CHAPTER 6

Cues and decision rules in animal migration

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Ice bars my way to cross
the Yellow River,
Snows from dark skies to climb
the T'ai-hang mountains!

(Hard is the journey,
Hard is the journey,
o many turnings,
And now where am I?)

So when a breeze breaks waves,
bringing fair weather,
I set a cloud for sails,
cross the blue oceans!

Li Po (701–762) 'Hard is the journey'

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6.1 Introduction

The sheer beauty and impressiveness of animal migrations have long puzzled observers and raised the questions of how these animals find their way, what initiates their migrations and how they manage to schedule their journeys at apparently the right times. There are many challenges that animals face before and during migration, and they can be grouped into two major categories namely '*where* to go?', dealing with orientation and navigation, and '*when* to go?', dealing with the timing of activities and migration schedules. As these questions are fundamentally different, we also expect different cues to provide relevant information. Furthermore, animals make decisions in relation to their physiological state and therefore, cues can be further categorized into internal and external signals.

In this chapter, we tackle these questions not in terms of *why* animals migrate (ultimate reasons), but *how* they make the right decisions before and during migration (proximate factors). Migrating animals rely on external and internal information such that they can tune their behaviour to their (changing) requirements and to the development of their seasonal environments. Here, we show that these cues, defined as 'signals or prompts for action' (*Oxford English Dictionary*), are not well understood, although they are most likely highly relevant both for advancing our fundamental understanding of migration and for increasing our capacity to manage and conserve migratory systems under the threat of environmental change.

In the following sections, we first characterize migration from different perspectives, as different migration types may require fundamentally different cues and decision rules. Thereafter, we introduce migration in the major migratory taxa that are readily observable to biologists, i.e. insects, fish, reptiles, birds and mammals, and seek to identify the cues that are used for the different steps during each of their migrations. We finish by highlighting the general lessons that can be drawn from this comparative study of cues and decision rules in migration.

6.2 Challenges in migration

6.2.1 Where to go?

Going along a specific track requires cues for positioning (navigation) and for finding the way towards the goal (orientation). Important cues for compass orientation include information from the magnetic field, the Sun and the related pattern of sky light polarization and stars, while information from, for example, landmarks and odours are used for navigation. Excellent reviews on orientation and navigation can be found in, for example, Åkesson and Hedenström (2007), and Newton (2008). However, for many migrating animals we still do not know how they find their way, which orientation and navigation abilities they have and which mechanisms they use (e.g. Alerstam 2006; Holland *et al*. 2006b).

6.2.2 When to go?

Photoperiod has been shown to be involved in the timing of activities for many species, e.g. initiating 'Zugunruhe' (restless behaviour as the premigration phase starts) or determining the speed of migratory progression. This may come as no surprise, as photoperiod is a reliable indicator of time of the year and thus can be a useful predictor for the phenology of resources (Fig. 6.1). Other local and short-term factors influencing timing of migration include prevailing weather conditions, e.g.

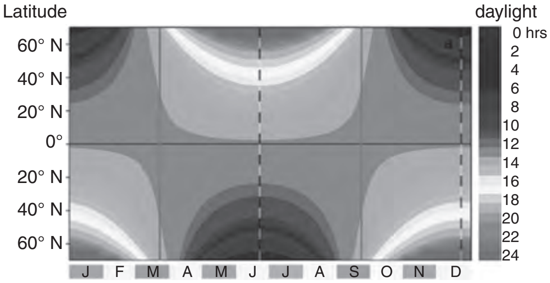

Figure 6.1 Photoperiod, i.e. day length, as a function of latitude and time of the year. Day length is here the time between dawn and dusk using civil twilight (Sun 6° below horizon). The different shades of grey indicate the day length with darker colours depicting continuous light or permanent darkness (from Bauchinger and Klaassen 2005).

temperature, wind, drought and precipitation, or water discharge in rivers, as these factors can significantly influence the costs of the travel ahead (Chapters 4 and 5).

There are also internal cues that serve as a clock or time-keeping mechanism. Additionally, physiological state and developmental stage are important cues as most migrants undergo morphological and physiological changes in preparation for migration and internal signals, e.g. hormone levels, indicate when these changes are completed (Chapter 5).

6.2.3 Seasonal and life-cycle migration

We can distinguish between two life-cycle patterns in migratory animals. In one type, which includes land reptiles, birds and mammals, most body transformations take place within the egg (reptiles and birds) or within the mother's womb (mammals), and the juveniles are only one or a few orders of magnitude smaller than the adult, and are generally well suited to the same environment as the adults. Migration in many of these animals is linked to a seasonal change in the environment and the cues involved typically predict these changes.

The alternative pattern includes organisms with complex life-cycles, such as arthropods, fish, amphibians and sea-reptiles, where animals spawn tiny eggs that develop into individuals with a body size several orders of magnitude smaller than the adults, and with a body form differing substantially from the adult form. During development, the major changes in the body plans often entail a habitat change and therefore, internal signals are required that are linked to these developmental processes as well as cues to locate the next favourable habitat. However, these organisms may also live in seasonal environments and, thus, the timing of ontogenetic processes will also depend on the phenology of the environment (Skelly and Werner 1990).

6.2.4 Travel with or without a predefined target

The best-known type of migration is that between a few specific localities, e.g. birds between wintering and breeding sites. In many cases, however, the migration does not lead to a specific locality or even to a certain more broadly defined area: In several species of pelagic fishes, both long-distance feeding and spawning migrations need not lead to a specific target. Feeding migration is often driven by continuous local food search (Huse and Giske 1998; Nøttestad *et al*. 1999), while the return spawning migration combines long-distance tracking of preferred spawning sites with physiological constraints from swimming costs (Huse and Giske 1998; Slotte and Fiksen 2000). Although some large insect migrants, such as Lepidoptera (butterflies and moths) and Odonata (dragonflies) have regular, bidirectional seasonal long-distance migrations that involve movements that are directed in predictable ways but not targeted at a specific site or region (e.g. Chapman *et al*. 2008a, 2008b; Wikelski *et al*. 2006), most insect migrations do not even involve movements in consistent, seasonally preferred directions.

6.2.5 Genetic or cultural transmission of migratory behaviour

How do offspring decide where and when to migrate? Migratory behaviour can be both genetically and culturally determined. In cultural transmission, the young copy their parents' (or other group members') behaviour. Consequently, species with culturally-transmitted migratory behaviour are expected to have a social life-style, longer lifespans and (in higher vertebrates) extended parental care. Prominent examples include schooling fishes (e.g. the culturally-induced change of migration patterns and over-wintering sites in herrings; Huse *et al*. 2002), geese and swans among birds (e.g. Von Essen 1991), and large herd-living mammals such as antelopes and wildebeest.

Alternatively, migratory behaviour, e.g. routes, threshold photoperiods, or preferred directions, can be genetically transmitted when there are no parents, peers, or elders—be it due to high mortality, short adult life-span, solitary life-style, absence of parental care or separation of age classes, e.g. age classes or generations have different requirements or constraints (differential migration). Examples of genetic transmission of migratory behaviour include some birds (e.g. the majority of small passerines and the European Cuckoo *Cuculus canorus*), all insect migrants and sea turtles (hatchlings complete their migration alone, and have to return to the same beach to breed when reaching sexual maturity many years later).

Besides the general insights, how (part of) migratory behaviour is transmitted is also highly relevant with regard to global and local environmental changes. A first review of the effects of environmental change by Sutherland (1998), concentrating on birds only, showed that none of the species with culturally determined migration routes had sub-optimal routes, i.e. longer than necessary, while approximately half of the species with genetically transmitted routes had become sub-optimal. There is thus a risk that environmental changes may occur faster than natural selection, particularly for long-lived and less fecund life forms. Whether these findings also apply to other taxa has yet to be shown. Exceptions to this general pattern appear to be zooplankton and insects—with their short generation times and high reproductive rates, many insect pests, for example, are able to adapt to changing conditions rapidly.

