THE
MIGRATION ECOLOGY OF BIRDS

IAN NEWTON

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Ian Newton

Monks Wood Research Station,
Cambridgeshire, UK

Illustrations by Keith Brockie

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Preface

From ancient days the migration of birds has excited the wonder of thoughtful observers. (J. A. Thomson 1913.)

The phenomenon of bird migration has long fascinated its human observers, who have been continually impressed by the sheer scale and regularity of the movements. It has repeatedly prompted familiar questions about birds, such as where do they go or come from, how do they know when and where to travel, and how do they find their way? For more than a century now, bird movements have been subjected to scientific study, and by increasingly sophisticated methodology. In the past 25 years, hardly a year has gone by 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. In this book, I hope to provide an up-to-date synthesis of much of this information, taking account of both older and newer findings. However, the emphasis throughout is on ecological aspects: on the different types of bird movements, how they relate to food supplies and other external conditions, and how they might have evolved. It is mainly in the weight of attention devoted to ecological aspects – which have received scant attention in previous reviews – that this book differs from earlier ones. It is also in these aspects that, with my own background, I feel most at home with the subject matter.

After a brief introduction and survey of methodology, the book is divided into five main sections. The first deals with the journeys themselves: with the constraints and limitations of bird flight, the influence of weather, fuelling needs, migration strategies, travel speeds, the problems of navigation, and vagrancy. The second section is concerned with the annual cycles of birds, with how migration relates to breeding and moult, and with the physiological control of these various processes. The third section describes geographical patterns in bird movements across the globe, and the various types of bird movements, such as dispersal, irruption and nomadism, emphasising the ecological factors that underpin them. The fourth section is concerned with the evolution of migration and other movement patterns of birds, with the role of glacial history in influencing current migration patterns, and with recent changes in migration related to climate change and other human influence. The fifth section discusses how the population ecology of migratory birds differs from that of sedentary ones, and the influence of migration events on the population levels of birds. In particular, it considers the extent to which migratory bird numbers are limited by conditions in breeding, migration or wintering areas. This section is followed by a glossary, references and index.

Although the book is intended mainly for research students, I have tried to write simply, in the hope that the text will appeal to anyone with an interest in this fascinating subject, including the many bird-watchers and ringers who have contributed so much over the years to its development. To keep the book within

bounds, I could not mention all recent work on bird migration, and have sought to cite examples rather than every study. Nevertheless, the reference list (up to and including 2006) relates to more than 2500 scientific papers and more than 50 books. It is inevitable in a book of this type that the same topics recur in different chapters, as they are relevant to more than one aspect of the subject, but I have tried to reduce this repetition to a minimum, and cross-refer between chapters. Nevertheless, each chapter is intended as a stand-alone read. So much of the book is concerned with geography that, while I have tried to provide some helpful maps in the text, some parts would be better read with an atlas, or preferably a globe, close at hand.

For permission to reproduce diagrams and other material from scientific journals, I thank the various publishers, ornithological societies and individuals involved, and for providing electronic copies of particular diagrams, I thank John Croxall, Thord Fransson, Mark Fuller, Sidney Gauthreaux, Yossi Leshem and Richard Phillips.

I owe a great deal to the many colleagues in the field who have discussed various aspects of the subject with me over the years, and to several friends for helpful comments on particular chapters, namely Bill Bourne (Chapter 4), Bill Clarke (Chapter 7), Alistair Dawson (Chapters 11 and 12), Barbara Helm (Chapters 11, 12, 20 and the Glossary), Lukas Jenni (Chapters 5 and 6), Peter Jones (Chapters 22, 24 and 25), Mick Marquiss (Chapters 15 and 18) and Tim Sparks (Chapter 21). Other colleagues, in their capacity as referees, commented helpfully on certain papers which preceded the book. I owe a particular debt to David Jenkins, who read the whole book in draft (some parts more than once), and offered many constructive suggestions for improvement. Finally, my wife, Halina, supported me through the writing process, and commented helpfully on the penultimate draft.

Ian Newton

Common Cranes *Grus grus* on migration

Chapter 1
Introduction

> *That strange and mysterious phenomenon in the life of birds, their migratory journeys, repeated at fixed intervals, and with unerring exactness, has for thousands of years called forth the astonishment and admiration of mankind.*
> (H. Gätke 1895.)

The most obvious feature of birds is that they can fly. This facility gives them great mobility and control over their movements. Many species can travel quickly and economically over long distances – up to thousands of kilometres, if necessary crossing seas, deserts or other inhospitable areas. They also have great orientation and navigational skills, and are able to remember and re-find remote places they have previously visited. Birds can thereby occupy widely separated areas at different seasons, returning repeatedly to the same localities from year to year, and adopting an itinerant lifestyle of a kind not open to less mobile creatures.

Although migration is evident in other animal groups, including insects, mammals, pelagic turtles and fish, in none is it as widely and well developed as in birds. The collective travel routes of birds span almost the entire planet. As a result of migration, bird distributions are continually changing – on regular

seasonal patterns, and on local, regional or global scales. Movements are most marked in spring and autumn, but can occur in every month of the year in one part of the world 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. One of the main advantages of flight is its speed, which is much faster than the alternatives of walking, running or swimming. Flight requires more energy per unit time, but because of the greater distance covered, it is also the cheapest mode of transport overall. One type of flight, by soaring–gliding, is cheaper still, but is practised mainly by larger species, such as albatrosses, which can travel the Southern Ocean with little more energy expenditure than sitting still (Chapter 3). Long-distance flight also allows birds to cross hostile areas that would otherwise act as barriers to their movements. Nevertheless, while most birds migrate by flying, penguins and some other seabirds migrate by swimming, and some landbirds by walking for part or all of their journeys.

Most birds are of a size that enables them to become airborne, and have wing shapes that ensure efficient flight. The wings are powered by massive breast muscles, the pectoralis and supra-coracoideus, which are responsible for 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. They are well supplied with blood vessels, and consist of fast-contracting fibres (red fibres), which in many species can beat the wings continuously for hours or days on end.

Compared with other animals, birds are not only homiothermic (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. The breathing mechanism of birds also results in much more efficient gas exchange than that in mammals. A bird's lung is connected by an array of tubes to a system of thin-walled air-sacs. Air is continuously directed through the lungs during both inspiration and expiration, thereby increasing the efficiency of oxygen extraction. By possessing all these various traits, birds are pre-adapted for the development of long-range movement patterns. Compared with resident bird species, migrants have these same features more highly developed as specialised adaptations for long-distance migration. It is this combination of features that enables some species of birds to perform some of the most remarkable migrations in the animal world.

TYPES OF BIRD MOVEMENTS

The terms resident and sedentary are usually applied to birds that occupy the same general areas year-round, and to populations that make no obvious large-scale movements resulting in changes in geographical distribution. The term migration is less easily defined because it means different things to different people. Ornithologists tend to use the word only for return movements between

breeding and non-breeding areas, but biologists working with other organisms often use the term more widely. For purposes of convenience in this book, I shall divide bird movements into six main types:

- First, there are the **everyday routine movements** centred on the place of residence, which occur in all birds, whether classed as resident or migratory. Typically, they include the flights from nesting or roosting sites to feeding sites, or from one feeding site to another, and can occur in any direction. In most birds these movements are short and localised, restricted to a circumscribed home range, and extend over distances of metres or kilometres. But in other species (not-ably pelagic birds) regular foraging movements can extend over hundreds of kilometres out from the nesting colony.

- Second, there are one-way **dispersal movements**. In both sedentary and migratory bird species, after becoming independent of their parents, the young disperse in various directions from their natal sites. Individual young seem to have no specific inherent directional preferences, so within a population, dispersal movements seem to occur randomly in all directions. In most bird species, dispersal distances can be measured in metres, kilometres or tens of kilometres, but in a few species (notably pelagic birds), such distances can be much greater (Chapter 20). Post-fledging dispersal of this type does not usually involve a return journey (see below), but in any case most 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 **migration,** in which individuals make regular return movements, at about the same times each year, often to specific destinations. 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 their annual non-breeding period at lower latitudes than their breeding period, but some migrate to similar latitudes in the opposite hemisphere where the seasons are reversed. Such 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.

- Fourth, there is another category of migration, which I have called **dispersive migration,** in which post-breeding movements can occur in any direction from the breeding site (like dispersal), but still involve a return journey (like other migration). Although these movements occur seasonally between breeding and non-breeding areas, they do not necessarily involve any change in the latitudinal distribution of the population, or any change in its centre of gravity. They are evident in some landbird species usually regarded as 'resident' (Chapter 17), 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 can disperse long distances in various directions from

their nesting colonies to over-winter in distant areas rich in food, returning to the colonies the following spring.

- Fifth, there are **irruptions (or invasion migrations),** 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 (the directions are roughly the same but often more variable between individuals than in regular migration). Such movements are usually towards lower latitudes, and occur in association with annual, as well as with seasonal, fluctuations in food supplies. In consequence, populations may concentrate in different parts of their non-breeding ranges in different years. Examples include some boreal finches that depend on sporadic tree-seed crops and some owls that specialise on cyclic rodent populations (Chapters 18 and 19).
- 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. The population may thus be concentrated in largely different areas in different years. This kind of movement occurs among some rodent-eating owls and raptors of tundra, boreal and arid regions, and among many birds that live in desert regions, where infrequent and sporadic rainfall leads to local changes in habitats and food supplies (Chapter 16). Because these changes are unpredictable from year to year, individual birds do not necessarily return to areas they have used previously, and may breed in widely separated areas in different years.

These different kinds of movements intergrade, 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 some species show both nomadic and irruptive movements (Chapters 18 and 19). Through migration, irruption and nomadism, birds exploit the resources of mainly different regions at different times. The birds thereby achieve greater survival and reproductive success (and hence greater numbers) than if they remained permanently in the same place, and adopted a sedentary (resident) lifestyle.

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 to occur 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 are suitable. Each of these aspects of bird behaviour can be independently influenced by natural selection (Chapter 20), giving overall the great diversity of movement patterns found among birds, related to the different circumstances in which birds 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 over-land 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 the two categories, but a continuum of variation in the distances travelled and terrain 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.

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 needs of breeding that tie birds to fixed localities for part of the year, because individuals need to remain at their nests, or visit their nests frequently, in order to feed their young. However, in some species, notably some seabirds, one parent can be away for long periods (often days, sometimes weeks 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 may be able to survive on its own for long periods, enabling both parents to be away foraging at the same time. Some of the foraging flights of albatrosses undertaken while breeding can cover up to 15 000 km, a distance far greater than the total annual migrations of the vast majority of landbirds.

In many bird species, 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 places 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 (Chapter 15). This holds for many kinds of seabirds, shorebirds, large raptors and others.

ADAPTATIONS FOR MIGRATION

One of the most amazing aspects of migration is how birds find their way over long distances. Many species are capable of migrating between exactly the same breeding and wintering places year after year, even if these places lie thousands of kilometres apart on different continents. Young birds migrating alone can find their own way to the usual wintering areas for their species, and back to their natal areas the following spring. Some pelagic seabirds wander widely over the oceans, yet each year return unfailingly to their own particular nesting islands. Great Shearwaters *Puffinus gravis*, for example, nest on the isolated Tristan da Cunha islands, lying at 40ºS in the South Atlantic and more than 2000 km from Africa, the nearest continent. In the non-breeding season these birds migrate northward in their millions, ranging over large parts of the North Atlantic. But they return each year with pinpoint accuracy to their tiny breeding islands, which are spread over only 45 km of ocean, and individuals occupy the same nest burrows from year to year, often lying within a metre of those of other individuals. These and other

seabirds that migrate long, overwater distances to small oceanic islands must surely be among the greatest of animal navigators, possessing extremely accurate orientation mechanisms.

Like human navigators, birds and other animals can find their way over long distances only with the aid of a reliable reference system by which to navigate. Research has confirmed that birds use at least two types of system, based on geomagnetic and celestial cues (the sun by day and the stars at night) respectively. However, a compass is of little value to a migratory bird unless it 'knows' beforehand – either by inheritance or experience – what course it needs to take. The mechanisms of bird orientation and navigation are discussed in Chapter 9.

