How Migrants Get There: Migratory Performance and Orientation

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Migratory animals show a suite of adaptations to cope with their journeys. These include not only morphological features for efficient locomotion and storage of energy but also behavioral adjustments to exploit winds and currents or to avoid drift caused by moving fluids. Migration strategies across locomotory modes can be analyzed in the context of optimality models, using some general principles concerning migration range and selection criteria. Comparisons of model predictions with natural behavior help researchers understand the selection pressures that underlie migration strategies. We give examples of typical migration speeds and distances for animals using different locomotion models. Successful migration also requires accurate orientation and/or navigation between distant areas for reproduction and survival. Animals can use a suite of different compasses, which may be cross-calibrated or integrated for direction finding, depending on the geographical and ecological situation, and may be used with an endogenous clock for time compensation.

Keywords: migration, strategies, navigation, migration routes, rules of thumb

Long-distance migration is the process of transportation between widely separated areas, typically divided in cycles of energy accumulation (fueling) and movement toward the goal. These cycles are repeated until the goal is reached. At this level of analysis, migration is deceptively simple. In reality, however, migration is a complex process that offers an ideal study system for the evolutionary biologist, as it involves specific adaptations involving morphology and physiology for efficient energy accumulation and locomotion, and behavioral adaptations for optimal use of external factors (winds, currents, orientation cues). Together these adaptations define the migration syndrome (i.e., the suite of characters that helps the animal to migrate more effectively than a resident). The experimental and modeling toolkit available to study migration has expanded dramatically in recent years, involving cross-disciplinary approaches and methods such as molecular genetics, isotope analyses, magnetic resonance imaging, ultrasound, electromagnetic coils, and wind tunnels.

The physical nature of locomotion, and hence of migration, makes it amenable to optimality analysis, as evidenced by the development of migration theory over the past two decades (Alerstam and Hedenström 1998). Here we discuss the opportunities and constraints provided by different media and modes of migration, at stages including fueling, locomotion, and orientation. In this article we will restrict ourselves to animals whose mode of locomotion is swimming, flying, or running. Migration also occurs in organisms at other (smaller) scales using other types of locomotion, but we believe the governing principles will nevertheless be similar. Our presentation is biased toward birds, partly because of our own background but also because research on bird migration processes has made more progress than that on other migratory organisms. For a thorough discussion on the definition of migration, we recommend Dingle (1996) and Dingle and Drake (2007).

Migration performance

A fanciful ideal migrant would be one that had infinite energy, moved with infinite speed, and could orient and navigate perfectly, as though it possessed a GPS (global positioning system). These "super-traits" would be characteristic of a Darwinian demon (an organism that reproduces at an infinite rate at no cost). Our "migratory demon" can serve as a starting point for discussing migration performance in real migrants.

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Migration is usually a process of alternate episodes of fueling and transportation toward the goal destination, a cycle that is repeated many times on a long journey (figure 1). Migration occurs in the first place as a result of resource fluctuations in a seasonal environment (Dingle 1996), and for several reasons it can be assumed that, in most organisms, natural selection favors traits resulting in fast migration. We also refer to this strategy as "time-selected migration," since minimum time and maximum speed amount to the same thing. In box 1, we outline some useful theoretical concepts of migration performance, illustrated in figures 2 and 3. We define migration speed as the overall rate of travel, including the time for acquiring energy as well as for transport; this rate should not be confused with instantaneous speed of locomotion (e.g., flight speed in a bird). For example, the overall migration speed in birds is typically one-eighth or less of the flight speed. Overall migration speed is determined by three variables: speed of locomotion, rate of energy deposition, and rate of energy (fuel) consumption during locomotion. Now, how could an animal maximize its migration speed?

Fueling episodes are an important component of migration performance (if not the most important) because the rate of fuel accumulation determines the overall migration speed (box 1). We should therefore expect adaptations that maximize food intake and its conversion into fuel stores. The most universally used biofuel is fat, which contains the most energy per unit of mass compared with the main alternatives, protein and glycogen. Our ideal migrant would fuel up instantly, but the real animal has to locate and ingest food, break it down (e.g., using the gizzard and digestive enzymes), absorb it, and create and transport fat bodies (lipoproteins) to specialized fat deposits. This requires special adaptations, which include physiologically flexible organs that grow and shrink in relation to the requirements of fueling and transportation. During fueling, bird migrants therefore ingest and process food at or close to their metabolic capacity (Kvist and Lindström 2003); they grow a larger intestine, gizzard, and liver to boost their food-processing capacity; and the flight muscles grow larger to lift increasing fuel loads. Just before takeoff, some parts of these organs are disposed of in order to keep the nonuseful payload to a minimum, thus reducing flight costs. In addition, the flight muscles may be partly consumed as fuel during long flights when the body gets lighter—a fine-tuning of the engine in response to changed requirements.

A high migration speed is also obtained by a high speed of locomotion. In birds, which have a U-shaped relationship between power consumption and speed (box 1, figure 2), a maximized migration speed is promoted by selecting an optimal (not maximal) flight speed that balances the marginal gain in speed against the marginal increase in flight cost (Alerstam and Hedenström 1998).

Migrants are expected to show morphological characters that minimize the cost of locomotion for efficient migration. The migration speed is pushed up by a low cost of locomotion, and promoted by wings (and flukes or tails) with a long and high aspect ratio, by streamlining of the body in swimmers, and by long legs in runners. Additional behavioral adjustments to save energy and maximize migration speed involve an appropriate selection of flight mode (powered flight versus thermal cross-country soaring) and flight in flock formation.

