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Mechanisms of animal global navigation: comparative perspectives and enduring challenges

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Animals navigate over a range of distances, but it has been the global navigation of species migrating among spatially restricted, seasonal homes separated by thousands of kilometers that continues to defy a thorough mechanistic explanation. We survey the navigational behavior of migratory salmon, whales, sea turtles, and birds, as well as dispersing monarch butterflies, to promote the idea that an explicitly comparative approach to global navigation can provide insight into the evolution and properties of navigational mechanisms. The navigational abilities of migrant birds and sea turtles are used to illustrate the concepts of true navigation and vector navigation, leading us to consider the selective forces that might shape the evolution of navigational mechanisms. We propose that different navigational mechanisms, with different scales of accuracy, are likely employed during the course of migration. Furthermore, superficially similar global migratory behavior in different taxonomic groups is likely characterized by different sensory, representational and neural mechanisms reflective of group-specific adaptation to the physical properties of a migratory environment.

KEY WORDS: grid-based navigation, map-based navigation, true navigation, vector navigation, migrant birds, migrant sea turtles.

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INTRODUCTION

The life history of many animal species is often punctuated by stunning migrations that traverse changing habitats for distances exceeding thousands of kilometers. They represent remarkable examples of animal navigators, even though in many respects the sensory mechanisms and representational strategies employed to carry out their global migrations continue to baffle researchers. We begin this paper by describing the global migratory behavior of a limited but diverse group of animals: migratory salmon, whales, sea turtles, and birds, as well as dispersing monarch butterflies (*Danaus plexippus*). Other animal groups engage in similarly impressive migrations; Atlantic eels (*Anguilla* sp.) and tuna (*Thunnus* sp.), as well as herds of arctic caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*) of the African savanna quickly come to mind. The taxonomically heterogeneous animal groups to be discussed offer a striking example of evolutionary convergence in behavior. Phylogenetic constraints may limit the effects of natural selection in shaping behavior. But the fact that the long-distance navigation in these animal groups evolved independently from related non-migratory species suggests that phylogenetic constraints have not been an obstacle impeding the evolution of global navigational ability.

Beneath the similarity in the phenomenology of global spatial behavior in the different taxonomic groups are likely adaptive differences in underlying sensory, representational and neural mechanisms that support navigation. Acknowledging that long-distance navigational mechanisms are not well understood, we propose that comparative contrasts can provide important insights into the evolution and properties of navigational mechanisms that guide migrations of a global scale. Many forms of navigation have been proposed (reviews: GALLISTEL 1990, WEHNER et al. 1996, HEALY 1998, JEFFERY 2003), mostly for smaller scale distances. In discussing global navigation, we will be especially concerned with the ability to navigate to an intended goal even when displaced to unfamiliar territory, so-called true navigation. We first characterize this ability, and then examine the extant literature for evidence of animals that exhibit true navigation. We then discuss candidate mechanisms and the evolution of global true navigation.

True navigation or vector navigation?

We make a distinction between the concepts of what we will call *vector navigation* and *true navigation* (Fig. 1). In the context of global migration, vector navigation is characterized by the ability of an animal to maintain a pre-determined orientation, typically a compass bearing, for a specified period of time or distance to reach a migratory goal. Movement in one direction or as a sequence of components (legs) in different directions can characterize vector navigation. It is well known that animals can use a variety of celestial cues (including the sun, skylight polarization, stars and moon), as well as the Earth's magnetic field, to take up and maintain a directional heading. For animals with suitable sensory capabilities, large scale landscape features (mountain ranges, rivers) encountered en route can also provide parallel information for maintaining a directional course similar to that described for short-range navigating insects (e.g., in bees: von Frisch & Lindauer 1954).

The programmed direction or vector used to guide vector navigation in a long-distance migrant can be conceptualized as a much scaled-up version of the vector representational strategy used by non-migrating animals to return to their home following a foraging episode of meters (fiddler crabs: Zeil 1998; Hemmi & Zeil 2003a, 2003b; Layne et al. 2003a, 2003b; hamsters in the lab: Etienne 2003, Etienne &

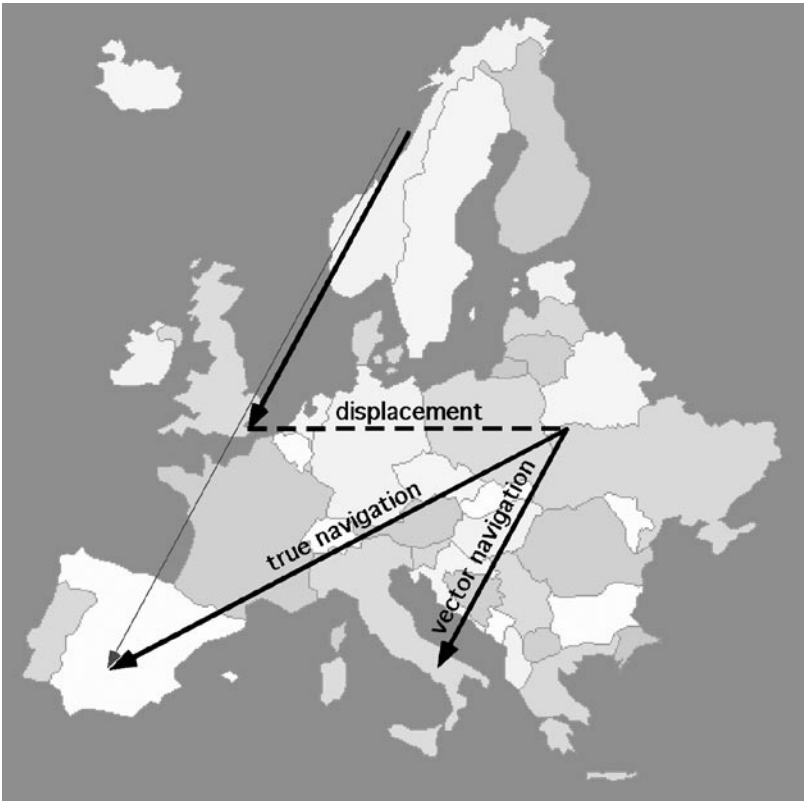

Fig. 1. — Schematic representation highlighting the distinction between true navigation and vector navigation of a hypothetical nocturnal songbird migrant in Europe. The traditional autumn migration route of this hypothetical species is from Norway to Spain (thin solid arrow). Similar to the starling experiment of Perdeck (1958), migrants en route are collected and displaced (dashed arrow) from their traditional migratory path to a distant, unfamiliar site in eastern Europe where they are released. True navigation (the thick solid arrow to Spain) is characterized by an ability to recover the traditional migratory path or return to the typical over-wintering site in Spain. Vector navigation (the thick solid arrow to Italy) is characterized by only an ability to continue having the distance and duration program being read off from the displacement site, and consequently an inability to reach the population specific over-wintering site in Spain.

Jeffery 2004), tens of meters (desert ants: Wehner 2003, Wehner & Srinivasan 2003) or hundreds of meters (honeybees: von Frisch 1967, Wehner & Srinivasan 2003). For the short-distance navigators, the basis for specifying the vector differs across species. Fiddler crabs and desert ants home on the basis of path integrating their outbound journey. Fiddler crabs measure the distance traveled by some form of step counting (Layne et al. 2003b), while honeybees measure distance flown primarily by means of optic flow experienced as they fly (Srinivasan et al. 1997, Wehner & Srinivasan 2003). Honeybees have in addition a dance language that specifies a vector (von Frisch 1967, Menzel et al. 2005). However, in contrast to the species described above, a first-time long-distance migrant cannot rely on an acquired representation of a recent foraging trip to guide its first migration. Rather, it would rely on an innately specified vector, as reviewed below.

We use the term *true navigation* in the sense of Griffin (1952) to describe the ability to navigate to a goal location even after displacement to unfamiliar locations outside the range of an animal's previous experience. A more detailed classification of possible true navigation was proposed by Papi (1992). One form of navigation Papi describes is *map-based navigation* (mosaic-map navigation of Able 2000) reliant on a learned representation of a mosaic of local cues, the most obvious example of which would be familiar landmarks (see also Bingman 1998). The stimulus elements that support map-based navigation, in particular familiar landmarks, could be used to directly guide the path of an animal, what is called *pilotage*, or be used in conjunction with an independently derived compass sense. Map-based navigation can support true navigation to the extent that familiar cues can be detected from beyond an animal's range of familiar space.

The other candidate form of true navigation Papi describes is *grid-based navigation* (gradient-map navigation of Able 2000) reliant on a learned representation of environmental physical or chemical gradients. Examples of environmental gradients that could be used to support grid-based navigation are variations in the distribution of chemical cues in the air or sea, or variations in the Earth's magnetic field. To use map-based or grid-based true navigation to carry out goal-directed course corrections following displacement, an animal must infer the spatial relationship between its current unfamiliar location and the migratory goal (Fig. 1). This ability depends on learning how the properties of environmental stimuli vary systematically in space.

The gold standard, behavioral-experimental evidence demonstrating a capacity for true navigation is the ability of an animal to re-orient in a goal-directed manner, in our case a migratory goal, following displacement away from a familiar migratory route. Although not migratory, the homing pigeon is the prototypical species capable of true navigation, although the range of mechanisms by which they achieve true navigation continue to be debated (see Wiltschko & Wiltschko 2003; Walraff, 2004, 2005a, 2005b). We now review selected literature in the chosen animal groups with a view to assessing experimental support for an ability to true navigate.