The timing of bird migration is equally remarkable. Many long-distance bird migrants arrive at their nesting or wintering places every year at around the same date. This implies the existence in the birds of precise timing mechanisms that, in response to external stimuli, trigger migration at about the same dates each year and maintain it for long enough to allow the bird to cover the distance required. Such mechanisms ensure that individuals arrive in their nesting areas as conditions become suitable for breeding and leave before conditions deteriorate and affect survival. The relatively small variations in timing that occur from year to year are mainly associated with variations in prevailing weather or food supplies (Chapter 12).

A third adaptation that facilitates seasonal migration is the ability of birds at appropriate times of year to accumulate large body reserves (mostly fat) to fuel the flights (Chapter 5). Small birds that cross large areas of sea or desert in which they cannot feed are able to double their usual weight beforehand through fuel deposition, and some species also reduce the mass of other body organs not directly concerned with migration, thus reducing the overall energy needs of the journey. The seasonal changes in body composition that occur in migratory birds are some of the most extreme of the animal world. Birds are also unusual in the speed and efficiency with which they can convert the fatty acids in fuel reserves to the energy needed to power the wings.

The migratory lifestyle requires that periods of movements are integrated with other events in the birds' annual cycle, especially breeding or moult. In most bird species, these events normally occur at different times of year, with minimal overlap between them. Because the act of breeding requires that birds remain within restricted localities, it is obvious that individuals cannot breed and migrate at the same time. And because feather replacement can temporarily reduce flight efficiency, it is also desirable that moult and migration are separated as much as possible. Studies of the annual cycles of birds, and the physiological control of migration within these cycles, are discussed in Chapters 11 and 12.

An interesting aspect of bird migration concerns the extent to which individuals are pre-programmed by inheritance to do the right things at the right times of year. Without innate programming, an individual would have little sense of when to migrate, in which direction to fly or for how long. Nor would it know when on its journey to do specific things, such as change direction or accumulate extra body reserves in preparation for a long sea-crossing. All these aspects require an endogenous schedule which promotes particular kinds of behaviour at appropriate times of year or stages in a journey. This inherent component of some bird movements adds an additional fascination to study of the controlling mechanisms (Chapter 12).

Yet despite being partly under genetic control, migration patterns among birds show great flexibility and facility for rapid change (Chapter 20). Many bird families contain both migratory and non-migratory populations, showing little phylogenetic constraint on the development of migratory behaviour. Within species, changes in migratory patterns are presumed to have occurred repeatedly through the Pleistocene glacial cycles and, more strikingly, even in recent decades, as particular populations have become more sedentary, or shortened their migrations, in apparent response to climate warming (Chapter 21). Further understanding of the evolution of migration systems can be inferred from present distribution and movement patterns, as well as from palaeontological and molecular evidence (Chapters 22 and 23).

To accommodate a long-distance migratory lifestyle, participants must be able to live in two or more different parts of the world, often on different continents. They must often occupy somewhat different habitats and climatic regimes, deal with different foods, and exist within different communities, filling distinct niches in both their summer and winter homes. Such split lives have consequences that a sedentary lifestyle does not. In particular, the population levels of migratory birds can be influenced by conditions in breeding, migration and wintering areas, and conditions experienced in wintering or migration areas can affect subsequent survival and breeding success (Chapter 26). Recent widescale declines in the numbers of many migratory species, from both the Eurasian–African and the North American–South American bird migration systems, have stimulated research into what limits the population sizes of migrants, and whether the limitation occurs primarily in wintering, breeding or migration areas (Chapters 26–28).

THE DIVERSITY OF MIGRATION

Migration occurs to some degree in most bird species that live in seasonal environments, from arctic tundras to tropical savannahs and grasslands. It is in strongly 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 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 food supplies, more than 50 billion birds 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. Thus, 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 acts as a major wintering area for Eurasian migrants, including up to two million waterfowl. Nevertheless, some birds from eastern Europe move southeast to winter in the Middle East, East Africa or India. Similarly, in much of North America, many birds move southeastward in autumn, towards the warm southeastern States, or onward to the Caribbean Islands or South America (most of which lies in longitudes east of North America).

Some bird species move almost directly east–west on their migrations. For example, the Pochards *Aythya ferina* which breed in Siberia move up to 4000 km in autumn to winter in western Europe, in the process crossing up to 80° of longitude (M. Kershaw, in Wernham *et al.* 2002). Many species in southern Africa move from the arid west in summer to the wetter east in winter (Brooke 1994). 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).

The Bald Eagles *Haliaeetus leucocephalus* that breed in southern North America show an unexpected pattern. The young are raised in winter or early spring, then move generally northwards for up to 2200 km, spending from May to September in Canada and Alaska, where they feed largely on salmon which fill the rivers at that time (Broley 1947). The young eagles therefore travel north in spring and south in autumn with the conventional migrants but, unlike them, they have been reared in the south before doing so. Many adult eagles also leave the south in spring, but it is not clear from ringing whether they travel as far as the juveniles. This migration was first established from ringing nestling eagles in Florida (Broley 1947), but more recently it has been confirmed in radio-tracked young from California (Hunt *et al.* 1992), and in colour-marked young from Texas (Mabie *et al.* 1994). This last study also showed that young returned to their natal areas to breed.

The young of several species of herons, raised in winter in the southern USA, disperse in various directions but mainly northward, again presumably to exploit the presence of fish in shallow water in the northern spring and avoid the effects of drought in more southern areas (Lincoln 1935a). Similar but less marked summer movements have been recorded among herons in Europe, and in the southern hemisphere some heron species in Australia also migrate to higher latitudes after breeding (Maddock 2000), as do flamingos in South America (Sick 1968b). In addition, the non-breeders of some seabird species, including the Little Auk *Alle alle* and several skua species, spread up to several hundred kilometres beyond their natal colonies in summer, exploiting the summer flush of food at higher latitudes, and some winter-breeding petrels and shearwaters also move to higher latitudes after breeding (see later).

Difficult journeys

Bird migrations may vary from a few tens to many thousands of kilometres, but it is the long and difficult journeys that best reveal the capabilities of migratory birds. Among landbirds, spectacularly long journeys are made by those species that fly regularly between northern Eurasia and southern Africa or Australasia,

Figure 1.1   Some long-distance migrations of birds. 1. Alaskan population of Pacific Golden Plover *Pluvialis dominica*; 2. Arctic Tern *Sterna paradisaea*; 3. Swainson's Hawk *Buteo swainsoni*; 4. Snow Goose *Chen caerulescens*; 5. Many North American breeding species that cross the Gulf of Mexico; 6. Ruff *Philomachus pugnax*; 7. Many European breeding species that cross the Mediterranean Sea and Sahara Desert; 8. Northern Wheatear *Oenanthe oenanthe*; 9. Amur Falcon *Falco amurensis*; 10. Arctic Warbler *Phylloscopus borealis*; 11. Short-tailed Shearwater *Puffinus tenuirostris*. Partly after Berthold (1993).

or between northern North America and southern South America or Australasia (**Figure 1.1**). Such long movements are performed each year by many shorebirds, and some seabirds, passerines and others. Even on the shortest routes, this entails some individuals flying more than 25 000 km on return migration each year. Some of the participants are small enough to be held comfortably in the palm of your hand. The major advantage in migrating so far between the northern and southern hemispheres derives from the fact that the seasons are reversed. The species involved thus pass both breeding and non-breeding seasons in summer conditions when food is plentiful, although no such birds are known to breed regularly at both ends of their migration route (Chapter 13).

Most birds that migrate overland have plenty of places to stop and feed. They can therefore migrate, rest and feed almost every day, accomplishing their journeys by a series of short flights. Other birds cross mainly hostile areas, where they cannot stop and feed. They therefore have to accumulate larger body reserves,

and make long flights between widely spaced stopping places (Chapter 5). For example, shorebirds typically complete their migrations in 2–4 long stages, refueling before each stage, and often travelling 1000–4000 km between suitable estuaries, even when mainly following coastlines. The flights themselves comprise long periods of muscular work without food or water, at great heights over inhospitable terrain, and usually require pinpoint navigation to widely separated refuelling areas. Flight paths and stopping sites of some shorebirds have been worked out in some detail from synchronised counts at different estuaries, from ring recoveries, and in some regions also from radar observations and studies of body weights.

To elaborate with one example, those Bar-tailed Godwits *Limosa lapponica* that winter in West Africa north of the equator have to face a journey of 10 000 km to their breeding grounds in Siberia (Piersma 1994a). Taking off from Guinea-Bissau at dusk, a bird could reach the next major mud flat, the Banc d'Arguin in Mauritania 1000 km away, by mid-day. From there, another 16 hours and 1000 km of flight would get the bird to the next suitable estuaries in Morocco and another 16 hours and 1000 km to the estuaries of the Loire and Gironde in western France, and yet another 10 hours and 600 km of flight to the Wadden Sea which fringes the northern Netherlands, Germany and Denmark. After a long period of refuelling on the Wadden Sea coast, most godwits seem to make the rest of their journey to Siberia in a single flight of 4000 km. In fact, most godwits also seem to fly from Banc d'Arguin to the Wadden Sea in one flight, as the Moroccan and French estuaries are used only by a small proportion of the population. Travelling at 60 km per hour (without the benefit of a tailwind), the entire journey translates to 167 hours of airtime, equivalent to a solid seven days and nights of flight, excluding breaks for refuelling (Piersma 1994a).

Some shorebird species that breed across the arctic show an astonishing array of migration routes. In the Ruddy Turnstone *Arenaria interpres*, for example, Alaskan birds migrate down the entire western seaboard of the Americas to winter as far south as Chile, while most of the Canadian birds head for the coasts of the Caribbean and beyond. The Greenland and eastern Canadian birds move to Britain and Ireland, and Scandinavian ones to West Africa. The central Siberian birds move south to the Middle East, the shores of the Indian Ocean and on to southern Africa, while the east Siberian/west Alaskan birds winter in southeast Australasia and Pacific Islands. Except at high ice-bound latitudes, few rocky shorelines anywhere in the world do not support wintering Ruddy Turnstones from one part of the breeding range or another.

Landbirds that migrate over oceans provide some of the most extreme examples of endurance flight and precise navigation. They travel without opportunity to feed, drink or rest, over vast stretches of open water devoid of helpful landmarks. They cannot stop, as birds do overland, when the weather turns against them. Yet millions of landbirds regularly cross the Mediterranean Sea and Gulf of Mexico at their widest points (about 1200 km), and smaller numbers regularly cross longer stretches, such as the western Atlantic between northeastern North America and northeastern South America (2400–3700 km), or the northern Pacific between Alaska and Hawaii and other central Pacific Islands (5000 km). However, the most impressive of all overwater migrations by a landbird is undertaken by the Bar-tailed Godwits *Limosa lapponica* from eastern Siberia and Alaska, which in

autumn apparently accomplish an astonishing 175-hour non-stop 10400 km flight to New Zealand (Chapter 6). Apart from the length of the journey, imagine the navigational precision required. From the departure point in Siberia or Alaska, the target area of New Zealand subtends an angle of only 5°, extending over a relatively tiny part of the southern Pacific. To judge from their normal flight speeds, landbirds would take more than 100 hours of non-stop flight in still air to accomplish the longer of their overwater journeys, but by taking advantage of favourable winds, they can shorten their flight times, sometimes by as much as one half. Participants include many passerines and shorebirds, but also waterfowl which, unlike the others, can rest on the sea if need be.

Some overland journeys are also difficult. Long desert crossings are made by the many species (including passerines) that travel between Eurasia and tropical Africa. Most west European species cross at least 1500 km of the Sahara Desert immediately after crossing the Mediterranean Sea, an overwater journey of up to 1200 km. In autumn some species may make this Mediterranean–Saharan flight without a break, a total journey of 1500–2500 km, depending on the route taken (Chapter 6). Other birds from further east cross the central Asian deserts, and then another 1700 km of southern Arabia and its bordering gulfs, before reaching East Africa. In Australia, some waders cross the central desert in moving between southern and northern coasts, a journey of more than 2000 km.