6.3 Cues in the different phases of migration

Migration can be divided into a few major steps—preparation, departure, on the way, and termination—a cycle that might be repeated if migration is suspended at intermittent stopover sites. Each of these steps potentially requires specific cues and decision rules as their demands on the animal's physiology and behaviour differ. Similarities might exist across taxonomic groups in how animals deal with each of these steps but differences may also be expected depending on the specific way of migrating or their particular environment.

6.3.1 Migration in plankton

The annual or seasonal migrations in plankton probably include a higher number of migrants than any other group (e.g. 10^{15} individuals of Antarctic krill *Euphausia superba*). As an example we present the much-studied *Calanus finmarchius*, which is among the most abundant species of marine calanoid copepods. These North Atlantic copepods reach an adult body size of a few millimetres, and spend most of the year in a survival mode in deep waters. Although the exact depth varies with local conditions and the state of the individual, and may range from a few hundred metres to >1000 m (Kaartvedt 1996), it is vital that they descend deeper than the winter mixing zone to avoid passive retransport to the surface layers during winter. The minimum energetic cost during over-wintering occurs where the organism is buoyant, so the individual variation in over-wintering depth probably comes from variation in storage tissue in the form of wax esters (Heath *et al*. 2004). Only a small fraction of the wax esters produced in the preceding feeding season are consumed during over-wintering (which is also sometimes called hibernation, diapause, dormancy or resting stage, Hirche 1996). Most is saved for conversion to eggs in or near surface waters in spring.

Preparation and departure: These copepods undergo a series of moults during their life, with six naupliar stages followed by five copepodid stages before adulthood. Overwintering is usually restricted to the fifth copepodid stage (C5). Since the maximum efficiency in converting food to storage occurs in the C3–C5 stages, the eggs of the over-wintering adults must hatch in time to grow and develop through the naupliar stages in time for C3–C5 to hit the spring-peak in phytoplankton production. Thus, ascent from deep waters must be timed well in advance of the peak. Depending on the food conditions in the surface waters, the copepods may produce one or several generations during spring and summer. Only the last of these generations will descend to the diapause depth. This migration pattern is therefore not genetically hard-wired, but also depends on one or more environmental signals.

On the way and termination: There are still several plausible suggestions for cues involved in the seasonal migrations for plankton in general and the species *C. finmarchicus* in particular. The matter is further complicated as this latter species lives in a very diverse range of environments in the North Atlantic Ocean and adjacent seas, and cues that are reliable in one area may not be so in another. Therefore, Hind *et al*. (2000) modelled the seasonal dynamics of the species in four different areas: the North Sea, the Norwegian Sea, the Iceland Shelf and in a northern Norwegian fjord, to test which set of cues would produce viable populations in all of these areas. They found only one set of cues that produced realistic population dynamics in all areas. This set consisted of four cues: (i) an external signal; (ii) an inherited threshold for the downwards migration; (iii) a physical characteristic of the over-wintering depth for the organism (buoyancy); and (iv) an internal cue for timing of ascent. If ambient food concentration is above the inherited threshold value for environmental food concentration, C4 copepodids develop towards adults and another generation in surface waters. If food levels are below the threshold, they sink after moulting to C5. Having reached the over-wintering depth, they continue to develop at a constant rate, but slower than for surface dwelling organisms. The cue for ascent to the surface is that the organism has completed 80% of the development of the C5 stage. However, one should bear in mind that this is only an ultimate test (population dynamics modelling) of the proximate mechanisms—neither the physiological nor developmental mechanisms are understood so far.

6.3.2 Migration in insects

Although migration occurs in all major insect orders, the actual migrations may often go unnoticed due to the small size of most insects, and the tendency of many species to migrate at great heights above the ground. However, the utilization of fast air currents allows many species to cover enormous distances (hundreds or even thousands of kilometres), often within just a few days and the consequences of these invisible large-scale insect movements may be highly conspicuous wherever they terminate. Some insect migrations are highly noticeable; among the most impressive of natural phenomena are the mass migrations in enormous cohesive swarms of a few species (e.g. the desert locusts *Schistocerca gregaria*, the dragonfly *Aeshna bonariensis*, and the monarch butterfly *Danaus plexippus*), which rival the largest flocks and herds of migratory birds and mammals in terms of biomass, and far exceed them in total numbers (Holland *et al*. 2006b).

Insect migrants typically do not make round-trip journeys, where the same individuals return to their natal area, nor do most species carry out bi-directional seasonal movements between separate breeding and wintering grounds. Instead, successive generations engage in windborne displacements through the landscape, most likely in an attempt to locate transient and patchily distributed favourable habitats. The majority of insect migrants take advantage of fast windborne dispersal and fly at altitudes of from several tens of metres up to a few kilometres above the ground. Relatively few species migrate predominantly within their flight boundary layer (FBL), i.e. the narrow layer of the atmosphere closest to the ground within which their airspeed exceeds the wind speed (Taylor 1974)—this is mostly restricted to large, day-flying species, such as butterflies and dragonflies (e.g. Dudley and Srygley 2008).

In most species, migration is restricted to the adult—winged—life stages and to a single brief time window of just a few days, due to the short adult life-span and further because migration typically takes place in the brief period of sexual immaturity immediately following metamorphosis from the immature stage to the adult (aka oogenesis-flight syndrome, Johnson 1969).

Preparation: The development of full-sized wings and associated musculature is obviously the most important preparation and many species, e.g. aphids, have the ability to produce offspring with varying levels of flight capability in response to environmental conditions, e.g. decreasing plant nutritional quality, and increased crowding. Exceptions to this general pattern exist in longer-lived species such as the monarch butterfly *Danaus plexippus*, which builds up substantial fuel reserves by foraging as adults, and tops these reserves up during intermittent stopover episodes.

The juvenile hormone and its esterase mediate a range of correlated factors associated with migration, e.g. timing of reproductive maturation, fuel deposition, development of larger wings and wing-muscles, and increased flight capability.

Departure: Owing to the very short window for migration in most species, opportunities to choose the departure time are rather limited and mainly concern questions of whether to migrate on a particular occasion and at what time of the day to migrate.

For time of the day, two basic options exist—diurnal migrants take advantage of the higher air temperatures and greater illumination (presumably facilitating orientation), while nocturnal migrants benefit from the absence of convective up-draughts and down-draughts and thus can control their altitude to a much greater extent than day-flying insects, taking advantage of warm, fast-moving, unidirectional air currents (Wood *et al*. 2006; Chapman *et al*. 2008b).

The decision whether to initiate migration on any particular occasion varies between species. Many insect migrants will not take off when wind speeds at ground level are too fast (more than a few m/s), as they cannot control their flight direction immediately after take-off (e.g. green lacewings *Chrysoperla carnea*, Chapman *et al*. 2006). However, as the migration window of most species generally lasts for just a short period (e.g. two nights in lacewings), they are unable to migrate if confronted with extended periods of strong winds, or are forced to do so in unfavourable conditions.

More complex decision rules are required for species that need to move in a particular direction, e.g. south in the autumn to escape northern hemisphere winter conditions. Some species are able to gauge the presence of favourable high-altitude tailwinds, facilitating southerly displacement in the autumn. An example for this is the potato leafhopper *Empoasca fabae*—a small insect that is entirely dependent on windborne displacement to escape deteriorating winter conditions in northern regions of the US by migrating to its diapause site in the southern US. Autumn migrants initiate their flights in response to falling barometric pressure, which is indicative of the passage of weather fronts that are followed by persistent northerly air flows, thus facilitating long-range transport of the leafhoppers to the south (Shields and Testa 1999).

