1 Introduction

The environmental conditions for most living beings on our planet are characterized by the continuous influence of two geophysical cycles: diurnal and annual periodicity. These are caused by the earth's rotation around its axis and the seasonally changing altitude of the sun's position. The resulting diurnal patterns and the four seasons, with their characteristic features, bring with them constant changes in environmental conditions to which animals must adapt if they are to survive and reproduce.

A common response to this periodicity is migration. It occurs in almost all groups of living creatures—from bacteria and simple algae, through the many forms of invertebrates and the representatives of all classes of vertebrates, to humans. Many aquatic life forms, such as plankton, undertake diurnal vertical migrations, following certain diurnal courses of light, temperature, food supplies, and so on. Legions of animals leave their secure burrows or hiding places at specific times of the day, wander around for a time, especially in search of food, and finally return to their cover.

Diverse forms of seasonal migration have developed in response to the seasons. The simplest cases are vertical migrations in a geographically limited environment. Many primitive animals, such as earthworms, snails, and crickets, which inhabit the surface during the warm summer months, withdraw to lower strata with the approach of winter. This also applies to many vertebrates—examples would include some fish species that seek shelter in the mud of freezing lakes as well as amphibia such as frogs and toads, reptiles such as lizards and snakes, and mammals such as moles and dormice—but not to a single species of bird. Birds' seasonal migrations invariably take them to more or less distant areas, and—with one exception—all species remain active throughout the year, regardless of whether they are migratory or resident. The one exception is the Poorwill (*Phalaenoptilus nuttallii*) from southwestern North America. Towards winter, members of this species retire to suitable caves, where they carry out a genuine hibernation in which their body temperature, up to 40 °C in active birds, sinks to about 10 °C.

In birds, too, the simplest seasonal migrations are vertical movements. Just as red deer leave their alpine pastures towards winter and retreat to lower ground, many alpine birds migrate down to the valleys. In high mountains and subalpine regions in Europe this behaviour is exhibited by the Alpine chough (*Pyrrhocorax graculus*), the Water pipit (*Anthus spinoletta*), and the Wallcreeper (*Tichodroma muraria*). In addition, Alpine choughs may commute between altitudes of 500 m and 2000 m in their daily search for feeding or roosting sites.

Whereas these relatively short-distance migrations receive scant attention, we are fascinated by the seasonal long-distance migrations of many other animals,

whether because we hanker to follow them to warmer climes away from the approaching winter, or because we are astonished by their remarkable migratory performances and navigational abilities, or because their movements are surrounded by an intriguing aura of mystery.

Seasonal long-distance migrations can be found in many arthropod species. Marine crustacea (for example crayfish and lobsters) may migrate for several hundred kilometres on the bottom of the sea; swarms of locusts are known to invade large parts of continents; the American Monarch butterfly (*Danaus plexippus*) migrates up to 4000 km from its northernmost habitats in Canada to its winter quarters in Mexico; and European butterfly species, such as the Painted lady (*Cynthia cardui*) and the Red admiral (*Vanessa atalanta*), may migrate from northern Africa over the Mediterranean as far as Scandinavia and Iceland.

In vertebrates, seasonal long-distance migration is pronounced in all systematic classes. Among fish, the best-known examples are eels, salmon, and tuna, some of them covering thousands of kilometres as anadromous (river-ascending) and catadromous (river-descending) migrants between the sea and rivers or as migrants between oceans. Among amphibians, newts and toads cover several kilometres to and from their spawning grounds. Among reptiles, the best-known examples are marine turtles such as the well-known Green turtle (*Chelonia mydas*), which covers some 3000 km to reach specific coasts of remote islands to lay its eggs. Among mammals, long-distance migration is found in marine species such as whales and seals, and in polar bears, which may carry out continent-wide migrations of up to 20 000 km, as well as in gregarious terrestrial species such as reindeer and wildebeest, which cover great distances of up to 1500 km annually (Baker 1991). But these are all surpassed by the complexity and extent of the migrations found in birds. Birds are predestined to migrate through their capacity for active flight, their size, and their homoiothermy (warm-bloodedness), as well as through their morphological diversity coupled with great ecological differentiation.

Birds have conquered virtually all parts of the earth, and their migration routes encompass most of the earth's surface like a mesh (Fig. 1.1). This means that bird migrations can also be found in the Southern hemisphere. Many of these austral (southern) migrations lead northwards from breeding areas in the south to wintering areas nearer the equator. In extreme cases migrants cover distances equivalent to the circumference of the planet; they cross all our oceans, deserts, mountains, and icefields, with the possible exception of the poles (Gudmundsson 1992), and there is not a single month in the year in which birds do not migrate somewhere over the earth's surface. Many specific adaptations and control mechanisms are needed to make this all-embracing system of migration possible—even today they continue to be developed. Swift and continual changes in the environment, mainly of human influence, require ever new adaptations from contemporary migratory species.