REVIEW OF GLOBAL MIGRATION: BEHAVIORAL PROFILES

The Monarch butterfly

Monarch butterflies are famous for their multi-generational, long-distance migrations across North America (Brower 1996, Calvert 2001) and Australia (Din-

GLE et al. 1999; although they are not native to Australia). The largest population takes the longest migratory route. In spring, this population travels between the Transverse Neovolcanic belt in Mexico, where they over-winter, through to northeastern USA and Canada. This migration can take three to five generations. The spectacular return journey, however, is completed in one generation; thus the same individuals can travel up to 3600 km in 75 to 90 days, from the Great Lakes to central Mexico. Both BROWER and CALVERT concluded that the butterflies use appropriate winds to aid them in their journey, saving valuable energy, and may possess some means to account for wind displacements. Other smaller populations head for the western parts of North America, and in Australia the cycle is 'reversed' in that they fly south in spring and north in autumn.

Monarchs fly their long migratory dispersal only once in their lives. Thus, the mechanisms guiding their behavior cannot depend substantially on accumulated experience. BROWER (1996) hypothesized that monarchs migrate in an innately specified direction that changes during the course of a year. Heading in a northerly direction when they leave Mexico, flight direction changes constantly through the circannual cycle by one degree per day. This accounts for the major patterns of movement of the butterflies that end up in northeastern North America. CALVERT's (2001) data on butterfly migrations are not completely consistent with BROWER's hypothesis. He found that some butterflies needed to correct their course in a direction other than that determined by BROWER's yearly-cycle model. CALVERT suggested that in addition to innately specified compass directions, large geographic features such as mountain ranges might also influence the butterflies' flight.

CALVERT (2001) suggested the use of a sun compass, and evidence for this has recently been identified (MOURITSEN & FROST 2002, FROY et al. 2003, STALLEICKEN et al. 2005). MOURITSEN & FROST (2002) recorded virtual flight paths of tethered monarchs for hours under simulated field conditions. Although they concluded that a compass based on polarized light was used, further testing in the same lab found that polarized light was neither necessary nor sufficient (STALLEICKEN et al. 2005). Instead, the butterflies appeared to use the sun itself, or associated intensity and spectral gradients, for orientation. A sun compass depends on a circadian clock; this is needed to account for the movement of the sun through the course of a day. Evidence for such a circadian clock has recently been found by clock-shifting the butterflies (MOURITSEN & FROST 2002, STALLEICKEN et al. 2005) or exposing them to constant light conditions (FROY et al. 2003).

Do monarch butterflies adjust their direction of travel after displacement? We found one study in which Monarchs were experimentally displaced on their autumn flight to Mexico. URQUHART (1965) sent tagged butterflies by post from localities in Ontario to various locations to the west, where they were released. URQUHART (1965: 28) concluded "that the flight direction remains the same when members of populations are transferred from one area to a remote area". But to us, this impressionistic conclusion, without the support of inferential statistics, is far from apparent in the data. The majority of the displaced butterflies' headings were in a southerly direction (8 of 13); this was a course-appropriate direction to get to Mexico. Proper controls were missing (i.e., butterflies shipped to localities within Ontario), but URQUHART's fig. 1 presents paths based on tagged releases of non-displaced monarchs. Most of their long-range recoveries show a southwesterly course. In summary, monarch butterflies disperse over long distances, have preferred routes of travel and can use a sun compass. However, it is unclear at the moment whether they can compensate for substantial geographic displacements. Therefore, although monarchs appear capable of carrying out a type of vector navigation, it is impossible to judge at the moment whether they exhibit true navigation.

Salmon

Salmonids are another group of animals that migrate large distances (QUINN & DITTMAN 1992). Unlike monarchs, experience-based information — learning — is very much involved in their navigation. Salmons hatch in freshwater rivers. They then migrate out to sea when still young and spend their pre-reproductive, adult years in open sea. Reproduction, however, takes place back in their natal rivers, and this presents them with a navigational challenge. It is not known how they navigate in the open sea, but nearer to home navigation is based on olfactory cues stemming from their natal river.

Recognition of the natal river can be explained by imprinting to a home stimulus quality (HASLER & SCHOLZ 1983) and does not require true navigation. Use of odor manipulations on hatchery-reared salmon, as well as observations of wild fish, offer conclusive evidence for a process of olfactory imprinting (HASLER & SCHOLZ 1983, QUINN & DITTMAN 1992, DITTMAN & QUINN 1996). This evidence includes the use of artificial odorants (reviewed by QUINN & DITTMAN 1992). Salmon are thought to have a sensitive period when they learn about the odor of their natal stream. Much about the neurophysiological basis of this process is also known (HASLER and SCHOLZ 1983; DITTMAN et al. 1996, 1997).

On the other hand, how salmon navigate the open sea and whether open-sea navigation is dependent on true navigation remain uncertain. Displacing salmon in the open sea has not been carried out, perhaps because this is logistically difficult to achieve. As one experimental strategy, we suggest capturing returning salmon at the mouth of their natal streams. The spatial behavioral responses of the fish to actual or 'virtual' displacements, for example by manipulating chemical or geomagnetic cues to simulate familiar or unfamiliar locations, could then be recorded. Such virtual displacements have proved successful in the study of sea turtle (e.g., LOHMANN et al. 2001, 2004; see section on sea turtles) and lobster (BOLES & LOHMANN 2003) navigation.

Mysticete whales

The extraordinary migrations of mysticete or baleen cetaceans are comparable in scale to those of migrant birds and sea turtles. For example, humpback whales (*Megaptera novaeangliae*) migrate between warm-water birthing sites and cold-water feeding sites throughout the Atlantic and Pacific oceans. Like monarch butterflies, the polarity of the humpback's seasonal migrations in northern and southern hemisphere populations is 'reversed', suggesting that their spatial behavior readily evolves adaptively to varying environmental conditions. Humpbacks have been reported to migrate for distances of more than 8,000 km (STONE et al. 1990) and display site fidelity to feeding grounds (STEVICK et al. 2003).

Little is known about the mechanisms that guide whale migration. In the case of the humpback, the migratory route of some populations often closely parallels coastal regions, suggesting that sensory contact with the coast, however accomplished, is used for orientation. But coastal contact cannot explain migrations from

Hawaii to Alaska (MATE et al. 1998) or from Antarctica to Australia. It has been proposed that whale navigation could be guided by sensitivity to the Earth's magnetic field either as a map of magnetic anomalies (landmarks), which are a common feature of ocean floors (KIRSCHVINK et al. 1986), or for compass orientation (WALKER et al. 1992). However, both coastal contact and geomagnetism as navigational mechanisms have not advanced beyond the speculative stage and underscore how little we know about how mysticete whales navigate. It is unknown whether whales can true navigate.

Sea turtles

Many of the seven species of extant sea turtles routinely engage in dramatic global migrations, typically between spatially restricted egg-deposition sites and more extensive feeding regions (CARR 1984, LOHMANN & LOHMANN 1996a) throughout the tropical and subtropical regions of the world's oceans. Their movements can extend over enormous distances, for example from Japan to Mexico and back to Japan in the case of some juvenile loggerhead turtles (*Caretta caretta*). Sea turtle migration can be remarkably precise. For example, for egg deposition green sea turtles (*Chelonia mydas*) successfully re-locate tiny Ascension Island in the middle of the Atlantic Ocean from feeding sites along the coast of Brazil (LUSCHI et al. 1998).

A young sea turtle is born into the world with an inherited predisposition to orient its first movements of crawling and then swimming toward the brighter sky over coastal water and into ocean waves (MROSOVSKY & SHETTLEWORTH 1968, LOHMANN & LOHMANN 1996a). From this modest spatial representational beginning, young sea turtles can quickly calibrate a directional response to the ambient magnetic field and use their directionally calibrated magnetic compass to guide their initial oceanic movements (LOHMANN & LOHMANN 1996a). When in the open ocean, the dispersal trajectory of hatchling sea turtles, which frequently display little or no active movement, will necessarily be controlled by the direction of the prevailing ocean currents (CARR 1987). However, the extent to which the migratory path of older sea turtles may be influenced by ocean currents as a directional or compass cue seems to vary among species and region (LUSCHI et al. 2003a, 2003b; HAYS et al. 2004). What is clear is that as sea turtles age and increasingly gain experience with spatial properties of their environment, the relatively simple spatial behavioral mechanisms that guide their hatchling orientation develop into a navigational system supporting precise migrations among egg-laying, ocean dispersal and feeding sites.

Can sea turtles accomplish true navigation? Different lines of recent evidence provide conflicting results. Displacement experiments carried out in the field have led one group of researchers to think no (LUSCHI et al. 2001, 2003c; ÅKESSON et al. 2003). Female green turtles returning to their nesting (and natal) beach during a period of egg deposition and post-nesting female loggerhead turtles returning to coastal, neritic feeding sites after completing egg deposition were displaced from different locations and tracked by satellite for distances ranging from 60 to more than 2,000 km from the capture site. Most of the turtles in these studies did eventually return to population-typical goal locations (see also AVENS et al. 2003). However, the routes taken by the turtles suggested strategies based on simple compass orientation (go west to reach the coast of Africa or South America) followed by movement along coastlines perhaps to find more spatially restricted goal locations. There was no indication that the turtles could compute a vector or trajectory directly to their goal location following displacement. Noteworthy was that the two loggerhead sea turtles in Luschi et al. (2003c) that were displaced the farthest ended up wandering the Indian Ocean without any indication of goal-directed navigation.