Green darner dragonflies have a number of simple decision rules that guide their autumn migrations along the eastern seaboard of North America in a favourable, southerly direction (Wikelski *et al*. 2006). They initiate migratory flights on days following two preceding nights of dropping temperatures, which are highly likely to be associated with persistent northerly air flows, and then simply fly in the downwind direction while avoiding being carried over large water bodies (and thus out to sea). Red Admiral butterflies also choose cold northerly tailwinds for their return migrations from Scandinavia—they fly at high altitudes when fast-moving winds from the north predominate, but low down when migrating in headwinds (Mikkola 2003).

On the way: Many insect migrants are too slow-flying compared with the speed of the air currents to influence the direction and speed of their movement. The most efficient strategy then is simply to fly downwind if the migrants are able to perceive the direction of the current (either through visual assessment of the direction of movement relative to the ground, or via some wind-related mechanism). There is considerable evidence that many high-altitude migrants are capable of aligning their headings in a more-or-less downwind direction (e.g. Reynolds and Riley 1997), and given that winds blow in favourable directions, displacement distances will be considerably longer than if the insects flew across or against the wind (e.g. Wood *et al*. 2006).

Migrants that fly predominantly within their flight boundary layer (FBL; Taylor 1974) can control their direction of movement irrespective of the wind direction. This is the case for butterflies, which are powerful fliers and can maintain migration speeds of 5 or 6 m/s for several hours a day, and for many consecutive days. To guide their migrations in seasonally-favourable directions, these butterflies must have a compass mechanism. A well-known example is the monarch, whose eastern North America population undergoes an annual autumn migration of up to 3500 km from the late-summer breeding grounds in eastern Canada and North-Eastern United States to the communal wintering site in central Mexico. But how do the monarchs orient their flight headings in the correct direction? Work by Mouritsen and Frost (2002) has demonstrated that autumn-generation monarchs have a preferred migratory heading towards the south-west, and that during sunny conditions they use a time-compensated solar compass to select and maintain this heading. In spring, successive generations of monarchs move progressively northwards through North America and presumably use the same orientation mechanism, but in reverse, to guide their migrations.

Migratory tracks of day-flying FBL insect migrants (butterflies over the Panama Canal) occur in predictable seasonal directions (from the Atlantic wet forest to the Pacific dry forest at the onset of the rainy season), and in at least two species (*A. statira* and *P. argante*) these preferred directions are maintained by reference to a time-compensated solar compass (Oliveira *et al*. 1998), i.e. use of visual landmarks on the horizon to compensate for crosswind drift away from their preferred migration directions (Srygley and Dudley 2008). Measurements of wind speed and air speed also indicated that these butterflies adjusted their air speed in relation to wind speed and their endogenous lipid reserves, so that they maximized their migratory distance per unit of fuel (Dudley and Srygley 2008; Srygley and Dudley 2008).

Chapman *et al*. (2008a, 2008b) have demonstrated that high-flying migrants, hundreds of metres above their FBL, can also influence their displacement direction even though wind speeds far exceed their own air speed. The moth *Autographa gamma* is able to select flight headings that partially compensate for crosswind drift away from its preferred seasonal migration directions, thus maximizing the distance travelled while influencing its migration direction in a seasonally-advantageous manner. Using a combination of altitude selection to fly in the fastest winds, and taking up advantageous headings, they can cover up to 600 km in seasonally adaptive directions during a single night's flight (Chapman *et al*. 2008a, 2008b).

Termination: The very act of migration slowly reduces the inhibition of responsiveness to 'appetitive' cues that is typical of migratory flight (Dingle and Drake 2007), and thus migratory behaviour itself slowly promotes its own termination. The vast majority of insect migrants only undertake one, or at most a few, bouts of migratory flight, and so the factors that bring about termination of a single bout of flight are often the same as those that bring about the termination of the whole migratory phase. These include depletion of fuel reserves, changes in photoperiod (e.g. nocturnal insects rarely migrate into daytime, and diurnal species rarely carry on into night-time: e.g. Chapman *et al*. 2004; Reynolds *et al*. 2008), and changes in temperature (e.g. migrations of nocturnal insects are often terminated due to a drop in temperature as the night progresses (Wood *et al*. 2006)). If the habitat after the termination of the initial migratory bout is suitable, then that will usually signal the end of the migratory phase, otherwise migration may continue for another bout. In some species, the flight muscles are autolysed and converted to increased egg mass after migration, i.e. they become effectively flightless.

6.3.3 Migration in fish

Although there are about 30 000 species of teleost fish, only a small fraction of them are currently known to be migratory. However, these few species are the dominant marine species in terms of biomass and numbers, and most of the world's fish catches are based on them. Many types of migration exist in fishes, e.g. from freshwater natal areas to the sea (or vice versa), and between feeding and breeding grounds in the sea. Here we illustrate some characteristics of fish migration by introducing two prominent examples, namely life-stage migration in salmon and feeding migration in herring.

6.3.3.1 Life-stage migration in Atlantic salmon

As predation pressure is considerable in the estuary and beyond, schooling behaviour is advantageous and therefore so is size similarity amongst smolt. This is achieved through growth control by the parr,

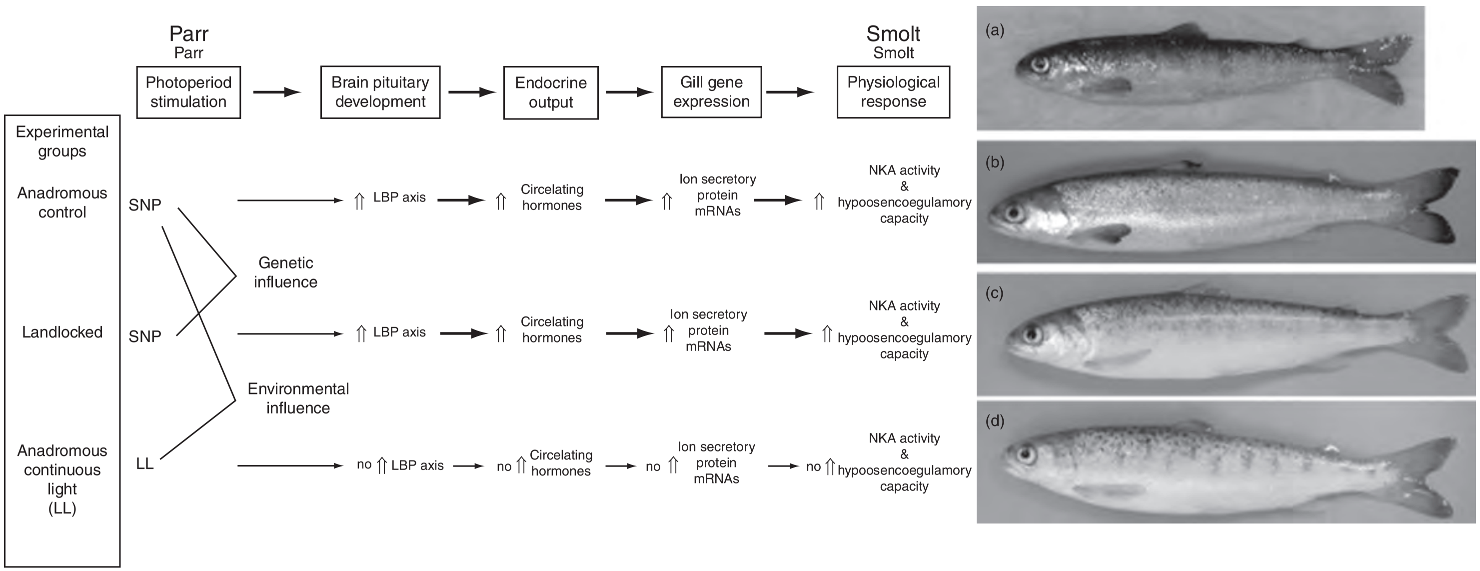

Figure 6.2 The sequence of events occurring during the parr–smolt transformation (smoltification) in salmon leading to hypo-osmoregulatory development, or not. Here three experimental groups of Atlantic salmon are presented: anadromous control, parr in February (A) and smolt in May (B) reared under simulated natural photoperiod (SNP); landlocked in May (C) reared under SNP; and anadromous control in May reared under continuous constant light (D) to demonstrate the importance of brain development of the light–brain–pituitary axis (LBP) early in smoltification on the downstream endocrine output, gill gene expression and hypo-osmoregulatory capacity. The degree of LBP development is reflected through all downstream processes including physiological development and Na^+, K^+-ATPase (NKA) activity (Ebbesson *et al*. 2007; Nilsen *et al*. 2007; Stefansson *et al*. 2007). Reproduced with permisson.