Yet other birds cross high mountain ranges, including the Himalayas and Tibetan plateau. One such species is the Bar-headed Goose *Anser indicus* which in the process can rise to more than 8 km above sea level, where the air is thin and very cold (Chapter 6). Other species cross extensive areas of pack-ice that lie in spring between Siberia and Alaska or between Norway and Svalbard. A few species cross 2000 km of the 2-km-high Greenland ice cap on journeys between northeastern Canada and western Europe. No landbirds regularly cross the Southern Ocean to Antarctica (which holds only seabirds), and none is known to cross the North Pole, even though the tundras on either side are only 2000–3000 km apart (Gudmundsson & Alerstam 1998). There would probably be no advantage in trans-polar movements, which in any case might also present navigational problems (Chapter 9).

The various migrations mentioned above are among the longest and most impressive undertaken by landbirds. Most long journeys involve movement from one hemisphere to another, but this is not true of all. Brent Geese *Branta bernicla* are restricted to northern latitudes, yet some of their breeding and wintering areas can be as much as 5000 km apart, involving substantial east–west shifts, as well as north–south ones. The journey from northeast Canada to Ireland involves these geese crossing polar seas, the Greenland ice cap and the North Atlantic.

At the other end of the spectrum, the shortest seasonal migrations by landbirds are undertaken by some altitudinal migrants, which move only a few kilometres from mountains to valleys for the winter, and by various gallinaceous birds which typically move over short distances (up to several tens of kilometres) between their breeding and wintering sites (Chapter 17). Such migrations often occur in various directions and intergrade with purely local movements.

Seabird movements are just as varied as landbird movements. Their study is hampered by the obvious improbability of getting ring recoveries from pelagic regions, but observations from ships and the satellite-based tracking of

radio-marked individuals have helped to fill out the picture (Chapter 2). Some species, as well as moving north–south, cross from one side of an ocean to another. In the Atlantic, Manx Shearwaters *Puffinus puffinus* move from western Europe to eastern South America after breeding, and Arctic Terns *Sterna paradisaea* from eastern Canada cross to West Africa, before continuing southward to the Southern Ocean. In addition, Sooty Terns *S. fuscata* cross the Atlantic from breeding colonies in the Caribbean to non-breeding areas off West Africa, but in the process make little or no latitudinal shift.

Like landbirds, many seabirds perform exceptionally long migrations, which are perhaps less demanding than the transoceanic flights of landbirds. This is partly because most seabirds are larger and more robust than the majority of landbirds, but also because many can more readily rest on the sea surface or feed en route. In moving between the Arctic and Southern Oceans, the Arctic Tern *Sterna paradisaea* may perform the longest migration of any tern, entailing a round trip of 30 000–50 000 km each year (this species is not known to rest on the sea). The birds move down the western coasts of South America and Africa, and on reaching the Southern Ocean, travel eastwards on the winds, some passing south of Australia and New Zealand. Many juveniles may continue eastwards, circling the Antarctic, before heading north again on their return flight, two or more years later (Salomonsen 1967b). These movements have been revealed by observations and by some striking ring recoveries, showing the presence in winter of North American birds off South Africa and of European birds off South Africa and Australia. Because some Arctic Terns may reach an age of 25 years, they might cover more than a million kilometres on migration during their lifetimes, about three times the distance between the earth and the moon. Some Common Terns *Sterna hirundo* from northern Europe have also been found off Australia, but this species apparently does not extend south towards Antarctica.

Conversely, some seabirds breeding in the southern oceans spend their non-breeding season in the northern hemisphere. Examples include the Sooty Shearwater *Puffinus griseus* which migrates between the South and North Atlantic, and between the South and North Pacific. Seventeen individuals from breeding colonies in New Zealand were tracked on migration using miniature archival tags to record geographical position, dive depth and ambient temperature (Shaffer *et al*. 2006). The tags revealed that these birds flew across the Pacific in a figure-eight pattern while travelling an average of 64 037 ± 9779 km round-trip. They took 198 ± 17 days over the journey, and reached speeds up to 910 ± 186 km per day. Each shearwater made prolonged stops in one of three discrete productive regions – off Japan, Alaska or California – before returning to New Zealand through a relatively narrow corridor in the central Pacific. The birds obtained food from the surface or down to depths of 68 m. Similar figure-eight migrations had previously been inferred from ring recoveries for the Short-tailed Shearwater *P. tenuirostris* which breeds on islands off southeast Australia and 'winters' in the north Pacific (**Figure 1.1**).

Several Antarctic seabirds, such as immature Southern Giant Petrels *Macronectes giganteus*, perform circumpolar migrations, flying eastward around the world in the Southern Ocean. Radio-tracking results from albatrosses have revealed the extraordinary distances travelled by some species in short time periods. For example, a Northern Royal Albatross *Diomedia epomophora* was found to fly up to

1800 km in 24 hours, and a Grey-headed Albatross *D. chrysostoma* circled the globe in just 46 days (Croxall *et al.* 2005). Albatrosses can cover long distances on routine foraging flights from their nesting islands, as well as on migration. Thirteen young Wandering Albatrosses *Diomedia exulans*, radio-tracked by satellite from their natal areas on the Crozet Islands, flew eastward in the southern Indian Ocean, where they foraged back and forth along a 2000 km strip of ocean, just north of the subtropical front. In their first year of life, they covered an average of 184 000 km (range 127 000–267 000 km), corresponding to a distance of 4.6 times round the earth at its widest part (Åkesson & Weimerskirch 2005).

Not all seabirds migrate to lower latitudes in winter. Some species that breed in winter migrate to higher latitudes after breeding, like the Bald Eagles mentioned earlier. In the northern hemisphere, they include the Black-vented Shearwater *Puffinus opisthomelas* and Brown Pelican *Pelecanus occidentalis* off western North America and Bonin Petrel *Pterodroma hypoleuca* of eastern Asia, and in the southern hemisphere they include the Kerguelen Petrel *Lugensa brevirostris* and the King Penguin *Aptenodytes patagonicus*. For those penguins nesting on the Crozet Islands, this involves swimming about 1600 km (over 8° of latitude) to exploit the rich food supplies available at the edge of the winter pack-ice (Bost *et al.* 2004). 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 *Fulmarus glacialis* and Kittiwake *Rissa tridactyla* in the northern hemisphere, and various albatrosses and petrels in the southern hemisphere. Those albatross species whose breeding cycle lasts more than a year have an off-year after each successful breeding attempt. This applies to Wandering Albatrosses *Diomedia exulans* nesting on the Crozet Islands in the southern Indian Ocean. The adults leave the foraging areas that they frequent while breeding and spend their sabbatical years in sea areas 1500–8500 km away, elsewhere in the southern Indian Ocean or in the southwest Pacific. The ocean areas they occupy then range from tropical–subtropical waters (females) to sub-Antarctic–Antarctic waters (males), and individuals probably visit the same areas in each sabbatical (Weimerskirch & Wilson 2000). These albatrosses do not therefore perform a seasonal north–south movement like other birds but, as different sectors of the population breed in different years, by moving far from their breeding areas the sabbatical birds avoid competing with others that are breeding that year and thus operating from the colony. In this sense, their movements are again food-related.

While many landbirds face the hazards of ocean crossings, some seabirds make long overland journeys. The birds are seldom seen because they fly too high for human vision, and the evidence for their overland movements is based on unusual events and ring recoveries. In both Eurasia and North America, part of the migrations of the marine Sabine's Gull *Xema sabini*, Long-tailed Skua *Stercorarius longicaudus*, Arctic Skua *S. parasiticus*, Arctic Tern *Sterna paradisaea* and several other seabirds may take place overland to and from their tundra nesting areas. Arctic Terns *Sterna paradisaea* may even cross the central parts of the Eurasian landmass en route between the Indian Ocean and the Siberian tundra. Occasional ringed birds were found dead more than 1000 km inland from any sea-coast (Bourne & Casement 1996).

The above examples give some idea of the variety of migration patterns found among birds from around the world, and of some of the more spectacular journeys.

Migration routes

For reasons of habitat and weather, birds do not always take the most direct (great circle) routes between their breeding and wintering areas; nor do they necessarily take the same routes in autumn and spring (Chapter 22). Thus, sea-ducks often migrate long distances around coastlines rather than taking over-land shortcuts between breeding and moulting or wintering areas. For example, most Eiders *Somateria mollissima* breeding on islands far up the St Lawrence River in eastern Canada fly a coastal route of 2250 km to reach a point on the coast of Maine scarcely 640 km distant from their nesting islands, a shortcut which is taken by only a minority of birds (Reed 1975). Such detours may offer several benefits to migrating birds, such as continuous suitable habitat in which they can stop and feed, or reduced risk from adverse weather or predators. Mainly because of wind conditions, some roundabout routes may also offer reduced energy costs, despite the longer journey (Chapter 3; Alerstam 2001). The trade-off between time-saving or energy-saving direct routes on the one hand and risk-reducing detours on the other may have favoured different patterns in different species, according to their flight capabilities and refuelling needs, as well as the habitat and seasonal weather patterns encountered en route.

Most bird species set off on a broad front between their breeding and winter-ing areas, but during the journey they may be concentrated to some extent along mountain ranges, sea-coasts and other 'leading lines'. Such streaming is particu-larly marked in waterbirds, which often migrate between specific sites, following river valleys or other routes offering wetland areas where they can rest and feed. It is also marked in raptors and other soaring birds that favour routes where ther-mals and other updrafts develop, and minimize any necessary water crossings. Because these features depend on geography and topography, such species tend to follow the same narrow traditional routes year upon year.

In taking roundabout routes, many birds divide their journey into distinct stages, each with a different main orientation. For example, most of the European passerines that migrate southwest to Iberia must then turn south or southeast if they are to reach West African wintering areas. Similarly, those that migrate from Europe southeast to the Middle East must then turn southwest to reach East African wintering areas. Their journeys are thus undertaken as two distinct stages, with different headings, although neither stage is necessarily accom-plished non-stop. Many Eurasian–Afrotropical migrants make their return north-ward flight somewhat to the east of their autumn southward flight, probably in response to prevailing wind or feeding conditions (Chapter 22).

The tendency to take different routes in autumn and spring is especially marked in those species, such as the American Golden Plover *Pluvialis domin-ica*, that migrate between northeastern North America and southeastern South America (**Figure 1.2**). In autumn, when winds are favourable, these birds take the shortest route over the Atlantic, but in spring when winds over the Atlantic would be against them, they take the longer overland route through Central and North America. Such loop migrations are performed by many species in many

Figure 1.2   Loop migration of the American Golden Plover *Pluvialis dominica* between breeding areas in North America and wintering areas in South America. The outward route occurs largely over the Atlantic Ocean and the return route largely overland. Partly from Byrkjedal & Thompson (1998).

different parts of the world, illustrating the effects of seasonal local conditions on the development of migration routes (Chapter 22).

Costs of migration

While migration allows participants to exploit the resources of different regions at different times of year, the travel involved is not without costs. In addition to the energy required for the journey, migrants must travel through unfamiliar and sometimes hostile terrain, adjust to atypical habitats, face unfavourable weather and intense competition for the limited resources at staging sites, and suffer the consequences of navigation errors (Chapter 10). As explained above, some species perform long and hazardous journeys on which they can neither feed nor rest. Although the mortality associated with such journeys is hard to estimate, it

may often be substantial, and storms have killed thousands or even millions of birds at a time (Chapter 28).

