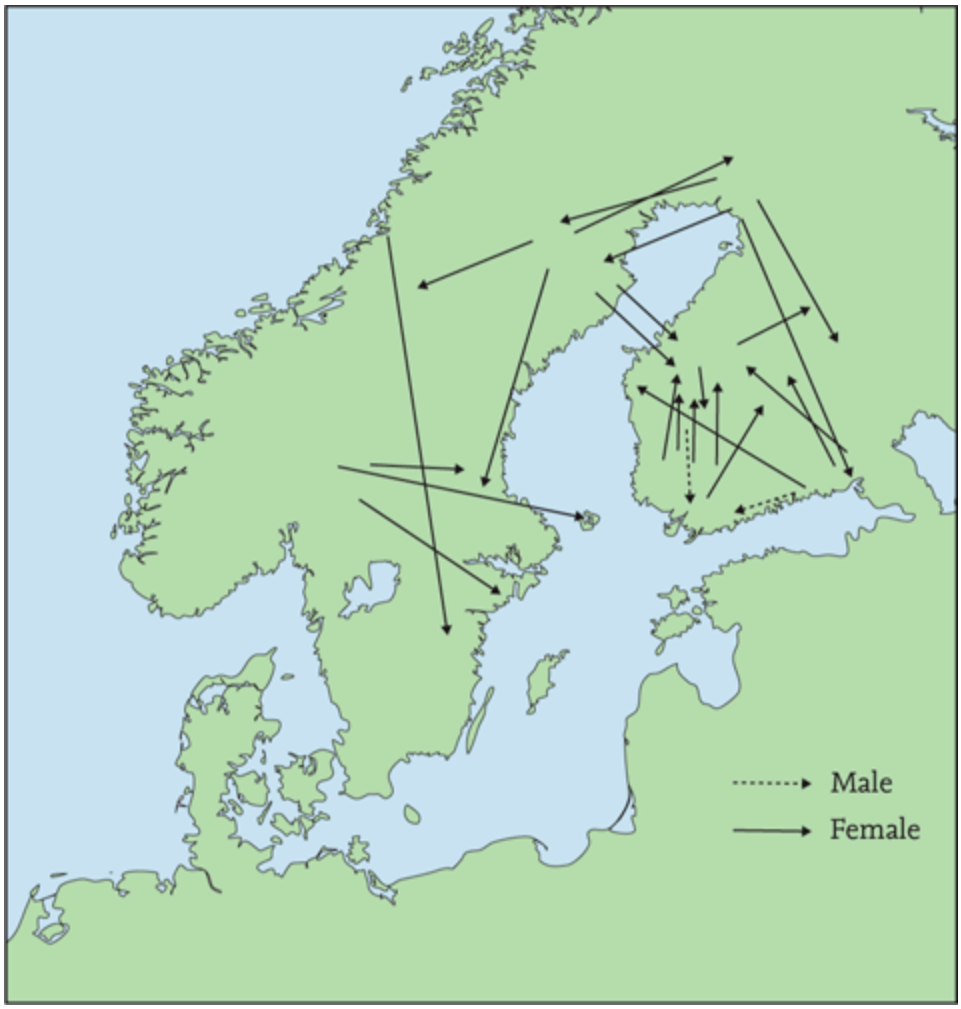


FIG 224. Annual fluctuations in the breeding densities of Short-eared Owls *Asio flammeus* in relation to Field Vole *Microtus arvalis* densities in an area of western Finland. (From Korpimäki & Norrdahl, 1991.)

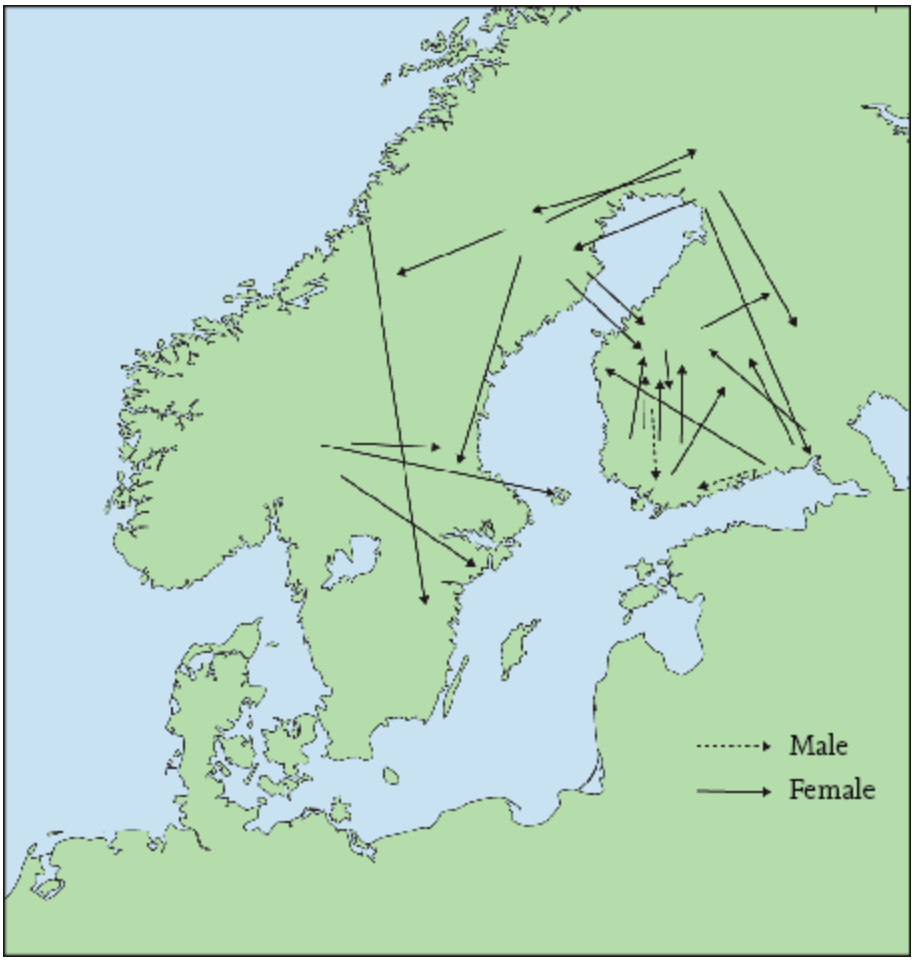


FIG 225. Ringing and recovery sites of adult Tengmalm's Owls *Aegolius funereus* that were identified in different breeding seasons. This species nests readily in boxes and has been studied at many localities in northern Europe. Only movements greater than 100 km are shown, which eliminated most recorded movements by males. The males are mainly resident and the females dispersive. Both sexes tend to stay in the same localities if vole densities remain high, moving no more than about 5 km between nest boxes used in successive years, but if vole densities crash, females move much longer distances, with many having moved 100–600 km between nest sites in different years. In contrast, fewer long distance moves were recorded from males, with only two at more than 100 km. The greater residency in males was attributed to their need to guard cavity nest sites which are scarce in their conifer nesting habitat, while their smaller size makes them better able than females to catch birds, and hence survive (without breeding) through low vole conditions. (Compiled from information in Löfgren *et al.,* 1986; Korpimäki *et al.,* 1987; and Sonerud *et al.,* 1988.)



FIG 226. Short-eared Owl *Asioflammeus,* whose breeding distribution changes from year to year, depending on vole populations. (Brian Irving © HELM-Images)



FIG 227. Long-eared Owl *Asio otus,* a resident and irruptive migrant in the British Isles. (Sean Gray/Grayimages)



FIG 228. Snowy Owl *Nydea scandiaca,* an arctic nesting species which erupts southward in poor lemming years, and occasionally reaches the British Isles. This individual appeared on the Scilly Isles in autumn 2008. (James Packer)



FIG 229. Long-tailed Skua *Stercorarius longicaudus,* a passage migrant seen along the coasts of the British Isles. Note the colour rings used to identify this individual on its arctic breeding area. (Edmund Fellowes)



FIG 230. Rose-coloured Starlings *Pastor roseus,* irruptive migrants from arid regions, of which small numbers occasionally reach the British Isles (above and left). A Common Starling *Sturnus vulgaris* on the left of the upper picture provides comparison. (Dick Forsman and Tim Appleton).