It is also questionable whether the ability of green sea turtles to locate Ascension Island reflects true navigation. Hays et al. (2003) found that homing following displacement is much better from the prevailing downwind direction compared to the upwind direction. They interpret their findings as indicating that wind-borne cues may serve as a beacon enabling green sea turtles to locate Ascension once within range of orienting wind-borne, chemical cues.

By contrast, laboratory experiments demonstrate that sea turtles can meaningfully re-orient their movement to altered ambient magnetic fields, at least altered fields indicating a north-south displacement. Juvenile sea turtles of various ages were tested in the laboratory for their orientation under ambient magnetic field conditions that reflected actual or simulated displacements. Under these experimental conditions, they consistently re-orient in a direction that would bring them back to their migratory route or goal (Lohmann & Lohmann 1994, 1996a, 1996b; Lohmann et al. 2001; Avens & Lohmann 2004). Most compelling are the data from Lohmann et al. (2004). Green sea turtles were exposed to simulated magnetic fields that would have corresponded to actual displacements several hundred kilometers north and south of their capture site. When tested for their orientation, the turtles "displaced" north showed a southerly orientation preference while the turtles "displaced" south showed a northerly orientation preference. The authors concluded that the corrective orientation behavior of the turtles was entirely consistent with true navigation based, at least in part, on variation in the Earth's magnetic field. The data, however, are limited in revealing sensitivity only to north-south displacements along a coastline. The authors acknowledged that geomagnetic cues may specify only the north-south position, while perhaps other environmental cues, such as the distance from a coastline, could be used to assess east-west position. It is uncertain how the turtles might have behaved if "displaced" east to the open sea.

In summary, we agree that sea turtles exhibit navigational sensitivity to global geomagnetic cues along the north-south axis, but this ability appears insufficient for true navigation, as indicated by the general failure of displaced sea turtles in the field to take up a direct route to a migratory goal. Rather than reflecting a true map of global space, the geomagnetic sensitivity along the north-south axis may function by eliciting corrective re-orientation responses that keep turtles within acceptable geographic limits (Fig. 2). Traveling too far north or south out of the North Atlantic gyre can bring sea turtles to dangerous and possibly fatal cold water currents (see Lohmann et al. 2001). In our view, a combination of vector-based navigational mechanisms and beacon guidance, coupled with corrective re-orientation behavior regulated by north-south sensitivity to the Earth's magnetic field, is sufficient to explain the global navigational ability of sea turtles. Our proposal, however, is certainly amenable to change with new data. Evidence of geomagnetic control of navigational behavior along the east-west axis would be most relevant.

Migratory birds

The migratory behavior of birds has been source of fascination to mankind since probably before recorded history. The precision by which some birds return to the same breeding site on close to the same day year after year is remarkable.

Regardless of the details of migratory behavioral ecology, most if not all bird species are superb navigators. It is not our intent to discuss all the variations in the migratory behavior of birds (see BERTHOLD 2001, 2003; ALERSTAM et al. 2003). Rather, we will use as an illustrative example the navigational behavior of typically diurnal songbird species that carries out the vast majority of its migration at night. These birds can successfully migrate to their intended destinations following both natural as well as experimental displacements to often very distant, unfamiliar locations (PERDECK 1958, MEWALDT 1964, MATTHEWS 1968, WILTSCHKO 1992). This ability to cope with displacement demonstrates true navigational ability, even if the mechanisms at a global scale are still poorly understood.

True navigation, however, is not exhibited in the first year of migration. During the course of its first summer, a young songbird develops the ability to orient its migratory behavior by the position of the setting sun and patterns of skylight polarization associated with it, the stars and the Earth's magnetic field (EMLEN 1970, ABLE & BINGMAN 1987, WILTSCHKO & WILTSCHKO 2003). These orientation mechanisms do

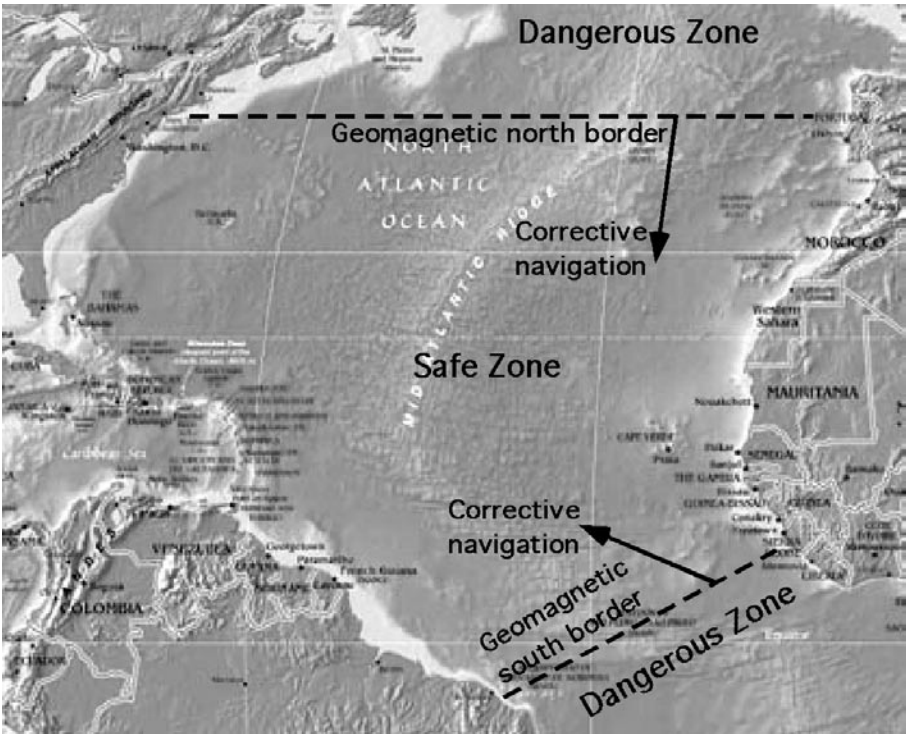

Fig. 2. — Hypothetical representation of how geomagnetic sensitivity in juvenile sea turtles can be exploited for navigation. We assume that young turtles are sensitive to a geomagnetic cue that specifies latitude. When these cues indicate that they are near the north or south border of their safe zone, corrective navigation is engaged. This consists of reorienting inward away from the ecological boundary separating migration-appropriate and inappropriate global zones. Geomagnetic information serves as a context cue used to engage a change in orientation that keeps sea turtles out of dangerous zones and close to their population specific migratory path within the North Atlantic gyre.

not develop independently; for example directional information from celestial cues routinely influence how a young migrant will orient to the Earth's magnetic field when it initiates its first migration (BINGMAN 1983, ABLE & ABLE 1990).

To gauge the distance to fly, many first-time migrants rely on an inherited temporal program specifying how long it should travel (BERTHOLD 2001, 2003). The onset of numerous behavioral and physiological adaptations for migration appears to be coordinated by largely inherited circannual rhythms, which shape the timing and the length of seasonal behavior. When held in captivity, species that fly longer distances display longer and more intense periods of migratory activity than species that migrate shorter distances. Even in the same species, birds from populations that migrate farther display longer and more intense periods of migratory activity than birds from populations that migrate shorter distances. Crosses between populations of short and long distance migrants of the same species lead to a F1 generation displaying intermediate levels of migratory activity.

The behavioral mechanisms that guide first-time nocturnal songbird migrants are a prototypical example of vector navigation because it is based on a determination of distance and direction from the departure point (BERTHOLD 2001, 2003). The behavior of first-time migrants using vector navigation contrasts with the behavior of experienced migrants using true navigation (Fig. 1). In a classic experiment carried out on diurnally migrating European starlings (*Sturnus vulgaris*), PERDECK (1958) banded and transported autumn migrants to an unfamiliar location, which was remote from the traditional migratory route to their winter home, where they were released. Subsequent recoveries of birds with previous migratory experience tended to cluster around the population specific winter home. The experienced starlings were able to navigate to their winter home following the experimental displacement, a signature of true navigation. By contrast, subsequent recoveries of first-year birds with no previous migratory experience tended to cluster in regions in a direction from the release site that would have corresponded to the direction they would have flown if they had not been displaced. That is, they continued to fly the vector they were executing, a signature of vector navigation.

DISCUSSION

True navigation in experienced migratory birds

Map-based global navigation? Map-based and grid-based navigation have been proposed as representational strategies that can support true navigation. The properties of map-based navigation resemble the characteristics of what has been called a "cognitive map" in the context of smaller-scale navigation (TOLMAN 1948, O'KEEFE & NADEL 1978, GOULD 1986, GALLISTEL 1990, MENZEL et al. 2005). (It should be noted that the term "cognitive map" is not without detractors (e.g., DYER 1991, BENHAMOU 1996, BENNETT 1996). A cognitive map would be characterized by a 'mosaic' representation of the spatial relationship among landmarks, or patches of distinct stimulus quality, which would enable the computation of a goal-directed trajectory. In vertebrates, map-like, landmark-based navigation is reliant on an intact hippocampal formation (turtles and perhaps fish: RODRIGUEZ et al. 2002; birds: GAGLIARDO et al. 1999; COLOMBO & BROADBENT 2000; rats: EICHENBAUM et al. 1990; monkeys: PARKINSON et al. 1988; ROLLS 1999; humans: BURGESS et al. 2002). The function of a cognitive map-like representation would be to allow an animal to navigate to any goal from any place within its familiar territory. Applied to true navigation, this notion must extend to encompass never-encountered unfamiliar locations. To be able to use a map-like representation from an unfamiliar place, the distinctive landmarks or stimulus patches that make up the mosaic must be perceptible and identifiable from great distances and from novel perspectives.