This survey first of all gives an overview of the origin of bird migration (Chapter 2) and a history of its investigation and study (Chapter 3). This is followed by an overview (Chapter 4) of the most important methods currently employed to study the course of bird migration and its basic control mechanisms, and a discussion of field observations and field and laboratory experiments.

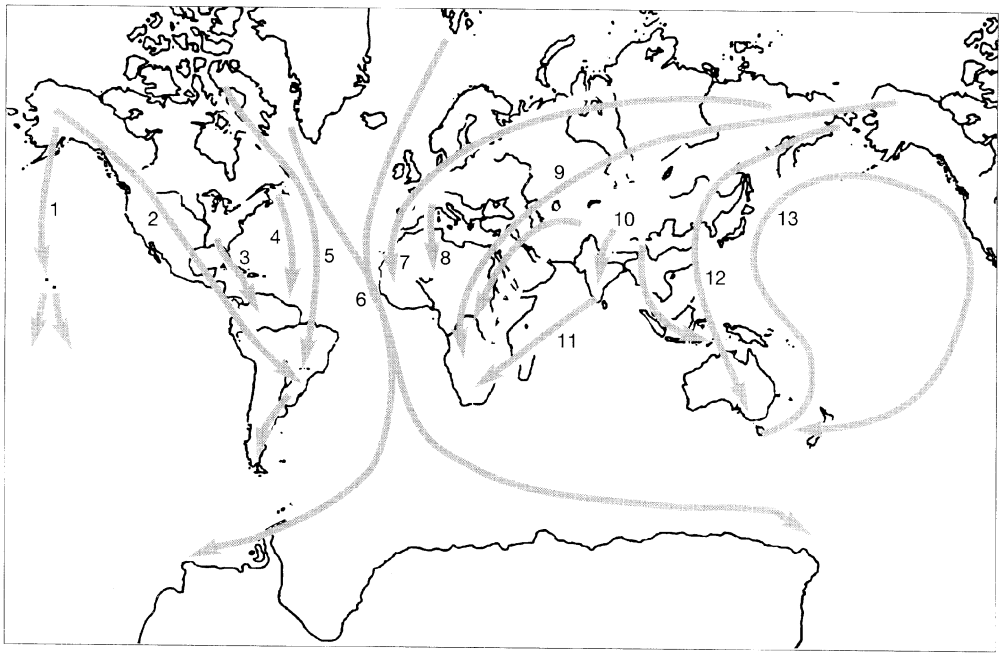

Fig. 1.1 Examples of migration routes of long-distance migrants during outward migration: (1) Alaskan population of American golden plover (*Pluvialis dominica*) and other waders to Pacific islands; (2) Swainson's hawk (*Buteo swainsoni*); (3) migration across the Gulf of Mexico by many North American species; (4) transatlantic migration of Blackpoll warbler (*Dendroica striata*); (5) and (12) Red knot (*Calidris canutus rufa* and *C.c. rogersi*); (6) Arctic tern (*Sterna paradisaea*); (7) Ruff (*Philomachus pugnax*); (8) trans-Saharan migration of many Eurasian species; (9) Alaskan population of Wheatear (*Oenanthe oenanthe*); (10) migration of three different Swallow (*Hirundo rustica*) populations to differing wintering areas; (11) Eastern Red-footed falcon (*Falco amurensis*)—only the transoceanic migration route is shown; (12) see 5; (13) circular migration route of Short-tailed shearwater (*Puffinus tenuirostris*).

Chapter 5 gives an impression of the variety of bird migrations and of record performances, and derives general rules. Chapter 6 discusses the physiological basis of migration, adaptations to its requirements, control mechanisms, and ecological factors. Chapter 7 deals with orientation mechanisms, especially the compass and navigation hypotheses, and Chapter 8 outlines how we can interpret the course and control of contemporary bird migration in the light of our present-day understanding of its mechanisms. Chapter 9 gives an up-to-date account of the current threats facing migratory birds and the conservation measures necessary for their protection. Chapter 10 deals with evolutionary aspects of present and future bird migration, and Chapter 11 explores the significance of bird migration for human society. Finally, Chapter 12 closes the survey with a short review of the future prospects of migratory birds and of research into migration.