In addition, at some stopover sites, where birds replenish their fuel reserves, large numbers of individuals must often gather at one time. Local food supplies can then be greatly depleted, leading to intense competition, to the detriment of many. Avian predators often concentrate at the same places, giving a high ratio of predators to prey, which increases mortality and disrupts the feeding of many individuals (Chapter 27). Moreover, in passing through a wide range of areas, migratory birds are likely to encounter a greater range of parasites and pathogens than are resident birds that remain in the same areas year-round. The high densities that migrants experience at some stopover sites favour the transmission of certain kinds of parasites and pathogens, which in turn can compromise the migratory performance, survival and breeding success of infected individuals. Compared to residents, some migrants have larger immune defence organs, such as spleen and bursa of Fabricius (Møller & Erritzoe 1998). The bursa is found only in sexually immature birds, but it is relatively larger in migrants, even before their first migration, than it is in residents. Disease agents may therefore play a greater role in the lives and deaths of migratory birds than in resident ones, and impose greater costs in terms of immunoprotection. In the process, migratory birds can also transport parasites and pathogens over long distances, as in recent years with the spread of the H5N1 strain of 'avian flu'. These are aspects of bird migration that have so far received little attention, and on which more research is needed. Overall, however, the benefits of migration to the participants, whether they accrue through increased survival, increased reproductive success or both, must on balance be greater than the mortality costs of the journey, for otherwise migration could not have evolved and could not persist.

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 and centre of gravity remain more or less the same all 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 Britain, as elsewhere, large numbers of many resident bird species have been ringed as chicks and adults, and the subsequent recoveries of birds found dead and reported by members of the public have given some idea of their 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 resident songbird populations, 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 such sedentary passerine species as House Sparrow *Passer domesticus* and Carrion Crow *Corvus corone*, and for non-passerines such as Moorhen *Gallinula chloropus* and Grey Partridge *Perdix perdix*. All these birds are likely to have made their longest movements in the immediate post-fledging period, soon after becoming free of parental care. 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.

The everyday movements that birds make to obtain their daily sustenance vary enormously between species, depending on their particular lifestyles. In species that live year-round in territories, individuals may spend their whole adult life in a confined area, varying from less than one hectare in some small songbirds up to a few hundred square kilometres in some large eagles (Newton 1979). In species in which breeding and feeding occur in different areas, everyday movements may be longer. For example, some radio-tagged female Brown-headed Cowbirds *Molothrus ater* studied in California travelled 9–16 km every day between their breeding and foraging areas, and even further to a communal roost (Curson *et al.* 2000). Other flock-feeding species, which base themselves in nesting colonies or communal roosts, forage over even larger areas. For example, radio-tagged Common Grackles *Quiscalus quiscula* studied in Oklahoma commuted an average of 24 km between roost and feeding area, and ranged during the weeks of study over an average of 325 km^2 (Bray *et al.* 1979). Among colonial seabirds, individuals may forage over very much larger areas, extending over many thousands of square kilometres, as mentioned earlier. In all such species, the same individuals may maintain the same distribution pattern year-round, or at least over large parts of each year.

HIBERNATION

While many birds alleviate seasonal food shortages by migrating elsewhere, many other animals cope with seasonally difficult periods by hibernating, remaining dormant for up to several months at a time. They survive at much reduced metabolic rate on body reserves, and emerge when conditions improve. At one time, the disappearance of most birds from high latitudes for the winter was attributed to hibernation rather than migration. In fact, at least one species of bird does hibernate in winter. This was discovered in 1946, when a Common Poorwill *Phalaenoptilus nuttallii* (a sort of nightjar) was found in a torpid state in a rock crevice in a California desert (Jaeger 1949). The bird was inert, its respiration and heart rate were barely detectable, and its body temperature was 18–20ºC, about half the usual level for birds. The individual was ringed, and in subsequent winters it was found hibernating again in the same crevice. Since then other poorwills have been found in similar sites in the same condition, and their physiology has been studied in laboratory conditions (Withers 1977). The energy consumption of torpid birds was so low that they could live off their body fat for more than three months. Other kinds of birds can also become torpid but remain so only overnight (hummingbirds) or for at most a few days at a time (swifts and colies). Evidently, long-term hibernation is at best extremely rare among birds, most escaping difficult conditions by migration instead.

SUMMARY

The large-scale movements of birds can conveniently be divided into dispersal, dispersive-migration, migration, irruption and nomadism, although these different types of movements intergrade with one another, and the same populations

may show more than one type of movement at different stages of their annual cycle. This book is concerned with all these types of movements, but chiefly with migration, defined as a seasonal return movement in fixed directions between separate breeding and wintering ranges. Migration occurs to some degree in most species of birds that live in seasonal environments. It leads to massive twice-yearly changes in the distributions of birds over the earth's surface.

Some migratory birds travel relatively short distances of a few tens of kilometres between their breeding and wintering areas, but others travel hundreds or thousands of kilometres, sometimes crossing long stretches of sea or desert or high mountain ranges, where they cannot rest or feed. They accumulate large reserves of body fat for the journey. Such birds show impressive navigational skills which enable individuals to return to the same breeding and wintering sites year after year. Although migration occurs mainly on a north–south axis, many species have a strong east–west component in their journeys, especially those that move from the seasonally hostile centre to the milder edges of the northern land masses. Individuals in so-called sedentary populations mostly move over short distances of at most a few tens of kilometres, and show no directional preferences, so that the population occupies essentially the same range year-round. Only one bird species is known to hibernate through the unfavourable season.

Ringing a Curlew Sandpiper *Calidris ferruginea*

Chapter 2
Methodology

The study of living birds by the banding method, whereby great numbers of individuals are marked with numbered aluminium leg rings, has come to be recognised as a most accurate means of ornithological research. (Frederick C. Lincoln 1935.)

The development of any area of science depends heavily on the methodology available. Migration studies began in the simplest possible way, by observation, and have developed over the past 120 years by the addition of progressively more sophisticated methodology, including in recent years the use of miniature radio-transmitters to track individual birds on their journeys. At no stage, however, has any method been dropped from the arsenal, and systematic observations can be just as revealing now as they were 120 years ago. In this chapter, different study techniques are described, highlighting their pros and cons. Two hundred years ago practically no evidence was available that birds migrated, apart from their seasonal appearance and disappearance in particular areas. Hibernation was often thought to be responsible for the disappearance of many species from high

latitudes in winter, a notion that gained support even from the scientific community, but again without evidence.

An early indication that individual birds could actually travel long distances to winter elsewhere was provided by a White Stork *Ciconia ciconia* which was seen in Germany in 1822 flying around with a spear stuck through its body. When the bird was shot it was found that the spear could be attributed from its design to a part of West Africa. This probably provided the first firm indication from Europe of a long-distance movement by an individual bird. Since that time, more than two dozen other storks have been recovered in Europe in similar circumstances. In more recent times, bird migrations have been studied by observations (made directly or with radar), by bird counts made in particular places at different dates, by widescale surveys of bird distributions at different seasons, by use of ring recoveries, or in recent years by the use of radio-transmitters and other devices fixed to individual birds which can then be followed on their journeys.

OBSERVATIONS OF BIRDS ON MIGRATION

It is widely known that, at particular localities, some bird species appear only in the breeding season, and others in the non-breeding season or at times of passage. Watching birds on migration has become a favourite pastime for thousands of bird watchers, and in many countries the concentration points (such as coastal promontories, offshore islets and mountain passes) are now well known. Hawk Mountain in Pennsylvania, which is famous as a viewing site for raptor migration, attracts about 20 000 raptors each autumn, but more than 100 000 human observers. Large numbers of people also visit Cape May in New Jersey each year, the Santa Ana Wildlife Refuge in southwest Texas, and Falsterbo in Sweden. At some sites, diurnal migration has been observed systematically over many years, giving information on the numbers, directions and passage periods of different species, on prevailing weather effects on migration, and on long-term changes in numbers and migration timing (Chapter 7).

For most bird species, however, counts of birds seen on the ground or flying over represent only a small and variable proportion of those passing overhead. This is because most migrating birds fly much too high to be seen with the naked eye or even with binoculars, and in any case many species migrate mainly at night. It is chiefly when they encounter headwinds that birds fly low enough to be easily seen. Migrants come to ground mainly to rest or refuel, or after they have drifted off course because of side winds, or been forced down by headwinds, mist or rain. Hence, visual counts of migrants cannot usually reflect the true volume of migration, or the weather conditions that most favour it (for a critique of observational methods of study, see Kerlinger 1989). On the other hand, any birds seen can usually be identified to species by their appearance or calls. Large-scale studies of visible bird migration, with observers posted at different localities, formed some of the earliest cooperative projects involving bird-watchers.

Watching seabirds on migration is most profitable when onshore winds cause birds to fly closer to land, and often thousands per hour can be seen streaming past headlands. Such counts depend on wind conditions bringing migrating

birds within view. In other conditions, migration would occur too far out to be visible to a land-based observer. Also, as seabird species forage at long distances from their nests, it is impossible at certain times of year to distinguish migration from foraging flights.

At night, ground-based observers are much more limited, but on clear nights low-flying birds can be seen as they cross the lit surface of the moon (moon-watching). The drawbacks of the method are that it can only be used near full moon in clear weather and the observation cone has a relatively small angle (on average 0.52º), covering only a tiny portion of the night sky. By adventurous calculations involving the moon's bearing and elevation, counts of birds crossing the face of the moon can be transformed into estimates of the numbers passing over, their direction of movement and even their height and speed (Nisbet 1959a). Using a telescope with 40× magnification, it was estimated that about 50% of the birds flying at 1.5 km distance from the observer were detected, reducing to zero at 3.5 km, based on comparison with radar and infrared observations (Liechti *et al.* 1995). The moon-watching method is also hard on the eyes, and ideally needs several observers taking turns. The most impressive large-scale count programme ever undertaken on the basis of moon-watching was in central Asia where, at the time it was done, no other study methods were available there (**Box 2.1**).

Other observers have used a strong spotlight directed skywards to count the birds passing through the beam. The best device for this purpose is a ceilometer, which is normally used at airports for measuring cloud height. In warm weather, the lower part of the beam tends to be full of insects, but birds seen flying through the upper part can be recorded in the same way as for moon-watching, but with limitations on distance as the beam typically extends only to a few hundred metres. Hebrard (1971) used a horizontally directed portable ceilometer placed on a tower to illuminate birds at they took off from the tree canopy at night.

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 3000 m or more. Birds call more during mist and poor visibility than in clear skies, and some species seem not to call at all, so the numbers of calls heard are only broadly related to the number of birds passing (Farnsworth *et al.* 2004). Nevertheless, the opportunity that listening affords for identifying species makes it a useful accessory to other methods.

Early indication of the numbers and species of birds migrating at night was provided by 'kills' of low-flying birds attracted to lighthouses and illuminated communication masts (Chapter 28; Gätke 1895, Clarke 1912). Spectacular slaughter has sometimes been recorded at particular sites, such as the 50 000 birds of 53 species killed at one site in Georgia in one night (Johnston & Haines 1957). Some species, such as Common Snipe *Gallingo gallingo*, Water Rail *Rallus aquaticus* and Common Grasshopper Warbler *Locustella naevia* in Europe, seem notoriously prone to such accidents. Mortality occurs mainly on overcast or foggy nights, and the resulting corpses have provided information on the migration seasons, body weights and condition of different species.

Indications that landbirds cross the sea have been obtained from coastal observations of birds flying out to sea, or from ships or oilrigs of birds passing over or stopping by, and from radar observations. The recent series of oil and gas

Box 2.1   The use of 'moon-watching' to assess migratory bird numbers in central Asia.

The most extensive series of counts ever made by moon-watching was obtained by a team of Russian observers stationed at various points across a 2200-km zone stretching from the Caspian Sea to the eastern part of the Tien Shan Mountains in central Asia (Dolnik & Bolshakov 1985). At each point, birds were counted in spring as they crossed the lit surface of the moon, using $30\times$ telescopes. The totals were converted to numbers of birds crossing 1 km of a latitude line, and then extrapolated to the whole 2200 km. Although skies were generally clear throughout the migration season, the observers could not count around times of a new moon, when too little of the moon surface was lit. For those darker nights they assumed that the same numbers of birds passed as on nights around full moon, when counts could be made. All the main types of birds expected were seen, but passerines formed 73–89% of the totals at different localities. Overall, an estimated 731 million birds crossed the 42°N parallel on spring migration. From the directions taken, 85% of these birds came from winter quarters in southern Asia (heading mainly north-northwest), and the rest (110 million) probably mainly from Africa (heading mainly northeast). The volume of migration was not uniform across the whole 2200-km stretch, perhaps because some birds were diverted by topographical features, including the Tien Shan Mountains.

