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Long-distance migration: evolution and determinants

Thomas Alerstam, Anders Hedenström and Susanne Åkesson

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Long-distance migration has evolved in many organisms moving through different media and using various modes of locomotion and transport. Migration continues to evolve or become suppressed as shown by ongoing dynamic and rapid changes of migration patterns. This great evolutionary flexibility may seem surprising for such a complex attribute as migration. Even if migration in most cases has evolved basically as a strategy to maximise fitness in a seasonal environment, its occurrence and extent depend on a multitude of factors. We give a brief overview of different factors (e.g. physical, geographical, historical, ecological) likely to facilitate and/or constrain the evolution of long-distance migration and discuss how they are likely to affect migration. The basic driving forces for migration are ecological and biogeographic factors like seasonality, spatiotemporal distributions of resources, habitats, predation and competition. The benefit of increased resource availability will be balanced by costs associated with the migratory process in terms of time (incl. losses of prior occupancy advantages), energy and mortality (incl. increased exposure to parasites). Furthermore, migration requires genetic instructions (allowing substantial room for learning in some of the traits) about timing, duration and distance of migration as well as about behavioural and physiological adaptations (fuelling, organ flexibility, locomotion, use of environmental transport etc) and control of orientation and navigation. To what degree these costs and requirements put constraints on migration often depends on body size according to different scaling relationships. From this exposé it is clear that research on migration warrants a multitude of techniques and approaches for a complete as possible understanding of a very complex evolutionary syndrome. In addition, we also present examples of migratory distances in a variety of taxons. In recent years new techniques, especially satellite radio telemetry, provide new information of unprecedented accuracy about journeys of individual animals, allowing re-evaluation of migration, locomotion and navigation theories.

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Migration has evolved independently among many animal groups, such as birds, fish, mammals (not least marine mammals and bats), reptiles (e.g. sea turtles), amphibians, insects and marine invertebrates. Furthermore, migration has constantly developed or become suppressed over the most recent time scale, as demonstrated by the evolutionary turmoil with respect to changes in migratory patterns that must have occurred during the few thousand years since the latest ice age. Many of these evolutionary transitions from residency to migration or vice versa, as well as changes in extent and pattern of migration, apparently occur without

important phylogenetic constraints. Many bird genera bear striking witness of this, incorporating a wide spectrum of residents, short-distance and long-distance migrants among closely related species. The same variation sometimes occurs even between populations of the same species. In partially migratory populations there is a selective balance between resident and migratory individuals, and there is often a distinct age-, sex- and dominance-dependent expression of the migratory urge (Lack 1968).

This great evolutionary flexibility in the appearance and disappearance of migration may appear surprising

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for such a seemingly complex attribute. Migration requires genetic instructions about (1) timing and duration of movement in the temporal/circannual program of the organism, (2) physiological adaptations for fuel deposition and metabolism, (3) behavioural adaptations for responding to the variable conditions (weather, wind, currents) during the journey and (4) control of orientation and navigation (Berthold 2001).

Although little is still known about the genetic constitution of these traits, they are probably based on the regulation of characters existing (but perhaps partly dormant) also among residents, so that migration builds on an extension of general seasonal adaptations in movement, homing, metabolism etc, rather than constituting an altogether separate quality (Lack 1968). Berthold (1999) stressed the evolutionary importance of partial migration, being an extremely widespread as well as ancient pattern. This indicates that important genetic features for migration have remained latent among birds since early times, never disappearing but becoming activated or suppressed as populations evolve into migratory or sedentary states, respectively (Berthold 1999). A striking example of rapid evolution of migration is provided by the house finch *Carpodacus mexicanus* introduced into eastern North America from a population in California. Although apparently sedentary, the parent population shows signs of harbouring the genetic basis for migration (Able and Belthoff 1998).

There remains a lot to be discovered and learned about the physiological, behavioural and navigational mechanisms and adaptations for migration, and about the genetic basis (Pulido et al. 1996) of these adaptations, before a full understanding of the evolutionary flexibility of migration will come within reach. Given this great flexibility one can expect that migration to a large degree evolves according to the ecological opportunities. There are indeed a lot of important ecological factors promoting but also limiting long-distance migration, which we will briefly summarise in this contribution.

The arctic tern *Sterna paradisaea* is one of the record species for long-distance migration, travelling a one-way distance of almost 20,000 km from breeding areas at northerly and often high arctic latitudes to survival and moulting areas in the Antarctic pack ice zone (Salomonsen 1967). Why this extravagant and risky way of life? This is the most common question from people hearing about this amazing feat. But is it really that risky? Consulting the literature gives at hand an average annual survival of adult arctic terns of almost 90% (Glutz von Blotzheim and Bauer 1982). This is not lower than the survival of other tern species, and indicates that the long migration takes no heavy toll. Thus, long-distance migration does not appear to increase the difficulty of a tern's life as much as we are inclined to believe. Even if we cannot explain the unique evolutionary trajectories of individual migratory species, we can address the general question "why?" by considering some crucial factors for long-distance migration. The ecological factors considered in this paper are summarized in Table 1.

Before discussing ecological factors pertaining to long-distance migration we will, as food for thought, briefly mention some examples of migrations among selected animals as listed in Table 2. For comparisons between animals of different size and mode of locomotion we also calculated the migration distance as number of body lengths (Table 2). In absolute distance the arctic tern has the longest migration between its high arctic breeding sites and the Antarctic, apparently only limited by the extent of Tellus. Also other bird species show impressive migrations, and in terms of number of body lengths a few species even surpass the arctic tern (Table 2). Among other groups, it is the flying insects (monarch and desert locust) and a bat that equal or approach the birds regarding relative migration distance. In swimming animals we find long-distance migrants among large whales, the elephant seal and sea turtles. The quoted movement of a loggerhead turtle refers to a trans-Pacific migration after release from a long time in captivity, which might be an unrepresentative movement of adults in this species. However, juve-

Table 1. Factors affecting the evolution and ecology in long-distance migrants and their likely implications on migration.