Speeds in the wild

As noted above, migration speed depends on fueling rate, energy consumption during locomotion, and speed of transport. Table 1 gives examples of migration speeds in flyers and swimmers. In birds using powered flight, the maximum speeds are found in small or medium-sized birds, such as the arctic tern (200 km per day) and the red knot (175 km per day), while the travel rate is much reduced in large birds such as swans (26 km per day). The reason for this is that the power required to fly scales with body mass (m) as $\propto m^{7/6}$ (Pennyuick 1975), whereas the mass-specific fueling rate declines with increasing body size. Some large birds get around this problem by switching to soaring flight, which has a lower metabolic cost than flapping flight (Hedenström 1993). The migration speeds of large raptors using thermal soaring are comparable to the highest speeds recorded for flapping flight in smaller birds, and even up to four times higher in albatrosses that use dynamic soaring (table 1).

The fastest long-distance swimmer may be the great white shark, which migrates 11,100 km across the Indian Ocean at 110 km per day. The green turtles of Ascension Island are also impressive swimmers, reaching 63 km per day across the Atlantic (table 1). These speeds

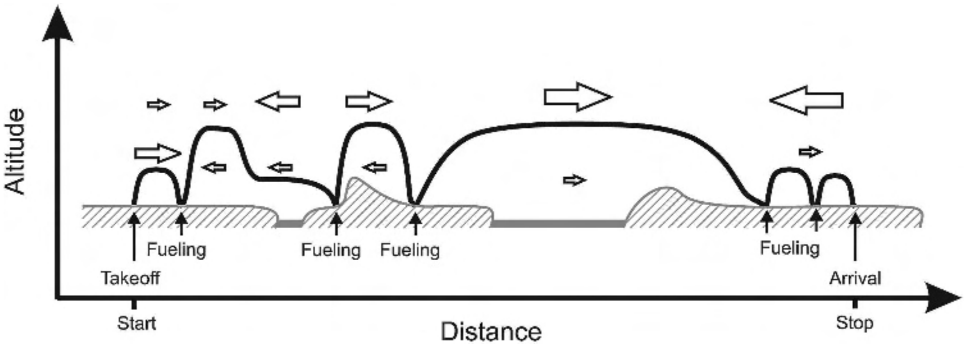

Figure 1. A schematic illustration of the migration journey of a hypothetical bird, showing how distance and altitude may vary as a result of barriers (e.g., mountains, seas) and winds. Arrows indicate wind direction and strength (by size of the symbol). The relative strength and direction of winds at different altitudes determine the cruising altitude.

Box 1. A theory of bird migration.

Migration theory can be summarized by a number of fundamental equations from which optimal strategies can be derived. When moving at speed U at a rate of energy consumption P_{loc}, the overall migration speed can be written as

$$U_{\mathrm{migr}} = UP_{\mathrm{dep}} / (P_{\mathrm{dep}} + P_{\mathrm{loc}}),$$

which includes time for fueling and transportation (Alerstam and Hedenström 1998). Figure 2 shows how U_{migr} can be solved graphically from a diagram showing the relationship between P_{loc} and speed of locomotion U. The illustrated example shows a typical bird power curve, but this can be replaced by any relevant relationship representing P_{loc} and U for a particular locomotion mode, and so this general equation applies to all types of locomotion. The flight speed associated with maximum overall migration speed U_{mt} is given by the tangent to the power curve from the point representing the fuel deposition rate P_{dep}. The optimal flight speed for minimum cost of transport is given by a tangent from the origin to the power curve and is denoted U_{mc} (mc for minimum cost; figure 2). The difference between U_{mt} and U_{mc} depends on the magnitude of P_{dep}, but in many cases $P_{\mathrm{loc}} >> P_{\mathrm{dep}}$, and so the expected difference between these alternate characteristic speeds is small and difficult to demonstrate in nature. However, in powered flight there is a characteristic U-shaped relationship between P_{loc} and U (figure 2; Pennyuick 1975) and hence an intermediate speed at which power consumption reaches a minimum (U_{mp}; figure 2). This latter speed is typically much lower than U_{mt} and U_{mc}, and should be selected by animals that aim at staying airborne for as long a time as possible.

A general form of the potential migration range as a function of the relative fuel load is given in figure 3. The diminishing return of flight range is due to the fact that the fuel already accumulated increases the weight and drag (through increased frontal area of the bird), and both factors contribute to increased energy cost of flight. This means that a migrant will save energy if it can avoid long flights involving heavy and costly fuel reserves by dividing the journey in several short steps associated with low fuel loads. There is a break-even detour around a barrier where the energy cost is equal to the direct flight across the barrier, if the detour can be divided into multiple flights with low fuel loads, avoiding a long nonstop flight with a high departure fuel load (Alerstam 2001). This may explain why many migrants tend to fly around seas such as the Mediterranean.

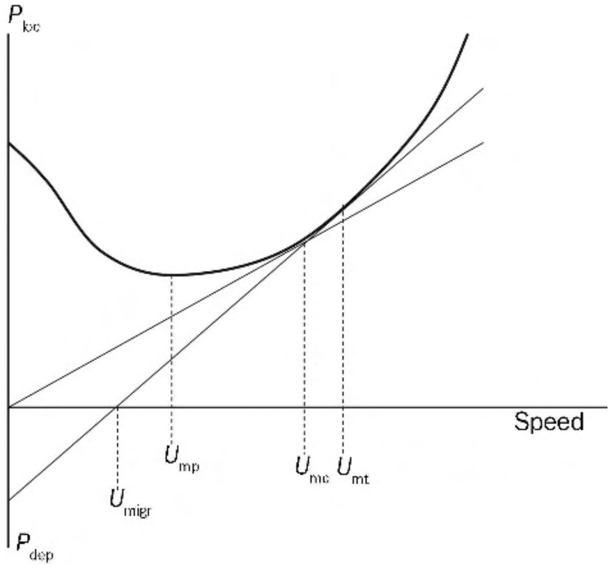

Figure 2. Power diagram showing the functional relationship between power required to fly (P_{loc}) for a bird and forward airspeed (U). The characteristic flight speeds associated with minimum power (U_{mp}), minimum cost of transport (U_{mc}), and speed resulting in minimum time of migration (U_{mt}) are indicated. U_{mt} depends on the rate of energy accumulation (P_{dep}) depicted on the negative ordinate, from which a tangent to the power curve gives U_{mt}, and also the overall migration speed (U_{migr}), where this tangent intersects with the abscissa.