FIG 231. Pallas' Sandgrouse *Synhaptes paradoxus,* an irruptive migrant from the Asian steppes which occasionally reaches the British Isles. Major irruptions to western Europe occurred in the late nineteenth century. This bird appeared on Shetland in May 1990. (Larry Dalziel)



FIG 232. Northern Pintail *Anas acuta,* which can breed in widely separated areas in different years, depending on rainfall and its effects on nesting habitat. (Edmund Fellowes)

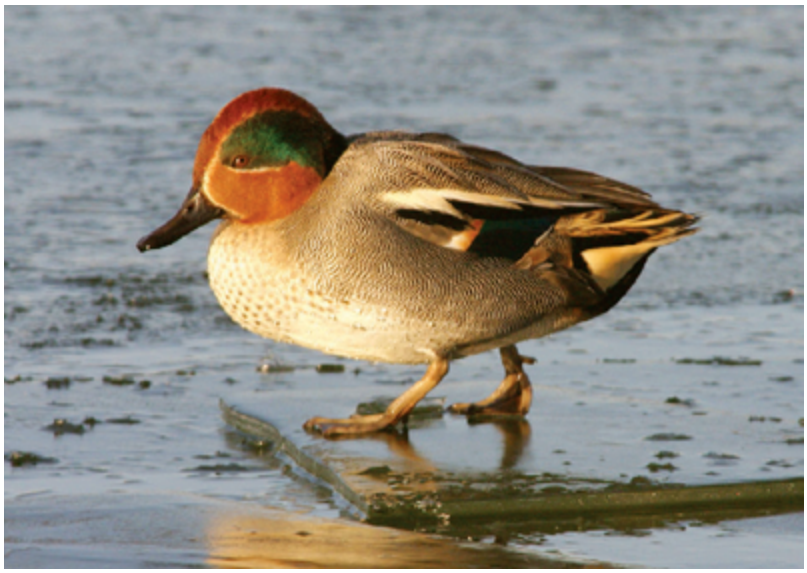


FIG 233. Common Teal *Anas crecca,* a shallow-water species whose widescale distribution in the breeding season varies with water levels, and in winter with ice cover. (Edmund Fellowes)



FIG 234. Skylark *Alauda arvensis,* a partial migrant, and well known weather migrant within the British Isles. (Jill Pakenham)



FIG 235. Dotterel *Charadrius morinellus,* in which females seek to mate with more than one male each year, laying a clutch of eggs for one male to incubate before moving on to lay another clutch for a different male elsewhere. (Edmund Fellowes)



FIG 236. Moulting Greylag Goose *Anser anser,* showing all the flight feathers in simultaneous growth, rendering the bird flightless for about five weeks each year. (Alan Martin)



FIG 237. Shelduck *Tadoma tadoma,* well known for a moult migration in which birds from much of Europe concentrate each summer on the Grosser Knechtsand in the German Wadden Sea to moult their flight feathers. (Brian Irving © HELM-Images)



FIG 238. Goosander *Mergus merganser,* in which most drakes leave the British Isles for a period each summer to moult their flight feathers in the north of Norway. Female Eiders *Somateria mollisima* in the foreground. (Edmund Fellowes)



FIG 239. Common Eiders *Somateria mollissima* (mainly drakes) assembling at an arctic moulting site. King Eider *Somateria spectabilis* drake in left foreground. (Jack Stephens)



FIG 240. Shag *Phalacrocorax aristotelis,* in which individuals disperse in various directions away from their nesting colonies after breeding, but return there the following year. Also, young birds tend to disperse further than adults. (Brian Irving © HELM Images)

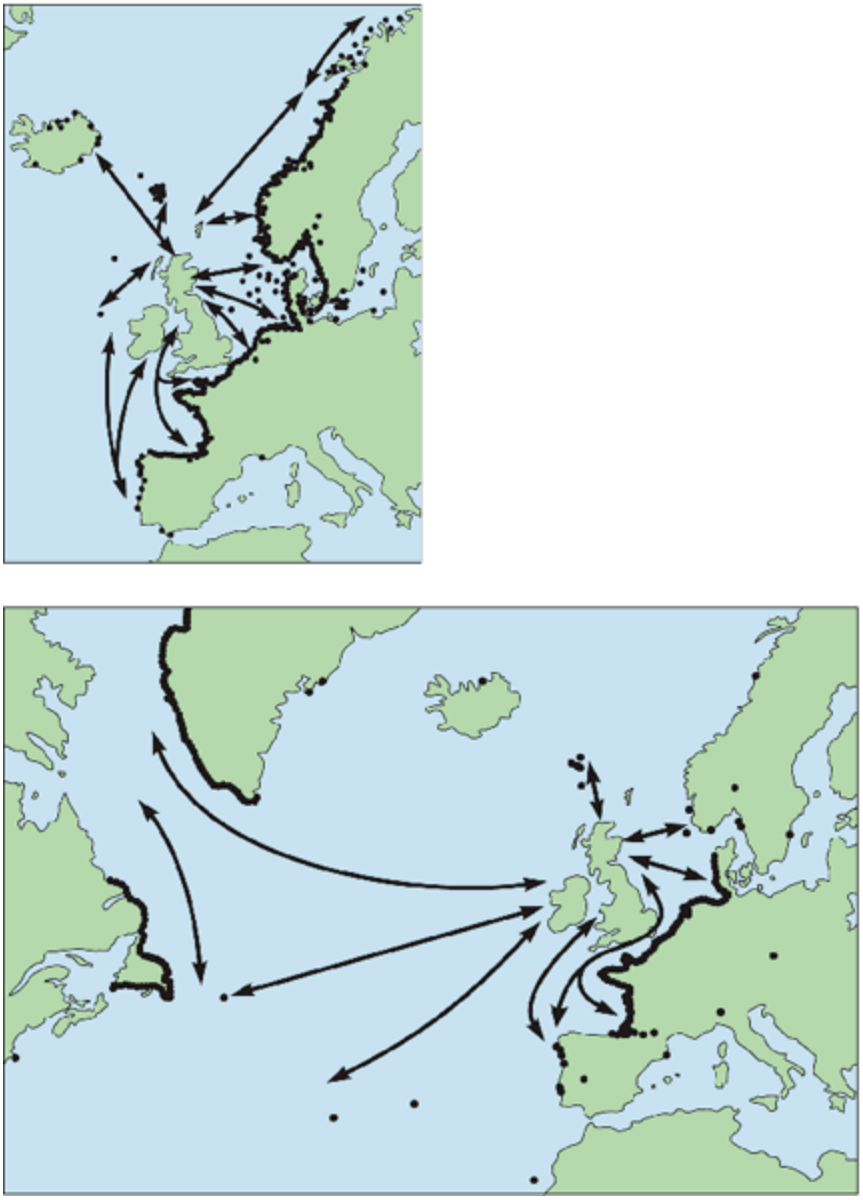


FIG 241. Dispersive migration of two species of seabirds based mainly on recoveries of birds ringed as nestlings in Britain: (top) Common Guillemot *Uria aalge;* (above) Black-legged Kittiwake *Rissa tridactyla.*



FIG 242. Red-necked Phalarope *Phalaropus lobatus* in breeding plumage, a rare breeder and passage migrant in the British Isles. (Edmund Fellowes)



FIG 243. Spotted Redshank *Tringa eiythropus* (in winter plumage), a long distance migrant in which females leave their northern breeding areas soon after egg-laying, leaving the males to hatch and raise the young. Mainly a passage migrant in the British Isles, but winters in small numbers. (Edmund Fellowes)