which is the life stage of young fish in the river before smoltification. Smoltification is the process in salmonid parr of preparing for their downstream, seaward migration and includes a suite of physiological, morphological, biochemical and behavioural changes (Fig. 6.2). Under very benign growth conditions, smoltification can happen during the first year of life, but in northern populations this may take up to seven years. The smoltification decision is based on internal stimuli but the relationship between the parr's body condition and the initiation of smoltification is poorly understood (Stefansson *et al*. 2008). According to Thorpe (1977), a bimodality in size appears in the second (or later) autumn. Only parr larger than 7.5–8.5 cm fork length eventually leave the river as smolt the coming spring. Once the decision on smoltification is made, the parr changes into a fast growth mode, where the growth rate may be 4–5 times higher than before. If the parr decides to wait, it even goes into anorexia during the winter (Stefansson *et al*. 2008).

The next external stimulus is the change in day length in the following spring, probably combined with exceeding a temperature threshold. This leads to growth of the brain and the pituitary gland, leading afterwards to the release of a series of endocrine hormones. This, in turn, activates gill genes and initiates the physiological processes leading to the smolt stage (Stefansson *et al*. 2008). The final downstream migration is triggered by a combination of light regime, temperature and river discharge (Hoar 1988), leading to simultaneous mass migrations into the estuary. The smolt will usually remain there for some months before migrating into the open ocean, usually as solitary individuals.

How can the salmon find its way back to its native river, small or large, hundreds of kilometres away and 1–4 years later? Homing to the river is also driven by a combination of internal and external factors. Several hypotheses have been suggested including a pheromone trail left by out-migrating fish, counter-current swimming, navigation by stars, and geomagnetism (Lohmann *et al*. 2008). It is quite clear that salmon utilize smell and learned cues in the later homing phase. Magnetic crystals have been found in the lateral line sensory system of salmon (Moore *et al*. 1990) and in the olfactory lamellae of trout (Walker *et al*. 1997), which they might use for long-distance navigation. Therefore, they probably use a combination of geomagnetic information (for long-distance directional migration) and smell and imprinting cues (for choosing the correct river and stretch of it).

Preparation in parr: While food abundance is the driving force for the seawards migration in all size classes, the change from hypo- to hyper-salinity requires a major transformation of the metabolism and, additionally, changes in behaviour and skin pigmentation as the young salmon transforms from a bottom-dwelling territorial parr into an open-water schooling smolt. As this decision is taken long before the actual migration, cues for preparations come from both internal and external sources—once a threshold body condition (size) is reached, day-length initiates the onset of body and metabolism changes.

Departure in smolt: After having completed all body changes, the smolt often waits for the autumn river discharge to depart and go downriver seawards.

On the way smolt: Seawards, the smolt remains for some time at the estuary to become imprinted and then leave for the ocean in groups, where they become solitary again and mainly follow food. On their way back, they probably initially use some sort of magnetic field orientation, and gradually change to olfactorial orientation when they are near the home-river (e.g. Healey and Groot 1987).

Termination in returning adults: Once they have arrived in their target area in the natal river, migration is suspended.

6.3.3.2 Feeding migration in pelagic fish: an undefined target

In several species of pelagic fish, long-distance migrations may be directional rather than to a specific localizable target, e.g. mackerel *Scomber scombrus* and blue whiting *Micromesistius poutassou* migrate northwards from spawning areas around the British Isles into feeding areas in the Norwegian Sea. Thereby, they benefit both from the later spring and summer further north, and also from the gradual increase in daylight-hours in the northern summer. Both factors contribute to prolonged high feeding and growth rates (Nøttestad *et al*. 1999). Similarly, herring *Clupea harengus* migrate westwards from the mild Atlantic waters off the coast of Norway towards the colder waters in the west, with delayed spring production (Varpe *et al*. 2005). For some decades, the whole adult population of Norwegian spring spawning herring has been over-wintering in the deep Tysfjord in northern Norway. Spawning migration in spring is southwards along the coast of Norway. The further south the eggs are spawned, the better the prospects for larval growth and survival. However, as migration is energetically costly, there is a trade-off between fecundity and migration distance such that small individuals migrate shorter distances and larger individuals longer, i.e. further south (Slotte and Fiksen 2000). Hence, the likely cues are a combination of physiological state (spawning migration in herring) and a seasonal signal such as day length (end of northwards or westwards feeding migration).

Very little, if anything, is know about how fish find their way and make decisions. Geomagnetism has been proposed for long-distance navigation (e.g. Lohmann *et al*. 2008). Many of the species also migrate in large schools, which may act as cooperative units for food searching (Clark and Mangel 1986) and decision-making (Huse *et al*. 2002). Thus schooling acts both to reduce predation risk, and to increase the chance of being on the right track for future food resources. During the feeding migration, models indicate that a long-distance direction finder may not be needed as the fish simply follow the seasonal development of the food, which will automatically lead them to profitable places (Huse and Giske 1998). However, models also indicate that a separate 'homing motive' is needed for the return migration, during which local gradients in food or temperature may not be helpful (Huse and Giske 1998). Unfortunately, it is not known whether the decision to return is based on some seasonal signal or the state of the organism, or both.

6.3.4 Turtle migration

Long-lived sea turtles regularly commute between two completely different environments, the open ocean for foraging and sandy shores for egg-laying. Some sea turtles, e.g. the leatherback turtle (*Dermochelys coriacea*), spend several years foraging in pelagic habitat (e.g. Hays *et al*. 2004) and accumulate body stores, which they later use for mating and producing eggs. These two habitats are usually separated by vast areas of unsuitable habitat and, consequently, migrations are often long.

Others, e.g. herbivorous green turtles (*Chelonia mydas*), also lay eggs on sandy beaches but forage as adults on sea grass and algae along shallow coastal areas (e.g. Mortimer and Carr 1987, Bjorndal 1997). One of the longest distance migrations is performed by Ascension Island green turtles, migrating between breeding sites at Ascension Island and foraging areas along the Brazilian and Uruguayan coasts (Carr 1984; Papi *et al*. 2000; Luschi *et al*. 2001).

It is well known that sensory information is important for navigation by hatchling sea turtles when they depart to the sea (Lohmann and Lohmann 1996; Lohmann *et al*. 2008), but it is less well understood what information is used by the adults when returning to breed (Luschi *et al*. 2001; Åkesson *et al*. 2003). Even less is known about the migratory behaviour and information used by sub-adult sea turtles (Godley *et al*. 2003) and how the transition takes place from the genetically programmed guidance of the hatchlings into the migration programme guiding the sub-adults and adults later in life (Åkesson *et al*. 2003). Most likely, the turtles use partly genetically encoded behaviours, but also learn to incorporate a number of cues into their navigational toolbox (Åkesson *et al*. 2003).