Ecological factor	Implication for long-distance migration
Seasonality	Resource exploitation
Habitats	Resources, competition
Barriers	Migration routes, physiology
History and genetics	Migration routes, breeding ranges, speciation
Competition	Migration patterns
Mortality cost	Migration distance, co-evolution predator/prey
Parasites and immunology	Habitat selection, exposure to different pathogen faunas
Energy cost of transport	Migration strategy, migration route
Time of migration	Migration strategy, migration distance
Moving fluid (transport medium)	Range, environmental transport, compensation for displacement
Size	Mode of locomotion, migration distance
Orientation and navigation	Migration routes, availability of sensory cues

Table 2. Examples of one-way migration distances in different animal groups. The examples give are not necessarily the longest exhibited by a species

Species		From-to	Distance (km)	Body length (m)	Distance (\times body lengths $\times 10^3$)	Source ^a
Mammals						
Caribou	<i>Rangifer tarandus</i>	Tundra-forest (Canada)	1200	2	600	S. Couturier pers. comm.
Elephant seal	<i>Mirounga leonina</i>	South Georgia-Antarctic peninsula	3000	3	1000	McConnel and Fedak 1996
Humpback whale	<i>Megaptera novaeangliae</i>	Hawaii-Alaska	5000	15	330	Darling and McSweeney 1985
Sperm whale	<i>Physeter macropcephalus</i>	Atlantic	5000	16	310	Lockyer and Brown 1981
Gray whale	<i>Eschrichtius robustus</i>	Baja California-Chukchi Sea	6000	14	430	Lockyer and Brown 1981
Nathusius' pipistrelle	<i>Pipistrellus nathusii</i>	Moscow area-Black Sea	1000	0.05	20000	Strelkov 1969
Birds						
Wandering albatross	<i>Diomedea exulans</i>	S Georgia-Tasman Sea	16000	1.2	13000	
Short-tailed shearwater	<i>Puffinus tenuirostris</i>	Tasmania-Bering Strait	12500	0.43	29000	
White stork	<i>Ciconia ciconia</i>	Baltic-S Africa	10000	1.01	9900	
Swainson's hawk	<i>Buteo swainsoni</i>	USA-Argentina	13500	0.52	26000	Fuller et al. 1998
Osprey	<i>Pandion haliaetus</i>	Sweden-Mozambique	10000	0.57	18000	Hake et al. 2001
Red-footed falcon	<i>Falco vespertinus</i>	Upper Lena-Namibia	14500	0.29	50000	
American golden plover	<i>Pluvialis dominica</i>	N Alaska-Tierra del Fuego	15500	0.26	60000	
Pectoral sandpiper	<i>Calidris melanotos</i>	Taymyr-Argentina	16500	0.21	79000	
Red phalarope	<i>Phalaropus fulicaria</i>	N Ellesmere-off SW Africa	12500	0.21	60000	
Long-tailed skua	<i>Stercorarius longicaudus</i>	N Greenland-Southern Ocean	16000	0.51	31000	
Arctic tern	<i>Sterna paradisaea</i>	Greenland-E Antarctic	19000	0.35	54000	
Swift	<i>Apus apus</i>	Lake Baikal-Angola	11500	0.17	68000	
Wheatear	<i>Oenanthe oenanthe</i>	Alaska-E Africa	13500	0.16	32000	
Willow warbler	<i>Phylloscopus trochilus</i>	Chukotka-S Africa	15500	0.11	141000	
Blackpoll warbler	<i>Dendroica striata</i>	Alaska-Bolivia	12000	0.14	86000	
Amphibians, reptiles						
Green turtle	<i>Chelonia mydas</i>	Ascension Island-Brazil	2900	1.4	2100	Papi et al. 2000
Loggerhead turtle	<i>Caretta caretta</i>	California-Japan	11500	1	12000	Nichols et al. 2000
Frog	<i>Rana lessonae</i>	Austria	15	0.09	170	Sinsch 1990
Striped whipsnake	<i>Masticophis taeniata</i>	Utah, USA	4	1.5	3	Hirth et al. 1969
Water python	<i>Liasis fuscus</i>	N Australia	12	3	4	Madsen and Shine 1996
Fish						
Herring	<i>Clupea harengus</i>	Norwegian Sea, N Atlantic	1500	0.35	4300	Slotte 1999, Harden Jones 1981
Eel	<i>Anguilla anguilla</i>	Baltic Sea-Sargasso Sea	6500	0.6	11000	Van Ginneken and van den Thillart 2000
Bluefin tuna	<i>Thunnus thunnus</i>	Atlantic	12000	3	4000	Mather et al. 1995
White shark	<i>Carcharodon carcharias</i>	California-Hawaii	3800	4.4	860	Boustany et al. 2002
Insects						
Collembola	<i>Hypogastrura socialis</i>	Scandinavia, on snow	1.5	0.002	750	Hågvar 2000
African armyworm moth	<i>Spodoptera exempta</i>	Kenya	150	0.012	12000	Rose et al. 1985
Monarch butterfly	<i>Danaus plexippus</i>	Mexico-North America	3600	0.05	72000	Urquhart and Urquhart 1977, Brower 1996
Desert locusts	<i>Schistocerca gregaria</i>	Arabian peninsula-Mauritania	5000	0.06	83000	Waloff 1959

^abased on handbook information unless reference given.

nile loggerhead turtles move large distances in the north Atlantic gyre (Lohmann and Lohmann 1998). Adult green turtles do however migrate as indicated (Table 2). Terrestrial amphibians and reptiles show rather moderate migration distances in comparison to flyers and swimmers. The caribou qualifies as a terrestrial long-distance migrant but still has a rather modest migration when compared to swimmers and flyers. The data shown in Table 2 are by no means complete, but could serve as examples of migration achievements by different animals when now turning to those ecological factors that we believe play important roles in biological adaptation for a mobile life.