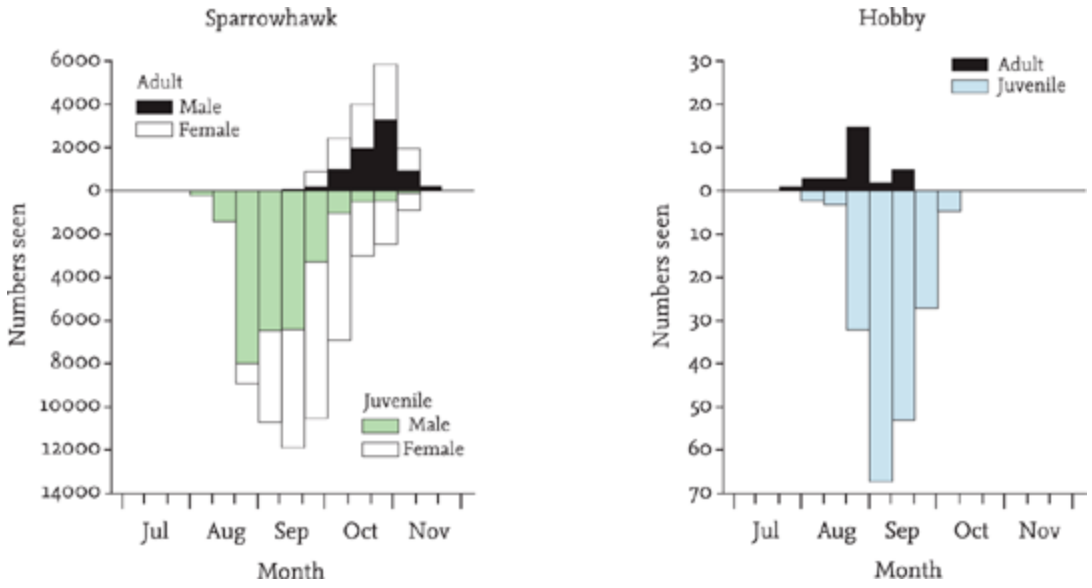


FIG 244. Numbers of (above left) Eurasian Sparrowhawks *Accipiter nisus* and (above right) Eurasian Hobbies *Falco subbuteo* seen migrating through Falsterbo, Sweden, at different dates in autumn. In the Sparrowhawk which is a partial migrant, juveniles moved before adults, on average. Similar patterns were shown by other partial migrants at this locality, including Northern Goshawk *Accipiter gentilis* and Red Kite *Mihus mihus.* In the Eurasian Hobby, which is a complete migrant, adults moved before juveniles, on average, but sexes could not be distinguished. Similar patterns were shown by other complete migrants at this locality, including Honey Buzzard *Pernis apivorus,* Montagu's Harrier *Circus pygargus* and Osprey *Pandion haliaetus.* (From Kjellén, 1992.)

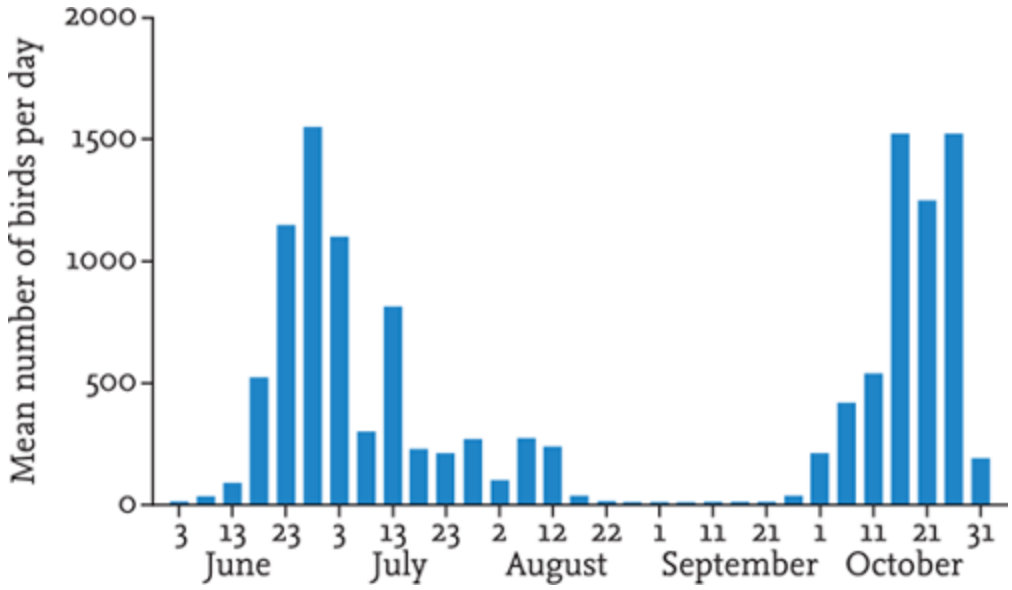


FIG 245. The twin-peaked post-breeding migration of Starlings *Sturnus vulgaris* as recorded at Ottenby in south Sweden. The first peak consists mainly of juveniles and the second mainly of adults, and the lull in between represents the moult period within the population. (From Svärdson, 1953.)



FIG 246. Ruff *Philomachus pugnax* (female), in which the larger males winter mainly in Europe and the smaller females mainly in Africa. (Edmund Fellowes)

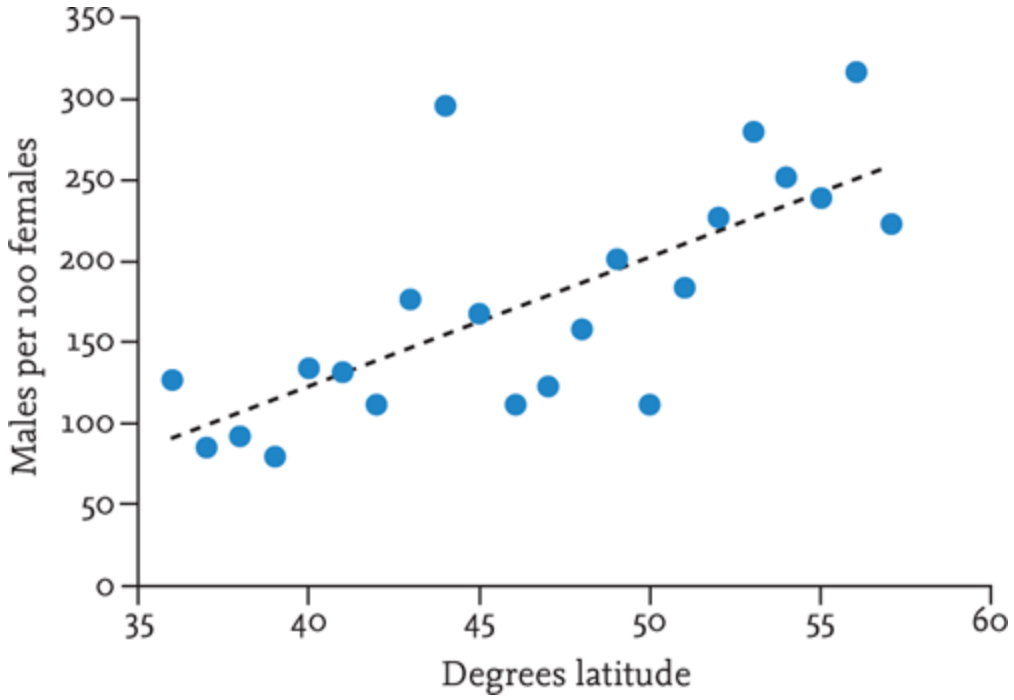


FIG 247. Winter sex ratios among Pochards *Aythya ferina* in relation to latitude in western Europe. (Redrawn from Carbone & Owen, 1995.)



FIG 248. Snow Bunting *Plectrophenax nivalis* (in winter plumage), a regular winter visitor to mountain areas and sandy or muddy coastlines, mainly in northern and eastern parts of the British Isles (for summer plumage see Figure 117). (Rebecca Nason)



FIG 249. Blue Tit *Cyanistes caeruleus,* which is resident within the British Isles, but a partial migrant in northern Europe. (Edmund Fellowes)



FIG 250. Robin *Erithaca rubecula,* a partial migrant in western Europe, in which dominance relationships seem to influence which individuals stay and which leave. (Edmund Fellowes)



FIG 251. Grey Plover *Pluvialis squatarola,* a winter visitor and passage migrant to the British Isles, which often defends feeding territories on coastal mud-flats. (Sean Gray/Grayimages)



FIG 252. Honey Buzzard *Pemis apivorus* (adult male), in which adults and juveniles tracked on migration from Sweden took different routes to their West African wintering areas—see text. (Dick Forsman)

