

THE NEW NATURALIST LIBRARY

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BIRD MIGRATION

EDITORS

SARAH A. CORBET, ScD
PROF. RICHARD WEST, ScD, FRs, FGS
DAVID STREETER, MBE, FIBIOL
JIM FLEGG, OBE, FIHort
PROF. JONATHAN SILVERTOWN

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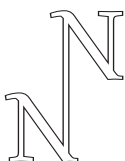
The aim of this series is to interest the general reader in the wildlife of Britain by recapturing the enquiring spirit of the old naturalists.

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.

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BIRD MIGRATION

IAN NEWTON



Collins

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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!

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.

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

[†] 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.

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FIG 1. Cuckoo *Cuculus canorus*, a summer visitor to the British Isles which spends the winter in tropical Africa. (Edmund Fellowes)

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 a body 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

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FIG 2. Common Redshanks *Tringa totanus*, whose wintering population consists of local breeders and winter visitors mainly from Iceland. (Brian Irving © HELM-Images)

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 efficient 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 different 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 post-breeding 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 non-breeding 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

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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,



FIG 3. Puffin *Fratercula arctica*, which nests on offshore islands around the British Isles, and winters widely over the West Atlantic, usually far from land. (Edmund Fellowes)

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 climates for the non-breeding period, they move mainly on a north-south axis. However, many

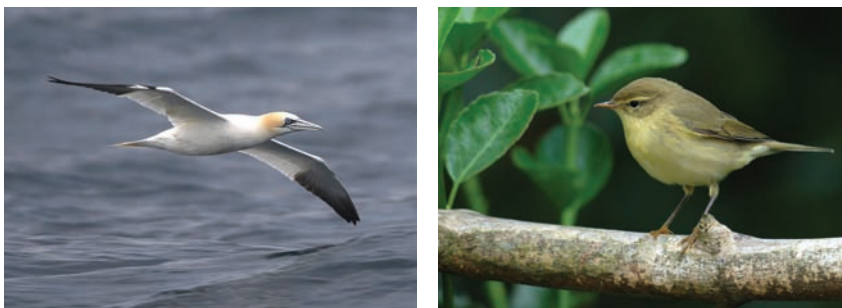
populations also have an easterly or westerly component in their movements, especially those that breed in the central parts of the northern landmasses and move to the warmer edges for the winter. The predominant autumn migration direction of intra-continental migrants in western Europe is southwestward, 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



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. (above left) Gannet *Morus 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); (above right) Willow Warbler *Phylloscopus trochilus*, which, despite its small size, performs some of the longest and most arduous migrations found among land-birds. (Frank Snijkers)

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 in 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

At the opposite end of the spectrum from migratory populations are sedentary (or resident) ones. A sedentary bird population can be defined as one whose distribution remains more or less the same year-round, and from year to year. Individuals of sedentary populations typically show no directional bias in their movements at any time of year (unless imposed by local topography), and generally move over much shorter distances than migrants. In the British Isles, as elsewhere, individuals of many resident bird species have been ringed in large numbers as chicks or adults, and the subsequent recoveries have given some idea of the overall movement patterns. Typically, most birds of non-migratory species were found (up to several years later) near where they were ringed, in all directions, but with progressively fewer at increasing distances. In many populations which are resident within the British Isles, the median distance moved between ringing and recovery sites was less than 1 km, but some individuals had reached more than 20 km. This pattern held for some passerine



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)

species such as the House Sparrow and Yellow-hammer, and for non-passerines such as the Moorhen and Grey Partridge. All these birds are likely to have made their longest movements in the immediate post-fledging period, soon after becoming independent of their parents. Of course, other 'sedentary' species make longer movements, yet in all such species the population as a whole retains the same broad-scale distribution year-round, with no obvious large-scale shifts. Some of the species that are sedentary in the mild climate of the British Isles are highly migratory in other parts of their range.

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.