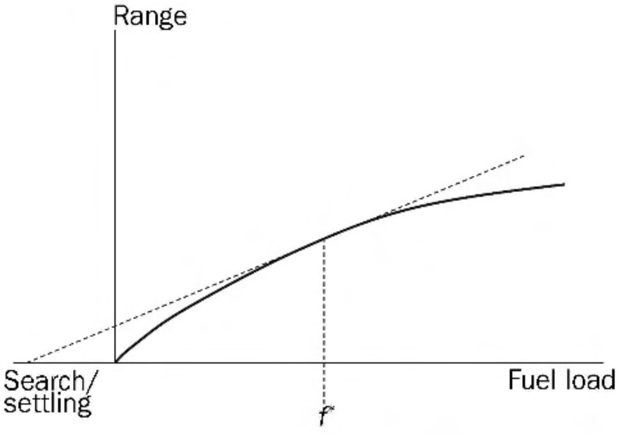

Figure 3. The potential migration range in relation to relative fuel load. The relative fuel load is expressed as $\mathrm{f} = (\mathrm{m}/\mathrm{m}_0) - 1$, where m is body mass with fuel and m_0 is lean mass. By constructing a tangent to the range curve, from a point on the negative abscissa representing the energy loss associated with search settling at a new stopover, the optimum departure fuel load f^* is obtained. Based on Alerstam and Hedenström (1998).

Table 1. Migration speeds observed in a set of flying and swimming animals.

Species	Mode of locomotion	Speed (km per day)
Great white shark (*Carcharodon carcharias*)	Swimming	110
Pacific bluefin tuna (*Thunnus orientalis*)	Swimming	21
Green turtle (*Chelonia mydas*)	Swimming	63
Elephant seal (*Mirounga leonina*)	Swimming	38
Bewick's swan (*Cygnus columbianus*)	Flapping flight	26
Red knot (*Calidris canutus*)	Flapping flight	175
Arctic tern (*Sterna paradisaea*)	Flapping flight	200
Willow warbler (*Phylloscopus trochilus*)	Flapping flight	85
Lesser spotted eagle (*Aquila pomarina*)	Thermal soaring	133
Honey buzzard (*Pernis apivorus*)	Thermal soaring	163
Grey-headed albatross (*Thalassarche chrysostoma*)	Dynamic soaring	880

Source: Hedenström and Alerstam (1998), with additional data from McConnell and Fedak (1996), Papi and colleagues (2000), Hake and colleagues (2003), Block (2005), Bonfil and colleagues (2005), and Croxall and colleagues (2005).

refer to time when swimming, uncorrected for time to refuel. Movements over longer periods, where time for energy accumulation is included, show lower but still impressive traveling rates, exemplified by the Pacific bluefin tuna, which moves at 21 km per day over nine months, and the southern elephant seal, which moves at 38 km per day (table 1).

Migration distance

In most animals, the migration range shows a diminishing return function with more fuel (box 1, figure 3), because fuel adds weight and drag due to the body's increased volume. Hence, the first gram of fuel accumulated is worth more than the last gram, since more fuel progressively raises the cost of locomotion. The three main modes of locomotion follow this general rule, but the penalty resulting from added fuel may vary because the relative cost of weight support and drag differs among types of locomotion and morphology. Swimmers are often buoyant and therefore pay mainly the cost of drag, runners pay mainly the cost of weight support, and flyers pay both these costs.

If there is a maximum limit for how much fuel can be stored—which is the case for birds, for purely mechanical reasons related to flight requirements—there is a maximum one-step migration distance. However, birds rarely fly this maximum distance (although certain fish do swim their maximum distance), unless they have to cross vast ecological barriers. Normally, the migration is divided in shorter distances associated with submaximum fuel loads when migrants travel across ecologically benign areas (see figure 1). In time-selected migration, there is a well-defined optimal departure fuel load and stopover duration determined by the fueling rate and the search and settling costs on arrival at the stopover site (box 1, figure 3). Experimental studies in which food was provided to manipulate the rate of fueling showed that songbirds adjust their departure fuel load in qualitative agreement with the prediction based on optimality reasoning (Alerstam and Hedenström 1998). There are, however, several factors that may cause birds to depart on migration flights at fuel loads different from those predicted on the basis of simple optimality for time-selected migration: for example, an ecological barrier or changing winds that affect the potential flight distance.

The theoretical maximum flight distance is approached by Alaskan breeding bar-tailed godwits (*Limosa lapponica*) when flying nonstop to their wintering area in New Zealand (Gill et al. 2005); circumstantial evidence and flight mechanical calculations suggest that they undertake a direct 11,000-km nonstop flight. Among the largest bird species using flapping flight (e.g., swans), the overall migration speed is so low (table 1) that the potential migration distance is severely restricted by the time allowed for migration in the annual cycle. The whooper swan (*Cygnus cygnus*) migrates between Iceland and Scotland, which is a sea crossing of about 800 km and an exceptional nonstop flight for a bird of this size using flapping flight. Satellite telemetry revealed that whooper swans made frequent and sometimes prolonged stops on the water (Pennyuick et al. 1996), but they were not able to refuel during these stops, and therefore the flights are nonstop from an energetic viewpoint. Since the time required for breeding and molt also increases with size in birds, the time left for migration decreases progressively with size, which is the reason there are no really long-distance migrants among large nonsoaring birds.