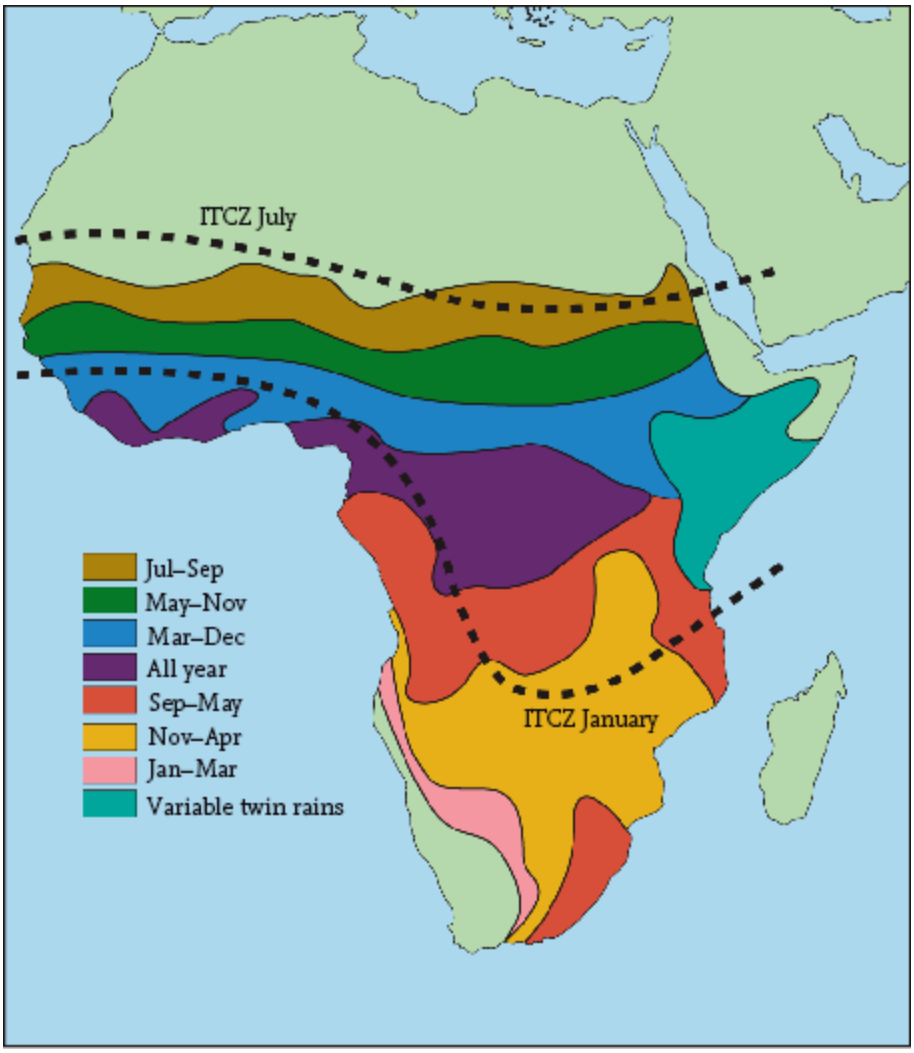


FIG 253. Rainfall patterns and vegetation zones in Africa. Rainfall determines vegetation, from rainforest (wettest), through woodland and savannah to desert (driest), giving equivalent vegetation belts both north and south of the equator (see text). ITCZ—Inter-Tropical Convergence Zone. (From Jones, 1995.)

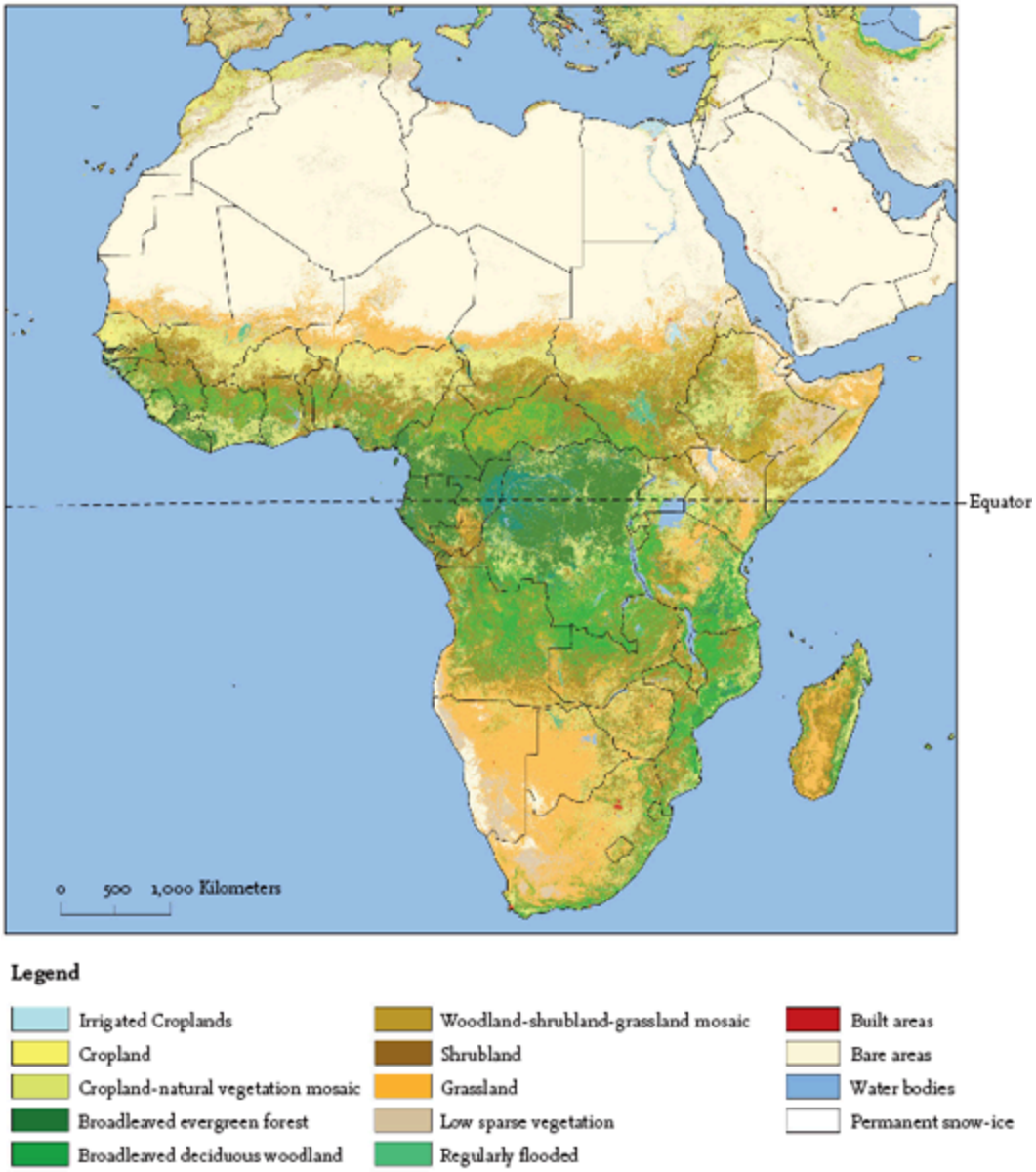


FIG 254. Satellite image of Africa, showing main vegetation zones. (Courtesy of Globcover Land Cover V2 database. European Space Agency/Globcover Project, led by MEDIAS-France, 2008.)



FIG 255. Garganey *Anas querquedula* (drake), a scarce breeder in southern Britain but one of the commonest Eurasian duck species found in winter in the northern tropics of Africa. (Sean Gray/Grayimages)



FIG 256. Wood Sandpiper Tringa *glareola,* a passage migrant in the British Isles, which winters on inland wetlands throughout Africa south of the Sahara. (Colin Turvey)



FIG 257. Curlew Sandpiper *Calidris ferruginea* (winter plumage), a common wintering shorebird on the coasts of Africa. (John Wright)



FIG 258. Turtle Dove *Streptopelia turtur,* formerly widespread in southern Britain, now localised and rapidly declining, which winters in the dry savannahs of northern Africa. (John Wright)



FIG 259. Spotted Flycatcher *Muscícapa striata,* in which individuals from some parts of the breeding range migrate as far as South Africa in winter. (Frank Snijkers)