  In autumn, the number of migrants would be expected to be at least twice the number counted in spring, owing to reproduction. This was equivalent to three times the autumn estimate made for North Africa which spans approximately double the length of latitude as the Asian survey. The implication was that about six times more migrants left this part of Asia in autumn than entered Africa. The difference may be due partly to the different methods of assessment, each with their own errors; to greater bird densities in central Asia where habitats have been less disturbed than in Europe; and to the fact that many of the Asian birds may have wintered south of 42°N, but at latitudes north of the northern latitude of Africa. The 220 million birds that could have been heading for Africa across this 2200-km front would form nearly 4.5% of the 5000 million Eurasian migrants estimated by Moreau (1972) to enter Africa each autumn.

drilling platforms in the North Sea has provided additional information on the movements of birds between Britain and continental Europe (Bourne *et al.* 1979, Anderson 1990).

RADAR AND OTHER DEVICES

The use of radar for the systematic recording of bird migration began in the 1950s. A radar emits short pulses of radio-waves and records their echoes from targets, whether birds or aeroplanes. Because 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 4). 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). Radar also swiftly disposed of the idea that migration occurred only in spring and autumn. Birds of one species or another could be seen migrating somewhere on earth at almost any time of year.

Individual birds can be followed by radar over enough of their journeys to reveal how they orientate during migration and react to different weather conditions, and hence how their flight behaviour is shaped by prevailing atmospheric conditions. The density of birds on a radar screen cannot be precisely related to the true number of birds flying over (because several birds flying close together may appear as a single echo-spot), but it provides a relative measure of abundance that can be used by day and night.

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 species are usually unknown, apart from broad categories distinguished by body size, flight speed, or wing-beat patterns. The radar echoes often show rhythmic fluctuations that can be recorded and used to estimate the wing-beat frequency. This procedure enables waders and waterfowl (continuous wing-beats) to be distinguished from passerines (wing-beats broken by pauses), and perhaps two size classes in each group. Other drawbacks are that birds flying close to the ground 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 fan-beam of wide vertical angle (10–30°) and narrow horizontal angle (up to 2°). By rotating the radar antenna, a wide swathe of sky can be scanned for echoes with a high horizontal resolution, but no altitude resolution. Spanning an area of more than 100 km across, surveillance radars are therefore good for studies of migration intensity, speed and general direction. On some modern radar sets, small songbirds can be detected to beyond 100 km, and larger birds to more than 500 km, providing they are high enough (Bruderer 1999). With most radar sets, the displays can be easily recorded on film for subsequent playback and analysis. A useful way of recording the slow-moving echoes of birds is with time-lapse photography, the radar screen with a clock beside it being photographed with a cine camera every 1–2 minutes. Projected at normal speed, a whole night's migration can then be viewed in a few minutes. The combination of records from many different surveillance radars at different locations has been used to provide a broad picture of bird migration on particular dates over large regions including much of North America (**Figure 2.1**; Lowery & Newman 1966, Gauthreaux *et al.* 2003). The latter study used a new system of WSR-88D weather surveillance radars. Nocturnal data on such a huge geographical scale could not have been obtained in any other way.
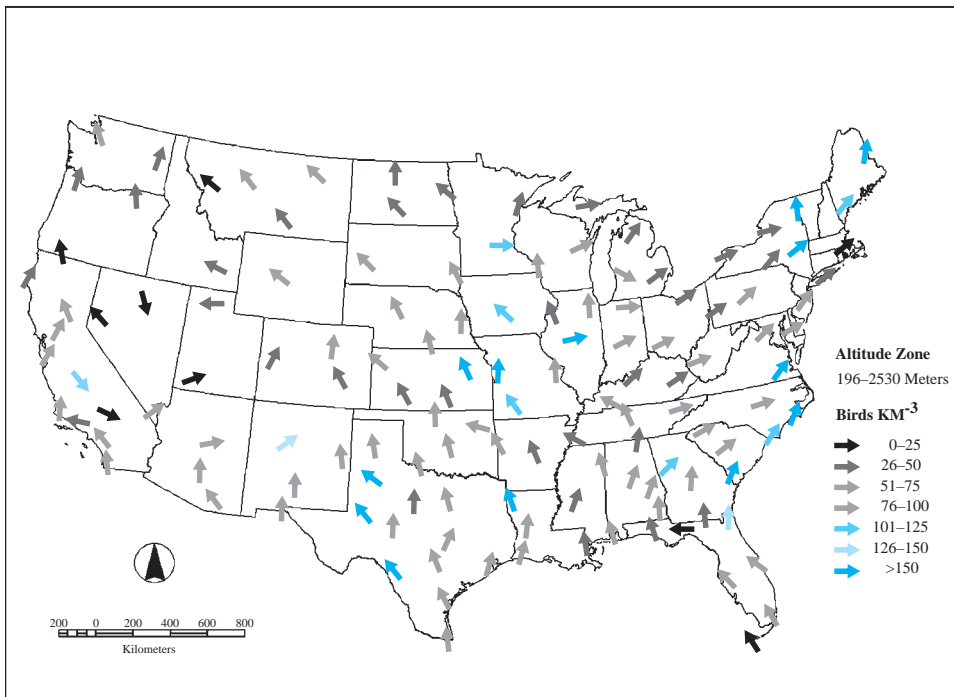
Figure 2.1   Map depicting bird migration over the United States within the altitude zone 196–2530 m on the nights of 10–11 May 2002. Arrows reflect the positions of weather surveillance radars, and show the directions and volumes of migration overhead. Map provided by S. Gauthreaux. For further details, see Gauthreaux *et al.* (2003).

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 distance, elevation and azimuth angles, from which the speed and direction of the tracked migrants can be calculated, and their flight trajectories plotted in three-dimensional space (Bruderer *et al.* 1995). Alternatively, the beam can be used in a conical scanning mode to provide information on the spatial distribution of migrants (although calculations of bird numbers from conical scanning present problems). Wind profiles can be obtained by using radar to track ascending weather balloons carrying aluminium foil for maximum reflectance. The heading and airspeed of the birds can then be calculated from the tracking data against the wind data. Another radar technique involves a vertical set designed to quantify the amount of migration taking place and the heights at which the birds are flying. This gives similar results to those obtained using a ceilometer, except that the radar can look through clouds and detect the birds at all heights.

Another method of remote detection involves the use of an infrared sensor to pick up the heat radiated from birds flying overhead. By pointing a thermal imaging device of 1.45° opening angle to the sky, migrating birds can be detected from 300 m up to 3000 m (Zehnder *et al.* 2001). Flight tracks are recorded on video,

and targets are grouped into size classes to estimate flight altitudes. Infrared sensors work best at night under clear skies, so are not good for assessing weather effects on migration. If such an instrument is combined with a distance measure, quantitative information on migration can be obtained.

The most comprehensive picture of migration is obtained by a combination of radar and visual observations by ground-based observers in the same area. However, in their studies of migration of soaring birds in Israel, Leshem & Yom-Tov (1996a) also used a motorised glider in which they could actually accompany flocks of large soaring birds on part of their journeys. This enabled these researchers to record in detail the ups and downs of the birds' flight, as they climbed in each thermal and glided, losing height, to the next.

DISTRIBUTION STUDIES

For many years museum collections formed our main source of information on bird distributions, especially of the wintering areas of those northern hemisphere birds that migrate to the tropics for the non-breeding season. The aim of skin collectors, operating mainly in the nineteenth century, was to preserve representative samples of all the species occurring in different areas. These specimens still provide invaluable 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 13). For some parts of the world these distributions have been depicted at relatively fine scale in recent 'atlas' projects. 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. The main value of such distributional data in our present context, however, is in showing where the same species occur at different times of year; in other words, in revealing breeding and non-breeding ranges, as well as migration routes.

RINGING

Around the end of the nineteenth century, research on bird migration received a major boost with the start of scientific bird ringing, which is still the mainstay of migration studies around the world. This activity began with the efforts of a school master, Hans Christian C. Mortensen, in Denmark in 1899, but it quickly spread to other places in Europe, North America and elsewhere. A ring (or band) 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. The British scheme currently uses rings of 20 sizes, with internal diameters of 2–26 mm. Each ring carries a unique engraved number, identifying the individual bird, and an address to which a recovery can be reported. The bird can be identified unequivocally,

and its whereabouts are thus known at least twice in its life – at ringing and recovery. In general, birds ringed as nestlings are of most value because their precise natal locality is known, whereas birds ringed as adults may be of less certain provenance; depending on when and where they were caught, they may have been local breeders, winter visitors or passage migrants. Some recoveries of ringed birds are provided by other ringers who trap the birds alive and release them again, while other recoveries are provided by hunters or by other members of the public who may report the birds dead or injured.

The recovery rates of ringed birds are generally low: in many small species less than 0.1% of ringed individuals are ever reported again, but in larger species, especially those that are hunted, the proportion can rise above 20%. Of course, for ringers operating repeatedly in the same place, local recapture rates can be very much higher, rising to nearly 100% in some species, but such local records reveal little about bird movements. In general, therefore, getting useful information about migration in this way depends on ringing very large numbers of individual birds, from which varying proportions may be subsequently reported from elsewhere. Moreover, because nestlings suffer higher mortality rates than older birds, many more nestlings than adults must be ringed to provide a given number of recoveries.

Another problem is that recovery rates can vary enormously along migration routes, according largely to the density and literacy of the local human population. For example, of nearly 300 000 House Martins *Delichon urbica* ringed in Britain, just over 1000 (0.4%) have been recovered. More than 90% of these reports were from within Britain and Ireland, and so were of little help in indicating migration routes, while only one came from Nigeria, within the presumed wintering range (I. A. Hill, in Wernham *et al.* 2002).

In 1903, following the pioneering work of Heinricke Gätke on Heligoland Island in the southern North Sea (**Box 2.2**), a modern-style bird observatory and ringing station was established at Rossitten (now Rybachi) on the Courland Spit in the southern Baltic, a site where migrant birds are concentrated. Subsequently, many other bird observatories were established at other sites in Europe and North America and most are still in operation. Together, they provide a network of well-placed sites, where migrants can be observed and, more importantly, trapped and ringed in large numbers. During the early twentieth century, many countries came to operate their own institutionalised ringing schemes, in most of which ringing was carried out largely by amateurs operating in their home areas, but also making ringing expeditions to more remote areas. Nowadays in Europe, the various national ringing schemes are linked by EURING, which coordinates techniques and the electronic handling of data, unifies standards and formats, and stimulates projects and analyses on a pan-European basis. All ringers are trained, tested and licensed before they can operate alone.

Many of the techniques used to trap birds are developments of ancient methods used to catch birds for food. One important development was a giant funnel trap, big enough to enclose bushes, known as the Heligoland trap, because it was first constructed on Heligoland Island. At the end of the funnel is a glass-fronted catching box into which birds are driven (**Figure 2.2**). However, the numbers ringed increased greatly in the 1950s with the development of more efficient trapping methods, including mist nets and cannon nets, which increased the range of species that could be caught in large numbers. Mist nets are essentially walls of fine, almost invisible netting, each up to 20 m long and up to 2 m high. Each net is erected on

Box 2.2   Heligoland Bird Observatory

The first bird observatory, of very different style from those of today, was established on the island of Heligoland (German Helgoland) in the southeastern North Sea, about 60 km west of Denmark and about 80 km north of the German town of Wilhelmshaven. The observatory became famous mainly through the work of one man, Heinrich Gätke, who spent more than 50 years on the island, observing and shooting birds. The skins were sold to museums and private collectors, providing a useful supplement to the income of Gätke and his local collaborators. In the process, Gätke amassed a great deal of information on the timing and volume of bird migration, and on the occurrence of vagrants on the island. The business of skin collecting meant that particular emphasis was paid to rarities, as in much of modern bird-watching. His famous book, *Heligoland as a Bird Observatory*, was translated into English and published in 1895. Until the spring of that year, he had recorded 398 different bird species on the island. The book is full of fascinating information, and most of his ideas and interpretations have stood the test of time, although in the absence of proper measuring devices, he greatly overestimated the speed and altitude of bird migration.