In swimming animals, north–south long-distance migration seems to be confined within hemispheres (Dingle 1996), and recent tracking studies of Atlantic bluefin tunas (*Thunnus thynnus*) and white sharks (*Carcharodon carcharias*) have shown transoceanic return migrations along a west–east axis (Block et al. 2001, Bonfil et al. 2005). In contrast with many birds, several migrating swimmers, such as salmonid fish, eels, sea turtles, and large marine mammals, fuel massively and then rely on this energy for the entire migration (McConnell and Fedak 1996, Van Ginneken et al. 2005), perhaps because the open ocean provides few feeding opportunities. The migrations of nonflying terrestrial animals are shorter still, with the longest one-way distance of 1200 km traveled by the caribou (*Rangifer tarandus;* Alerstam et al. 2003), while the famous migration by wildebeest (*Connochaetes taurinus*) on the East African plains is only about 200 km (Dingle 1996). The reason for relatively short migrations among land-based animals is probably that they have a higher specific cost of transport than swimmers and flyers, and hence need more energy to move a certain distance. Topographical barriers such as mountains, seas, and rivers may also prevent migration to a larger extent for terrestrial migrants than the corresponding barriers for swimmers and flyers.

Barriers

Migrants are often confronted with ecological barriers—seas, deserts, ice fields, or mountains—that provide no habitats suitable for feeding and refueling. When confronted with such a barrier, the migrant can either store enough fuel to cross it in one go, or take an alternative but longer detour around the barrier. On their way to African wintering quarters, large birds use thermal soaring to avoid an open sea crossing over the Mediterranean, instead taking detours via Gibraltar or the Bosporus and Middle East. Cross-country thermal soaring enables them to fly at a much lower cost than that of flapping flight, making it favorable to take the detour even if it is two to three times longer than the direct barrier crossing (box 1; Alerstam 2001). The detour ratio (box 1) may explain the apparent "suboptimal" routes found in some bird species, as well as the migration routes around barriers such as the Himalayas and the Mediterranean (Alerstam 2001).

When encountering a barrier, migrating birds are often observed temporarily retreating (reverse migration), presumably to find suitable fueling sites some distance from the barrier (Åkesson et al. 1996). Environmental cues, such as Earth's magnetic field (Fransson et al. 2001), may trigger extra fueling in anticipation of a forthcoming long migration step, which in turn requires that positional information is encoded in the inherited genetic program.

Winds and currents

An animal that flies or swims moves through a medium (air or water) that is almost always moving by itself. Depending on the direction and strength of this flow, migrants may benefit if it is in the same general direction as the intended migration course or may be hindered or prevented from migrating if the flow is in an opposing direction. In cross flows, an animal may drift off its intended migration course unless it can detect and compensate for this flow. Clearly the migrant is confronted with a difficult problem here. Typically, wind strength is of the same order of magnitude as the airspeed of a bird (defined as its speed in relation to the surrounding air). The relationship between the airspeed (U_a) and wind speed (U_w) determines the scope of orientation available to a migrant. When $U_w < U_a$, the scope is always an unrestricted 360°; when $U_w = U_a$, the scope is restricted to 180°; and when $U_w > U_a$, the scope of orientation declines with increasing wind speed. This implies that smaller birds and insects, with relatively low airspeeds, may exhibit a higher degree of wind selectivity than larger migrants (see Dingle 1996 for examples).

The relationship between a migrant's track, heading, and wind is shown in figure 4. The track vector is the sum of the wind or current vector and the heading vector. Complete compensation can be achieved by a relatively low airspeed paired with a large angle of compensation (α) or vice versa (figure 4). The optimal flight speed (defined here as the speed with the minimum energy cost per unit distance) depends on the marginal gain in ground speed with increased airspeed (Liechti et al. 1994). With cross flows, it will be optimal to speed up as the angle α between the track and heading vectors (figure 4) increases; in flow parallel to the flight direction, it will be optimal to speed up if heading into the flow and to reduce the airspeed if moving with the flow. This latter prediction is generally supported by studies of migrating birds and, among insects, of dragonflies (Hedenström et al. 2002, Srygley 2003). It remains to be established, however, whether birds adjust their speed adaptively in crosswinds according to the theory.

If migration is divided into many steps, and winds or currents vary, then an adaptive drift strategy should be adopted in which a migrant allows drift when far from the goal and gradually increases the degree of compensation as the goal is approached (Alerstam 1979). Birds usually show partial drift far from the migration goal, and some data suggest that they do gradually increase compensation as they approach the goal, as predicted by the model (Green et al. 2004). An analysis of the effect of crosswinds on drift showed an age-related difference in two raptor species, with adults compensating to a larger extent than juveniles (Thorup et al. 2003), possibly as a result of greater experience or greater incentive in adults