Visual landmarks are often used for landmark-based navigation on a relatively small scale (e.g., bees: Menzel et al. 2005; homing pigeons: Gagliardo et al. 1999; Biro et al. 2004; Lipp et al. 2004). But for true navigation operational over thousands of kilometers, visual landmarks are too local to be a source of map-like information.

It has been convincingly demonstrated that homing pigeons can use the distribution of atmospheric odors in the region of the home loft to navigate (Wallraff 2003, 2004, 2005a, 2005b). It is unclear whether odors are represented as a mosaic map (Ioalè et al. 1978) or a grid (Wallraff 2003, 2004). But whether map-based or grid-based, the range of olfactory navigation extends to perhaps hundreds of kilometers beyond a pigeon's familiar space (Benvenuti et al. 1994, Wallraff 2004). Global navigation on a scale of thousands of kilometers is unlikely to be based on olfactory cues alone (but see Nevitt & Bonadonna 2005).

What landmark-like stimuli can be perceived over thousands of kilometers? The ability to detect very low frequency sounds, referred to as infrasounds, has been suggested (Quine & Kreithen 1981, Hagstrum 2000). Infrasound has the desirable quality of attenuating only very slowly in space, so that a sensory system can detect it from a very long distance. Often suggested as stable sources of infrasound are ocean waves, mountain winds and, at least periodically, anthropogenic sources such as aircraft take-offs. Hagstrum (2000) documented circumstantial evidence for the use of infrasound in homing pigeons, and also discussed what infrasounds might be used. The examples of stable sources of infrasound, however, are not point-source landmarks, but mountain ranges and ocean waves. Therefore, these large-scale landscape features are more likely to serve as references defining compass directions rather than landmarks defining points in space, which would be necessary to support true navigation.

In summary, because we can identify no appropriate source of sensory information of a global scale, we consider a map-based mechanism of global true navigation unlikely.

Grid-based global navigation? Wallraff (1974, 2004) has best articulated the concept of gradient-based navigation. Using homing pigeons as an example, passing through the home loft would be at least two environmental gradients with differing directional axes. For explanatory purposes, it is easiest to assume that the gradient axes are orthogonal to each other, although in reality this need not be the case (Benhamou 2003). For example, a gradient in the intensity of stimulus x would increase to the north and decrease to the south of the loft; a gradient in the intensity of stimulus y would increase to the east and decrease to the west. After displacement to some unfamiliar location, a pigeon could compare the local values of gradients x and y with the values at the home loft. It could then determine its displacement relative to the home loft in the x and y plane, and compute a homeward vector or at least direction (see Wallraff 2004 for a fuller explanation). The point is that once a pigeon learns how the gradients vary in directional space away from the home loft, a determinate (not trial-and-error) algorithm of extrapolation can be employed to compute a homeward vector. As in the case of map-based navigation, such a gradient grid can in principle guide navigation over global distances.

The first thoroughly discussed candidate hypothesis of a gradient grid was MATTHEWS' (1953) sun-elevation hypothesis. The idea was that birds could use the maximum elevation of the sun during the day as a measure of latitude, and temporal differences in the course of the sun's movements during the day (the solar ephemeris) between the present location and home as a measure of longitude. Differences in latitudinal and longitudinal measures between current location and home could then be used to compute the homeward vector. The challenge to true navigating by the sun is that the path and timing of the sun's daily journey across the sky vary enormously across the globe as well with the seasons. The computational obstacles in learning such a gradient grid appear prohibitive, and indeed, experimental findings in homing pigeons (see KEETON 1974) led researchers to reject the possibility of such a navigational system.

After the rejection of the sun-elevation hypothesis, there emerged a resurgent interest in the possibility that variations in the Earth's magnetic field could serve as a basis for grid-based true navigation. This notion was nurtured by the gradient-like variations of geomagnetic parameters such as intensity, inclination, and declination as well as the established ability of birds to use the Earth's magnetic field for compass orientation (WILTSCHKO & WILTSCHKO 1995). Again it has been homing pigeons that have served as the principal experimental subjects to test the hypothesis of a geomagnetic grid map, and the experimental support for this hypothesis has been scant (WALCOTT 1991; WALLRAFF 1999, 2004, 2005a, 2005b). Pessimism also emerges from consideration of the frequently "noisy" quality of geomagnetic information, i.e., local deviations in the prevailing gradient of geomagnetic parameters over distances typically navigated by homing pigeons (WALRAFF 1999; see also ÅKESSON & ALERSTAM 1998) as well as temporal variation (REILLY 2002). Sea birds such as albatrosses and petrels also engage in impressive homing flights between foraging areas and nest sites (WEIMERKIRCH et al. 1993, 2002), with little support for the notion that their homing behavior is guided by geomagnetic map cues (BENHAMOU et al. 2003, MOURITSEN et al. 2003, BONADONNA et al. 2005).

The homing pigeon (as well as breeding sea birds) is grounded to one location, the home loft (or in the ancestral rock dove, a roosting site on a Mediterranean cliff), and displacements in space would be prevailingly measured relative only to the location of the home loft. By contrast, a migrant bird traveling thousands of kilometers may have many home bases, including the nest site in summer as well as over-wintering, dispersal and migratory stopover sites. A migrant has far more opportunity to sample the ambient geomagnetic field over a period of weeks from a vast range ("perspective") of locations. The more dispersed sampling can serve to reduce statistical noise and at a scale of thousands of kilometers, even noisy data may support low-resolution navigation. We thus propose that the failure of a geomagnetic map to explain homing pigeon navigation should not preclude considering geomagnetism as a source of information used by long-distance migrants. In support of this idea are noteworthy, recent physiological studies demonstrating trigeminal magnetic sensitivity that could support *coarse*-resolution detection of geographic variation in some geomagnetic parameter(s) (SEMM & BEASON 1990, MORA et al. 2004). The orientation behavior of captive, migrant birds subjected to simulated geomagnetic displacements (FISCHER et al. 2003) and theoretical considerations (WALKER 1998) are permissive of a hypothesis of a *global* grid map based in part on predictable variation in the Earth's magnetic field.

Re-thinking global true navigation in birds. Migratory birds are capable of true navigation, but the mechanisms that guide their incredible sense of global space remain elusive. We offer the following considerations in the hope of promoting new research approaches to the challenge of avian global navigation.

(1) It is theoretically likely that multiple representations at different scales are used in global migration (Fig. 3). Even on a small scale of meters, theorists have found representation at multiple scales necessary in animals (CHENG 2005) and in artificial intelligence (DAVIS 1986). As an illustrative example, a low-resolution global grid (hypothetically a "noisy" geomagnetic grid could work as this scale) may guide migration over large stretches of unfamiliar regions. An olfactory grid or map of atmospheric odors may guide migration in regions within a few hundred kilometers of a goal location. A landmark-based map may then guide migration over familiar regions tens of kilometers from the goal, and the recognition of the goal (beacon) may guide the final approach (Fig. 3). Each phase of operation only needs enough resolution to bring it within the 'catchment' area of the next phase. Navigational mechanisms at different scales can vary at both the sensory and representational levels; i.e., grid-based and map-based navigational representational mechanisms can operate at different spatial scales and be reliant on different sensory information.

Landmark-based navigation is well understood on a neurophysiological level, although much remains to be unraveled. In homing pigeons, the hippocampal formation is crucial for the operation of map-based navigation reliant on familiar landmarks (GAGLIARDO et al. 1999, WHITE et al. 2002, WALLRAFF 2005a), but plays no role in the operation of true navigation in unfamiliar areas (BINGMAN et al. 1984). Generalizing from this work, demonstrating hippocampal involvement in migration would suggest the use of landmark-based navigation at some point during the migratory journey, an idea supported by HEALY et al. (1996) and CRISTOL et al. (2003). An important lesson from research on the hippocampus and navigation in homing pigeons is that sensory, representational and neurobiological experiments can interface with each other to provide general insight into navigational (behavioral) mechanisms. A similar battery of research approaches could reveal much about global navigation.

(2) Proposing multiple mechanisms/representations for navigation brings on the problem of coordinating them. What, for example, brings Phase 1 to a close and engages Phase 2? Sequential servomechanisms are thought to guide insect navigation over short distances (COLLETT & COLLETT 2002, CHENG in press). In this case, appropriate contextual cues are thought to trigger each servomechanism. A servomechanism is launched only when appropriate triggering cues are present (Fig. 4A). By contrast, all strategies may operate in parallel from the start. At different stages of the journey, a different operation may take the leading role in navigation (Fig. 4B). A parallel scheme simplifies control architecture, and also means that at some points along the journey, multiple mechanisms might control navigation. The use of multiple mechanisms may be beneficial in providing better navigational accuracy as a consequence of using multiple sources of information (see also GUILFORD et al. 2004 for short-distance navigation by homing pigeons). Of course, mixtures of parallel and sequential control processes are also possible.