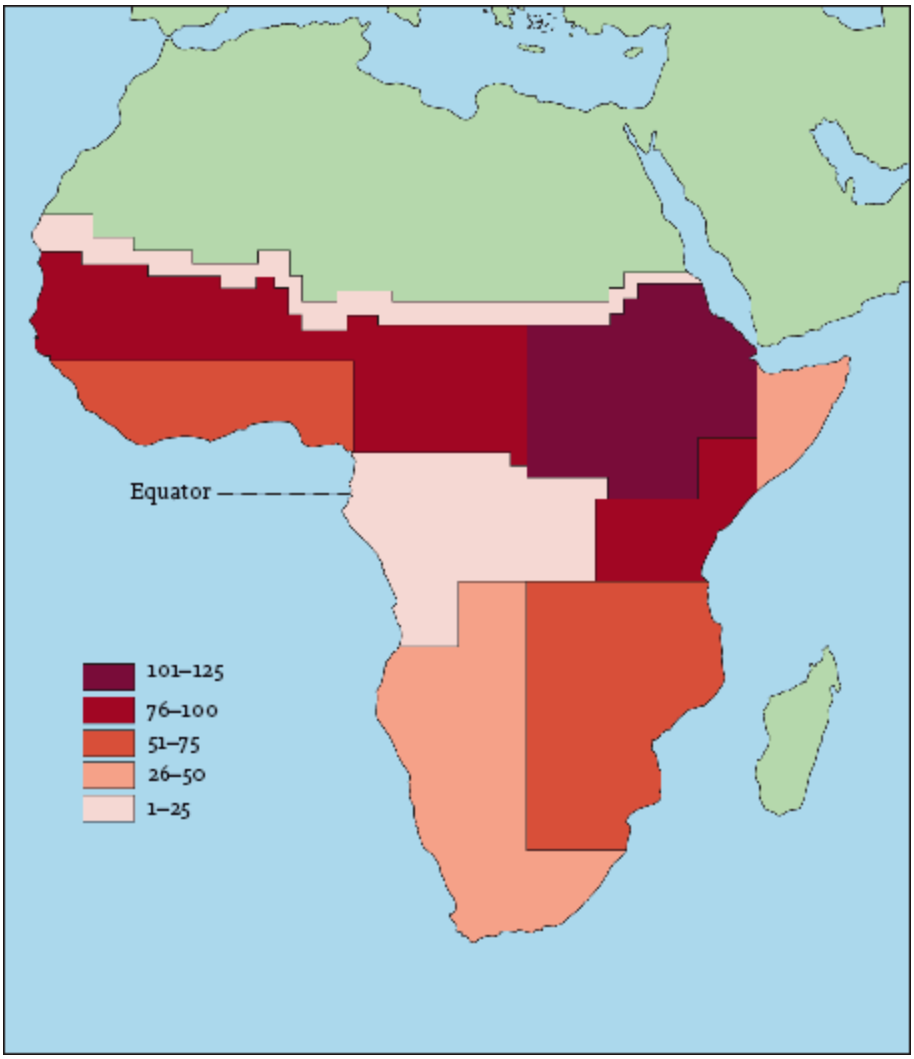


FIG 260. Numbers of Eurasian migrant species found in different parts of subsanaran Africa during October-March. In addition, a few migratory species occur around oases in the Sahara in winter, and in some parts of the Arabian peninsula, but in numbers that form a trivial proportion of the total. (From Newton, 1995a.)



FIG 261. Green Sandpiper *Tringa ochropus,* which winters on freshwater wetlands from Britain south to southern Africa, with individuals normally returning to the same localities year after year. (Sean Gray/Grayimages)



FIG 262. Red-footed Falcon *Falco vespertinus* (male left, female right), which winters in southern Africa, forming huge communal roosts and ranging over surrounding land in search of insects. (Colin Turvey)

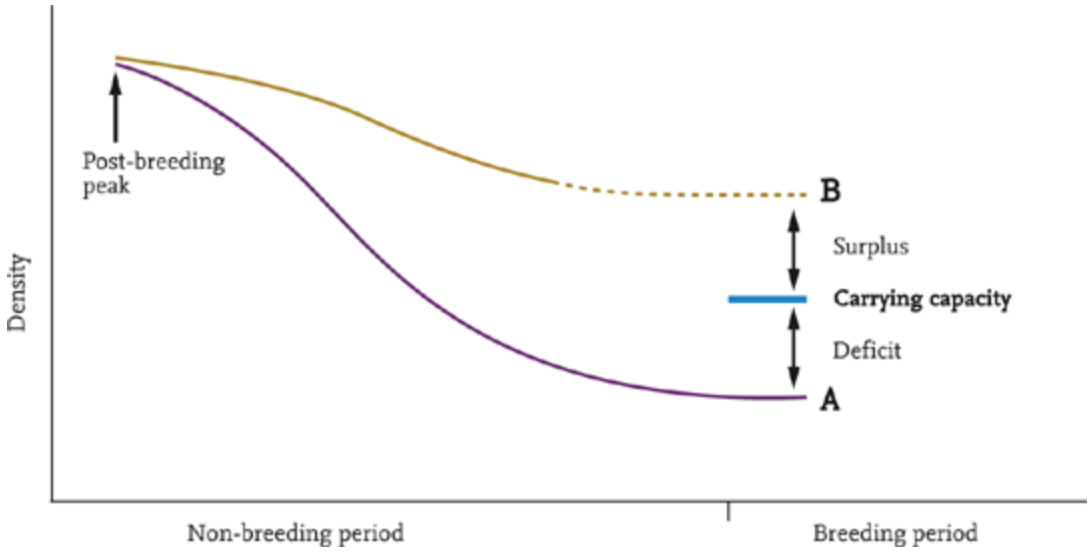


FIG 263. Model showing seasonal changes in the total bird numbers of a species in relation to the carrying capacity of the breeding area (thick line). In the lower curve (A) numbers left at the end of the non-breeding season are fewer than the nesting habitat could support, and in the upper curve (B) numbers are greater than the nesting habitat could support, leading to a surplus of non-territorial, non-breeders. In (A), breeding numbers are limited by conditions in the areas occupied in the non-breeding season, and in (B) by conditions in the area occupied in the breeding season. (From Newton, 1998b.)



FIG 264. Pied Flycatcher *Ficedula hypoleuca,* a summer visitor which in many parts of Europe is limited by shortage of tree-cavity nest sites. (Sean Gray/Grayimages)

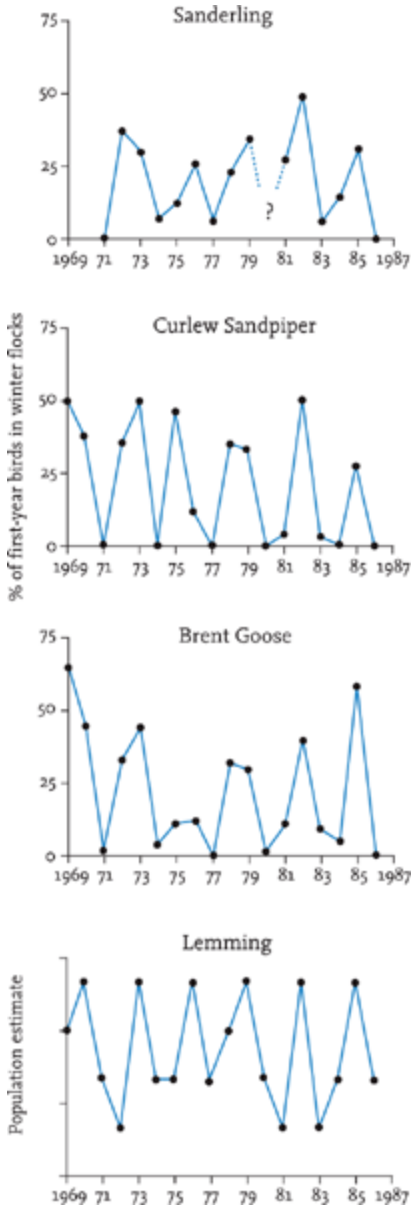


FIG 265. Demography and population change. (a) Relationship between annual survival of adult Barn Swallows *Hirundo rustica* and annual change in breeding density (from Møller, 1989). (b) Relationship between annual breeding output of Pied Flycatchers *Ficedula hypoleuca* and annual change in breeding density (from Virolainen, 1984). Significance of relationships: Barn Swallow, $b = 3.44$, $r^2 = 0.93$, $P < 0.001$; Pied Flycatcher, $b = 0.15$, $r^2 = 0.74$, $P < 0.001$.