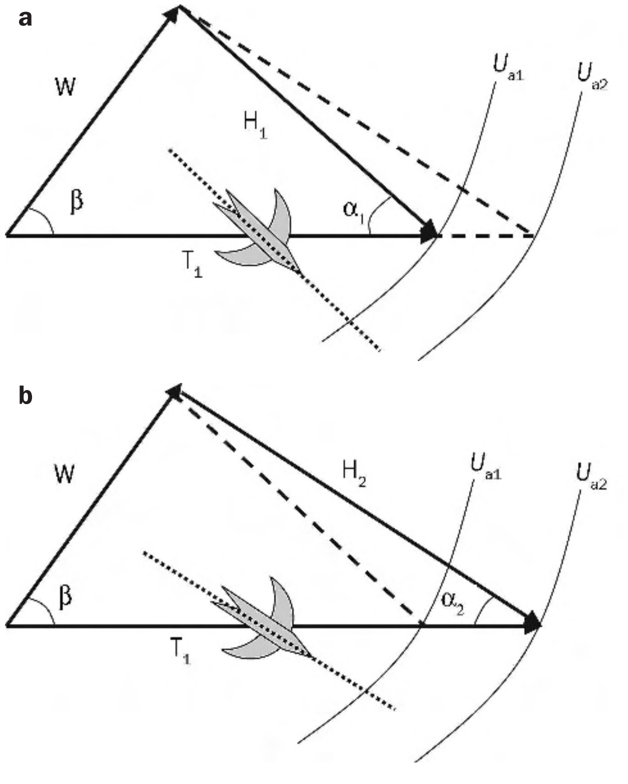

Figure 4. Compensation for wind drift by adjusting the self speed U_a and the heading α (angle of compensation) with respect to a wind or current. The track vector T (track direction, ground speed) is the sum of the wind vector W and the heading vector H (heading direction, airspeed). Optimal compensation can be achieved by (a) a relatively low speed (U_{a1}) and a large angle of compensation (α_1), or (b) a relatively high speed (U_{a2}) paired with a small angle of compensation (α_2). The optimal balance between U_a and α is given by $P' = P/U_g \cdot U_g'$, where P is power required to fly and U_g is speed over ground (speed of track vector T), and depends on the marginal gain in ground speed with increasing airspeed, which is equal to 1/cos α. Based on Alerstam and Hedenström (1998).

to revisit previous migration routes or wintering sites. It should be noted that compensation for crosswinds requires some fixed frame of reference, and so the possibility of compensating is restricted if this frame is hard to discern, as, for example, when flying above fog and clouds or over a moving wavescape when crossing water.

Because winds have such a big impact on migratory progress in birds, it can be expected that departures from stopover sites should be timed to take advantage of following winds. Without winds, there is an optimal departure fuel load predicted from models, which depends on the flight range curve and on the costs of searching and settling (box 1, figure 3). Because winds change the utility of the current fuel load (potential flight distance), we should expect birds, if they are attempting to maximize their overall migration speed, to depart before the optimal fuel load in still air conditions has been reached if there is a sudden tailwind, whereas they may stay longer if there is a persistent headwind. Observations seem to confirm the applicability of this model, as they indicate that departures occur mainly with weak or following winds (Åkesson and Hedenström 2000). Bar-tailed godwits also seem to depart with tailwinds on their epic flight between Alaska and New Zealand, with prospects of encountering favorable winds during significant parts of the flight (Gill et al. 2005).

A related strategy is the selective tidal stream transport used by fish, in which the fish come up into midwaters when the tidal stream flow is in the intended migration direction, whereas they remain on the bottom when it is flowing in an unhelpful direction (Dingle 1996). On a smaller scale, crab larvae have been found to use tidal stream transport (Cronin and Forward 1979). Stable wind patterns may influence the evolution of loop migration routes in birds (Alerstam 1981), such as the oceanic migrations of shearwaters. The movements of sea turtles are also affected by currents (Luschi et al. 2003), and juvenile loggerheads (*Caretta caretta*) move around the North Atlantic gyre (Lohmann et al. 2001). Young eels (leptocephali) rely on currents for their 6000-km migration between the Sargasso Sea and Europe (McCleave and Kleckner 1985), while the adults have evolved an extremely low energy cost of swimming to power their migration from Europe back to the Sargasso Sea (Van Ginneken et al. 2005). Winds and currents make a big difference for migrants, and it is therefore not surprising that migrants use them where possible to help them move toward their migration goal, but it is also clear that stationary current patterns mold the evolution of migration routes.

Altitude

It is well known that altitude affects an animal's physiology in a number of ways. Temperature, oxygen concentration, and air density decline with increasing altitude, affecting animals' water economy (risk of dehydration), respiratory efficiency, and aerodynamic properties (Carmi et al. 1992). Winds and vertical air currents may also influence the selection of flight altitude. The selection of cruising altitude is relevant mainly to flyers, but to some extent the cruising depth of swimmers could also be under selection. Migrating birds are regularly observed flying up to 6000 m above ground level (agl; Alerstam 1981), and the bar-headed goose (*Anser indicus*) regularly reaches heights of about 8000 m when crossing the Himalayas. Recently, migrating birds were found between 5000 and 9000 m agl over the Negev desert in Israel, exploiting low-level jet streams to reach ground speeds of up to 50 m per second (Liechti and Schaller 1999). In a statistical analysis of factors likely to determine cruising altitude, the horizontal wind component was found to be the single most important factor (Bruderer et al. 1995), and climbing–descending flight seemed to be used for sampling the most favorable winds. Monarch butterflies reach altitudes of up to 1000 m during thermal soaring (Dingle 1996), and corn leaf aphids (*Rhopalosiphon maidis*) have been recorded up to 1200 m agl, allowing them to travel 400 to 1100 km in 24 to 48 hours on following winds (Achtemeier et al. 1987, cited in Dingle 1996). When confronting high barriers, such as mountains, birds should either make a detour around the barrier or climb high enough to clear the mountain or ice cap. If such a barrier is encountered shortly after departure, when the birds carry heavy fuel reserves, the rate of climb per se may restrict the barrier crossing, especially in large birds where the power margin is low. This is probably the case for brent geese (*Branta bernicla*) crossing the Greenland inland ice, and the climbing is divided into many short flights, possibly using anaerobic muscle work (Gudmundsson et al. 1995). Interestingly, these geese also made a detour in relation to the direct ice cap crossing, perhaps to cross the ice where its height is lower than it is along the direct route.

Animal swimmers have the capacity to reach impressive depths (Boyd 1997), but their migratory movements are often close to the sea surface (Hays et al. 2001, Bonfil et al. 2005). This may reflect the need to stay near the surface for breathing, but perhaps also to watch celestial cues for orientation (see below).