(3) WALLRAFF (2003, 2005b) has already proposed a simpler and perhaps more parsimonious model of global navigation that combines both direction (vector)-based and map-like navigation. His model includes all the map-like representations of increasing scale up to and including the olfactory gradient grid and dispenses with the largest-scale global map. Different odor grids and landmark maps would be used for different familiar regions such as breeding and over-wintering sites. In between

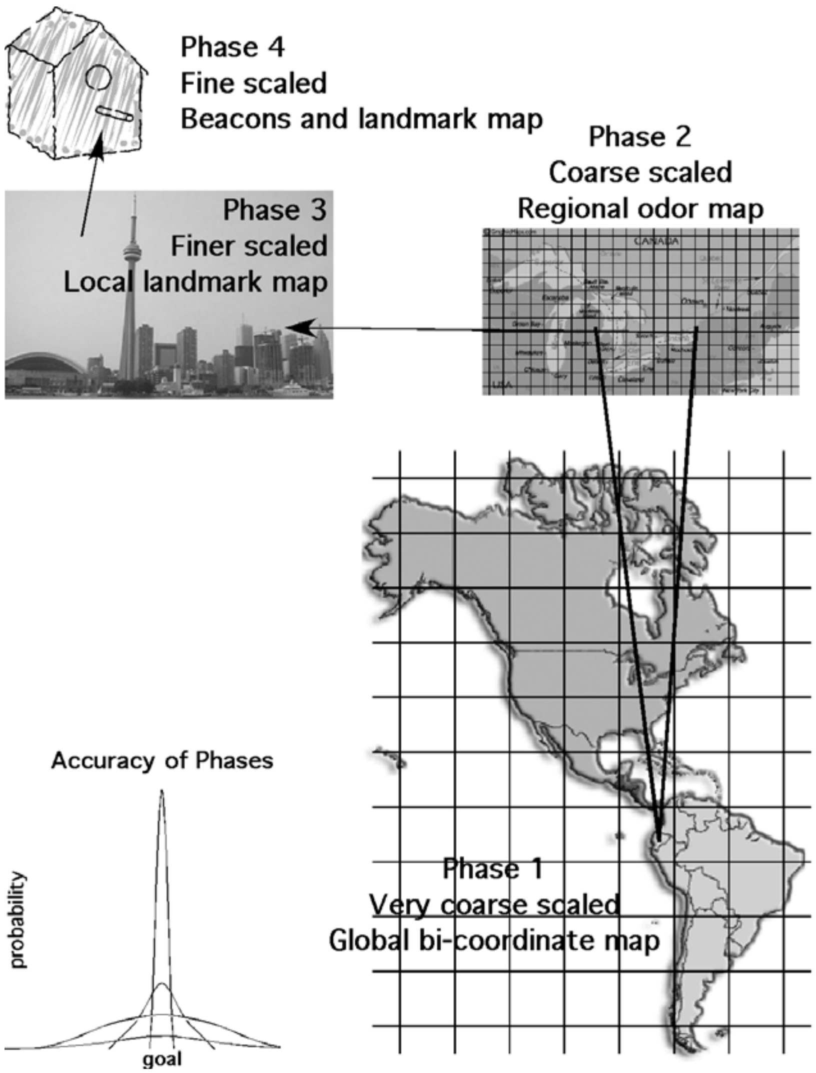

Fig. 3. — Schematic representation of the proposed phase model of global-navigational mechanisms of different scalar resolutions. For illustrative purposes, an experienced nocturnal migrant begins its spring migration in South America and heads in an approximate direction toward the breeding site in Ontario, Canada, exploiting low-resolution bi-coordinate, grid-based navigation reliant, hypothetically, on variations in the Earth's magnetic field (Phase 1). As the migrant approaches its breeding area, control of its navigational behavior switches to a higher-resolution bi-coordinate, grid-based navigation based on variation in atmospheric odors (Phase 2). Getting closer to its breeding site, control of the migrant's navigational behavior again switches to even higher-resolution map-based navigation based on familiar visual landmarks (Phase 3). The migratory journey closes as the bird beacons in on its breeding territory of the previous year (Phase 4). The spatial resolution of the different navigational mechanisms can be interpreted using the inset to the lower left. The increasing accuracy of successive phases are represented by narrower probability distributions around the target (goal) direction. Thus, the later phases are more likely to get the bird close to its goal than the earlier phases. The use of multiple phases represents a judicious use of different trade-offs between the range of a map and its resolution.

these familiar regions, a migrant would leapfrog over unfamiliar terrain by directional tendencies or vectors. The danger of such a mechanism is that if a bird were blown off course to unfamiliar space, it would be disadvantaged in recovering sensory access to familiar navigational cues. This type of navigation does not explain the remarkable ability of birds to recover from large, global-scale displacements such as some of the experimentally displaced subjects described in MATTHEWS (1968).

(4) It is possible that different axes of a grid are composed of different sensory information. For example, one axis might be composed of some quality of atmospheric odors and the other axis some geomagnetic stimulus quality. It may even be worth re-examining whether only one global axis, for example orthogonal to the migratory route, is represented as a global, large scale-low resolution map; a map which would support true navigation only when birds are displaced along that axis (away from the migratory route).

(5) We have framed our paper discussing environmental stimuli that have dominated the literature. But conforming to these precedents necessarily impedes searching for alternative compatible mixes of sensory ability and environmental stimulus quality that could support global navigation and migration. Researchers

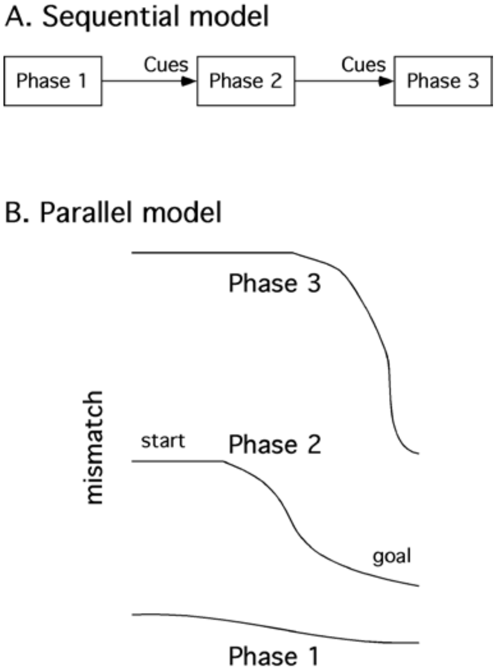

Fig. 4. — Two models of how different phases of navigation are controlled. In the sequential model (A), control switches sequentially from one phase of operation to the next, based on cues that trigger the operation of a mechanism. In the parallel model (B), all phases (mechanisms) operate simultaneously from the start of the journey. Mismatch refers to the discrepancy between relevant parameters at the target and at the current location. The animal is assumed to be moving from left to right. In doing so, it is attempting to reduce the mismatch in all phases (mechanisms) in parallel. The different steepness of the mechanisms at different points in the journey means that different mechanisms play the major navigational role at different stages of the journey.

should be open to thinking of alternatives to the historical panoply of environmental stimuli thought to guide migration.

Evolution of true navigation: selective pressures and neural constraints

We begin this part of the paper by comparing migratory birds and sea turtles, the species groups we know most about with respect to the mechanisms of global navigation. We then consider other species in light of the comparative inferences drawn from birds and sea turtles. We recognize first that migratory birds are capable of true navigation. Sea turtles are sensitive to global geomagnetic cues, and exhibit an ability to use these cues to re-orient following latitudinal displacement. However, we tentatively conclude that this ability falls short of true navigation. For the moment, the general failure of displaced sea turtles to goal orient (see above) in the field offers compelling evidence against a capacity for true navigation.

Mechanisms of global navigation in sea turtles and migratory birds display both convergent and divergent properties. Fig. 3 proposes that global navigation consists of components operating at different scales that are reliant on different sensory and representational mechanisms. The representational mechanisms that guide the use of local beacons (a type of sensory taxis) and familiar landmarks (map-based navigation) near goal locations are likely shared by both migratory birds and sea turtles. The avian hippocampal formation participates in map-based navigation (GAGLIARDO et al. 1999). The hippocampal formation of turtles (sea turtles were not tested) seems also to participate in map-based navigation reliant on landmarks (RODRIGUEZ et al. 2002) suggesting similarity based on homology rather than convergence in the neural mechanisms supporting landmark (map-based) representations of space. But at a global scale, why is true navigation easily demonstrated in migratory birds and tenuous at best in sea turtles?