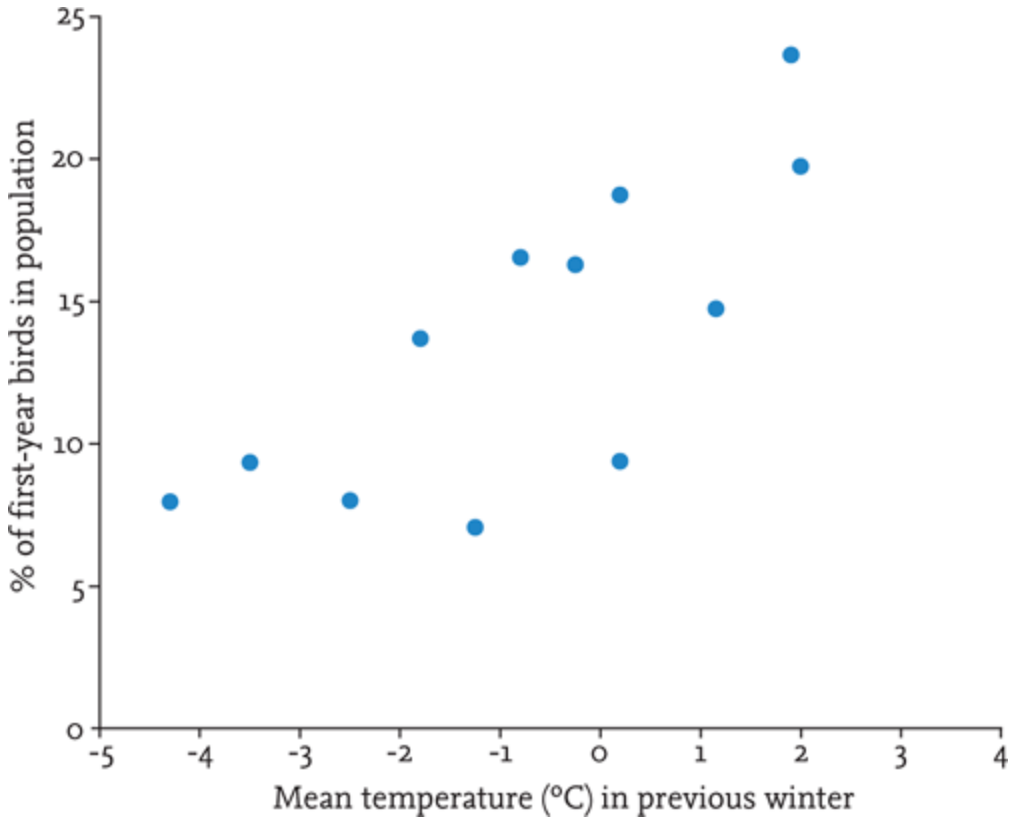


FIG 266. Proportion of first-year birds in wintering populations of various bird species that breed on the Taimyr peninsula of Siberia, shown in relation to densities of lemmings on the breeding grounds in different years. High production of young in Sanderlings *Calidris alba,* Curlew Sandpipers *C. ferruginea* and Brent Geese *Branta bernicla* occurred about every three to four years when lemming numbers were also high, providing alternative food for predators. (From Summers & Underhill, 1987.)



FIG 267. Sand Martin *Riparia riparia,* whose breeding numbers in the British Isles are reduced by Sahel droughts. (Colin Turvey)



FIG 268. Stone Curlew *Burhinus oedicnemus* at nest in farmland. (Bobby Smith)

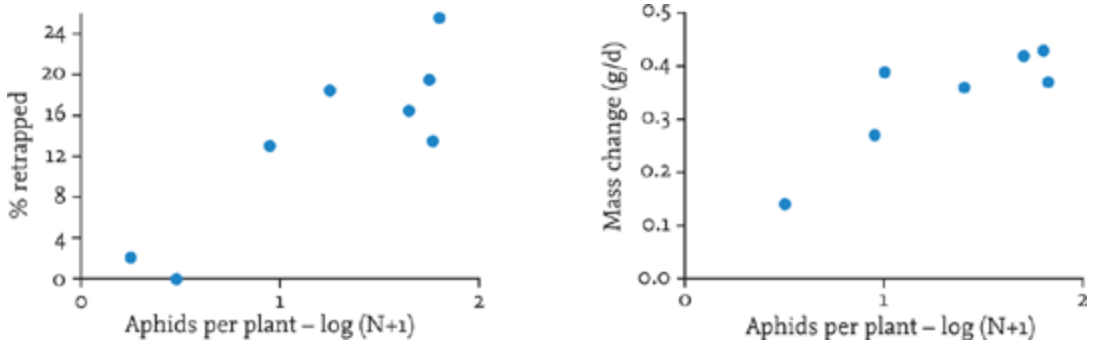


FIG 269. Proportion of young among Whooper Swans *Cygnus cygnus* wintering in Sweden in relation to mean temperature in the preceding winter. Following cold winters, the swans produced fewer young, as evident in subsequent counts. (From Nilsson, 1979.)

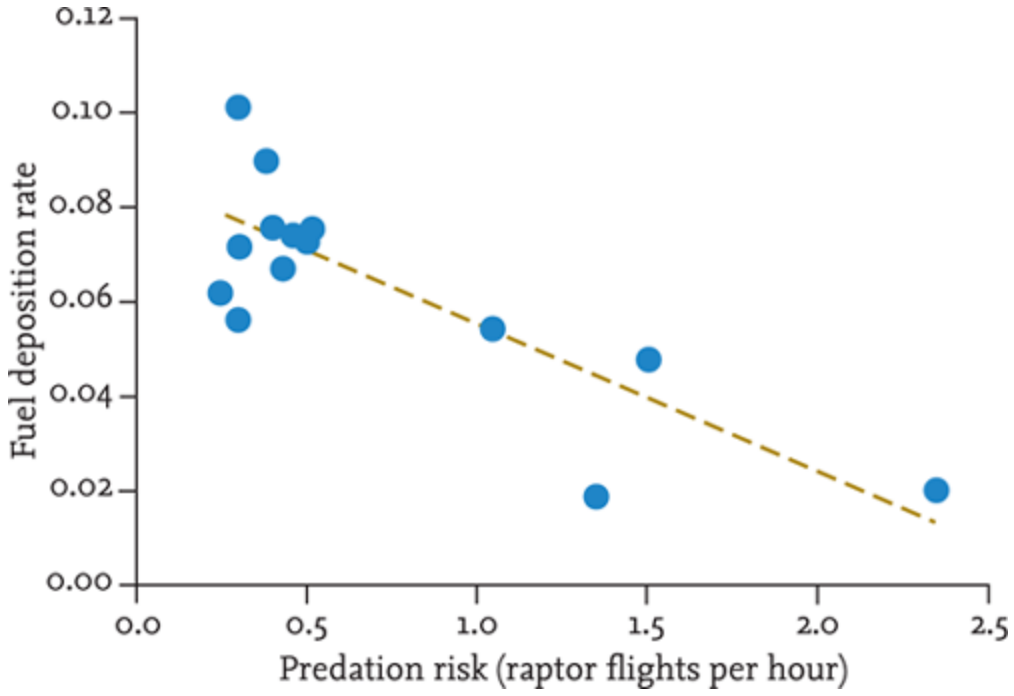


FIG 270. Relationship between food supply (aphid density) at a stopover site and (above left) tendency to stay, and (above right) rate of migratory weight gain in Sedge Warblers *Acrocephalus schoenobaenus*. Aphid densities plotted on a log scale. (From Bibby & Green, 1981)



FIG 271. Winter Knots *Calidris canutus* in flight. (Sean Gray/Grayimages)

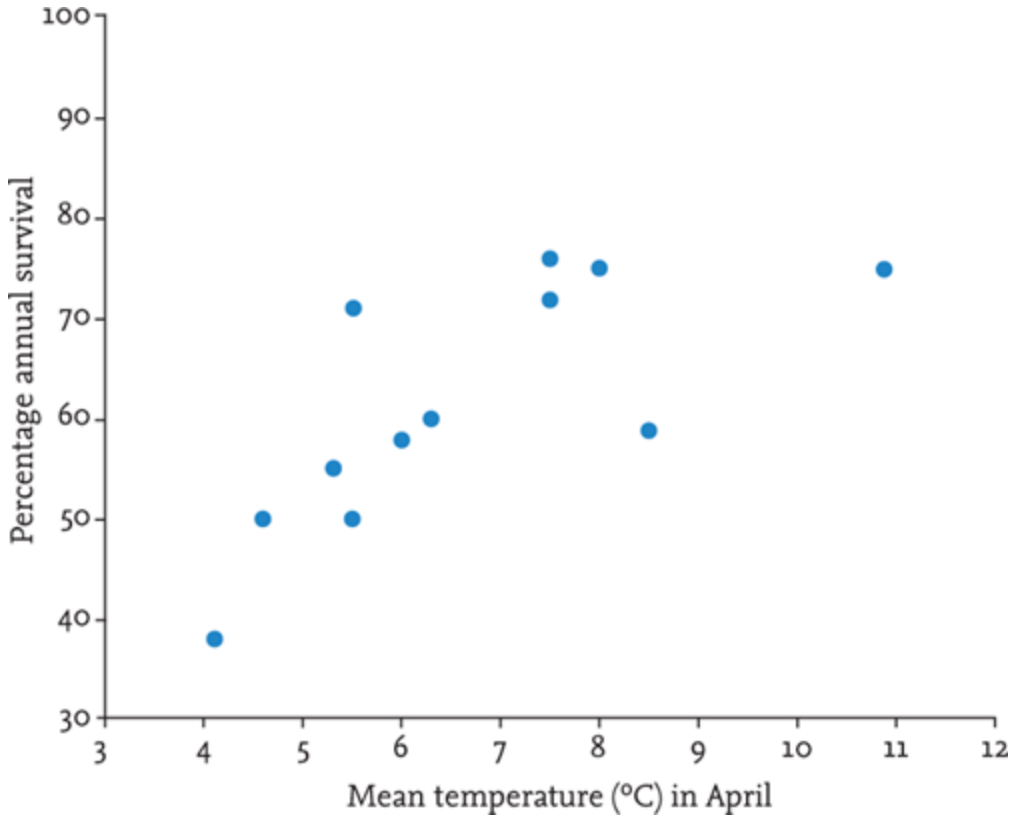


FIG 272. Daily fuel deposition rates in Northern Wheatears *Oenanthe oenanthe* in relation to the frequency of over-flights by raptors (mainly Sparrowhawks) on Heligoland Island. Fuel deposition rate is a relative measure calculated as body mass gain divided by lean body mass, obtained from Wheatears that stayed more than three days. Birds were weighed whenever they perched on a digital balance placed on the ground. Fuelling rates were lower in the presence of raptors which caused Wheatears to 'freeze' or hide for long periods (usually 1–7 minutes, occasionally up to 33 minutes), reducing their feeding and fattening rates. (Modified from Schmaljohann & Dierschke, 2005.)