Compass orientation

Perhaps the most intriguing aspect of migration is how animals are able to find their way. They do so using the most sophisticated sensory adaptations and navigation capabilities that are found in animals ranging from, for example, amphibians moving a few kilometers on land to large whales moving thousands of kilometers between foraging and reproductive areas in the ocean (Alerstam et al. 2003). To orientate means to determine and keep a compass course, while navigation refers to moving from a starting point to a specific goal. To do so, animals are expected to use one or several compasses in combination with a map (Able 2001, Åkesson 2003).

Migratory animals have access to several compasses for orientation, based on information from the sun (and the related pattern of skylight polarization), stars, and Earth's magnetic field (box 2). A geomagnetic compass encoding inherited migratory directions based on the field's angle of inclination has been demonstrated in several bird species, amphibians,

Box 2. Compass mechanisms.

The sun and the related pattern of skylight polarization

The sun compass is based on a time-compensation mechanism, enabling the animal to compensate for the sun's apparent movement over the sky, and is connected to the animal's internal time sense. By experimentally shifting the internal clock for a few days, in so-called clock-shift experiments, and recording the selection of courses in homing or orientation cage experiments, a time-compensation mechanism has been revealed in a wide range of animals. The expected degree of compensation varies with latitude and time of year, and has not been studied in great detail. Polarized skylight, associated with the position of the sun, can be used by insects, fish, amphibians, and probably other vertebrates, such as birds, to detect the position of the sun even if it is hidden behind clouds (Wehner 1998). The pattern of polarized skylight is used as a compass cue in path integration by, for instance, desert ants of the genus *Cataglyphis* navigating the desert floor in search for food, or by honeybees for compass information during foraging flights in open fields (Wehner 1998). Still, the mechanism by which the polarized skylight is detected is not well understood for several vertebrates (Horváth and Varjú 2004).

Stars

Stars provide compass information at night, when the sun and the related polarization pattern are no longer visible. However, stars are not used with a time-compensation mechanism; rather, the rotation center of the night sky encodes the geographical north direction (Emlen 1975). The birds need, however, to experience a rotating, starry sky during their development to be able to develop and use a star compass (Emlen 1975). Star patterns close to the rotation center seem to be learned by birds, but there is no inherited mechanism encoding particular star patterns observed under natural conditions. A very simplified pattern, based on artificial light sources, seems sufficient to stimulate this behavior (Weindler et al. 1996). Finally, to find the migratory direction leading to the population-specific wintering area, a migratory songbird needs to experience a combination of a rotating starry sky and a natural magnetic field (Weindler et al. 1996).

Earth's magnetic field

Earth's magnetic field provides information about compass courses, but could also be used to define the geographic position on the basis of field intensity gradients. The geomagnetic compass information represents migratory directions toward the poles and toward the equator, respectively, on the basis of the angle of inclination and not the polarity of the field (Wiltschko and Wiltschko 1995). A similar mechanism has been described in newts and sea turtles, for example, while a polarity compass has been reported for mole rats (for reviews, see Wiltschko and Wiltschko 1995, 2006). The inclination compass mechanism most probably is based on radical pair processes involving photopigments (Wiltschko and Wiltschko 2006). (A radical pair process is started by the absorption of a photon by an acceptor molecule resulting in an electron transfer; the donor and acceptor molecules then each have one unpaired electron that holds a magnetic moment; Ritz et al. 2000.) The intensity of the magnetic field could be detected by receptors containing magnetite crystals (Wiltschko and Wiltschko 1995, 2006). A magnetite-based receptor mechanism has been reported in birds and fish (Wiltschko and Wiltschko 1995, 2006).

The inclination compass encodes population-specific migratory courses, where experience from both the rotating night sky and geomagnetic information is crucial (Weindler et al. 1996). However, an inherited shift in orientation in relation to the angle of inclination is necessary for birds crossing the equator on migration to reach their final winter destinations (Wiltschko and Wiltschko 1995).

and sea turtles (Wiltschko and Wiltschko 1995). Celestial rotation encodes courses relative to geographic north (Emlen 1975). A combined experience during development of both the rotation center of stars in the sky and the natural geomagnetic field seems crucial for songbirds to find the inherited migratory direction to a population-specific wintering area (Weindler et al. 1996).

In polar areas, light summer nights make star navigation impossible, but animals will experience steep magnetic field lines and large shifts in magnetic declination (i.e., the angular difference between geographic and geomagnetic north) between nearby sites. In areas where the declination varies a lot between sites, the geomagnetic field and the sun could indicate conflicting information. How can animals cope with this disparity and select appropriate migration directions in such areas? Either a mechanism downgrading one of two compasses or, alternatively, a sophisticated calibration system coordinating the two types of information would seem to be needed. Both geomagnetic and solar compasses have been shown to be recalibrated with reference to the alternative compass information (for review, see Muheim et al. 2006a). Experiments with *Catharus* thrushes in North America showed that the magnetic compass course is calibrated by sun-related cues once per night (Cochran et al. 2004). Recently, Muheim and colleagues (2006b) showed that it is the pattern of skylight polarization near the horizon that is crucial for the calibration of the magnetic compass.