Seasonality

Migration is in many cases primarily an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression. The trajectory of the arctic tern through the Earth's spatiotemporal landscape of solar energy input provides a good example (Fig. 1).

For a sedentary population the degree of seasonal fluctuation in resources within its range (bottleneck effect) presumably determines the general level of re-

productive output as suggested by Ashmole (1963) and evaluated by Ricklefs (1980) and Yom-Tov and Geffen (2002). Hence, for bird species at high latitudes there will be more excess resources available for breeding relative to the resource level during the survival (winter) period, giving room for larger clutch sizes than for species at equatorial latitudes. Migration will have the effect of modulating the amplitude in seasonal resource fluctuations for the populations concerned. Comparing residents and migrants among northerly breeders, the migrants will experience a reduced amplitude in seasonal resource levels (because they migrate south to richer survival regions) and they will thus be expected to have smaller clutch sizes than ecologically similar resident species. Conversely, comparing resident and migrant species sharing benign equatorial or mid latitudes during the survival season, the migrants, by travelling to breed at higher latitudes, will experience the largest relative seasonal resource fluctuation and thus be expected to have larger clutch sizes than the equatorial residents. However, for such differences in reproduction and survival to arise between residents and migrants it requires that there exist ecological segregation and asymmetric competition to uncouple the demographics between the three categories of northerly residents, southerly residents and migrants (Ricklefs

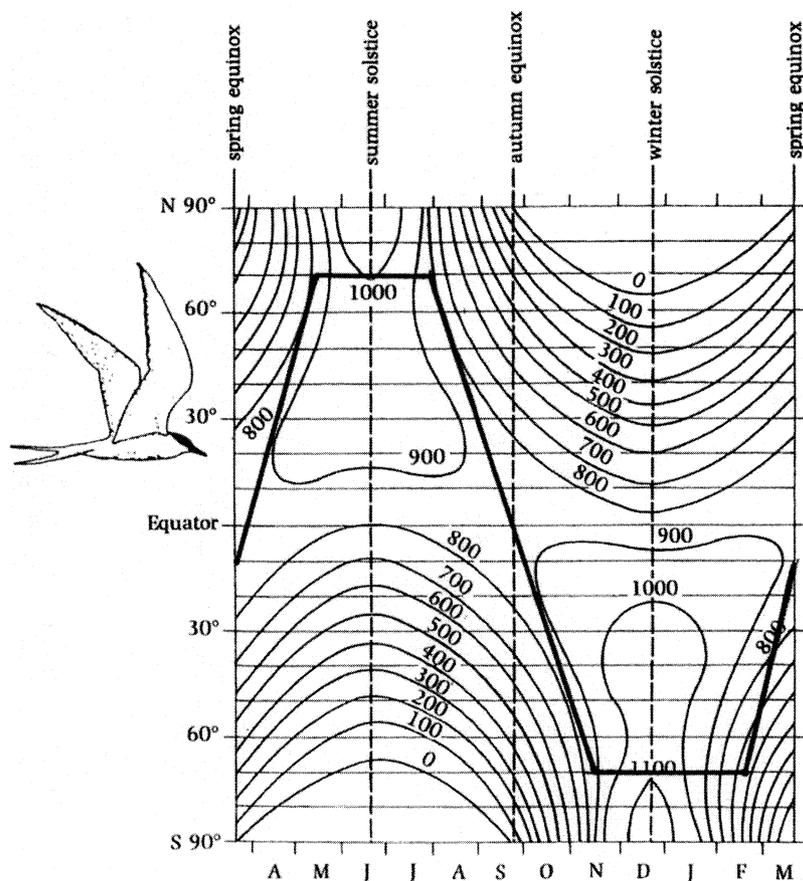


Fig. 1. Daily solar energy (cal cm^{-2}) reaching the Earth at different latitudes and times of the year (based on Lamb 1972). The thick line shows the trajectory in this spatio-temporal 'energy landscape' of arctic terns migrating between Arctic breeding latitudes and Antarctic survival and moulting latitudes.

1992). Also, Yom-Tov and Geffen (2002) showed that residents experiencing heavy competition from migrants during the non-breeding season tend to have a larger reproductive output than residents encountering fewer migrants. This is in accordance with Ashmole's (1963) suggestion that an influx of migrants during the non-breeding season increases the difference in relative resource levels between seasons for the residents.

By venturing far south into the Southern Hemisphere for its survival period, the arctic tern may seem to reduce the amplitude of seasonal resource fluctuation to almost nil (Fig. 1), leaving room for only a small reproductive output. The relative amount of resources available for reproduction and survival of migrating animals is, however, seldom a simple function of only latitude and climate but may in fact vary widely (and be very difficult to estimate) because widely different habitats are exploited for reproduction and survival.

Habitats

The transition between residency and migration probably occurs through a density-dependent selection process where resident or migratory populations will become outcompeted or there will remain a balance of partial migration (Bell 2000). Important for the outcome of this competition are the relative advantages of the extra seasonal gain in reproduction or survival for the migrants and of prior occupancy for the residents when they meet the returning individuals of the migratory population within their range (Alerstam and Enckell 1979). There are important habitat segregation and dominance relationships between sedentary and migratory individuals on the common non-breeding grounds, as demonstrated for blackcaps *Sylvia atricapilla* in Spain (Pérez-Tris and Telleria 2002). The benefit associated with prior occupancy and site fidelity is small or nonexistent in unstable or unpredictable habitats, favouring the development of obligate migration in species from such habitats (Alerstam and Enckell 1979).