 The bird observatory still survives on Heligoland, but like other modern observatories, it has become a centre for ringing and scientific study. It is the original home of the so-called Heligoland trap, a large horizontally placed wire-netting funnel, big enough to enclose many bushes, and through which birds can be driven and caught in a glass-fronted box at the end.
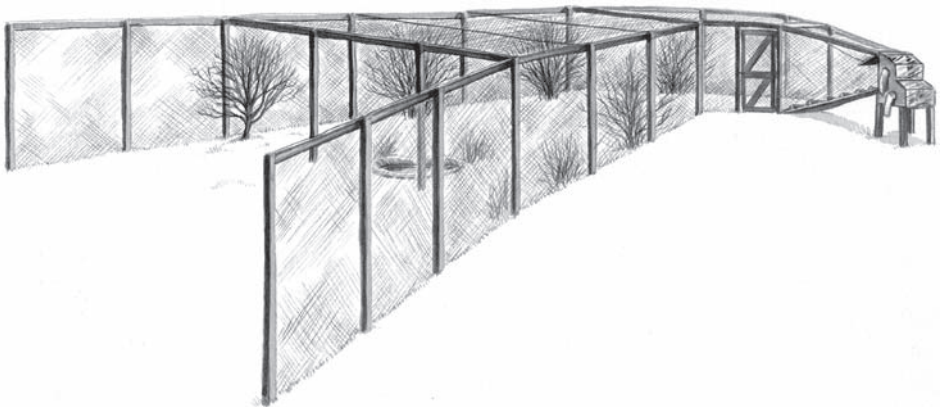
Figure 2.2   Drawing of a Heligoland bird trap, a large funnel through which birds can be driven and caught in a glass-fronted box at the end.

poles, and set against a background of trees and shrubs to ensure that the net does not show against the sky. Any small bird that hits the net slides into a pocket of net formed by one of three or four shelf strings, which are threaded horizontally at different levels through the length of the net.

Figure 2.3   Cannon-netting of Oyster-catchers *Haematopus ostralegus*.

A different method was developed for catching waders, waterfowl or others that gather in large concentrations on the ground. A cannon- or rocket-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.

By the end of the twentieth century, using a variety of trapping methods, more than 200 million birds had been individually ringed worldwide, giving hundreds of thousands of recoveries, revealing the movement patterns of different populations. Over the years, several 'atlases' of bird movements, based on ringing data, have been published (e.g. Schüz & Weigold 1931, Zink 1973–85, Wernham *et al.* 2002, Bakken *et al.* 2003).

Ringing activities tend to be concentrated in particular regions, where opportunities and interest levels are high. Although many of the ringed birds then move on, the subsequent recoveries are probably biased, as mentioned above, towards areas with high-density, literate human populations. Even in so well studied a region as western Europe, spatial variation in the reporting of ring recoveries could give an unrepresentative idea of migration patterns. Over this whole area, much migration occurs on a northeast–southwest axis, as amply confirmed by ring recoveries; but almost certainly ring recoveries greatly underestimate the amount of migration that occurs on a northwest–southeast axis. This is because the chances of getting ring recoveries from southeast Europe are much lower than from elsewhere on the continent. Yet other information from migrants caught in central and eastern Europe indicates that many species show predominantly southeast directional preferences in autumn, their movements not being picked up to any significant degree by subsequent ring recoveries (Busse 2000, 2001).

Care is therefore needed in the interpretation of ring recoveries, although they can still be useful in defining the flyways and wintering areas of particular breeding populations, the annual and seasonal timing of movements, and any sex and age differences in movements that might occur within species (Chapter 15). Some of the most geographically complete information on migration relates to North American waterfowl. It results from a planned, geographically dispersed ringing effort over many years, and subsequent recoveries provided from all parts of the continent by millions of hunters.

Overall, ring recoveries comprise our main source of information on bird movements. Taken together, they have revealed a network of bird migration routes that encompass all habitable parts of the globe, and that are travelled annually by millions of migrating birds. It has sometimes been possible to set up coordinated collaborative projects in a wide range of localities along a migration flyway, in which many observers collect data on the same species in a standardised way. The EURING projects on Barn Swallow *Hirundo rustica* and other European–African songbird migrants provide examples.

One drawback of ringing is that the ring can only be re-read if the bird is in the hand, alive or dead. Not surprisingly, therefore, researchers have been keen to develop methods that enable the re-sighting of marked birds without the need to trap them. Marking has been achieved in many different ways depending partly on the species, such as colour rings on the legs, large rings bearing numbers or letters that can be read through a telescope, coloured or numbered neck collars or wing tags. Such colour-marking schemes have greatly increased the rate of information gain for some species, especially waterfowl and waders, and have often yielded multiple records of the same individuals at different places. They have given more accurate information than ring recoveries on the speeds of migration and the duration of stopovers. The information yield from such schemes is, of course, greatly increased if observers along the potential migration route are alerted to look out for tagged birds. For example, in the Black-tailed Godwit *Limosa limosa* in Britain only 2.5% of ringed birds were ever recovered, but following the introduction of a colour-marking programme and additional observer input, more than 80% of marked birds were subsequently reported, many at several different places on the migration route. In the same way, the use of colour leg-tagging has greatly increased our knowledge of shorebird migration in Eastern Asia–Australasia and in North–South America, providing information on the timing and speed of migration, and of the locations of important stopover sites (Minton 2003).

Birds trapped for ringing can be sexed and aged, enabling differences in timing and other aspects of migration between sex and age groups to be identified. Individuals in the hand can also be measured and weighed, providing information on weight gain and fat deposition in different species, which can be related to the types of journeys undertaken. Laboratory analyses of carcasses have revealed that substantial changes in body composition accompany migration, not simply the gain and loss of fat (Chapter 5). In some species caught on migration, measurements (mostly wing and bill) can give some idea of provenance, enabling the passage periods of different populations to be assessed. Nowadays this type of information can often be augmented from ring recoveries or studies on DNA or isotope markers (see later). Blood samples can provide information on the levels of specific hormones, metabolites or red blood cells, all of which can help in understanding migration. Details of plumage development also reveal how moult is fitted into the annual cycle of different species, along with breeding and migration (Chapter 11).

From early in the twentieth century, bird ringing led to the experimental manipulation of birds in order to learn more about their navigation abilities. Large-scale displacement experiments, in which birds were caught in one locality and released in another far away, were done to see whether birds could re-find their home areas, or how translocation affected their migrations, using subsequent

ring recoveries to provide the necessary information. No less than 24 such large-scale experiments, involving a wide range of species from Barn Swallows *Hirundo rustica* to White Storks *Ciconia ciconia*, were done in the first half of the twentieth century at Vogelwarte Rossitten on the Courland Spit (Schüz *et al.* 1971), followed by others in other parts of Europe and in North America (Chapter 9). Recoveries of birds trapped, ringed and released without displacement provided the control comparisons. Such experiments revealed much about the orientation and navigational abilities of birds, and about differences in behaviour between young and older individuals. In more recent years, much work on orientation and navigation has involved homing pigeons, which are easy to keep and handle. Or it has involved wild birds which were trapped at migration times and their directional preferences assessed in 'orientation cages', after which they were released to continue their journeys (see later). Such captive birds were sometimes subjected to simulated displacements by adjusting the celestial or magnetic cues to which they were exposed, and their directional preferences then re-assessed.

RADIO-TRACKING

In recent decades an additional study method has become available, namely the day-by-day tracking of radio-tagged birds on their journeys. Initially, aircraft were used to follow the tagged birds (Chapter 8; for various thrushes see Cochran *et al.* 1967; for raptors see Hunt *et al.* 1992; for cranes see Kuyt 1992). But since the mid-1980s, however, tracking has been made much easier by use of satellite-based receivers (Chapter 8). The transmitters, called platform transmitter terminals (PTTs), can be tracked individually and automatically by the Argos satellite system. This is a joint French–American venture, originally designed to locate objects on earth such as floating weather stations and buoys. It is based on satellites that continually circle the globe over the poles, and is capable of detecting signals from anywhere on earth, with an accuracy of 150–3000 m depending on the angle of the satellite pass and the quality of the PTT signal. The satellites then transmit the information to a ground station. By measuring the Doppler shift of the emitted signal, the system can measure the exact distance between the transmitter and the satellite, and knowing the parameters of the satellite orbit, the system can also calculate the exact coordinates of the transmitter. The method is expensive, but the data provided are some of the best available on the movements of migratory birds. As the accuracy of each reading is known, the less reliable ones can be discarded if necessary.

The use of PTTs 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 (Chapter 8). With this new method, fieldwork on bird migration is advancing in new directions, providing information on migration routes and progress, stop-over location and durations, flight speeds, wind and weather effects and orientation abilities.

In one of the earliest radio-tracking studies, six male Wandering Albatrosses *Diomedea exulans* had satellite transmitters attached to them at their nests on the Island of Crozét, midway between South Africa and Antarctica (Jouventin & Weimerskirch 1990). Four of the six birds were followed for about a month as they

wandered around the ocean looking for food. One albatross covered a distance of 10 427 km over 27 days. The satellite located it 314 times and its maximum flight velocity between location points was 63 km per hour. Another albatross flew a total of 15 200 km during 33 days. The satellite located it 385 times, and its maximum flight velocity between location points was 81 km per hour. On one day this albatross covered a total of 936 km. For some years, satellite tracking provided the only way to obtain such information, especially in birds that cover such huge distances over the open sea. Additional information gained from the satellite-based tracking of albatrosses and other birds is discussed in Chapters 8 and 17.

Because of their weight, PTTs could until recently be carried safely only by birds weighing at least 1 kg (since reduced to 600 g), which excludes the majority of bird species (ideally the transmitters should not exceed 3–4% of the bird's weight). Most studies have involved swans and geese, raptors, cranes, storks, pelicans and albatrosses. Each transmitter provides information for a period of months or years, until the battery or transmitter fails. It gives immediate information on the daily movements of individuals and, if necessary, also on aspects of the physiology of the wearer and on the conditions of the environment through which the bird passes. Various devices, such as intermittent transmission, can be used to lengthen the life of a battery-powered transmitter, but as yet few battery-operated PTTs have lasted longer than a year. However, from 1995 solar-powered transmitters became available which, unlike battery-powered ones, could in theory last for many years. The current world record holder is a White Stork *Ciconia ciconia*, so far tracked (with periodic transmitter changes) over a 10-year period on six outward and six return journeys between its nesting place in Germany and its wintering places in different parts of Africa. In some years, this adult female wintered at localities within a few degrees of the equator in East Africa (about 7000 km from its nesting place) and in other years it wintered at places in southern Africa (about 11 000 km from its nesting places) (Chapter 8; Berthold *et al.* 2004). Only radio-tracking has so far revealed that individual storks have wintered in widely separated places in different years. For other species, satellite-based radio-tracking has also revealed previously unknown breeding or wintering areas (Meyburg *et al.* 1998, Ueta *et al.* 2002).

Other kinds of electronic and data-storage tags can now be used to track migrating birds on a worldwide scale. Geolocation systems (GLS) are based on continual measurements by photosensors of the ambient light intensity to record the geographical coordinates (latitude from daylength and longitude from absolute times of dawn and dusk), while global positioning systems (GPS) receive data from satellites for calculating the position of the bird. When first introduced, both systems required the recapture of the birds to recover the tags (attached to leg rings) and accumulated data. This was not difficult with seabirds, for example, returning annually to the same nest sites (e.g. Croxall *et al.* 2005). However, recent developments to link GLS and GPS to satellite transmitters now allow the data stored on the bird to be retrieved without the need for recapture, and some current solar-powered models can operate over periods exceeding ten years, providing that light levels are sufficient to generate the necessary power. GPS operate through a network of satellites launched by the United States Department of Defense. The bird is equipped with a GPS receiver, which collects locations at pre-set intervals (say every hour) from the GPS satellite network. These data can then be relayed to ground-based Argos processing centres, again at pre-set intervals (say every

few days) (Seegar *et al.* 1999). Because the locations determined in this way 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 as often as required. Used in conjunction with high-power satellite images or aerial photographs of the ground, a bird can be placed accurately within a landscape situated thousands of kilometres from the observer who is seated comfortably at home in front of a PC. Other sensors can be added to a PTT in order to measure other environmental variables, such as altitude of flight or ambient temperature, but they also add weight.