Genetic programs

Young solo migrants do not just need inherited compass courses to reach their destination; they also need to know how far they should continue. One answer to this problem is to rely on an inherited endogenous program that encodes both direction and distance to migrate (for a review, see Gwinner and Helm 2003), as well as the amount of energy needed for longer nonstop flights. However, it is hard to generalize across animal taxa about what type of information is used and how, since some animals are able to learn migration routes from their parents (geese, cranes, swans, whales), or apparently by joining flocks of migrating conspecifics (waders, ducks, storks, tunas, caribou), while others clearly do not have this opportunity and migrate singly (many birds, albatrosses, sea turtles, butterflies). Also in typical flock migrants, where migration routes are believed to be transferred from adults to juveniles by tradition, major parts of the migration program used nevertheless have a genetic component. Experiments have shown that young white storks (*Ciconia ciconia,* a flock migrant) that were delayed and displaced in autumn still migrated to their normal wintering area in Africa, including appropriate course shifts when flying around the eastern Mediterranean, and that they could compensate for displacements to some degree (Chernetsov et al. 2004).

Recent experiments with long-distance migrating loggerhead sea turtles suggest that the behavioral responses resulting in course shifts during migrations are triggered by the combination of external geomagnetic parameters, including the field's angle of inclination and intensity, typical for a particular geographic location (Lohmann et al. 2001). In songbirds, the angle of inclination of the geomagnetic field seems to be important to define the latitude, and thus to trigger the consecutive expected course shifts during migration (Wiltschko and Wiltschko 1995).

Migration routes

Even if it uses an endogenous program, finding the way from its site of birth to its nonbreeding destination is not a trivial undertaking for a first-time migrant. How do birds solve this problem? Do we find strictly algorithmic strategies guiding them from the starting site to the exact location of the destination? Or do migrants apply some rule of thumb to approach the goal, during all or part of the route? Are there any ways we can find out? One way is to compare observed migration routes with those predicted by theoretical models. There are several alternative routes an animal could take: for example, the shortest route (great circle), fixed geographic or geomagnetic routes, and magnetoclinic routes (i.e., routes in which the Earth's magnetic field has the same apparent angle of inclination; box 3, figure 5). Arctic waders migrating by long-distance nonstop flights could use a sun compass mechanism without compensating for the time shift for orientation when departing from breeding areas on high Arctic tundras for wintering areas in the Southern Hemisphere, which takes them very close to a great circle route (Alerstam et al. 2001).

Box 3. Migration routes.

How does a migrant choose the best route and then find the way over it? Figure 5 shows alternative courses for American golden plovers (*Pluvialis dominica*) migrating from breeding areas in high arctic North America to wintering areas in South America. To achieve appropriate migration routes, the following mechanisms may be used.

Orthodromes (great circle routes)
The shortest route between two locations, the great circle, is at first view a rather complicated task to achieve, since the animal needs to gradually shift the compass course. However, if an animal uses a sun compass, without compensating for the sun's movement by shifting its internal clock with local time during transport across longitudes, it will follow approximately a great circle route (Alerstam et al. 2001).

Geographic loxodromes (rhumb-line routes)
An alternative to a great circle route is a constant geographic course, or rhumb-line route, between two sites, but this is a longer route, which is energetically more costly.

Magnetoclinic routes
It has also been suggested that migrating birds follow so-called magnetoclinic routes (i.e., routes where the animal's magnetic sensor indicates the same apparent angle of inclination relative to the bird's heading; Kiepenheuer 1984). These will normally lead to curved routes, and in some areas are close to routes followed by birds on natural migrations (see figure 5).

Magnetic loxodromes
Birds may also follow constant magnetic courses, or magnetic loxodromes (i.e., routes with a constant angle between a bird's heading and the horizontal component of the geomagnetic field; Alerstam et al. 2001). In polar areas, such courses often spiral in toward the geomagnetic North Pole (Muheim et al. 2003), and are therefore not likely to be followed.

Other routes
There are of course other routes an animal could take, such as learned routes between traditional stopover sites, or migration along coastlines or other topographical features. Migrants may also shift course rather abruptly between different sections of the migration route, for reasons not necessarily related to the geomagnetic field, but rather relative to large-scale topography or patterns of evolutionary migratory history (Alerstam et al. 2003).

*Figure 5. Selection of alternative hypothetical migration routes for American golden plovers (***Pluvialis dominica***), following a great circle route (A), a rhumb-line route (B), a magnetoclinic route (C), and a magnetic loxodrome (D) from breeding areas in northern Canada and wintering areas in South America. The constant magnetic course is given for an initial great circle route and will spiral away from the breeding area around the magnetic North Pole. The map is an orthographic projection.*

So far there is very limited support for the use of magnetoclinic routes in songbirds (box 3), while course shifts encoded in the endogenous program seem to be rather widespread among migrating songbirds and marine turtles (Wiltschko and Wiltschko 1995, Lohmann et al. 2001). Some of these course shifts are triggered by external information from the geomagnetic field.

Despite our comprehensive knowledge of evolutionary processes and migration patterns across animal taxa (Alerstam et al. 2003), relatively little is known about what information animals use to navigate and how often they need to select a new course during actual migratory transport (i.e., when airborne for birds). Computer simulations suggest that birds need to update their courses repeatedly during a flight, if they are to maintain the precision inferred in individual migrants from bird ringing studies, satellite telemetry, and radar tracking (Sandberg and Holmquist 1998). However, whether a simple clock-and-compass model is sufficient for orientation by juvenile songbirds migrating for the first time is controversial. Ringing recovery data from European long-distance passerine migrants suggest that an additional navigation mechanism (some positional system involving a map sense) as a supplement to a simple clock-and-compass mechanism is required to find the migration route during the first migration. Different species of *Sylvia* warblers appear to head for specific regional goal areas before they engage in crossing two large ecological barriers, the Mediterranean Sea and the Sahara (Fransson et al. 2005). Further support for the use of a navigation mechanism by songbird species during their first migration comes from recoveries reported from a very restricted corridor in East Africa (Pearson 1990), suggesting they are converging through this narrow corridor when migrating south.