Preparation: Many sea turtles need several years to recover from a major migration and egg-laying event and during this time they store fat as fuel. For example, female Ascension green turtles migrate to the island to lay eggs, where they do not forage at all for 5–6 months. Apparently they exhaust most of their reserves during the event, such that their recovery and preparation for the next migration and breeding bout requires approximately 3–4 years (Carr 1984).

Departure: Hatchlings: When the hatchlings in a clutch escape from the nest, they first climb to the surface of the sand during the day and await the night. At that stage they are stimulated by their nestmates' movements such that all siblings leave at night in a synchronized fashion. Once in the water, they mix with other hatchlings and depart on their independent migratory journeys. When they depart to open sea, their movement is both active and passive, i.e. partly swimming and partly drifting with the currents. The timing of departure relative to the season very much depends on the timing of egg-laying, which again depends on the foraging conditions encountered in the wintering areas (Godley *et al*. 2001).

On the way: Sea turtles have been shown to use a number of different cues to orientate and navigate during migration (e.g. Lohmann and Lohmann 1996, Åkesson *et al*. 2003). Loggerhead turtle hatchlings (*Caretta caretta*) respond to light when leaving the sand and moving along the beach; later they have been shown to swim against the waves to leave the shore and, once they are in more open water, they probably use magnetic field information for navigation as has been shown in experiments manipulating the magnetic field (Lohmann *et al*. 1999, 2001). Studies on adult green turtles have tried to identify cues used during migration, but also when searching for the breeding island after displacement. It was found that successfully homing turtles responded to local information, suggesting they are using information carried with the wind from the island (Papi *et al.* 2000; Luschi *et al*. 2001; Åkesson *et al.* 2003).

Termination: For all sea turtles, breeding migration ends as soon as they have reached the breeding grounds. During foraging migrations, differences exist between the pelagic species, such as the leatherback turtle, that can be considered to be constantly moving and exploring the open ocean environment (Hays *et al*. 2004), and coastal foragers, such as the green turtle, which forage along shallow coastal sea-grass beds.

6.3.5 Bird migration

The classic bird migration is the biannual migration between breeding and wintering grounds. The breeding grounds are suitable for nesting and hatchling/fledgling survival, whereas the wintering grounds are more suitable for post-fledgling and adult survival. Because birds are able to fly, they can travel long distances relatively cheaply and quickly (Chapter 4), e.g. the longest non-stop migratory flight recorded is that by bar-tailed godwits (*Limosa lapponica*) crossing the Pacific Ocean from Alaska to New Zealand, a distance of more than 10 000 km (Gill *et al*. 2009).

Exceptions to this are moult and facultative migrations. In moult migrations, birds appear to migrate to predator-free areas where they can safely shed their flight feathers. In facultative migrations, birds only migrate long distances when food is sparse, e.g. many finches (Newton 2006). At an extreme end of the spectrum are birds that are nomadic, like the grey teal (*Anas gracilis*) looking for ephemeral water and food sources in a desert landscape in Australia (Roshier *et al*. 2008).

Two main flight modes exist—flapping and soaring—each having particular consequences: Flapping flight is very costly but can be used under a wide range of weather and topographic conditions, whereas for soaring, thermals or wind are needed (Chapter 4).

The majority of birds cannot feed while flying, and in many cases the total travel distance exceeds the maximum flight distance. Thus, the birds need stopover sites where they can replenish their reserves. A good example is tundra swans (*Cygnus columbianus*), which migrate 4000–5500 km (Nolet 2006), whereas their maximum recorded non-stop flight is 2850 km (Petrie and Wilcox 2003). These swans mainly refuel on energy-rich, below-ground parts of macrophytes in shallow lakes and wetlands along the route (Beekman *et al*. 1991).

Preparation: Before actually embarking on migration, most birds partly change the composition of their bodies, e.g. increase flight muscles at the expense of leg muscles, atrophy digestive and metabolic organs (Piersma and Gill 1998; Biebach 1998; van Gils *et al*. 2008; Bauchinger and McWilliams 2009) and accumulate body stores. Photoperiod is an important external signal for preparations; it has been shown to initiate 'Zugunruhe', i.e. migratory restlessness in many migratory passerines (Gwinner 1990), but also many geese, swans and waders start accumulating body stores, altering their digestive system and building up flight muscles from a particular day length onwards. The specific value of day length at which these transformations are started is under strong genetic control, as evidenced by hybridization, parent–offspring comparisons and effects of changing selection pressures (Newton 2008). Birds kept under constant day length for up to several years still showed a circannual rhythm with the right sequence of annual events (migratory fat deposition and restlessness, gonad development, and moult) suggesting that getting into the migratory state is under internal control (Gwinner 1977). But these cycles tend to drift and be either shorter or (most often) longer than a calendar year. This internal control is most rigid in long-distance migrants that are normally confronted with most variation in day length.

Thus, under natural conditions the exact timing of events is most likely determined by a combination of internal and external factors such that the internal system is adjusted by seasonal changes in photoperiod, as has been shown with experiments with extra light or shorter than annual cycles (Newton 2008).

Departure: The exact timing of migratory departure is fine-tuned by secondary factors like temperature, wind, rain and food supplies (Newton 2008). Birds have been shown to choose favourable flight conditions and preferably leave on days with tailwinds and no rain. In the Swainson's thrush (*Catharus ustulatus*), departure decisions are best predicted by both a high daily temperature (>20°C) and low wind speeds (<10 km/h) at the time of presumed take-off. If one of these conditions is not met, the individual will not take off. However, such apparently strict rules also lead to serious errors, e.g. individuals take off at low local winds, and yet ascend into air streams that will push them backwards against their flight direction (Cochran and Wikelski 2005).

One means by which birds may forecast improving weather conditions before they actually occur has been hypothesized to be sensing air pressure changes (Newton 2008, Keeton 1980). In facultative migrants, departure may also be delayed until weather conditions for refuelling deteriorate (Newton 2008; Gilyazov and Sparks 2002).

The decision to depart from a stopover site is probably based on rather simple behavioural rules. Passerines that lose or increase fuel stores at a high rate leave a site quickly, whereas the intermediate birds stage the longest (Schaub *et al*. 2008). Geese use a mixture of endogenous and external cues, with the endogenous cues having a stronger effect as the season progresses (Bauer *et al*. 2008, Duriez *et al*. 2009).

On the way: Birds have been shown to use several cues to guide them in the right direction on long-distance migrations. The combination of cues may be essential for correct navigation as directional cues change with place (e.g. the magnetic compass; Wiltschko and Wiltschko 1972) and time (e.g. the sun compass; Kramer 1959). Birds use a combination of cues for recalibration. For instance, recent experiments suggest that birds use cues from the setting Sun to re-calibrate their magnetic compass before migrating at night (Cochran *et al*. 2004). At sunrise or sunset, birds can use skylight polarization, especially visible close to the horizon, as a compass (Able 1982; Muheim *et al*. 2006). Uniquely to birds, star patterns that indicate the axis of rotation of the night sky have been hypothesized to be a directional tool (Newton 2008). However, laboratory-based experiments on stellar orientation in birds could also be explained by the fact that individuals have the rule to use the single brightest and non-moving light as the main orientation cue.

If birds do not compensate for the change in local time when travelling across longitudes, a sun compass would lead them along routes similar to great circle routes (Alerstam and Pettersson 1991). In contrast, if they compensate and reset their internal clocks regularly while crossing longitudes, they would follow a constant rhumbline route (Fig. 6.3). Birds following one (Alerstam *et al*. 2001) or the other (Green *et al*. 2002) have been found.