Costs and benefits are useful to consider. From the viewpoint of costs, we can assume that a more extensive neural architecture is required for learning-based true navigation compared to typically inherited programs of vector navigation. Developmentally, representational mechanisms that support true navigation in migratory birds are thought to build from the baseline of inherited vector navigation (PERDECK 1958, WILTSCHKO & WILTSCHKO 2003). True navigation presumably recruits the participation of brain regions not involved in vector navigation. For example, the avian forebrain, which is characterized by hypertrophied anterior pallial regions analogous to the neocortex in mammals, is much larger compared to similar brain regions in reptiles including sea turtles (when corrected for body weight). Morphologically, birds have substantially more neural hardware in associative forebrain regions compared to sea turtles (BUTLER & HODOS 1996). The evolution of a larger forebrain in birds may be an important, divergent evolutionary event permitting avian true navigation of a global scale as either adaptation or exaptation (adoption of a character that had one use in an ancestral form into a new, different use in a descendant form). At the very least, the costs of evolving a larger forebrain (ATTWELL & LAUGHLIN 2001, LAUGHLIN 2001) have not prevented the evolution of true navigation in birds (but see WINKLER et al. 2004).

Turning to benefits, birds migrate in a volatile medium, air, with a variable movement pattern (wind) that can lead to rapid, transient, and substantial displacements away from a goal (migratory) trajectory. True navigation on a large scale allows a bird to compute a goal-directed, corrective navigational trajectory following such displacements, saving valuable time and energy. In some cases, such savings can mean the difference between life and death. Other less learning-dependent corrective strategies include the tendency of nocturnal migrant birds to selectively migrate on nights with favorable winds (GAUTHREAUX & ABLE 1970, ÅKESSON et al. 2002, ERNI et al. 2002), corrective morning flights (GAUTHREAUX 1978, BINGMAN 1980) and perhaps the use of large-scale geographic landscape features (e.g., GUDMUNDSON et al. 1995).

By contrast, the ocean currents in which sea turtles migrate are more stable in space and time than the air above it. Currents are much slower than the winds (although it must be admitted that turtles are also slower migrants than birds), and when they change, they change gradually and are seasonally stable in their new state. Therefore, an inherited strategy of vector navigation may not carry the same disastrous potential in sea turtles as it does in birds. For sea turtles, the benefits of true navigation as evolved in birds may not sufficiently outweigh the costs to be supported by natural selection.

But ocean currents can displace a traveler. The corrective re-orientation of sea turtles following north-south geomagnetic displacements may represent a less learning-dependent evolutionary solution to manage the perhaps more modest displacements that would occur in ocean currents. From a cost-benefit perspective, one would especially expect sensitivity along the north-south axis, as the climatic changes associated with this dimension can pose greater dangers. We would not expect a similar sensitivity to navigational drift in animals that are unlikely to get displaced, such as those that travel on land.

Our account suggests that the function of global true navigation is the ability to carry out goal-directed corrections after large displacements to unfamiliar space, a capacity demonstrated to date only in birds. This benefit may only be worth the costs in a selective landscape where the possibility of such displacements is substantial: traveling in the medium of air. Following from this view, phylogenetic constraints, including neural hardware, may play a smaller role in determining the evolution of navigational ability. Such constraints may have a greater influence on representational mechanisms and dependence on learning than on behavioral ability as measured in the field. Rather, it is our proposal that the properties of geophysical factors that displace or drift animals, i.e., winds and currents, are important selective agents in shaping global navigational behavior in a relatively unrestrained evolutionary space; an evolutionary space which can lead to an ability as extraordinary as avian global true navigation. Therefore, pressure for the evolution of true navigation would be highest in global air travelers, next in sea travelers, and least in land travelers. This leads us to suggest some key species to test this broad hypothesis.

(1) Migratory bats, which typically travel distances comparable to short-distance bird migrants, offer a compelling challenge to our thesis. As flying mammals that can migrate long distances (e.g., lesser long-nosed bats, *Leptonycteris curasoae*, WILKINSON & FLEMING 1996) and home (DAVIS 1966, WILLIAMS et al. 1966), numerous bat species inhabit a selective landscape, and if necessary, possess the neural hardware that would predict a capacity for true navigation.

(2) As proposed for sea turtles, sea mammals, fish and even marine invertebrates may use a combination of vector navigation coupled with a capacity for corrective behavior following displacement to guide global navigation. Salmon displacement experiments are worth attempting. On the west coast of North America, the coastline runs roughly north-south, and therefore an ability to detect latitudinal displacement might be among the most important navigational needs. Research

suggests that currents and eddies might influence the latitude at which salmon find the coast (THOMSON et al. 1992, HEALEY et al. 2000). Worth mentioning as well is a study on lobsters (BOLES & LOHMANN 2003) demonstrating corrective re-orientation following north-south geomagnetic displacements.

(3) Some insects do fly global distances, such as the monarch butterfly. But is the small brain of an insect too limited for true navigation? Worth considering is the superb spatial ability found in short-distance navigating honeybee (MENZEL & GIURFA 2001). Recent data show that bees can correct their course after displacement in familiar territory (MENZEL et al. 2005), although they do this only after executing route-based navigation first. WEHNER's (1992) review of arthropod navigation found no evidence for true navigation at any scale of distance, but it may be worth examining monarch butterflies more closely.

CONCLUDING WORDS

As implied in the discussion, we think that research addressing both the mechanistic and the evolutionary characteristics of global navigation needs to proceed in parallel. Methodologically central to both these fronts is the displacement and tracking of migrating animals coupled with experimental manipulations in the field (e.g., PAPI et al. 2000). This is now greatly aided by satellite-tracking and route-recording techniques, with the necessary hardware getting smaller year by year. To complement behavioral tracking in the field, we also need lab-based behavioral and neurobiological experiments inspired by a comparative perspective. In the end, the study of global navigation should be grounded in the integration of both behavioral ecology and neuroethology research approaches.

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REFERENCES

ABLE K. 2000. The concepts and terminology of bird navigation. *Journal of Avian Biology* 32: 174-183.

ABLE K. & ABLE M. 1990. Daytime calibration of magnetic orientation in a migratory bird by celestial rotation. *Nature* 347: 378-380.

ABLE K. & BINGMAN V.P. 1987. Ontogeny of the orientation and navigation behavior of migratory birds and pigeons. *Quarterly Review of Biology* 62: 1-29.

ÅKESSON S. & ALERSTAM T. 1998. Oceanic navigation: are there any feasible geomagnetic bicoordinate combinations for albatrosses? *Journal of Avian Biology* 29: 618-625.

ÅKESSON S., BRODERICK C., GLEN F., GODLEY B.J., LUSCHI P., PAPI F. & HAYS G.C. 2003. Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? *Oikos* 103: 363-372.

ÅKESSON S., WALINDER G., KARLSSON L. & EHNBOM S. 2002. Nocturnal migratory flight initiation in reed warblers (*Acrocephalus scirpaceus*): effect of wind on orientation and timing of migration. *Journal of Avian Biology* 33: 349-357.

ALERSTAM T., HEDENSTRÖM A. & ÅKESSON S. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247-260.

ATTWELL D. & LAUGHLIN S.B. 2001. An energy budget for signaling in the grey matter of the brain. *Journal of Cerebral Blood Flow Metabolism* 21: 1133-1145.

AVENS L. & LOHMANN K.J. 2004. Navigation and seasonal migratory orientation in juvenile sea turtles. *Journal of Experimental Biology* 207: 1771-1778.

AVENS L., BRAUN-MCNEILL J., EPPERLY S. & LOHMANN K.J. 2003. Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Marine Biology* 143: 211-220.

BENHAMOU S. 1996. No evidence for cognitive mapping in rats. *Animal Behaviour* 52: 201-212.

BENHAMOU S. 2003. Bicoordinate navigation based on non-orthogonal gradient fields. *Journal of Theoretical Biology* 225: 235-239.

BENHAMOU S., BONADONNA F. & JOUVENTIN F. 2003. Successful homing of magnet-carrying white-chinned petrels released in the open sea. *Animal Behaviour* 65: 729-734.

BENNETT A.T.D. 1996. Do animals have cognitive maps? *Journal of Experimental Biology* 199: 219-224.

BENVENUTI S., IOALÈ P. & NACCI L. 1994. A new experiment to verify the spatial range of pigeons olfactory map. *Behaviour* 131: 277-292.

BERTHOLD P. 2001. Bird migration. A general survey, 2nd Ed. *Oxford: Oxford University Press*.

BERTHOLD P. 2003. Genetic basis of evolutionary aspects of bird migration. *Advances in the Study of Behavior* 33: 175-229.

BINGMAN V.P. 1980. Inland morning flight behavior of nocturnal passerine migrants in eastern New York. *Auk* 97: 465-472.

BINGMAN V.P. 1983. Magnetic field orientation of savannah sparrows with different first summer experience. *Behaviour* 87: 43-53.

BINGMAN V.P. 1998. Spatial representations and homing pigeon navigation, pp. 59-85. In: Healy S., Edit. Spatial representation in animals. *Oxford: Oxford University Press*.

BINGMAN V.P., BAGNOLI P., IOALÈ P. & CASINI G. 1984. Homing behavior of pigeons after telencephalic ablations. *Brain, Behavior and Evolution* 24: 94-106.

BIRO D., MEADE J. & GUILFORD T. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences* 101: 17440-17443.

BOLES L.C. & LOHMANN K.J. 2003. True navigation and magnetic maps in spiny lobsters. *Nature* 421: 60-63.

BONADONNA F., BAJZAK C., BENHAMOU S., IGLOI K., JOUVENTIN P., LIPP H.P. & DELL'OMO G. 2005. Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society (B)* 272: 489-495.

BROWER L.P. 1996. Monarch butterfly orientation: Missing pieces of a magnificent puzzle. *Journal of Experimental Biology* 199: 93-103.

