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Conflicting Evidence About Long-Distance Animal Navigation

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Because of conflicting evidence about several fundamental issues, long-distance animal navigation has yet to be satisfactorily explained. Among the unsolved problems are the nature of genetic spatial control of migration and the relationships between celestial and magnetic compass mechanisms and between different map-related cues in orientation and homing, respectively. In addition, navigation is expected to differ between animal groups depending on sensory capabilities and ecological conditions. Evaluations based on modern long-term tracking techniques of the geometry of migration routes and individual migration history, combined with behavioral experiments and exploration of the sensory and genetic mechanisms, will be crucial for understanding the spatial principles that guide animals on their global journeys.

Migration emerges and becomes suppressed among birds, fish, insects, sea turtles, bats, and sea mammals with apparent evolutionary ease. It has evolved numerous times without important phylogenetic constraints; closely related species or populations are often nonmigratory. Furthermore, post-glacial changes in travel patterns indicate a high fundamental understanding of animal navigation, and the emerging picture is complex and intricate. Yet after longstanding and intensive migration research, we are still far from a fundamental understanding of animal navigation, and the emerging picture is complex and intricate. Linnaeus, in his treatise Migrations Avium (1757), appealed for field observations from all over the world that would reveal birds’ migration routes. Over the next two centuries, banding of birds and fish produced a wealth of information, and displacement experiments revealed impressive homing performances. Orientation cage experiments proved to be powerful for discovering and exploring celestial as well as magnetic compass mechanisms. The map sense that is required in addition to a compass sense to explain the homing capabilities of animals attracted increased attention (2, 3). Animal tracking studies have benefited during the recent decades from increasingly sophisticated techniques, such as radar registration, satellite-based radio telemetry, and electronic geolocation and data storage tags. However, current research is characterized by conflicting evidence and interpretations about several fundamental questions (Table 1).

Until recently, it was believed that juvenile birds (among species traveling solitarily) on their first journeys relied solely on an endogenous spatiotemporal program, defining the journey in terms of direction and distance along one or a few main legs (Table 1B). Adding successive travel steps for migrants guided by such a simple inherent clock-and-compass program, with some variation between each step, will lead to a geographic spread of a population of migrants that increases with distance as a parabola along the migratory axis. Ringing recovery distributions of some bird species fit nicely with this predicted pattern (4).

However, migration patterns converging toward narrowly defined species-specific passage or wintering areas can hardly be the result of such simple endogenous control (5, 6) (Fig. 1). Rather, these patterns indicate that migrants use external cues, such as geomagnetic coordinates (e.g., magnetic field strength and inclination). Thrush nightingales (Luscinia luscinia) that were experimentally moved in geomagnetic space (while retained geographically in Sweden) to their target stopover area in Egypt increased their fuel deposition as expected when preparing to cross the Sahara desert (7). The best evidence for geomagnetic coordinates as regional markers comes from experiments with hatching loggerhead sea turtles (Caretta caretta) (8). The turtles changed their orientation in relation to geomagnetic position so as to remain along the migration route at the North Atlantic gyre. However, inherent magnetic map guidance is not without complications. The current difference in magnetic coordinates between northern Florida and the northeastern gyre will be obliterated in less than fifty years because of differential geomagnetic secular changes at these two places. Geomagnetic coordinates at the thrush nightingale’s target area, in 100 to 150 years time, will have changed to those that today are found at the target area of the blackcap (Sylvia atricapilla) (Fig. 1). How is it possible for evolutionary change in the animals’ genetic migration program to keep pace with such secular changes in the Earth’s magnetic field (Table 1)?

Homing may be an important element in migration of experienced animals that return to favorable sites visited earlier, such as breeding and wintering destinations and goal areas along the route (Table 1C). If the geomagnetic field provides information for migration control, it may also be an important basis for the map sense used by homing animals, an idea that has been considered several times since the end of the 19th century (3). Recent experiments in which animals have been displaced in geomagnetic (but not geographic) space have provided support for this possibility among salamanders, spiny lobsters, and sea turtles (9–11). However, the hypothesis of homing based on a magnetic map sense is controversial. Supporting experiments have demonstrated homing responses to geomagnetic north-south displacements but not yet to east-west displacements, where the differential changes in geomagnetic parameters are more critical. It also remains to be shown whether geomagnetic gradients allowing unambiguous navigation are actually available within the local natural homing ranges of the experimental animals. An even more serious difficulty for the magnetic navigation hypothesis is the failure reported in several experimental attempts to disrupt homing success by attaching magnets to the animals (3).