Furthermore, there are many habitats that offer excellent conditions for survival but cannot be used for reproduction. Such survival resources can be efficiently exploited by migrants, travelling to different and often distant and seasonal habitats for reproduction (Alerstam and Högstedt 1982). In fact, migration to a large degree serves as an adaptation for exploiting different habitats for survival and reproduction, and for combining these fractional niches into a complete basis of existence. Thus, exploiting different habitats for survival and reproduction (and sometimes for special purposes like moulting) and exploiting the effects of seasonality are equally fundamental (and only partly interdependent) conditions for the evolution of migration.

If there is a surplus of survival resources in relation to reproductive resources or vice versa will be of crucial importance for the timing and age-dependence of migration and for the general life history traits of the migratory species (Alerstam and Högstedt 1982).

Barriers

Barriers, like oceans (for terrestrial animals), continents (for marine animals), mountain ranges, deserts or glaciers, have a profound influence on the evolution of migration. The importance of deserts and mountain ranges for the Palaearctic-African bird migration systems was highlighted by Moreau (1972). Barriers may have at least three main consequences: (1) they may simply put a stop to further migration. (2) They may lead to the evolution of detours, where the crossing of barriers is avoided or reduced. Detours may evolve even if e.g. birds have the potential capacity for a direct crossing. The detour may be associated with a reduced cost of transport because of e.g. improved conditions for favourable flight techniques like soaring migration (Kerlinger 1989), increased wind assistance (Gauthreaux 1980), or reduced cost for carrying heavy fuel reserves (Alerstam 2001). (3) Long-distance crossing of barriers requires that special instructions are incorporated into the migrants' endogenous spatiotemporal circannual programme (Gwinner 1996, Berthold 2001) about increased fuel deposition and sometimes changes in the orientation (Gwinner and Wiltschko 1978) at the barrier. Possibly such changes in fuel deposition and orientation are triggered by map-related external cues provided by e.g. the geomagnetic field (Fransson et al. 2001).

Historic and genetic factors

It is an old idea that migratory pathways reflect the colonisation routes during the range expansions of migratory species. The underlying assumption is that there are elements of evolutionary inertia and constraints pertaining to the inherited genetic program for migration, allowing successive extensions of the programme but not too complex and abrupt changes. Sutherland (1998) reviewed recent changes in the migration patterns of birds and found several cases of expanding populations having retained their original, but now apparently or possibly sub-optimal, migration routes and winter quarters. Interestingly, all these cases referred to species where the juveniles migrate independently from the adults and rely on their genetic programme for the first autumn migration (there were also many cases of changed routes among species in this category). There were no such cases of apparently

sub-optimal routes among species where the juveniles accompany the adults on migration, indicating that learning between generations (cultural evolution) enhances the flexibility of migration for these species (Sutherland 1998).

This type of evolutionary constraint, imposed by the genetic migratory programme, was suggested as an explanation for the paradoxical fact that long-distance migrants among land birds have been less successful colonists between North America and Eurasia than sedentary species (Böhning-Gaese et al. 1998) and that migratory species have on average a smaller breeding range than residents across the Eurasian boreal zone (Bensch 1999).

The idea of important constraints for evolutionary transitions to novel migratory programmes stands in some contrast to the great flexibility of migration as pointed out earlier and to the indications of novel migration patterns evolving very rapidly also without cultural transmission (Berthold et al. 1992, Berthold 1999). Another possible explanation for relatively smaller range sizes among migratory birds is the antagonistic effects of dispersal. Even if migratory birds had a great potential as colonisers by a high dispersal capability, extensive dispersal may contribute to restriction of a species' range through swamping of local peripheral adaptations by large gene flow from the centre of the range (Kirkpatrick and Barton 1997). Furthermore, for an expanding population of migrants to develop a novel migration pattern there are more difficulties to overcome than those associated with a change in the migratory programme – habitat requirements must be satisfied and the environment of competitors and parasites must be manageable at the new winter quarters.

Competition

Migration habits often differ among populations, age and sex classes of the same species/population (reviewed by Alerstam and Hedenström 1998). When leapfrog migration occurs, northerly breeding populations migrate longer distances than southerly breeding populations, which in the ideal case are over-flown by the northern birds (Salomonsen 1955). If chain migration occurs the migration distances might be more or less similar among populations, although they breed and migrate between different areas. Within a population a common pattern is that juveniles and females migrate farther than adults and males. To explain such migration patterns and differential migration, competition is often invoked, either among individuals of different populations or between individuals of the same population, in combination with migration costs, suitability gradients and/or seasonal productivity. In differential

migration, dominants (typically adults and/or males) displace sub-ordinates (juveniles and/or females) which move to wintering sites further away from the breeding area than dominants. No matter what the critical resource is, e.g. wintering sites allowing early spring arrival, some form of competition is often an important ingredient in models of the evolution of migration and patterns thereof. Hence, migration behaviours should be considered as components of the suite of life-history trait adopted by migratory organisms. In this sense, migration has probably co-evolved in concert with other traits, e.g. timing of moult and breeding, breeding effort, nesting habits, etc, thereby defining the ecology of a population or species.