BURGESS N., MAGUIRE E.A. & O'KEEFE J. 2002. The human hippocampus and spatial and episodic memory. *Neuron* 35: 625-621.

BUTLER A.B. & HODOS W. 1996. Comparative vertebrate neuroanatomy: Evolution and adaptation. *New York: Wiley-Liss*.

CALVERT W.H. 2001. Monarch butterfly (*Danaus plexippus* L., Nymphalidae) fall migration: Flight behavior and direction in relation to celestial and physiographic cues. *Journal of the Lepidopterists' Society* 55: 162-168.

CARR A. 1984. The sea turtle: so excellent a fishe, 2nd Ed. *Austin: University of Texas Press*.

CARR A. 1987. New perspectives on the pelagic stage of sea turtle development. *Conservation Biology* 1: 103-121.

CHENG K. 2005. Reflections on geometry and navigation. *Connection Science* 17: 5-21.

CHENG K. (in press). Arthropod navigation: Ants, bees, crabs, spiders finding their way. In: Wasserman E.A. & Zentall T.R., Edits. Comparative cognition: Experimental explorations of animal intelligence. *Oxford: Oxford University Press*.

COLLETT T.S. & COLLETT M. 2002. Memory use in insect visual navigation. *Nature Review Neurosciences* 3: 542-552.

COLOMBO M. & BROADBENT N. 2000. Is the avian hippocampus a functional homologue of the mammaliam hippocampus? *Neuroscience and Biobehavioral Reviews* 24: 465-484.

CRISTOL D.A., REYNOLDS E.B., LECLER C.E., DONNER A.H., FARABAUGH C.S. & ZIEGENFUS C.W.S. 2003. Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal Behaviour* 66: 317-328.

DAVIS E. 1986. Representing and acquiring geographical knowledge. *London: Pitman*.

DAVIS R. 1966. Homing performance and homing ability in bats. *Ecological Monographs* 36: 201-234.

DINGLE H., ZALUCKI M.P. & ROCHESTER W. 1999. Season-specific directional movement in migratory Australian butterflies. *Australian Journal of Entomology* 38: 323-329.

DITTMAN A.H. & QUINN T.P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* 199: 83-91.

DITTMAN A.H., QUINN T.P. & NEVITT G.A. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 53: 434-442.

DITTMAN A.H., QUINN T.P., NEVITT G.A., HACKER B. & STORM D.R. 1997. Sensitization of olfactory guanylyl cyclase to a specific imprinted odorant in coho salmon. *Neuron* 19: 381-389.

DYER F.C. 1991. Bees acquire route-based memories but not cognitive maps in a familiar landscape. *Animal Behaviour* 41: 239-246.

EICHENBAUM H., STEWART C. & MORRIS R.G.M. 1990. Hippocampal representation in place learning. *Journal of Neuroscience* 10: 3531-3542.

EMLEN S.T. 1970. Celestial rotation: its importance in the development of migratory orientation. *Science* 170: 1198-1201.

ERNI B., LIECHTI F., UNDERHILL L.G. & BRUDERER B. 2002. Wind and rain govern the intensity of nocturnal bird migration in central Europe — A log-linear regression analysis. *Ardea* 90: 155-166.

ETIENNE A.S. 2003. How does path integration interact with olfaction, vision and the representation of space, pp. 49-66. In: Jeffery K.J., Edit. The neurobiology of spatial behaviour. *Oxford: Oxford University Press*.

ETIENNE A.S. & JEFFERY K.J. 2004. Path integration in mammals. *Hippocampus* 14: 180-192.

FISCHER J., MUNRO U. & PHILLIPS J.B. 2003. Magnetic navigation by an avian migrant?, pp. 423-432. In: Berthold P. et al., Edits. Avian migration. *Heidelberg: Springer Verlag*.

FRISCH K. VON 1967. The dance language and orientation of bees. *Cambridge, MA: Belknap*.

FRISCH K. VON & LINDAUER M. 1954. Himmel und Erde in Konkurrenz bei der Orientierung der Bienen [Sky and Earth un competition in the orientation of bees]. *Naturwissenschaften* 41: 245-253.

FROY O., GOTTER A.L., CASSELMAN A.L. & REPPERT S.M. 2003. Illuminating the circadian clock in monarch butterfly migration. *Science* 300: 1303-1305.

GAGLIARDO A., IOALÈ P. & BINGMAN V.P. 1999. Homing in pigeons: The role of the hippocampal formation in the representation of landmarks used for navigation. *Journal of Neuroscience* 19: 311-315.

GALLISTEL C.R. 1990. The organization of action. *Cambridge, MA: MIT Press*.

GAUTHREAUX S.A. JR 1978. The importance of daytime flights of nocturnal migrants: redetermined migration following displacement, pp. 219-227. In: Schmidt-Koenig K. & Keeton W.T., Edits. Animal migration, navigation and homing. *Heidelberg: Springer Verlag*.

GAUTHREAUX S.A. JR & ABLE K.P. 1970. Wind and the direction of nocturnal songbird migration. *Nature* 228: 476-477.

GOULD J.L. 1986. The locale map of honey bees: do insects have cognitive maps? *Science* 232: 861-863.

GRIFFIN D.R. 1952. Bird navigation. *Biological Reviews* 27: 359-400.

Gudmundson G.A., Benvenuti S., Alerstam T., Papi F., Lilliendahl K. & Åkesson S. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proceedings of the Royal Society of London (B)* 261: 73-79.

Guilford T., Roberts S., Biro D. & Rezek I. 2004. Positional entropy during pigeon homing II: navigational interpretation of Bayesian latent state models. *Journal of Theoretical Biology* 227: 25-38.

Hagstrum J.T. 2000. Infrasound and the avian navigational map. *Journal of Experimental Biology* 203: 1103-1111.

Hasler A.D. & Scholz A.T. 1983. Olfactory imprinting and homing in salmon. *Berlin, Heidelberg, New York, Tokyo: Springer Verlag*.

Hays G.C., Åkesson S., Broderick A.C., Glen F., Godley B.J., Papi F. & Luschi P. 2003. Island finding ability of marine turtles. *Proceedings of the Royal Society of London (B)* 270 (*Suppl*. 1): 5-7.

Hays G.C., Houghton D.R. & Myers A.E. 2004. Pan-atlantic leatherback turtle movements. *Nature* 429: 522.

Healey M.C., Thomson K.A., Leblond P.H., Huato L., Hinch S.G. & Walters C.J. 2000. Computer simulations of the effects of the Sitka eddy on the migration of sockeye salmon returning to British Columbia. *Fisheries Oceanography* 9: 271-281.

Healy S. (Edit.) 1998. Spatial representation in animals. *Oxford: Oxford University Press*.

Healy S.D., Gwinner E. & Krebs J.R. 1996. Hippocampal volume in migratory and non-migratory warblers: Effects of age and experience. *Behavioural Brain Research* 81: 61-68.

Hemmi J.M. & Zeil J. 2003a. Burrow surveillance in fiddler crabs I. Description of behaviour. *Journal of Experimental Biology* 206: 3935-3950.

Hemmi J.M. & Zeil J. 2003b. Burrow surveillance in fiddler crabs II. The sensory cues. *Journal of Experimental Biology* 206: 3951-3961.

Ioalè P., Papi F., Fiaschi V. & Baldaccini N.E. 1978. Pigeon navigation: effects upon homing behaviour by reversing wind direction at the loft. *Journal of Comparative Physiology (A)* 128: 285-295.

Jeffery K.J. (Edit.) 2003. The neurobiology of spatial behaviour. *Oxford: Oxford University Press*.

Keeton W.T. 1974. The orientational and navigational basis of homing in birds. *Advances in the Study of Behavior* 5: 47-132.

Kirschvink J.L., Dizon A.E. & Westphal J.A. 1986. Evidence from strandings for geomagnetic sensitivity in cetaceans. *Journal of Experimental Biology* 120: 1-24.

Laughlin S.B. 2001. Energy as a constraint on the coding and processing of sensory information. *Current Opinion in Neurobiology* 11: 475-480.

Layne J.E., Barnes W.J.P. & Duncan L.M.J. 2003a. Mechanisms of homing in the fiddler crab *Uca rapax* 1. Spatial and temporal characteristics of a system of small-scale navigation. *Journal of Experimental Biology* 206: 4413-4423.

Layne J.E., Barnes W.J.P. & Duncan L.M.J. 2003b. Mechanisms of homing in the fiddler crab *Uca rapax* 2. Information sources and frame of reference for a path integration system. *Journal of Experimental Biology* 206: 4425-4442.

Lipp H.-P., Vyssotski A.L., Wolfer D.P., Reneaudineau S., Savini M., Tröster G. & Dell'Omo G. 2004. Pigeon homing along highways and exits. *Current Biology* 14: 1239-1249.

Lohmann K.J. & Lohmann C.M.F. 1994. Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *Journal of Experimental Biology* 194: 23-32.

Lohmann K.J. & Lohmann C.M.F. 1996a. Orientation and open-sea navigation in sea turtles. *Journal of Experimental Biology* 199: 73-81.

Lohmann K.J. & Lohmann C.M.F. 1996b. Detection of magnetic field intensity by sea turtles. *Nature* 380: 59-61.

Lohmann K.J., Cain S.D., Dodge S.A. & Lohmann C.M.F. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science* 294: 364-366.