FIG 273. Sparrowhawk *Accipiter nisus,* a common predator of small birds concentrated at stopover sites. (John Wright)



FIG 274. Merlin *Falco columbarius* (above left) and Peregrine *F. peregrinus* (above right), common predators of birds at stopover sites. (Edmund Fellowes)



FIG 275. Lapland Bunting *Calcarius lapponicus* (female), an arctic nesting species which is a rare winter visitor to the coasts of the British Isles, and elsewhere has occasionally suffered massive mortality from snow-storms while on spring migration. (Edmund Fellowes)



FIG 276. Little Auk *Alle alle,* a winter visitor from the far north to the offshore waters of the British Isles, occasionally found in 'wrecks' of starving birds blown inland. (Rebecca Nason)



FIG 277. Common Sandpiper *Actitis hypoleucos,* a summer visitor vulnerable to cold weather in the spring arrival period. (Brian Irving © HELM-Images)

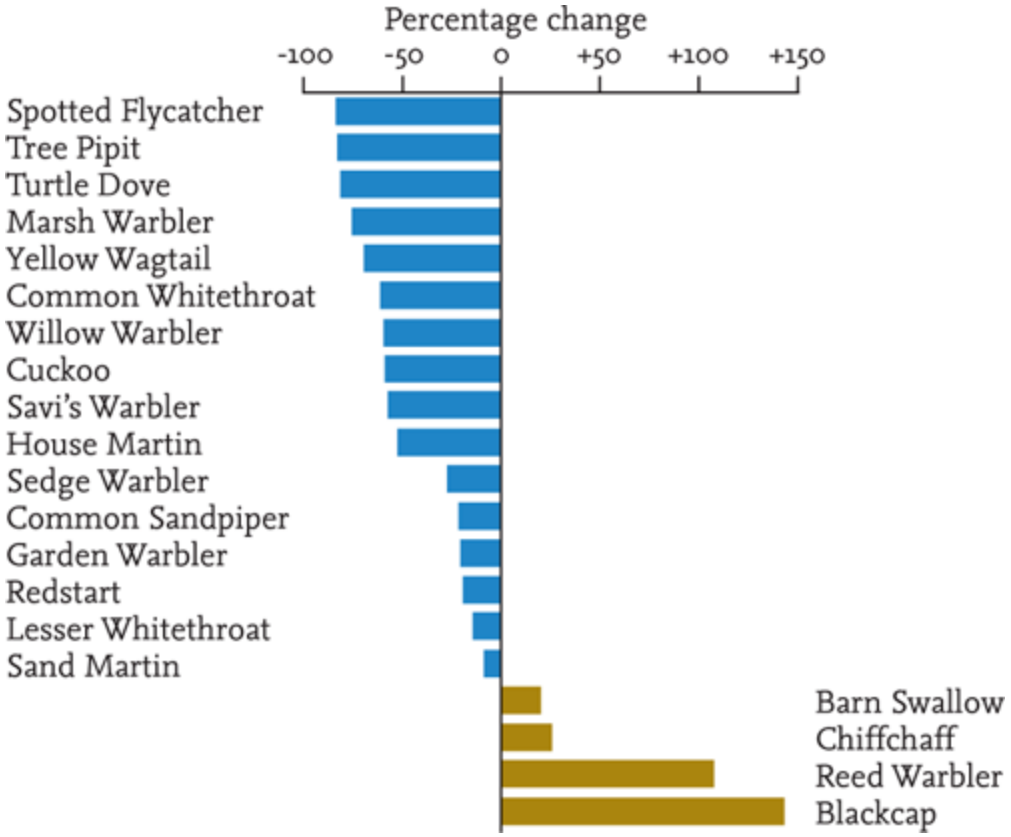


FIG 278. Relationship between annual survival of Common Sandpipers *Actitis hypoleucos* (y-axis) and mean temperature in the latter half of April (x-axis), soon after arrival in breeding areas, England, 1977–89 ($y = 0.074x + 0.40$, $r = 0.82$, $P < 0.001$). Birds suffered higher mortality than usual in years when snowstorms occurred in the days following their arrival, so that breeding densities in these years were reduced. (From Holland and Yalden, 1991.)



FIG 279. Lighthouse on the Isle of May in the Firth of Forth. Soon after this picture was taken, cloud obscured the moon, the sky darkened, and thousands of nocturnally-migrating birds appeared at the light. (Bobby Smith)



FIG 280. Wind turbines are often considered a potential hazard to migrating birds. These turbines, at Tarifa in southern Spain, are placed on a major bird migration route. They form part of a complex which has killed many raptors and other large birds. (John Wright)

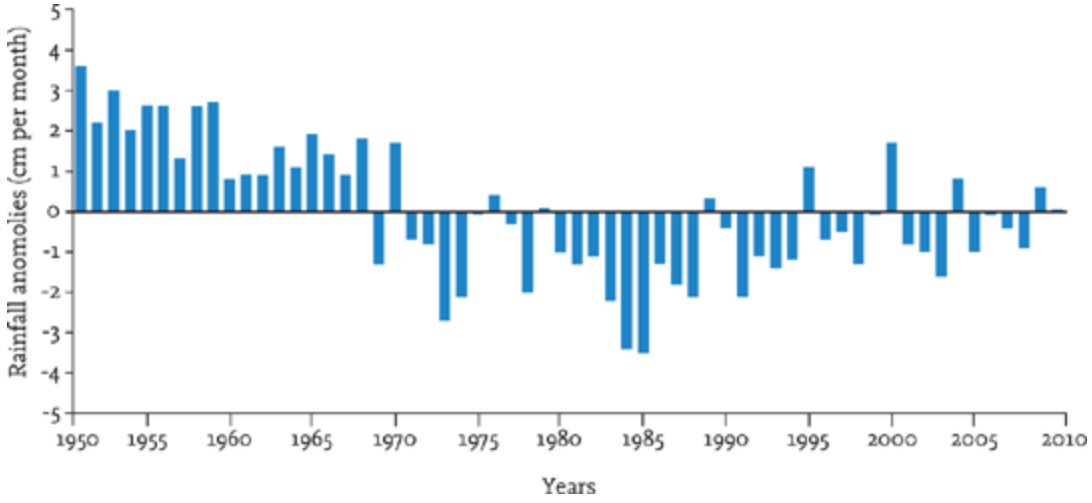


FIG 281. Net population changes in 20 species of European-African migrants during the period 1967–2005 as measured in British breeding areas by counts organised by the British Trust for Ornithology. Negative values on the left indicate

population declines and positive values on the right indicate increases. For further details see Table G.