Sea turtles, petrels, and albatrosses equipped with disturbance magnets and recorded by satellite tracking show oceanic navigation performance similar to that of control individuals (12–15).
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These results imply that magnetic cues are not essential for successful homing if alternative navigation cues are available. A possible alternative homing mechanism is olfactory navigation. Seabirds have an excellent sense of smell and local emissions of scents released by phytoplankton may create an odor landscape that seabirds use for their navigation and homing (16). Green turtles (Chelonia mydas) that were displaced away from Ascension Island and recorded by satellite tracking relocated the island most efficiently from the downwind direction, suggesting that they used wind- or water-borne cues for their homing (17, 18). For homing pigeons, olfactory navigation remains theoretically possible on the basis of observed large-scale gradients of atmospheric chemical substances (19).

For birds, the intercalibration between different compass mechanisms has been studied in cue-conflict cage experiments (in which birds are exposed to both celestial and magnetic cues, with one or both of these cues manipulated such that they give conflicting compass information (Table 1D)). A consensus seemed to emerge that, for nocturnal migrants, twilight and star compasses are recalibrated to the geomagnetic field during the migratory period (whereas during the juvenile premigratory period celestial rotation constitutes the calibration basis for the magnetic compass (3)). However, this view was recently disputed by an elegant experiment in which Catharus thrushes were exposed to a deflected magnetic field during twilight and tracked by radio telemetry on their subsequent night flights (20). The outcome indicated, contrary to expectation, that the thrushes recalibrated their magnetic compass in relation to the twilight cues and then relied on their (miscalibrated) magnetic compass for the nocturnal flight, apparently ignoring stellar cues. The experimental birds changed to normal orientation again on succeeding nights when they had recalibrated their magnetic compass back to normal. A recent review of cue-conflict experiments proposes that the birds’ view of the twilight sky near the horizon may be decisive for the calibration rank between magnetic and celestial cues (21). There may also exist important differences between species in compass mechanisms and their hierarchical organization. New studies, particularly of birds under natural free-flying conditions, are now needed for a re-evaluation of the compass calibration issue.

The geometry of migration trajectories may indicate whether animals travel on constant compass courses over longer distances and, if so, which compasses are dominant (Table 1E). Tracking by ground-based radio telemetry suggested that a Catharus thrush oriented at a constant angle in relation to the sunset azimuth during six successive nocturnal flights over a total distance of 1500 km (20). Radar studies have indicated that shorebirds follow flight trajectories similar to great circles on long-distance flights across the Arctic Ocean at Siberia and arctic North America. Sun compass orientation, without correction for the longitudinal shift in local time, provides a possible mechanism for great circle orientation at polar latitudes (22). However, great circle routes are not universal. There are also several cases where bird migration routes conform most closely with a constant compass course. Trajectories of raptors in both the Old and New World were generally more consistent with constant geographic courses (implying dominant orientation by celestial cues) than constant geomagnetic courses (23). Further and closer analyses of the geometry of migration routes seem to be a promising avenue for the future.

Table 1.

Examples of unsolved problems and questions with conflicting evidence and interpretations in the field of animal navigation

| A | How can the existence of complex mechanisms in animal navigation and migration be reconciled with short evolutionary transition steps between nonmigratory and migratory statuses? |
| B | How important are external signals from map-related factors in the spatiotemporal control of migration of naïve animals? |
| C | How important are geomagnetic, olfactory, and other map-related cues in the homing of different animals? |
| D | What is the relative importance of the individuals’ multiple compass mechanisms based on celestial and magnetic cues, and how are the different compasses calibrated in relation to each other? |
| E | How do orientation and navigation mechanisms influence the geometry of migration routes, and to what extent do migrants travel on constant compass courses or along great circles? |
| F | How does learning during early migration episodes influence subsequent journeys with respect to, e.g., route and goal area fidelity, and how does navigation develop with age? |
| G | How do specific and total demands on brain capacity differ between migrants and residents? |
| H | What are the possibilities and constraints for rapid evolution of new migration routes? |