Navigation to the goal

Many birds return to known stopover sites and wintering areas used year after year (Åkesson 2003), and they even follow very similar or identical migration routes between years (Alerstam et al. 2006). There is ample evidence that displaced migrants can find their way to a goal from which they have been transported, either passively or actively, with high success rates (Åkesson 2003), demonstrating an ability to navigate over long distances. The ability to return after displacement is mostly pronounced in experienced migrants (Åkesson 2003). What information do these migrants use to find their way to the destination? There are several alternative strategies by which an animal can navigate using mainly global cues or recording its own movements in relation to the starting point, such as path integration (Wehner 1998, Able 2001). Results from long-distance passive displacements with migratory birds (i.e., displacements where birds are transported in a cage by the researcher, as opposed to self-propelled movement) speak against the latter type of navigation, suggesting the animals used local cues to define their position relative to the goal. These studies thus favor the use of a navigation mechanism based on global cues (Åkesson 2003).

The most difficult navigation task seems to be finding a suitable system for establishing longitude; latitude is much more easy to establish, on the basis of both celestial (i.e., elevation of celestial bodies) and geomagnetic (i.e., angle of inclination, field intensity) cues (Wehner 1998, Åkesson 2003). Recently, results from displacements of white-crowned sparrows in high arctic North America indicate that the geomagnetic field in combination with celestial information (e.g., declination) might be used to define longitude in this area (Åkesson et al. 2005), although this still is probably not a trivial task.

Conclusions

Migrating animals are confronted with a multitude of tasks, each one requiring decisionmaking and appropriate responses. Even such straightforward problems as the selection of flight speed in birds are affected by several factors operating simultaneously (Hedenström et al. 2002). As researchers, we may solve this problem using an engineering approach, by working out what information is required in a simplified model and what the optimal response is. Animals do not use calculus, vector algebra, or trigonometry, but natural selection has resulted in sensory organs and behavioral responses that are so sophisticated that we often take them as "optimal" when watching animal migration feats. However, to understand how migrants actually solve their daily problems, whether choosing a flight speed or migration direction, we probably have to look for simple rules of thumb that implement an approximation to the best solution. The use of a time-compensated sun compass to fly along great circles is one example of a simple mechanism that solves a difficult problem (box 2).

How does an animal know when it has reached its optimal fuel load at a stopover and it is time to depart? Simple calculus provides an answer (box 1), but a wild animal most likely follows a simple rule that gives a "good enough" solution not far from the theoretical optimum. Since birds cannot weigh themselves, and hence gauge when the optimal departure fuel load has been reached, they may stay and feed for a fixed number of days and then depart with tailwinds or no winds. If there is still a headwind after an additional number of days, they will depart anyway. They must also have reliable orientation cues available to allow the selection of an appropriate direction, and take account of possible signals from the genetic program about barriers. This is an example of how a simple algorithm could be set up that implements an approximation to an optimal migration strategy.

Orientation research is still very much concerned with the different compass mechanisms and senses. We still do not know how the different cues are integrated in wild birds, and the sensory mechanism for the magnetic compass sense remains obscure, though it is likely to be associated with photoreception in the eye. Controlled experiments in the laboratory are needed to answer questions designed to study alternative navigation mechanisms, such as what information can be used by the animal and thus how the individual reacts to controlled manipulations. However, a laboratory environment is likely to deprive animals of information available in the natural habitat, possibly causing stress and resulting in a limited behavioral repertoire. Therefore, it is also important to use field experiments in which migrants confront a range of natural cues, especially if we are to better understand the integration of information from different cues.

Some research paradigms have resulted in contradictory results. For instance, simulated displacements in the laboratory have resulted in support for the use of geomagnetic information for navigation (Lohmann et al. 2001), whereas experiments in the field show small or no effects as a result of magnetic manipulations (Bonadonna et al. 2005). Since the magnetic sense seems so fantastic, researchers may have overestimated its importance on the basis of laboratory experiments. In nature, it may be only one of several direction cues available to the migrant, some of which may be dispensable.

We strongly believe that future research in animal migration will become increasingly interdisciplinary, and that biologists must reach out to other scientific disciplines, such as physics, to better understand such an extraordinary system as a migrating animal. As we have seen, there are many different problems an animal must solve, yet animals seem to solve all these problems simultaneously and without great effort. Mathematical modeling can help to define problems and to solve them; sensory biology can show what animals are capable of; and experimental manipulations and behavioral studies can help disentangle how animals actually do it. Tracking of individual migrants with ever smaller devices of increasing sophistication, combined with experimental manipulations of sensory inputs in the wild, will be increasingly important in the quest to find out more about how free-living migrants work.

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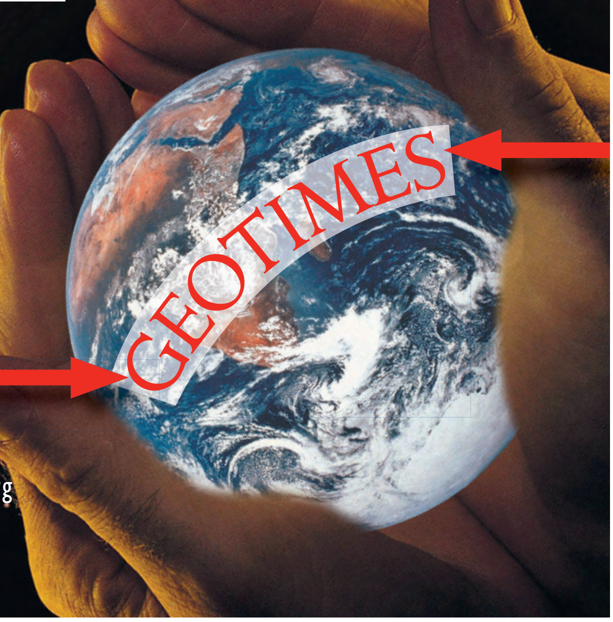

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