To be of most value, radio-tags and sensors should ideally have no effect on the flight or other behaviour of the wearer. In practice, the capture and handling of birds (for whatever purpose) is likely to cause some temporary stress, and there could be an energy cost to carrying any extra load. However, birds are normally able to compensate for such effects, so that they are not obvious to the observer, and the weight of the attachment can be trivial compared to the weight of a meal or internal body reserves. Attempts to test the effects of tags on the flight performance of birds have either used experimental approaches (such as comparing the flight or energy consumption of tagged and untagged birds flown in wind tunnels, e.g. Holliday *et al.* 1988), or have compared the migratory timing and progress of radio-tagged birds with those of untagged birds, where this was measured (Beekman *et al.* 2002, Igual *et al.* 2005). So far as I am aware, no such study has revealed significant impacts of radio-tags or sensors on the flight performance of migrants, providing these items weighed less than 3–4% of the birds themselves. Michener & Walcott (1966) could detect no differences in the flight performance of homing pigeons *Columba livia* carrying transmitters weighing as much as 15% of pigeon body weight, although some effects were detected in a later study of homing pigeons by Gessaman & Nagy (1988). Hence, although we can generally assume that the data on migrations obtained by radio-tagging have not been significantly distorted by the effect of the tag on the wearer, this may not necessarily have been true of all such studies (for further discussion see Kenward 2001, Phillips *et al.* 2003).

ISOTOPES AND OTHER MARKERS

The use of markers present within the tissues of migratory birds to analyse broad-scale movement patterns offers an alternative approach in species that yield few or no useful ring recoveries, and are too small to carry PTTs. In particular, analyses of stable isotopes (different forms of the same element) in bird tissues can provide information on the broad provenance of trapped migrants. Stable isotopes of several abundant elements, including hydrogen (H), carbon (C), strontium (Sr) and others, have spatial distributions that vary consistently either across broad geographical regions or between bird habitats and food types (Hobson 1999). For example, in North America, the ratio of hydrogen to its isotope deuterium (δD) in precipitation varies across the continent, from deuterium-enriched in the southeast to deuterium-depleted in the northwest. These patterns are transferred through food webs from plants to higher organisms. 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, or the habitat and type of food. 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 their body tissues. Keratinous tissues, such as feathers, are metabolically inert following synthesis, and maintain an isotopic signature reflecting the food eaten at the time and place of their formation. Other tissues are metabolically active, and retain their signatures for periods ranging from a few days (in the case of liver or blood plasma) to several weeks (in the case of muscle or whole blood), to the lifetime of the individual in the case of bone collagen (Hobson 2003). Isotope ratios also change as the chemicals concerned pass from prey to predator, upwards through food webs, because of differential loss through excretion and respiration, but these changes are known and can be allowed for.

In practical terms, by catching a bird and pulling a single feather, analysing by mass spectrometry its isotope signature, and comparing this with known geographical patterns in isotope ratios, it is possible to find (in very broad terms) where the bird grew its feathers. Even without a baseline reference, one can tell whether different breeding populations have their own distinct wintering areas, or whether wintering populations have their own distinct breeding areas. It is thus not necessary to re-capture birds, and the method is equally applicable to museum specimens.

Many birds moult in their breeding areas, and retain the feathers grown there for up to a year. In migration studies, linkages between breeding and wintering sites have been established using this approach. For example, in Black-throated Blue Warblers *Dendroica caerulescens*, $\delta^{13}C$, δD and $\delta^{87}Sr$ values in feathers varied systematically across the breeding range, while equivalent values from wintering sites in the Caribbean region indicated that the birds there had been drawn from northern parts of the breeding range. The δD and $\delta^{13}C$ values among individuals from local wintering sites showed greater variation than those among individuals from local breeding sites, which implied that migrants sampled at each wintering locality were drawn from more than one part of the breeding range (Chamberlain *et al.* 1997). Even more strikingly, δD signatures for five species of Neotropical migrants sampled at a single locality in Guatemala represented individuals from across the breeding ranges of these species (Hobson & Wassenaar 1997); and δD signatures for Northern Bullfinches *Pyrrhula p. pyrrhula* obtained in Scotland in 2004 indicated that these irruptive migrants derived from a large part of the European boreal region, as far east as the Urals (Newton *et al.* 2006). In contrast, material from Wilson's Warblers *Wilsonia pusilla* showed isotopic evidence for 'leap-frog migration', where more northern birds migrate to wintering areas further south than those of southern breeders (Kelly *et al.* 2002).

In contrast to the above species, Eurasian Willow Warblers *Phylloscopus trochilus* moult in summer and winter, and analysis of carbon and nitrogen isotopes of winter-grown feathers plucked on European breeding areas confirmed that the two subspecies (*Phylloscopus t. trochilus* and *P. t. acredula*) found breeding in different parts of Sweden winter in different (west and east) parts of Africa (see **Figure 22.2**; Chamberlain *et al.* 2000). Similarly, stable isotope analysis of Barn Swallow *Hirundo rustica* feathers (grown in winter) has indicated that Swiss and English breeding birds probably winter in different parts of Africa (the $\delta^{13}C$ signatures being more depleted in Swiss birds, which indicates wintering in more wooded areas than the

English birds, Evans *et al.* 2003a). More surprisingly, analyses of Barn Swallows breeding in Denmark revealed that isotopes in feathers grown in winter quarters had a bimodal distribution, suggesting two different wintering areas (Møller & Hobson 2004). The two types of birds also differed in phenotype, as did their off-spring. Depending on the season of moult, different species are suited for summer or winter population differentiation, while a twice-yearly moult makes some species useful for study in both summer and winter areas. The same is true for species with split moults, which grow some of their feathers in breeding areas and others in wintering areas (Chapter 11).

Sometimes migrants from northern areas winter within the range of more southern birds which are resident. It is then hard to tell the relative proportions of migrants and residents in the same wintering area. Using measurements of deuterium (δD) and $\delta^{13}C$ values in feathers of Loggerhead Shrikes *Lanius ludovicianus*, it was established that northern breeders made up about 10% of the Florida population in winter, 4% of the Texas population and 8% of the Mexican population (Hobson & Wassenaar 2001). The differences in proportions between States were not statistically significant, but the figures showed that northern migrants formed only a small part of these lower-latitude wintering populations. This would have been difficult to establish reliably by ringing.

Although useful in identifying the regional origins of migrants, and filling gaps in other information, the method of isotope analysis cannot provide anything near the geographical resolution that is possible with other approaches, such as ringing or radio-tracking. The levels of deuterium (δD), which follow patterns in rainfall, are perhaps the most useful in studies of migratory birds: they give good latitudinal precision, but less good longitudinal precision (Hobson 2005). However, $\delta^{15}N$ and $\delta^{13}C$ values are of less value in this respect because drought conditions can enrich both, and natural regional variations in both are increasingly modified by human activities, such as fertilizer use and atmospheric pollution, reducing their value as geographical markers. Nevertheless, the method of isotope analysis provides better-than-nothing information for species with low recovery rates in the regions concerned, especially where analysis of several elements rather than one can give greater discrimination power.

Isotope analyses of soft tissues have also been used to address other questions, such as: (1) whether eggs were formed from food eaten in the immediate breeding area or from food imported to the breeding areas as body reserves accumulated in migration or wintering areas (Chapter 5; Hobson *et al.* 2000, Klaassen *et al.* 2001); (2) whether birds breeding in one region had accumulated body reserves on the same or different stopover sites (Atwell 2000, cited by Hobson 2003); and (3) whether particular individuals examined in a breeding area had spent the winter in good or poor habitat (knowledge which can then be related to migration and breeding performance, Marra *et al.* 1998). In addition, analyses of muscle have provided information on the changes in feeding areas and diets that occur during the course of a single migration (see Minami *et al.* 1995 for shearwaters migrating from the Southern Ocean to the North Pacific).

Analyses of trace elements in feathers have also been used to indicate the broad geographical origins of birds. This is possible because the proportions of different elements in feathers vary from region to region, according to geological substrate. Sand Martins *Riparia riparia* breeding in different parts of Europe

differed markedly in the elemental composition of their tail feathers, indicating that the birds from different breeding areas had moulted in different parts of Africa. 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 (Szép *et al.* 2003). Other studies of this type have involved Peregrine Falcons *Falco peregrinus* (Parrish *et al.* 1983), and various species of geese (Hanson & Jones 1976).

Some other bird populations drawn from the same species can sometimes be distinguished by their DNA. Using as a reference DNA samples from different breeding areas, birds sampled on migration or in wintering areas could be assigned to one or more of these areas (for Dunlin *Calidris alpina* see Tiedemann 1999, Wennerberg 2001, for passerines see Smith *et al.* 2005 for review see Wink 2006). However, the use of DNA markers is limited among birds because of the weak genetic differentiation found in many populations. This in itself results partly from the mobility of birds, and the consequent genetic exchange between populations in different breeding areas, and partly from their recent (postglacial) colonisation of northern regions, which has given too short a time for spatial genetic variation to arise (Chapter 22). In addition, DNA-based methods tend to be expensive and time-consuming.

CONNECTIVITY

All these various methods, from ringing and radio-tracking to isotope ratios and other internal markers, provide information on 'connectivity' – the geographical linking of populations at different times of year between specific breeding, migration and wintering areas. Connectivity can be classed as strong or weak (diffuse) depending on the degree to which individuals from different breeding areas mix in their non-breeding areas, or vice versa (Boulet & Norris 2006). It can be classed as strong if all individuals from a limited breeding area migrate to the same limited wintering area, and as weak if such individuals scatter among many wintering areas, intermixing with individuals from elsewhere. The importance of understanding connectivity is that conditions experienced by individuals in one part of the world can affect their subsequent performance in another part, hundreds or thousands of kilometres away (Chapter 26). These carry-over effects can be studied only if the birds from particular breeding areas can be linked to specific wintering and migration areas. They can occur at the population level (as with density-dependent effects on reproduction and mortality), or at the individual level (as when body condition at one time of year influences performance at another). Understanding such geographical linkages is also relevant to questions of the ecology, disease transmission and genetic structure of populations, and for effective conservation (Webster & Marra 2005).

STOPOVER ECOLOGY

Some birds perform their entire migration with a single bout of flying. This is true of some short-distance migrants which can cover the whole distance within a single day or night and of shorebirds and others whose migration routes lie entirely

over water or other unsuitable habitat, and may take up to several days and nights of non-stop flight (Chapter 6). However, the majority of birds break their journeys for hours, days or weeks at a time in places where the food situation can influence their fattening rates, and subsequent breeding or survival (Chapter 27). The term stopover ecology has been increasingly used for studies at stopover sites, where birds are often crowded, present for only a short time, and feeding hard in order to replenish their depleted body reserves and continue their journeys. Attempts are made to estimate the periods that individual birds are present, and by repeated trapping and weighing, to determine their rates of fuel deposition.

Stopover periods are generally hard to measure because one can seldom be sure exactly when particular birds arrive or leave. However, precise measures have been obtained for marked individuals of conspicuous species that can be seen throughout their stay (such as cranes and swans), radio-tagged birds that can be monitored daily, and other birds that visit such small sites that they can be caught within hours of their arrival, and then seen throughout their stay, and where there is no danger of confusing migrants with local residents, as at the garden of St Catherine's monastery in the Sinai desert (Lavée *et al.* 1991). Otherwise birds are often present in an area before they are seen or captured, and may also stay some time after the last observation or capture. Hence, in most studies stopovers have been estimated as minimum values between first and last sighting or first and last capture. Such estimates can be improved in various ways, for example by use of various statistical methods (Kaiser 1999, Schaub *et al*. 2001).