The direction of migration is also under endogenous control (Gwinner and Wiltschko 1980; Helbig 1991). The direction is reversed when the return migration starts (Newton 2008). Together, the inherent period and direction of migration result in naive migrants being able to stop in the right area. Juvenile starlings that were trapped on migration and displaced by aeroplane to Switzerland, east of the usual wintering area of the population, continued their migration in the same direction and over the same distance that they would otherwise have flown and ended up in southern France or Spain (Perdeck 1967). In contrast, the trapped adult star-

Figure 6.3 Two extremes: a global view of the Earth from space (insert; orthographic projection centred in the Wadden Sea 54 °N, 8.5 °E), and a Mercator projection flattening and stretching the globe. On the Mercator projection all straight lines are constant geographic bearings (loxodromes, rhumblines), whereas straight lines through the centre of the orthographic projection represent great circles (orthodromes). Note that the scale at the Equator is similar on both maps (from Gudmundsson *and* Alerstam 1998). Great circle routes are thus the shortest distance between any two points on the Earth's surface whereas rhumbline routes may be easier for navigation as they require no re-adjustments of headings but always cross meridians at the same angle. The difference in distance between both routes is small (<1%) at high latitudes and distances of less than 30° longitude but increases significantly thereafter. For instance, for travelling along 50° latitude and across 180° longitude, the rhumbline route is 45% longer than a great circle route.

lings were found in their traditional wintering area in northern France and England, so they must have used goal orientation. Interestingly, the juveniles returned to their new wintering area in the subsequent years, showing they also switched to goal orientation in later life. Similarly, white-crowned sparrows (*Zonotrichia sp*.) were caught in Washington while migrating from Alaska to California, and were flown to the US East coast. From there, adults headed back towards Californian wintering grounds, whereas juveniles headed south, presumably in an innate direction (Thorup *et al*. 2007).

Some migrations require changes in direction or migratory steps along the way, e.g. to avoid inhospitable environments. Birds from populations that change direction during migration show a corresponding change in direction in orientation cages as the season progresses, indicating that this is also under genetic control (e.g. Gwinner 1977; Helbig 1991). In other cases, local conditions serve as cues. For instance, pied flycatchers *Ficedula hypoleuca* changed their directional preference only when confronted with the magnetic conditions where they normally change direction, and not when mag-

Figure 6.4 Adult dark-bellied Brent geese (*Branta b. bernicla*) arriving at their still largely ice-covered breeding grounds in Taimyr, northern Siberia. In experienced birds, the decision to stop migrating is influenced by cues indicating that a familiar nesting locality has been reached (Photo: Andries Datema, Alterra Wageningen-UR).

netic conditions were kept constant (Wiltschko and Wiltschko 2003). Thrush nightingales *Luscinia luscinia* that were captured in southern Sweden at the start of their first autumn migration were exposed either to the local magnetic field or to an artificial magnetic field typical of northern Egypt, where they are thought to prepare for crossing the Sahara (Fransson *et al*. 2001). The latter group responded by accelerating fat deposition, suggesting that there is a built-in genetic response to local conditions.

Replenishment of the fat store itself may act as a cue to continue migration: in several experiments it was demonstrated that migratory restlessness and inclination to leave were higher in fatter than leaner individuals. Most of these studies were performed at localities where the birds were preparing for a major crossing (Newton 2008).

Termination: When tested under identical conditions in the lab, the duration of migratory restlessness is longer in long- than in short-distance migrants, even within species (Berthold and Querner 1981). Cross-breeding experiments showed that this is an inherited trait (see also Berthold 1999 for an experiment with hybrids of redstarts). In birds from the same species, those wintering furthest away from the breeding grounds show a tendency to start spring migration earlier (King and Mewaldt 1981). Juvenile blue-winged teal *Anas discors* caught in the autumn and held captive for a while, migrated less far than normal after release at the same site (Bellrose 1958). This shows that the decision to stop is at least partly under genetic control. However, in adult birds the opposite was found, with the migratory restlessness continuing longer than normal when held captive for a while during spring migration (Newton 2008). Also, when held at the breeding location, indigo buntings *Passerina cyanea* did not migrate after release in the spring, whereas the control birds that were displaced 1000 km to the south did (Sniegowski *et al*. 1988). The same was true for white storks *Ciconia ciconia* reared in captivity and released in a reintroduction programme (Fiedler 2003). In experienced birds, the decision to stop is therefore apparently influenced by cues indicating that the familiar locality has been reached (Fig. 6.4).

6.3.6 Migration in mammals

6.3.6.1 Migration in bats

Even though bats are mammals, their ability to fly makes them more like birds in terms of their opportunities for and ecology of migration, but relatively little is known about their migration biology in comparison with birds. This is probably because temperate bats have adopted hibernation as their main strategy for surviving periods of resource depression in a seasonal environment. Yet, in the family Vespertilionidae, migration occurs in 23 out of 316 species classified (7%), and has evolved in 15 genera with apparently little phylogenetic inertia (Bisson *et al*. 2009). The distances of bat migrations are shorter than for birds, with maximum migration distances around 2–3000 km (Hutterer *et al*. 2005). In temperate bats, long-distance migration occurs mainly in species that use trees for roost sites (Fleming and Eby 2003), but in these species migration is combined with hibernation at the wintering site. Migration also occurs in tropical species but movement distances are generally rather short and, in most cases, are driven by the phenology of fruiting trees (Fleming and Eby 2003). Differential migration is common in bats, with females migrating further north than males to raise their young, presumed to be due to higher resource needs for raising the young (Fleming and Eby 2003). As in birds, partial migration also occurs, i.e. part of the population migrates and the other part is resident.

Preparation. Bats accumulate fat deposits before hibernation (e.g. Kunz *et al*. 1998), and therefore fat is probably the main fuel used during migration (McGuire and Guglielmo 2009).

Departure. Bats most likely depart during the early night hours, similarly to nocturnally migrating birds. Departure conditions are little studied, but is seems as if migration activity is highest when wind speeds are low (Petersons 2004).

On the way. It has recently been shown that bats possess a magnetic sense (Holland *et al*. 2006a), and it therefore seems likely that this is involved in orientation during migration. Otherwise, next to nothing is known about orientation and navigation in bats, although recent evidence suggests that the greater mouse-eared bat *Myotis myotis* calibrates a magnetic compass with sunset cues (Holland *et al*. 2010). Some frugivorous species seem to track the phenology of their main food source on migration (Fleming and Eby 2003).

Long-distance migration generally consists of several cycles of fuelling followed by migratory flight. It remains to be shown whether bats follow this model, but there are some indications that they do stop over for fuelling (Petersons 2004). Since bats are mainly nocturnal they must divide their active period (the night) between foraging and migratory flight during migration. Because migrating bats' rate of energy consumption is typically much higher than that of fuel accumulation, it is expected that the proportion of time spent on stopovers should be much longer than that spent on migratory flights (Hedenström 2009). One way of saving energy on migration is to use torpor during periods of fuelling, i.e. lowering the body temperature during daytime roosting and thereby increasing the net rate of fuel accumulation (and hence overall migration speed).

In flight, there are alternative 'optimal' flight speeds predicted from flight mechanical theory (Hedenström 2009), with the maximum range speed being the best option for minimizing energy cost per unit distance. A comparison between foraging and commuting flights in *Pipistrellus kuhlii* showed that these bats select flight speed according to this prediction. Overall, bats seem to fly at slower speeds than birds of similar sizes (Hedenström *et al*. 2009).