Lohmann K.J., Lohmann C.M.F., Ehrhart L.M., Bagley D.A. & Swing T. 2004. Geomagnetic map used in sea-turtle navigation. *Nature* 428: 909-910.

Luschi P., Åkesson S., Broderick A.C., Glen F., Godley B.J., Papi F. & Hays G.C. 2001. Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behavioral Ecology and Sociobiology* 50: 528-534.

Luschi P., Hays G.C., Del Seppia C., Marsh R. & Papi F. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proceedings of the Royal Society of London (B)* 265: 2279-2284.

Luschi P., Hays G.C. & Papi F. 2003a. A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos* 103: 293-302.

Luschi P., Hughes G.R., Mencacci R., De Barnardi E., Sale A., Broker R., Bouwer M. & Papi F. 2003c. Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea. *Marine Biology* 143: 793-801.

Luschi P., Sale A., Mencacci R., Hughes G.R., Lutjeharms J.R.E. & Papi F. 2003b. Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the ocean. *Proceedings of the Royal Society of London (B)* 270 (*Suppl*. 2): 129-132.

Mate B.R., Gisiner R. & Mobley J. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. *Canadian Journal of Zoology* 76: 863-868.

Matthews G.V.T. 1953. Sun navigation in homing pigeons. *Journal of Experimental Biology* 30: 243-267.

Matthews G.V.T. 1968. Bird navigation, 2nd Ed. *Cambridge: Cambridge University Press*.

Menzel R. & Giurfa M. 2001. Cognitive architecture of a mini-brain: the honeybee. *Trends in Cognitive Sciences* 5: 62-71.

Menzel R., Greggers U., Smith A., Berger S., Brandt R., Brunke S., Bundrock G., Hülse S., Plümpe T., Schaupp F., Schüttler E., Stach S., Stindt J., Stollhoff N. & Watzl S. 2005. Honeybees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences* 102: 3040-3045.

Mewaldt L.R. 1964. California sparrows return from displacement to Maryland. *Science* 146: 941-942.

Mora C.V., Davison M., Wild J.M. & Walker M. 2004. Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature* 432: 508-511.

Mouritsen H. & Frost B.J. 2002. Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proceedings of the National Academy of Sciences* 99: 10162-10166.

Mouritsen H., Huyvaert K.P., Frost B.J. & Anderson D.J. 2003. Waved albatrosses can navigate with strong magnets attached to their heads. *Journal of Experimental Biology* 206: 4155-4166.

Mrosovsky N. & Shettleworth S.J. 1968. Wavelength preference and brightness cues in the water finding behaviour of sea turtles. *Behaviour* 32: 211-257.

Nevitt G.A., & Bonadonna F. 2005. Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters* 1: 303-305.

O'Keefe J. & Nadel L. 1978. The hippocampus as a cognitive map. *Oxford: Oxford University Press*.

Papi F. 1992. General aspects, pp. 1-18. In: Papi F., Edit., Animal homing. *London: Chapman Hall*.

Papi F., Luschi P., Åkesson S., Capogrossi S. & Hays G.C. 2000. Open-sea migration of magnetically disturbed sea turtles. *Journal of Experimental Biology* 203: 3435-3443.

Parkinson J.K., Murray E.A. & Mishkin M. 1988. A selective mnemonic role for the hippocampus in monkeys: memory for the location of objects. *Journal of Neuroscience* 8: 4159-4167.

Perdeck A.C. 1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., as revealed by displacement experiments. *Ardea* 46: 1-37.

Quine D.B. & Kreithen M.L. 1981. Frequency shift discrimination: Can homing pigeons locate infrasounds by Doppler shifts? *Journal of Comparative Physiology (A)* 141: 153-155.

Quinn T.P. & Dittman A.H. 1992. Fishes, pp. 145-211. In: Papi F., Edit. Animal homing. *London: Chapman Hall*.

Reilly W.I. 2002. Magnetic position determination by homing pigeons. *Journal of Theoretical Biology* 218: 47-54.

RODRIGUEZ F., LOPEZ J.C., VARGAS J.P., GOMEZ Y., BROGLIO C. & SALAS C. 2002. Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *Journal of Neuroscience* 22: 2894-2903.

ROLLS E.T. 1999. Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus* 9: 467-480.

SEMM P. & BEASON R.C. 1990. Sensory basis of bird orientation. *Experientia* 46: 372-378.

SRINIVASAN M.V., ZHANG S.W. & BIDWELL N.J. 1997. Visually mediated odometry in honeybees. *Journal of Experimental Biology* 200: 2513-2522.

STALLEICKEN J., MUKHIDA M., LABHART T., WEHNER R., FROST B. & MOURITSEN H. 2005. Do monarch butterflies use polarized skylight for migratory orientation? *Journal of Experimental Biology* 208: 2239-2408.

STEVICK P.T., ALLEN J., BÉRUBE M., CLAPHAM P.J., KATONA S.K., LARSEN F., LIEN J., MATTILA D.K., PALSBØLL P.J., ROBBINS J., SIGURJÓNSSON J., SMITH T.D. & ØIEN N. 2003. Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology, London* 259: 231-237.

STONE G.S., FLÓREZ-GONZALEZ L. & KATONA S. 1990. Whale migration record. *Nature* 346: 705.

THOMSON K.A., INGRAHAM W.J., HEALEY M.C., LEBLOND P.H., GROOT C. & HEALEY C.G. 1992. The influence of ocean currents on latitude of landfall and migration speed of sockeye salmon returning to the Fraser River. *Fisheries Oceanography* 1: 163-179.

TOLMAN E.C. 1948. Cognitive maps in mice and men. *Psychological Review* 55: 189-208.

URQUHART F.A. 1965. Monarch butterfly (*Danaus plexippus*) migration studies: Autumnal movement. *Proceedings of the Entomological Society of Ontario* 95: 23-33.

WALCOTT C. 1991. Magnetic maps in pigeons, pp. 38-51. In: Berthold P., Edit. Orientation in birds. *Basel: Birkhäuser Verlag*.

WALKER M.M. 1998. On a wing and a vector: a model for magnetic navigation in birds. *Journal of Theoretical Biology* 192: 341-349.

WALKER M.M., KIRSCHVINK J.L., AHMED G. & DICTION A.E. 1992. Evidence that fin whales respond to the geomagnetic field during migration. *Journal of Experimental Biology* 171: 67-78.

WALLRAFF H.G. 1974. Das Navigationssystem der Vögel. *Munich: Oldenbourg Verlag*.

WALLRAFF H.G. 1999. The magnetic map of homing pigeons: an evergreen phenomenon. *Journal of Theoretical Biology* 197: 265-269.

WALLRAFF H.G. 2003. Zur olfaktorischen Navigation der Vögel. *Journal für Ornithologie* 144: 1-32.

WALLRAFF H.G. 2004. Avian olfactory navigation: its empirical foundation and conceptual state. *Animal Behaviour* 67: 189-204.

WALLRAFF H.G. 2005a. Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds. *Connection Science* 17: 91-106.

WALLRAFF H.G. 2005b. Avian navigation: Pigeon homing as a paradigm. *Berlin: Springer Verlag*.

WEHNER R. 1992. Arthropods, pp. 45-144. In: Papi F., Edit. Animal homing. *London: Chapman Hall*.

WEHNER R. 2003. Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology (A)* 189: 579-588.

WEHNER R., LEHRER M. & HARVEY P. (Edits) 1996. Navigation. *Journal of Experimental Biology* 199: 1-261.

WEHNER R. & SRINIVASAN M.V. 2003. Path integration in insects, pp. 9-30. In: Jeffery K.J., Edit. The neurobiology of spatial behaviour. *Oxford: Oxford University Press*.

WEIMERKIRCH H., SALAMOLARD M., SARRAZIN F. & JOUVENTIN P. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110: 325-342.

WEIMERKIRCH H., BONADONNA F., BAILLEUL F., MABILLE G., DELL'OMO G. & LIPP H.P. 2002. GPS tracking of foraging albatrosses. *Science* 295: 1259.

WHITE A.R., STRASSER R. & BINGMAN V.P. 2002. Hippocampus lesions impair landmark array spatial learning in homing pigeons: A laboratory study. *Neurobiology of Learning and Memory* 78: 65-78.

WILKINSON G.S. & FLEMING T.H. 1996. Migration and evolution of lesser long-nosed bats, *Leptonycteris curasoae*, inferred from mitochondrial DNA. *Molecular Ecology* 5: 329-339.

WILLIAMS T.C., WILLIAMS J.M. & GRIFFIN D.R. 1966. Homing ability of the neotropical bat *Phyllostomus hastatus*. *Animal Behaviour* 14: 468-473.

WILTSCHKO R. 1992. Das Verhalten verfrachteter Vögel. *Vogelwarte* 36: 249-310.

WILTSCHKO R. & WILTSCHKO W. 1995. Magnetic orientation in animals. *Berlin: Springer Verlag*.

WILTSCHKO R. & WILTSCHKO W. 2003. Avian navigation: from historical to modern times. *Animal Behaviour* 65: 257-272.

WINKLER H., LEISLER B. & BERNROIDER G. 2004. Ecological constraints on the evolution of avian brains. *Journal of Ornithology* 145: 238-244.

ZEIL J. 1998. Homing in fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *Journal of Comparative Physiology (A)* 183: 367-377.