Mortality cost of migration

Heavy fuel loads will affect flight performance negatively (Hedenström 1992, Lind et al. 1999), and so a fat bird might be more vulnerable to predation than a lean bird. If predation risk is mass-dependent, then the optimal departure fuel load is reduced in relation to that associated with time-minimization migration. Hence, an alternative optimization rule for migration could be the minimization of mortality per unit distance migrated (Alerstam and Lindström 1990). Cage experiments indicate that birds exposed to artificial predator attacks reduce their body mass (fat load) in relation to controls (Lilliendahl 1997, but see Fransson and Weber 1997), which could be interpreted as adaptive behaviour in accordance with the theory. However, recent data from a small island stopover indicate that relatively lean birds are more vulnerable to predation than heavy birds (Dierschke 2003). If and how birds in the wild adjust their fuel levels and hence their migration speed when exposed to predator attacks remains to be shown.

Studying predator attacks against chaffinch *Fringilla coelebs* and brambling *F. montifringilla* at autumn stopovers, Lindström (1989) estimated that 10% of the finches were killed during their six-week migration period. This indicates that predation during migration may be an important mortality factor in small birds. In a recent population study of black-throated blue warblers *Dendroica caerulescens*, Sillett and Holmes (2002) assessed the survival rates during the summer breeding period in New Hampshire, during the winter period in Jamaica and during autumn and spring migration, respectively. They found that most mortality occurs during the migration episodes with an apparent mortality rate at least 15 times higher during migration compared with the stationary periods, and that more than 85% of apparent annual mortality occurs during migration. These data support the notion that migration might be hazardous and that adaptations to reduce predation/mortality risks should be expected. Such adaptations

could involve habitat selection regarding fuelling rate with respect to predation risk (Lindström 1990) and possibly timing of migration to avoid peak predator migration (Lank et al. 2003). The Old World falcons, Eleonora's *Falco eleonora* and sooty falcon *F. concolor*, have adjusted their breeding season to coincide with peak autumn songbird migration between Eurasia and Africa (Walter 1979a, b). The distribution of Eleonora's falcon colonies probably matches the migration density and even if estimated numbers of prey taken by the Eleonora's falcon are impressive ($> 10^6$; Walter 1979a), they constitute $< 0.1\%$ of the total number of birds migrating through the Mediterranean region. Possible co-evolution of migration timing and routes between predators and prey species remains an interesting, but poorly investigated, research question.

Parasites and immunology

The prevalence and spread of infectious diseases are affected by a variety of factors, such as density of hosts, parasite transmission mode, and the spatial structure of host populations (Getz and Pickering 1983, Antonovics and Thrall 1995, Lockhart et al. 1996). Thus, the seasonal movements adopted by many animal hosts are likely to affect pathogen prevalence. Gylfe et al. (2000) indicated that the stress of autumn migration reactivated latent *Borrelia* infections among redwing thrushes *Turdus iliacus*. The selection of parasite-free habitats has been suggested to be an important reason for long-distance migration in shorebirds (Piersma 1997). A similar explanation has been put forward for the occurrence of migration in reindeers (Folstad et al. 1991), and the alternation between sleeping groves by yellow baboons *Papio cyanocephalus* (Hausfater and Meade 1982). The ecological costs associated with parasite infections are likely to be high in hosts and have been intensively studied for example in birds (reviewed by McCurdy et al. 1998 and Norris and Evans 2000), and therefore selection should favour behaviours minimizing exposure to parasites during migration. This could be achieved in migration systems where animals are shuttling between habitats with relatively few parasites, such as the arctic tundra and coastal marine habitats (arctic waders, Piersma 1998).

Altizer et al. (2000) examined how variation in parasite prevalence relates to host movement patterns, by studying the obligate parasite *Ophryocystis elektroscirrha* (McLaughlin and Myers 1970) and its host, the Monarch butterfly *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae). The three main populations of Monarch butterflies in North America showed differences in the occurrence of the parasite *O. elektroscirrha* correlated with the migratory distance (Fig. 2, Altizer et al. 2000). Thus, the highest parasite prevalence was observed in

the non-migratory Florida population, while the lowest numbers of parasites were counted in the easternmost and long-distance migrating population (Fig. 2). Furthermore, the average parasite loads of summer-breeding adults decreased with increasing distance to the wintering sites, suggesting that the most heavily infected individuals were not successful in reaching the most northerly breeding sites. Thus, parasite transfer seems to occur during migration and wintering, presumably as a consequence of the typical clustering behaviour of the host butterflies, and had a high impact on the Monarch ability to perform long migrations (Altizer et al. 2000).

Animal migrants regularly spending time in different habitats during migrations are likely to be exposed to variable parasite faunas, characteristic for each geographical area and habitat. Parasite faunas may vary not only between geographical areas, but also over time (Bensch and Åkesson 2003). Cross-species transfer of avian haemosporidian parasites, *Haemoproteus* and *Plasmodium*, has been shown to occur between resident bird species and long-distance migrants in the wintering areas in Africa (Waldenström et al. 2002). Some of these parasites are likely to have high fitness costs for the birds. Thus, exposure to new lineages of parasites may be a potential cost of migration having important consequences for the evolution of migration routes and winter distributions.

Transport cost: energy

Any movement involves an energy cost, which is typically taken from stored fuel during long-distance migration. It has been suggested that certain aerial foragers, such as swallows, might feed while migrating, but also they seem to deposit fuel stores before flights as other birds do (Pilastro and Magnani 1997, Rubolini et al. 2002). Energy substrate for metabolism may differ between animals, but for long-distance migration an energy-dense substrate is preferred because the cost of transporting the fuel itself is kept at minimum. Therefore, energy reserves to be used for migration are usually stored as fat adipose tissue (Jenni and Jenni-Eiermann 1998).