The overall migration speed includes time for fuelling and flight (Hedenström *et al*. 2009), and is predicted to be about 46 km/day on the basis of fuel accumulation rate, energy consumption during flight and flight speed. Ringing recoveries of Nathusius's bat *P. nathusii* showed a migration speed of 47 km/day (Petersons 2004), which is comparable to that of short–medium distance migrating birds. Flight altitudes of bats on migration appear to be rather low (Ahlén *et al*. 2009), although free-tailed bats *Tadarida brasiliensis* may reach altitudes of about 3000 m when foraging (Williams *et al*. 1973).

Termination. Birds have an inherited migration programme that determines when to cease migration, but whether bats have a similar mechanism is not known.

6.3.6.2 Migration in large herbivores

Seasonal nomadism and migration have been documented numerous times in terrestrial mammalian herbivores and occur on every continent (Fryxell and Sinclair 1986). There are three types of situation in which herbivore nomadism or migration are common, perhaps even typical. The first situation is species inhabiting montane environments, such as elk, mule deer; red deer, and montane ecotype caribou (Albon and Langvatn 1992; Brown 1992; Horne *et al*. 2007; Hebblewhite *et al*. 2008). Migration is relatively common in herbivore species inhabiting open savannah or tundra environments, such as tundra ecotype caribou in North America, wildebeest, zebra and Thomson's gazelles in the Serengeti and Tarangire ecosystems of Tanzania, white-eared kob and tiang in the Boma ecosystem of Sudan, and Mongolian gazelles (Pennycuick 1975; Inglis 1976; Fryxell and Sinclair 1986; Durant *et al*. 1988; Fryxell *et al*. 2004; Boone *et al*. 2006; Mueller *et al*. 2007; Holdo *et al*. 2009). Finally, seasonal migration by ungulates also occurs in temperate regions subject to severe climatic variability, such as woodland caribou, pronghorn antelope, saiga antelope, white-tailed deer or mule deer (Rautenstrauch and Krausman 1989; Nelson 1998; Johnson *et al*. 2002; Ferguson and Elkie 2004; Berger *et al*. 2006; Sawyer *et al*. 2009; Singh *et al*. 2010).

Seasonal onset of vegetation growth is strongly temperature-dependent in montane ecosystems in temperate to arctic regions. As a consequence, snow melt occurs later at high elevations and vegetation growth is retarded relative to lower elevations (Pettorelli *et al*. 2005). It is common for terrestrial herbivores to exhibit seasonal shifts in accordance with seasonal green-up (Albon and Langvatn 1992; Horne *et al*. 2007; Hebblewhite *et al*. 2008; Berger *et al*. 2006; Sawyer *et al*. 2009). In low-lying forbs and grasses, structural compounds, such as lignin and cellulose, are incorporated more and more into stem and leaf tissues as the plant grows taller, reducing digestibility and lengthening the processing time in herbivore digestive tracts (van Soest 1982). As a consequence, optimal rates of nutrient intake can often be best achieved by feeding on relatively immature ramets (McNaughton 1984; Hobbs and Swift 1988; Fryxell and Sinclair 1988; Illius and Gordon 1992). By appropriate timing of migration up the elevation gradient, herbivores are able to access young vegetation and maintain optimal nutrient intake over a prolonged period. Over the course of the winter, animals usually retreat to low-lying areas, which are less exposed to severe climatic conditions and have residual plant standing crop from the growing season. A similar pattern is seen in tundra systems, with animals retreating to woodland margins during winter, but venturing far out on to the tundra during the brief growing season.

In savannah environments, animals usually follow rainfall gradients, from the more arid rangelands used during the brief growing season to higher rainfall areas used during the driest part of the year (Pennycuick 1975; Fryxell and Sinclair 1988; Mueller *et al*. 2007). As nutrient quality is often inversely related to annual rainfall levels (Bremen 1983), migrants are able to access young vegetation at an optimal growth stage during the growing season in the arid areas, while retreating to high rainfall areas when arid lands dry out. Nomadism is characteristic when rainfall is unpredictable in space (Fryxell *et al*. 2004; Mueller *et al*. 2007, 2008), though this is often superimposed on a relatively dependable migratory pattern at coarser temporal and spatial scales (Wilmshurst *et al*. 1999; Boone *et al*. 2006; Holdo *et al*. 2009).

In temperate regions with extreme seasonal variation in climate, it is common to see migration from summer home ranges, presumably chosen primarily to obtain food and reduce predation risk, to winter ranges with less snow cover or improved shelter from snow and wind (Rautenstrauch and Krausman 1989; Nelson 1998; Johnson *et al*. 2002; Ferguson and Elkie 2004; Berger *et al*. 2006; Sawyer *et al*. 2009, Singh *et al*. 2010).

It seems likely that there is at least some learned or cultural component to migration behaviour in terrestrial herbivores, though this question has received relatively little attention in the ungulate literature. The cultural conjecture is based on well-documented examples of altered migration routes, adoption of migration by previously resident animals and even cessation of migration within a single generation (Nelson 1998). Longitudinal studies clearly suggest that partial migration is typical of northern white-tailed deer, with young individuals typically mimicking the migratory behaviour of their mothers, but capable of shifting to different strategies (resident or mixed) later in life (Nelson 1998). Similarly, elk in Banff National Park were largely migratory before the 1990s (Woods 1991). Re-invasion of wolves into areas in the Bow Valley from which they had been extirpated led to a dramatic change in space use patterns by elk over the course of 10 years (Hebblewhite *et al*. 2005), with most individuals concentrating year-round near towns that provided security from predation as well as improved nutrient intake on a year-round basis (McKenzie 2001; Hebblewhite *et al*. 2005, 2008).

Preparation and departure. Because large herbivores are highly mobile, feed while they travel, and have relatively slight energetic costs of movement relative to other taxa, there is little indication of extensive physiological preparation for seasonal movements. Cues for the initiation of migration and nomadism are thought to include seasonal changes in temperature, precipitation, and water quality (Pennycuick 1975; Rautenstrauch and Krausman 1989; Albon and Langvatn 1992; Nelson 1998; Wolanksi and Gereta 2001; Mahoney and Schaefer 2002; Boone *et al*. 2006; Gereta *et al*. 2009), although evidence is largely anecdotal. For example, Serengeti wildebeest have been seen to reverse direction and return to previously vacated areas when temporary periods of drought interrupt the usual onset of the rainy season (Pennycuick 1975). This suggests that rainfall is a key variable for this species, but it is hard to disentangle that from other putative causal variables (young vegetation abundance, water quality) that co-vary with rainfall.

On the way. Once underway, it is not clear what proximate cues migratory herbivores use to guide their movements. Some species have specific migration routes that are travelled year after year, such as pronghorn antelope in the mountains of Wyoming, Idaho, and Montana (Berger 2004, 2006), mule deer in Wyoming (Sawyer *et al*. 2009), and montane caribou in Alaska (Horne *et al*. 2007). In each case, specific individuals travel the same corridors as they shift from winter to summer ranges. Anthropogenic habitat changes that create bottlenecks in such migration corridors are a source of considerable conservation concern, because there are clear examples of migrants being negatively affected by anthropogenic barriers to movement (Williamson et al. 1988; Mahoney and Schaefer 2002; Berger *et al*. 2006; Ito *et al*. 2005, Chapter 11).

Migration routes in other systems seem much less repeatable within individuals from year to year (Wilmshurst *et al*. 1999; Thirgood *et al*. 2004; Boone *et al*. 2006), suggesting cues may be regional in nature. For example, movement trajectories of Serengeti wildebeest and Thomson's gazelles can be fairly precisely predicted in coupled map lattice models on the basis of local rainfall, grass biomass and soil nutrient levels (Fryxell *et al*. 2004; Holdo *et al*. 2009), but only when animals are capable of choosing new locations to move to within ranges of the order of 100s of km^2. Smaller zones of perception would probably lead individuals to concentrate in areas of local fitness peaks, thereby disrupting the migration that is repeatedly observed at a coarser spatial scale. In a particular area, residents can prefer different habitats from migrants (M. Hebblewhite, pers. comm.), suggesting either that migrants and non-migrants differ in their selective constraints or that migrants are unable to choose the best local resources because of lack of familiarity with the area.