FIG 282. Nightingale *Luscinia megarhynchos,* once found widely in southern Britain, now more localised. (John Wright)



FIG 283. Whinchat *Saxicola rubetra,* once found breeding over much of Britain and Ireland, now restricted to the uplands, where it continues to decline. (Brian Irving © HELM-Images)



FIG 284. Nightjar *Caprimulgus europaeus* at nest. This species has generally declined in Britain, but has experienced local increases, largely in response to favourable forestry management. (Bobby Smith)



FIG 285. Corncrake *Crex crex,* which disappeared from most of the British Isles through changes in grass-harvesting Proc.edures, but has recovered in limited areas where more favourable methods have been reinstated. (Edmund Fellowes)



FIG 286. Spotted flycatcher *Muscícapa striata* at its nest-site in an old door, another once familiar but rapidly declining summer visitor which winters in western and southern Africa. (Bobby Smith)

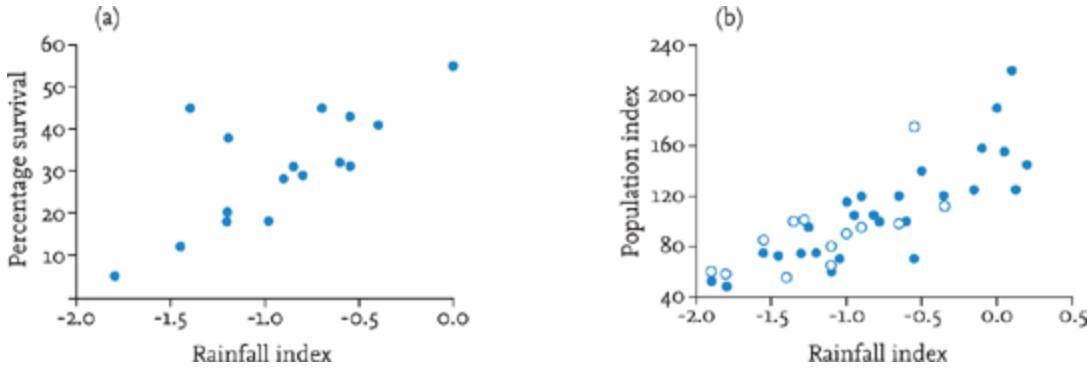


FIG 287. Annual rainfall anomalies in the western Sahel zone during 1950–2008 (10°–20°N, 20°W–io°E). From JISAO data, attributed to the NOAA Global Historical Climatology Network.



FIG 288. Common Whitethroat *Sylvia communis,* a summer visitor affected by Sahel droughts. (Frank Snijkers)

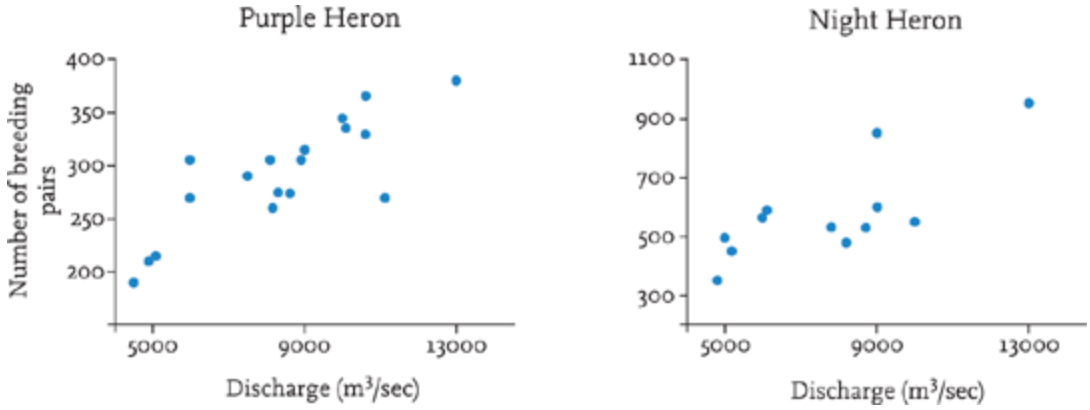


FIG 289. Relationships between (a) annual survival of Sedge Warblers *Acrocephalus schoenobaenus* at various sites in Britain, or (b) annual spring population index in Britain, and preceding annual rainfall in the Sahel zone of Africa, where Sedge Warblers spend part of the winter. (Redrawn from Peach *et al.,* 1991.)



FIG 290. Night Heron *Nyctocorax nycticorax,* one of the heron species whose breeding numbers in western Europe have fluctuated from year to year according to rainfall in West African wintering areas. (Frank Snijkers)



FIG 291. Relationship between the numbers of migratory herons nesting at colonies in western Europe and wetland conditions in West Africa during the preceding year. Purple Herons *Ardea purpurea* were counted at one major colony in the Netherlands, and Night Herons *Nycticorax nycticorax* at several colonies in southern France. Wetland conditions measured as the sum of the maximum

monthly discharges through the Senegal and Niger rivers. Both relationships were statistically significant (on Kendall's rank correlation test, P0.005). (From den Held, 1981.)



FIG 291. Eleonora's Falcon *Falco eleonorae,* which nests on islands around the Mediterranean Sea, breeds in July-October, and preys upon passing migrants en route to Africa. (Colin Turvey)



FIG 292. Hobby *Falco subbuteo,* one of the few Eurasian–African migrants whose numbers and distribution in Britain have expanded greatly in recent decades. (John Wright)



FIG 293. William Eagle Clark, 1858–1938, on Fair Isle, 1912. (Fair Isle Bird Observatory Trust)



FIG 294. Arthur Landsborough Thomson, 1890–1977.

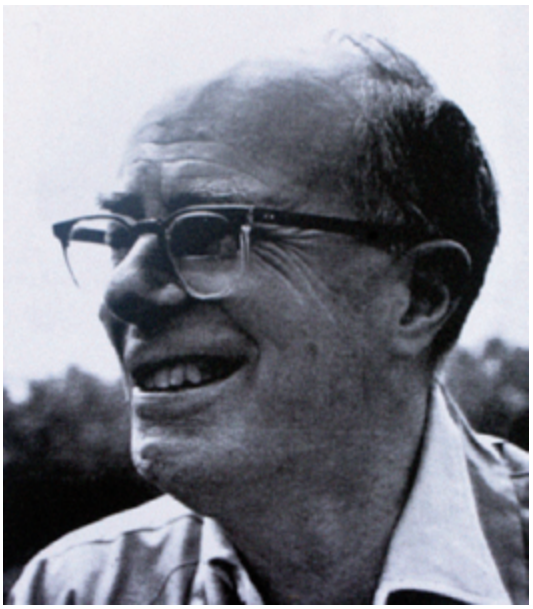


FIG 295. David Lambert Lack, 1910–72.

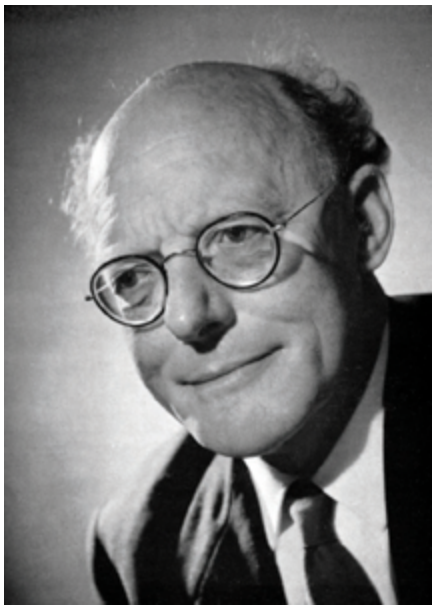


FIG 296. Reginald Ernest Moreau, 1897–1970.

Copyright

This edition published in 2010 by Collins,
An imprint of HarperCollins Publishers

HarperCollins Publishers
77–85 Fulham Palace Road
London W6 8JB
www.collins.co.uk

First published 2010

© Ian Newton, 2010

All rights reserved under International and Pan-American Copyright Conventions. By payment of the required fees, you have been granted the non-exclusive, non-transferable right to access and read the text of this e-book on-screen. No part of this text may be reproduced, transmitted, down-loaded, decompiled, reverse engineered, or stored in or introduced into any information storage and retrieval system, in any form or by any means, whether electronic or mechanical, now known or hereinafter invented, without the express written permission of HarperCollins e-books.

EPub Edition © OCTOBER 2010 ISBN: 978-0-007-37972-9

A cip catalogue record for this book is available from the British Library.

Hardback
ISBN 978-0-00-730731-9

Paperback
ISBN 978-0-00-730732-6



About the Publisher

Australia
HarperCollins Publishers (Australia) Pty. Ltd.
25 Ryde Road (PO Box 321)
Pymble, NSW 2073, Australia
http://www.harpercollinsebooks.com.au

Canada
HarperCollins Canada
2 Bloor Street East - 20th Floor
Toronto, ON, M4W 1A8, Canada
http://www.harpercollinsebooks.ca

New Zealand
HarperCollinsPublishers (New Zealand) Limited
P.O. Box 1 Auckland,
New Zealand
http://www.harpercollinsebooks.co.nz

United Kingdom
HarperCollins Publishers Ltd.
77-85 Fulham Palace Road
London, W6 8JB, UK
http://www.harpercollinsebooks.co.uk

United States
HarperCollins Publishers Inc.
10 East 53rd Street
New York, NY 10022
http://www.harpercollinsebooks.com