Since carrying large and heavy fuel reserves increases the transport cost (applies to all modes of locomotion) the energy cost of migration will be minimized if the travel is divided into short episodes that can be covered with small fuel reserves. If the food or suitable habitat for a particular species are patchily distributed (Bibby and Green 1981), the energy cost will be increased since longer distances without refuelling must be undertaken. The maximum fuel storage capacity (sensu Hedenström and Ålerstam 1992) might therefore limit the distances that an animal can move without refuelling (see below on size).

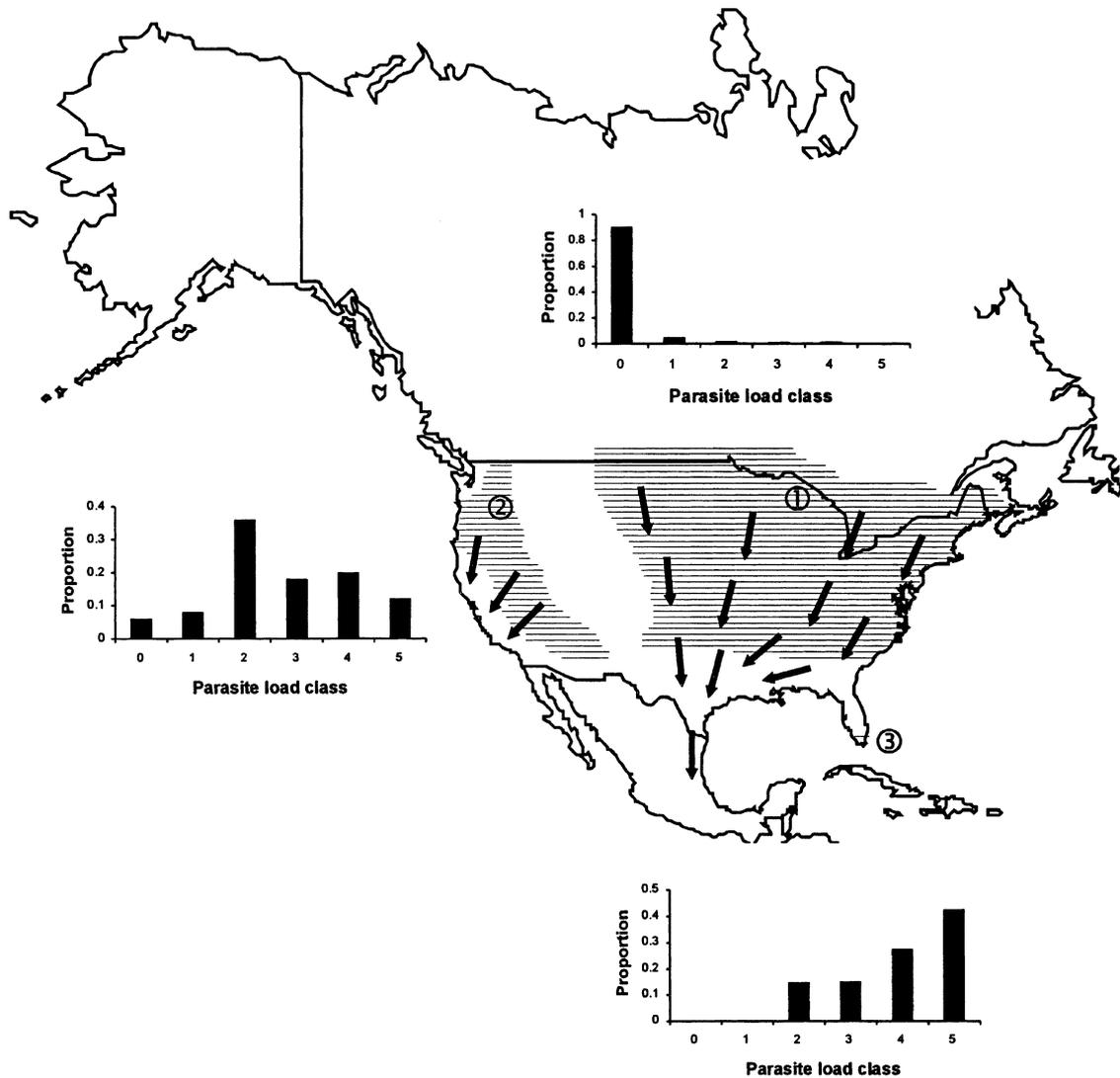


Fig. 2. Summer breeding ranges and main migration routes for three populations of North American monarch butterfly: 1. eastern migratory population, 2. western migratory population, 3. southern Florida resident population. Inserted histograms show frequency distributions of parasite loads for the respective populations. Based on Altizer et al. (2000).

Generally, if migration is sub-divided into stages of movement with stopover interludes, the total energy consumption during migration can be written as

$$E = \frac{PD}{V} \left(1 + \frac{x}{P_{\text{dep}}} \right) \quad (1)$$

where P is power of locomotion, D is migration distance, V is locomotion speed, P_{dep} is rate of energy deposition at stopovers, and x is the field metabolic rate at stopovers (Hedenström and Ålerstam 1997). Eq. (1) can be used to compare the total investment in migration among, for example, animals of different size and using different modes of locomotion. The ratio $x:P_{\text{dep}}$ determines the ratio between energy consumed during

stopovers and cost of locomotion, which in a typical passerine bird may be about or larger than 2:1. From Eq. (1) it is also evident that minimizing the ratio $P:V$, a measure closely related to cost of transport, will minimize the energy cost of migration. By comparing the cost of transport among animals that run, swim or fly, Schmidt-Nielsen (1972) found that swimmers move with the lowest cost and runners with the highest, with flyers at intermediate levels. Hence, depending on the mode of locomotion long distance migration should be favoured in swimmers and flyers, while runners might be constrained by energy to develop long-distance migration. Indeed, among swimming and flying animals (e.g. whales and arctic tern; Table 2) we find the true globetrotters.