6.4 Discussion and Integration

In this chapter, we have considered the cues that are used in several phases of migration across taxonomic groups. Although naturally many differences appear due to the specifics of each species' migration, considerable similarities appear to exist in the cues involved in the different phases of migration (Table 6.1).

In all species, preparations for migration involve entrainment to time of the year, as all environments are seasonal to some degree, thus particular times are more suitable for particular activities. Indeed, even at very low levels of seasonality, animals should migrate in order to make use of the varying levels of food in different areas (Barta *et al*. 2008). Therefore, the occurrence of photoperiod as a cue in almost all taxa is not surprising.

However, as migration is a daunting activity in the life-cycle or annual cycle, it also requires bodily changes, such as the accumulation of energy stores, the build-up of the locomotion apparatus—often at the expense of the digestive and/or reproductive system, and the transformation of a freshwater- to a seawater-adapted life-form or the achievement of a particular developmental stage. Whenever these changes are accomplished, an internal cue is produced indicating that the animal is ready to depart.

Table 6.1 Summary of the cues identified for the four major steps of migration, in all major migratory taxa

Cues for	Preparation	Departure	On the way	Termination
Plankton: ***Calanus finmarchicus***	Undergo all naupliar stages and reach 5th copepodid stage. Storage of wax esters	Descending migration: Food level below threshold Ascending migration: C5 stage to 80% developed	Continue until buoyancy depth and below mixing depth	Descend: arrival in buoyancy depth; Ascend: arrival in surface waters
Insects	Photoperiod, Crowding during immature stages, Habitat deterioration (food, predation or parasitism)	Favourable flying conditions, e.g. tailwinds	Time-compensated sun compass	Migration reduces inhibition to appetitive cues (in mig. bout); depletion of fuel reserves, changes in photoperiod or temperature
Fish	Reach minimum body size; for some: physiological adaptation to new environment	Salmon: Autumn river discharge	Local food search, or long-distance spawning location tracking	Arrival in locations favourable for spawning
Turtles	Light regime, internal status, and migratory restlessness	Favourable departure conditions, e.g. night, with currents	Visual information (bright skylight), direction of waves, geomagnetic field, wind	Arrival on specific target location, e.g. feeding or wintering grounds
Birds	Photoperiod, Build-up flight apparatus, Reduction digestive system	Favourable flight conditions (wind, rain, air pressure). Fuelling rate and body stores. Cumulative temperature or related proxy	Sun compass, magnetic field, skylight polarization, star pattern. Direction under hormonal control, sometimes responses to local conditions	Arrival on specific target location, e.g. breeding or wintering grounds. Naïve birds have an inherent migratory period
Mammals: Bats	Accumulate fat deposits (torpor during fuelling periods)	Early night hours, low wind speeds	Not much known, probably use magnetic field calibrated by direction of sunset	Unknown
Large mammals	No particular (physiological) preparations	Seasonal changes in temperature, precipitation and water quality but evidence anecdotal	Not much known; may follow gradients.	Unknown

For the actual departure, another external cue is often involved, which is usually related to travel conditions, e.g. wind, precipitation, temperature. Thus, animals prefer to depart during periods of favourable conditions, for instance, flying animals wait for tailwinds in their preferred directions; swimming animals use river discharge or sea-currents.

On the way, orientation and navigation determine the migration route taken but they may also be involved in indicating when migration is to be terminated. Animals heading for a specific location need to recognize this location, which is an option only for experienced animals, whereas naive individuals (e.g. first-time migrants) need to have a genetic programme that signals when to stop. Alternatively, migrations without clear endpoints, e.g. between feeding locations, may involve physiological cues for the termination of migration. Here again, internal signals play a greater role as they indicate when a threshold state is reached, e.g. sufficient body reserves have been accumulated for a subsequent breeding attempt.

Although we can make very rough generalizations such as these, we need to realize that currently we know the full set of cues and decision rules used throughout their annual cycle for hardly any species. For most species, we don't have any idea which cues and decision rules, orientation and navigation mechanisms they use during (specific parts of) their migration. However, such knowledge is all the more urgently required in the face of human-induced environmental changes. These changes affect the size and quality of habitats as well as the distances that separate suitable environments. Furthermore, climatic conditions are changing, but to complicate matters some areas on the globe are expected to be affected much more than others. For migratory animals, such changes pose particular challenges as they visit multiple, distant sites during their annual or life cycles—often even in different ecosystems. If we are to predict the consequences of such changes for migratory animals, we need to close the gaps in our current knowledge and gain a thorough understanding of the cues and decision rules used during migration as well as animals' orientation and navigation mechanisms.

To this end, we need to overcome the considerable bias both in the species and taxa studied and also in the type of questions asked and the approaches used. Birds are by far the best-studied taxon at present, followed by the economically relevant fish species, while comparatively little is known for the other taxa.

Most studies on navigation, orientation and decision rules have so far been conducted in captivity. Although such studies can provide important first indicators of the processes involved in natural migration, the relative importance of different cues can only be established in complex environments. Hence, it will be essential to study migratory decisions of wild, naturally migrating individuals (Wikelski *et al*. 2007).

Traditionally, migrations of animals (in particular, birds) have been identified using recoveries and resightings of marked individuals. Especially for larger birds such as swans and geese, individual marking, e.g. with neck-rings, has been possible, allowing detailed observations along their routes. More recently, the advent of increased communication possibilities and technological advances have led to significant progress in, for example, the development of satellite transmitters, geolocators, or the miniaturization of existing devices such that the movement of individuals of smaller and/or clandestine species can be followed in great detail (e.g. discovery of migratory routes in turtles, Hays 2008).

Data obtained with these devices can provide insights into the *individual* level of decision-making involved in the different steps during migration and thus provide mechanistic rather than phenomenological insights (Chapter 8). Such individual movement data can be analysed across taxa (www.movebank.org). Furthermore, these tracks can be integrated with detailed geographical and dynamic meteorological information allowing the identification of both the internal and external (environmental) determinants of migration decisions.

Another avenue for further advances in our understanding is improved integration of theoretical and empirical efforts (Bauer *et al*. 2009; Chapter 8). Significant progress in science has often been achieved when theoretical developments have inspired new experiments or when startling empirical findings have inspired the development of new theories. Despite pioneering efforts (e.g. Alerstam and Lindström 1990), the interaction between theoreticians and empiricists has been too limited to date in the study of animal migration. Several modelling approaches exist, ranging from simple optimality models (e.g. Alerstam and Hedenström 1998), dynamic optimisation models (e.g. Houston and McNamara 1999), game-theoretic models (e.g. Kokko 1999), individual-based models (e.g. Pettifor *et al*. 2000) to models based on evolutionary methods (genetic algorithms and neural network models, e.g. Huse *et al*. 1999). Again, the use of these models has been highly biased, with birds being the most studied taxon with the widest variety of theoretical approaches used.

Methods for the identification of cues and decision rules are numerous and include (but are not restricted to) translocation/displacement experiments (e.g. Luschi *et al*. 2001), cross-breeding experiments (Helbig 1991) and a combination of theoretical and empirical approaches (confronting models with data), e.g. simulation models (e.g. Duriez *et al*. 2009) and proportional hazards models (e.g. Bauer *et al*. 2008).

We believe that much could be learned by overcoming taxonomic borders and integrating theoretical and empirical efforts—particularly in our rapidly changing world that challenges migratory animals with 'large-scale experiments'; this will give us important new insights and advance our understanding of migration.

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A Synthesis

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