LABORATORY RESEARCH ON PHYSIOLOGY, MIGRATORY RESTLESSNESS AND DIRECTIONAL PREFERENCES

Laboratory research on bird migration began in the mid-1920s and rapidly gained ground. 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 (Chapters 11 and 12). An important discovery was that, at migration times, migratory birds in captivity developed migratory restlessness (*Zugunruhe* in German), in which they hop and flutter around their cages, an activity that can be registered automatically by use of electronic trips under perches (Chapter 12). Migratory restlessness in captive birds occurs either by day (in diurnal migrants) or at night (in nocturnal ones), and has been regarded by some as the laboratory equivalent of migration itself (see **Box 12.1**). It appears chiefly in birds from migratory populations and much less so, or not at all, in birds from resident populations. The number of days on which migratory restlessness is shown has been found to correlate with the natural duration of migration (and hence distance travelled) in the population concerned. Migratory restlessness therefore provides 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 12).

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. Metabolic rates, food consumption, fat deposition, body weights and migratory activity can all be studied at the same time.
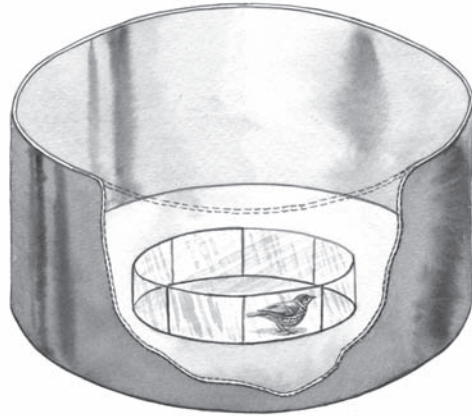
Figure 2.4   Equipment for measuring directional preferences of birds in field conditions: protective non-transparent wall around, and test cage within. The cage is shaped like a round cake. It is made of two circles of wire, connected by eight vertical wires. The top is covered with wire-netting through which the test bird can see the sky. The sidewall 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 the cage. The cage is placed in the centre of a circular fence of uniformly coloured solid plastic that prevents the bird from seeing any landmarks other than the sky. After a standard time (say 10 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. 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. From Busse (1995, 2000).

Another discovery was that captive birds also developed strong directional preferences at migration times. 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 inkpad on the floor. The pattern of footprints up the sides of the funnel (lined with white filter 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 (e.g. 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). The simplest of all such cages was designed by Busse (1995) specifically for use in the field on birds trapped on migration (**Figure 2.4**). Using only two cages, up to six birds can be tested each hour by a single observer.

Orientation cages can provide unbiased information on the directional preferences of birds caught at migration times at particular localities (Ozarowska *et al.* 2004). Most methods of analysing directional preferences (so-called circular statistics) start with the assumption that the birds sampled show only one main directional preference. Yet many individual birds that have been tested have

shown more than one migratory axis which is best expressed as a bi-vector individual pattern (see Busse & Trocinska 1999 for analytical method). In addition, when samples of migrants are caught and tested at particular localities, two or more migration axes frequently emerge, as birds migrating through the same locality but from different areas take somewhat different directions (Busse 2000). This is another reason for using a statistical method that can pick out the different directional preferences, rather than calculate a single amalgamated mean from all birds tested. While in theory directional information could be obtained from ring recoveries, in practice many years of data are needed, and geographical bias in ring reporting can distort the picture.

Another major benefit of studying migratory orientation in caged birds is that the external information received by the bird can be manipulated. For example, the perceived position of the sun can be altered by use of mirrors, star patterns can be modified in a planetarium, or the geomagnetic field can be altered using large magnetic coils (Wiltschko & Wiltschko 1995). These procedures facilitate study of the external cues that might be used by birds to determine their migratory direction (Chapter 9).

Wind tunnels

Recently developed wind tunnels have revealed much about the mechanics and energy needs of bird flight (Pennycuick *et al.* 1997). A wind tunnel creates a smooth (laminar) air flow in a test section where birds are trained to fly. The artificial wind speed can be adjusted so that, when the bird flies against the wind, it maintains a constant position in an observation section. Low turbulence is important in order to generate a natural situation reflecting flight through non-turbulent air but, if desirable, turbulence can be created by inserting nets or other objects upstream from the test section. Wind tunnels have been used to test flight mechanical theory (Chapter 3), to measure the metabolic costs of flight and to study flight style using high-speed video cameras. To yield meaningful results, especially on energy consumption, birds must be trained in the wind tunnel beforehand, so that they 'feel at home' there, and fly steadily, maintaining constant position against the wind for long periods.

In consequence of work with captive birds, we now have some understanding of how birds orientate on migration, of the energy costs of flight, and of the physiological preparation for migration that occurs at appropriate times of year, including the deposition of internal body reserves to fuel the flights.

BREEDING PROGRAMMES

Large-scale breeding programmes for captive migratory birds have revealed much about the genetic control and inheritance of different aspects of migration behaviour, whether timing, duration or directional preferences (Berthold 1996). The most convincing results have come from cross-breeding individuals of the same species but drawn from populations with different migratory behaviour (Chapter 20). 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 the least migratory individuals, populations became increasingly non-migratory. These experiments, conducted mainly on Blackcaps *Sylvia atricapilla*, confirmed that all major aspects of migratory behaviour were genetically controlled, and could be altered by selection (Chapter 20).

MATHEMATICAL MODELS

It is not enough in biology to know what animals do and how they do it. It is also important to understand the adaptive significance of morphological and behavioural features, and hence why animals have evolved to look and behave the way they do. Evolution can be regarded as a process of improvement (or optimisation) as animals become better adapted to what they have to do in order to survive and reproduce in contemporary environments. So-called optimisation analysis is a powerful approach to the study of adaptation, and has been increasingly used to test hypotheses about bird migration (Alerstam & Lindström 1990, Alerstam & Hedenstrom 1998a). Models are used to predict behavioural and other patterns that 'should' be observed if individuals follow one strategy or another, and the predictions are compared to field observations or experimental findings to see how well they fit, and hence to infer the likely strategy being followed by the bird. Optimal behavioural decisions during migration may involve matters of habitat selection, flight speed and altitude, whether to fly now or later, whether by day or by night, by flapping or soaring flight, which direction to head, how much account to take of winds, and so on. The theory of bird flight yields quite specific predictions on the speed and altitude of flight and how it is expected to vary with wind or fuel loads, all of which can be tested with field data.

Although the combination of modelling and field observation comprises a potentially powerful method for studying migratory adaptations, such models are heavily dependent on the assumptions on which they are based. These assumptions may be unrealistic and in any case are dependent on current knowledge which may be inadequate. Such models are nonetheless important in directing research, through defining more precise questions and the types of data that need to be collected. So far in migration research, models have proved especially useful in understanding flight behaviour, patterns of fattening, the timing and duration of the individual flights and stopovers that comprise migration, and the responses of birds to wind conditions (see papers in Alerstam & Hedenstrom 1998b). At present, there are more models than critical tests of their assumptions and predictions, giving plenty of scope for further research. Like any other ideas, however, formal models (often couched in mathematical terms) must be continually tested against experiments and field observations. Progress is often most rapid when predictions fail or are not supported by new data, showing that seemingly plausible ideas are probably wrong.

Optimality models have another potential pitfall. Optimality does not require that all individuals in a population behave identically. It requires only that individuals make decisions that maximise their own fitness, including making the best of a bad job. Different individuals may therefore pursue different tactics, dependent on their own physical condition at the time, and on the prevailing

environment as it affects them. Considerable variation in individual behaviour might then occur. The population might appear to be following no particular strategy, when in reality all individuals are behaving optimally for their own particular circumstances. One cannot interpret the significance of variability without information on the environmental conditions that affect the state and performance of the birds themselves at the time. Factors that influence individual variation are increasingly being incorporated into optimality modelling. In this book, I shall not dwell on the mathematical details of the various models (which are under continual revision), but with the physiological and ecological understanding that has emerged from their use.

As the study of migration has progressed over the years, rigorous statistical techniques have been developed to analyse the resulting data. Examples include the estimation of migration routes (Perdeck & Clason 1983), rates of movement (Nichols & Kaiser 1999), stopover durations and turnover rates of migrants at particular sites (Kaiser 1999), as well as the application of so-called circular statistics to the analysis of directional information (Batschelet 1981, Busse & Troćinska 1999).

CONCLUDING REMARKS

The scientific study of bird migration has developed over a period of about 120 years, beginning with the observations conducted at bird migration hotspots, such as Heligoland in the southern North Sea (Gätke 1895) and Fair Isle off northern Scotland (Clarke 1912). Early studies were mainly observational, but were frequently augmented by use of a gun to aid identification. The ringing and release of live birds began around the turn of the nineteenth century, and rapidly expanded as a scientific and recreational pursuit throughout the twentieth century, bringing an end to shotgun ornithology in migration studies. Observation and bird ringing were the major methodologies used through the first half of the twentieth century, but bird ringing also facilitated large-scale transplantation experiments designed to study the homing and navigational skills of birds. Throughout the latter half of the twentieth century, newer and increasingly more sophisticated methodologies were continually added, gradually spreading migration research to an increasing range of species, and enabling previously intractable questions to be addressed. Most of these methodologies, including radar and radio-tracking, were developed for very different purposes, but soon proved of value in studies of bird migration. Different approaches are being increasingly applied through collaborations between different specialists, integrating approaches which combine theory, field observations and laboratory studies, and linking physics, physiology and ecology with behaviour.

Migration research has been heavily dependent on the complementary contributions of amateurs and professionals. Amateur participation has greatly increased the numbers of active investigators and the geographical spread of studies. This has been especially evident in studies that depend on large-scale ringing and recovery (see the recent migration atlases, such as Wernham *et al.* 2002). Moreover, unlike many aspects of science, old methods (such as observation and ringing) are still contributing greatly to the growth in understanding. The cheapness of these methods means that they can be used effectively by anyone with an

interest in birds, however impecunious, and even the most ardent rarity-hunter has added usefully to our understanding of bird migration (Chapter 10).

Looking to the future, further breakthrough is likely once tracking devices have been miniaturised to such an extent that they can be used without ill-effect on smaller birds, when effective migration studies have spread to parts of the world where there has so far been little or no interest, and when better means are available for measuring the physiological condition of individual birds throughout their journeys. Intellectual breakthrough is also needed in several aspects, notably in the study of bird navigation.

SUMMARY

Bird movements have been studied by observations (made directly or with radar), by bird counts at particular localities in different seasons, by widescale distribution surveys, by use of ring recoveries to elucidate routes, and in recent years by the use of radio-transmitters or position locators fixed to individual birds which can then be tracked day by day on their journeys.

Most bird migration occurs at heights too great to be seen only with binoculars, and many species travel by night, so counts of migrating birds seen from the ground represent a small and variable proportion of those passing overhead. For most species, visual counts cannot, therefore, reveal the true volume of migration, or the weather conditions that favour it. At night, birds can be seen through binoculars or a telescope as they cross the lit surface of the moon, or through a powerful upwards-directed light beam. Night migrants can also be heard passing overhead, especially with a parabolic reflector and amplifier. The best measures of the volume of bird migration are made using radar, which can be used day or night in all weathers, but can seldom give precise identification of species.

Ringing is the main means by which the migration routes and wintering areas of breeding birds have been studied, together with any age or sex differences within populations. Ringing identifies individuals unequivocally, but tends to be concentrated in particular regions with high human interest. Similarly, recoveries tend to be biased towards areas with high human populations and literacy. Live birds in the hand can also be measured and weighed, providing information on weight gain and fat deposition; they can also be tested in orientation cages for directional preferences. Colour rings and other conspicuous tags enable birds to be identified at a distance without their being recaptured or killed.

Satellite-based radio-tracking can be used to follow individuals precisely on their journeys, wherever in the world they may go but, because of their weight, PTTs can be used safely only on large birds. Analyses of isotope or trace element signatures in bird feathers or other tissues have provided additional insights, linking birds from particular breeding areas with particular wintering areas, or vice versa.

Laboratory work has revealed relevant physiological processes and controlling mechanisms, and wind tunnels have been used to study various aspects of bird flight, including energy consumption. Studies of migratory restlessness and migratory orientation on captive birds have provided details of migratory timing and directional preferences in particular populations. Such studies are being increasingly extended to free-living birds.