Transport cost: time

For animals living in a seasonal environment the management of time in relation to ecological conditions is crucial. The reproductive activities (display, nest building, incubation/gestation, raising young to independent age, etc) require time, as well as moult (in birds), leaving a limited amount of time for other activities including migration. Generally, the time required for migration can be written as

$$T_{\text{migr}} = \frac{D}{V} \left(1 + \frac{P}{P_{\text{dep}}}\right) \quad (2)$$

where P , P_{dep} and V are defined as for Eq. (1). The relationship between stopover and transportation time is P/P_{dep} , which was estimated to be $\geq 7:1$ for a small bird (Hedenström and Ålerstam 1997). Given some limited time available for migration, Eq. (2) indicates that there is a maximum return distance (D_{max}) that an animal can achieve. The time of migration is reduced by low locomotion cost (P) and high transportation speed (V) and fuelling rate (P_{dep}), and so adaptations for low energy cost of transport and high rates of fuel deposition are expected in long-distance migrants. For example, physiological flexibility should occur mainly in long-distance migrant birds (Weber and Hedenström 2001). Also the optimal scheduling of life-history events and extent of migration may differ between animals using different modes of locomotion.

Moving fluids

A feature shared by swimmers and flyers is that they move in a medium, which typically is itself in motion, and this flow can aid or counter a migrant depending on the relative speed vectors of the animal and the surrounding fluid. It is generally surmised that terrestrial animals are relatively unaffected by e.g. winds, although they may have a notable effect in open landscapes. Locomotion costs in terrestrial animals are instead affected by compliance and resilience of the substratum on which they walk or run (Alexander 2000). For swimmers and flyers, predictable oceanic currents and winds may be exploited for migration and could perhaps also influence the evolution of certain migration routes, such as loop migration patterns. Radar studies indicate that birds usually migrate with following winds more often than expected by chance (Richardson 1978, Gudmundsson et al. 2002). During some particularly spectacular long-distance flights, like those across the western Atlantic by Nearctic shorebirds and possibly passerines, birds adjust their departure from Nova Scotia in relation to the passage of weather fronts to gain initial tail wind during the first SE leg of the flight (Richardson 1979, Stoddard et al.

1983), while enjoying the easterly trade winds when approaching the Caribbean or the north coast of South America.

Winds can be used by birds in strategic ways for optimisation of migration economy, both by using varying winds between days and by combining partial drift and overcompensation (Richardson 1990). The vertical wind speed gradient provides large seabirds with the possibility of dynamic soaring, in which energy is extracted by a sequence of climbs into the wind and gliding descents with the wind (Rayleigh 1883). Upwards deflected winds and gusts near wave crests are however probably more likely sources of energy for the majority of soaring seabirds (Pennycuik 2002). Air and water turbulence are likely to affect locomotion of flyers and swimmers, but there are no systematic study of what those effects might be.

Over land, slope lift, thermal convection, thermal streets and lee waves provide birds with energy for soaring flight migration.

In swimmers, sea currents are exploited for migration like winds by birds. For example, plaice *Pleuronectes platessa* migrating in the North Sea use selective tidal stream transport, where the fish come up into midwater when the tidal stream is flowing in the appropriate migration direction, while they remain on the bottom when it is flowing in the opposite direction (Metcalf and Arnold 1990). The famous migration by the European eel *Anguilla anguilla* to the Sargasso Sea (6000 km) is probably aided by sea currents, even though the energy cost of swimming is comparatively low in eels (Van Ginneken and van den Thillart 2000).

An animal's own speed in relation to the surrounding medium limits the scope of compensation for lateral fluid motion, depending on the strength and direction of the flow. Storms are therefore a potential hazard, especially to small birds which may be displaced or even succumb. Fluid motion and physical properties are facilitating long-distance migration, but may cause problems as well.

Size

How traits change with body size – scaling – is a fundamental question in biology, and migration performance is no exception. In flying birds, the load-carrying capacity decreases with increasing body mass (Hedenström and Ålerstam 1992), which applies to the maximum fuel load. This means that the maximum flight range decreases with increasing size, although large birds compensate this to some extent by relatively longer wings (Rayner 1988). Also the duration of breeding (incubation, rearing of young, etc) and moult increase with size in birds, leaving less time to complete a return migration within an annual time budget. Be-

cause of progressively increasing flight cost with increasing body size, the overall migration speed, $V_{\text{migr}} = D/T_{\text{migr}}$, is decreasing with body size in birds using flapping flight. Combined with reduced time available for migration, the overall speed of migration can constrain the potential migration distance in large birds, provided an annual time budget constraint for breeding, moult and migration (Hedenström and Ålerstam 1998). Possibly, this could explain the relationship between size and total migration distance among, for example, the three swan species in Europe, where the smallest species *Cygnus bewickii* migrates the farthest distance and the largest species *C. olor* the shortest distance. In gliding/soaring flight migration speed should increase with size (Hedenström 1993), as well as the energy cost of transport will decrease compared with flapping flight, which favour soaring flight by large-bodied long-distance migrants. However, thermal soaring requires migration over land and so migration routes are constrained by the geographical distribution of land-masses, often leading to migration along detours (Pennycuik 1972). Hence, there are interesting trade-offs depending on size and mode of locomotion.

In swimmers and runners the overall migration speed scales approximately as $m^{0.1}$ and $m^{0.17}$, respectively, if assuming that the rate of energy deposition is proportional to the resting metabolic rate (Hedenström 2003). Hence, in animals using these locomotion modes long-distance migration should be favoured by increasing body size, which is consistent with the size of swimming migrants (whales, whale shark) and animals using terrestrial locomotion (e.g. caribous or wildebeests).