Fig. 1. Ringing recoveries in the eastern Mediterranean region of trans-Saharan passerine migrants (both adults and juveniles). Triangles indicate endpoints. Birds with similar general habitat requirements from Fennoscandian breeding grounds show species-specific autumn passage and stopover areas, as exemplified for the thrush nightingale (Luscinia luscinia) (yellow) and the blackcap (Sylvia atricapilla) (red). Responses by the migrants to external navigational signposts or triggers seem to be required for locating such well-defined target areas. Thin lines connect ringing and recovery locations but do not show the routes followed by the birds between these two points. [Image based on (6)]
The exploration of long-distance migration has entered a new era with a rapid growth of individual-based tracking data of increasing spatial resolution and prolonged coverage during multiple years and journeys. This will be crucial to understand how migration is organized into phases of dispersal, exploration, compass orientation, and homing, and how learning during one journey affects succeeding journeys (Table 1F). Individuals of North Sea plaice (Pleuronectes platessa) showed a high degree of fidelity to previous routes and destinations on their 250-km-long journeys between feeding grounds and spawning areas, sometimes within 20 km of their positions in previous seasons (24). Bluefin tuna (Thunnus thynnus) were also faithful to their spawning sites but with migration patterns developing with age in a complex way, as recorded for individuals continuously tracked during 3 to 5 years (25). Migration patterns of gray-headed albatrosses (Thalassarche chryostoma) tended to fall into different categories with individuals in the most common category undertaking complete circumnavigations around the Antarctic continent (26). Adult ospreys (Pandion haliaetus) revisited one or a few individual intermediary goal areas during their repeated journeys between north Europe and West Africa (27). Between these goal regions route fidelity was low, and flight paths by the same individual often ran several hundred kilometers apart on different journeys, far beyond visual landmark contact (Fig. 2). It is likely that the ospreys could find the next goal region by regional map-based navigation possibly in combination with path integration.

Long-term tracking of individuals will also provide a basis for comparative evaluations between fish, sea turtles, and birds and for critical displacement experiments. Such displacement experiments of individuals subsequently tracked by satellite have already begun (28, 29). Unraveling the entire migration history of individuals, starting as juveniles, which has not yet been achieved for any species, will reveal how an inherent spatiotemporal control program is complemented by imprinting and learning during the first and successive long-distance journeys. Another unresolved question is what determines whether migrants drift by wind and water currents or compensate for the drift. Age-dependent drift (30) may have important consequences for the individual migration history.

Information that is likely to be learned during the first journeys includes positions of goal areas, large-scale gradient maps as well as local site-specific maps, stopover habitat, vegetation, and food. Does this mean that migrants have a special long-term memory capacity for such information (Table 1G)? This was indeed suggested by a recent experiment (31) in which memory time of a particular feeding site was shown to differ between a long-distance migrant bird species (memory lasted at least 12 months) and a closely related nonmigratory species (memory retained for only some weeks). This fits well with an increase in hippocampus size from the first to the second year in the migratory species but not in the resident species (31). However, in spite of the special challenges of navigation and memorization, migratory passerines have smaller relative overall brain sizes than residents, a difference that may reflect the foraging challenges faced by residents during the nonbreeding season (32).

Analyses of the variability in individual migration history within and between populations with different migratory habits will be important to understand the evolution of new migration patterns (Table 1H). There is evidence that new migration patterns based on endogenous programs can evolve extremely rapidly, over only a few decades (33), but there are also opposing suggestions of evolutionary inertia, where migration routes seem to reflect the historic colonization process rather than being optimal under present conditions (34). Furthermore, range expansion of migratory species may be limited in comparison with residents because of constraints in the evolutionary change of genetic migratory programs (35).

Research about long-distance animal navigation does not, of course, only rely on tracking studies and field and behavioral experiments. Exploration of the sensory, neurobiological, and genetic mechanisms is also crucial. Current progress in revealing the mechanisms of magnetoreception is encouraging (36–38). However, we are still far from understanding how animals integrate different cues for long-distance navigation under natural conditions. Finding the spatial principles behind the details and complexities of the animals’ journeys demands an unexpectedly long-lasting research effort.

References and Notes
1. J. Grinnell, Auk 48, 22 (1931).
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How and Why Do Insects Migrate?
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Countless numbers of insects migrate within and between continents every year, and yet we know very little about the ultimate reasons and proximate mechanisms that would explain these mass movements. Here we suggest that perhaps the most important reason for insects to migrate is to hedge their reproductive bets. By spreading their breeding efforts in space and time, insects distribute their offspring over a range of environmental conditions. We show how the study of individual long-distance movements of insects may contribute to a better understanding of migration. In the future, advances in tracking methods may enable the global surveillance of large insects such as desert locusts.