Orientation and navigation

The ability to find the way during migrations is likely to have a strong impact on the evolution of distances and routes adopted by migrating animals. Birds and other animals can use a number of different compasses for orientation during long-distance migrations, based on information from the sun and the related pattern of skylight polarisation, stars and the Earth's magnetic field (reviewed by Able 1980, Emlen 1975 and Wiltschko and Wiltschko 1995). The sun compass is based on a time-compensation mechanism (Schmidt-Koenig 1990), while the rotation centre of the night sky indicated by the stars gives the direction towards geographical poles (Emlen 1975). Geomagnetic compass courses are given by the angle of inclination among for example birds and sea turtles, while sub-terranean mole rats and homing newts respond to the polarity of the geomagnetic field (Wiltschko and Wiltschko 1972, for review see Wiltschko and Wiltschko 1995). The reliability of these compasses might vary between areas and with time of the year, such that for instance the sun

compass cannot be used if the sky is completely obscured by clouds, the star compass might not be available for orientation at high geographical latitudes during the polar summer (Ålerstam 1996), and a geomagnetic compass based on the angle of inclination is unusable at the geomagnetic poles and the geomagnetic equator (Wiltschko and Wiltschko 1972, Åkesson et al. 2001). A sun compass mechanism without compensation for the time-shift when passing the longitudes enables birds to fly close to the shortest routes between distant geographical areas, a situation that probably applies to long-distance migrating waders in the high arctic (Ålerstam et al. 2001). Furthermore, magnetic compass orientation has been shown to be possible in very steep geomagnetic fields for two species of passerine migrants near to the North magnetic pole (Sandberg et al. 1998, Åkesson et al. 2001). The results show that both a sun and a geomagnetic compass mechanism may be used in the navigationally complicated area near the geographic poles. The complementary significance of different compass mechanisms, depending on geographic position, time of season and availability of cues, is evaluated further by Muheim et al. (2003).

Besides the biological compasses animals can use other cues for navigation (Papi 1992). To return annually to known territories with familiar foraging and protective sites during migration is of great importance for many animals. In most cases it is still unknown which cues animals use for long-distance navigation. However, animals have been suggested to use geomagnetic bi-coordinate maps based on angle of inclination and the total field intensity for navigation over large geographical areas (Phillips 1996, Walker 1998, but see Wallraff 1999), recently supported by work on sea turtles in the North Atlantic (Lohmann and Lohmann 1996a, Lohmann et al. 2001). Newly hatched loggerhead sea turtles *Caretta caretta* have been shown to respond to and change migratory courses when exposed to site-specific combinations of geomagnetic field parameters, i.e. angle of inclination and total field intensity, that they are expected to meet during their circular migration around the Sargasso sea (Lohmann et al. 2001). Hence, the juveniles are born with a migration program that is triggered by external cues, and which direct them during their oceanic migration. Experiments with adult green turtles *Chelonia mydas* nesting on Ascension Island, suggest that they are relying on geomagnetic cues for navigation neither during migration (Papi et al. 2000) nor during homing (Luschi et al. 2001, Åkesson et al. 2003), suggesting that this species behaves differently than the loggerhead sea turtles studied in the North Atlantic or that other information (Carr 1972) is used for navigation as the sea turtles gain experience in life. Instead the Ascension Island green turtles seem to use local cues, transported with wind to locate the island after displacements (Luschi et al. 2001, Åkesson et al. 2003).

The distribution of geomagnetic gradients provides a basis for bi-coordinate geomagnetic navigation in some areas of the globe (north and south Atlantic Ocean, Lohmann and Lohmann 1996b, Åkesson and Alerstam 1998), while the combinations of parameters result in great difficulties to navigate in other areas, for instance, in the south Indian Ocean where wandering albatrosses *Diomedea exulans* are foraging and migrating over extensive areas of open ocean (Åkesson and Alerstam 1998). It is still unknown how these and other bird species inhabiting the same geographical area navigate during these long foraging and migration flights. Further difficulties for the use of bi-coordinate magnetic maps may be the secular variation, by which the geomagnetic parameters at a geographic location are gradually changing (Skiles 1985), which can be extensive during a sea turtles' lifetime (Courtillet et al. 1997). Diurnal variations of the geomagnetic parameters might also complicate the perception of geomagnetic field variables, especially since variations occasionally can be large during so-called magnetic storms (2–3% variation in field intensity, Skiles 1985). Despite these difficulties, it seems as if some animals have overcome these problems and have adapted to use the geomagnetic field for navigation (Lohmann and Lohmann 1996a, b, Fischer et al. 2001, Lohmann et al. 2001, Boles and Lohmann 2003), as well as for a triggering of physiological changes in the migration programs (Beck and Wiltschko 1988, Fransson et al. 2001). Still we need to find out if these responses to the geomagnetic field are widespread among animals, and which orientation cues have been important to facilitate the evolution of long-distance migration.

Concluding remarks

The compilation above of factors bearing on long-distance migration in animals reveals the inherent complexity of a mobile life-style. New field techniques, such as satellite transmitters (see examples in this volume), have revolutionized the tracking of individual migrants during their entire round-trip journeys. We still face purely natural history questions regarding how for instance small songbirds carry out their entire migration (but see Cochran 1987). Flow tanks, wind tunnels and treadmills help researchers investigate physiological and mechanical properties of locomotion, while new molecular genetic techniques provide information about parasites and pathogens affecting migrating animals. Evidently migration research represents a truly integrative field, where students of different background, such as ecologists, physiologists, biomechanists, etc. continue to leave significant contributions to the fabric of understanding the biological adaptations required by migratory organisms.

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