Large-scale movements of insects have enormous implications for human welfare (1), including catastrophic losses of crops (2), the spread of diseases to people and livestock (3), and the provisioning of essential ecosystem services such as crop pollination (4). In sheer numbers of individuals, insect migration far outweighs other migratory phenomena (5). Moreover, in terms of total moving biomass, the migrations of individual insect species rival and sometimes outstrip the largest extant herds and flocks of some well-known migratory mammals and birds (Table 1). And yet there is at least one fundamental difference between insect and most vertebrate migrations (6, 7): As a rule, individual insects do not make a round-trip journey that returns them to the area from which they departed. Even in the case of the monarch butterfly (Danaus plexippus) (Fig. 1A), one of the best-studied migratory insects, few if any of the individuals wintering in Mexico return to their natal areas. Instead, monarchs repopulate northern latitudes through a process of intergenerational migration, whereby successive broods advance northward (8, 9). Thus, return migration, the most common type of migration in birds and mammals (7), has yet to be documented in insects.

Migration Strategies in Insects
Researchers accustomed to viewing long-range animal movements through the prism of classic return (i.e., round-trip) migration would likely categorize many so-called insect migrations as dispersal events (6). Entomologists, however, would disagree. Indeed, major reviews of this subject in the entomological literature have recommended abandonment of the term “dispersal” to describe insect movements; instead, all long-range movements of insects would be considered “migrations” (1, 7, 10, 11). Migration by vertebrates is often viewed as a mechanism for exploiting high-quality resources that are available during only a portion of the year [typically the breeding season (7, 10)]. In the case of insect migrations, which we define here as repeated phenomena of directional movement that are cyclical in nature, the ultimate reasons are less clear. If insects are not able to return to a high-quality patch in a subsequent year, then why migrate at all? Although considerable progress has been made toward understanding patterns of insect migration (1, 11), especially with respect to certain moths (12), the ultimate selection pressures resulting in these spectacular and ubiquitous movements remain mysterious. Intuitively, one expects migratory movements to evolve only when the fitness benefits exceed those of remaining in the current habitat (13). Whether this reasoning applies in the case of insect migrations is unclear. Because insects do not have to provide long-term care for their offspring, they can in theory reproduce in their natal area, along a migratory route, or in a discrete “winter range.” This differentiates them from the classic vertebrate return-migration model. By spreading their breeding efforts both spatially and temporally, insects have the ability to “hedge their bets” by distributing their offspring across a range of areas and conditions that may be amenable for future reproduction (14).

To determine whether this bet-hedging hypothesis is a valid explanation for most (or any) insect migrations, one would need to know the reproductive output (and, ideally, success) of individual insects along their migratory route. Do

**Table 1.** Biomass of migrating animals.

<table>
<thead>
<tr>
<th>Class</th>
<th>Species</th>
<th>Location</th>
<th>Size of herd, swarm, or flock</th>
<th>Biomass (tons)</th>
<th>Source (reference)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insects</td>
<td>Darter (dragonfly), Aeshna bonaiensis</td>
<td>Argentina</td>
<td>4–6 billion</td>
<td>4000</td>
<td>(15)</td>
</tr>
<tr>
<td></td>
<td>Monarch butterfly, Danaus plexippus</td>
<td>Winter grounds in Mexico</td>
<td>100–200 million</td>
<td>40–80</td>
<td>(39, 40)</td>
</tr>
<tr>
<td></td>
<td>Desert locust, Schistocerca gregaria</td>
<td>Africa, Middle East, Asia</td>
<td>10^4–10^11</td>
<td>200,000</td>
<td>(5)</td>
</tr>
<tr>
<td>Mammals</td>
<td>Wildebeest, Connochaetes taurinus</td>
<td>Serengeti, Kenya and Tanzania, Africa</td>
<td>1.3 million</td>
<td>280,000</td>
<td>(41)</td>
</tr>
<tr>
<td></td>
<td>Mexican free-tailed bat, Tadarida brasiliensis mexicana</td>
<td>Carlsbad Cavern, New Mexico, North America</td>
<td>20 million</td>
<td>300</td>
<td>(42)</td>
</tr>
<tr>
<td>Birds</td>
<td>Lesser sandhill crane, Grus c. canadensis</td>
<td>Platte River, Nebraska, North America</td>
<td>450,000</td>
<td>1440</td>
<td>(43)</td>
</tr>
</tbody>
</table>