Animal navigation: A noisy magnetic compass?

Johnsen, Sönke; Lohmann, Ken; Warrant, Eric

Published in:
Journal of Experimental Biology

2020

Document Version:
Peer reviewed version (aka post-print)

Link to publication

Citation for published version (APA):
Johnsen, S., Lohmann, K., & Warrant, E. (2020). Animal navigation: A noisy magnetic compass? *Journal of Experimental Biology*, *223*(18), Article jeb164921.

Total number of authors:
3

Animal Navigation: A Noisy Magnetic Sense?

[1]Sönke Johnsen, [2]Kenneth J. Lohmann, and [3]Eric. J. Warrant

[1]Biology Department, Duke University, Durham, NC, USA, 27708

[2]Biology Department, University of North Carolina, Chapel Hill, NC, USA, 27599

[3]Lund Vision Group, Biology Department, Lund University, Lund, Sweden

Contact information:

Sönke Johnsen
Biology Department, Box 90338
Duke University
Durham, NC 27708
919-660-7321
919-660-7293 (FAX)
SJOHNSEN@DUKE.EDU

Abstract

Diverse organisms use Earth's magnetic field as a cue in orientation and navigation. Nevertheless, eliciting magnetic orientation responses reliably, either in laboratory or natural settings, is often difficult. Many species appear to preferentially exploit non-magnetic cues if they are available, suggesting that the magnetic sense often serves as a redundant or 'backup' source of information. This raises an interesting paradox: Earth's magnetic field appears to be more pervasive and reliable than almost any other navigational cue. Why then do animals not rely almost exclusively on the geomagnetic field, while ignoring or downplaying other cues? Here we explore a possible explanation: that the magnetic sense of animals is 'noisy', in that the magnetic signal is small relative to thermal and receptor noise. Magnetic receptors are thus unable to instantaneously acquire magnetic information that is highly precise or accurate. We speculate that extensive time-averaging and/or other higher-order neural processing of magnetic information is required, rendering the magnetic sense inefficient relative to alternative cues that can be detected faster and with less effort. This interpretation is consistent with experimental results suggesting a long time-course for magnetic compass and map responses in some animals. Despite possible limitations, magnetoreception may be maintained by natural selection because the geomagnetic field is sometimes the only source of directional and/or positional information available.

Keywords: magnetoreception, orientation, migration, signal-to-noise

Summary statement: *Magnetic orientation responses in animals are often weak and difficult to elicit experimentally. A possible explanation is that the magnetic compass is 'noisy' and cannot acquire precise magnetic information over short time periods.*

Introduction

Numerous organisms detect Earth's magnetic field and use it to guide their movements over a wide range of spatial scales (reviewed by Johnsen and Lohmann, 2005; Mouritsen 2013; Nordmann et al., 2017). In many ways, the geomagnetic field appears to be an ideal navigational cue. In contrast to most other sensory cues, it exists everywhere on Earth, is continuously present throughout the day and night, and is largely unaffected by season and weather (though potentially affected by solar storms that wax and wane over an 11-year cycle – e.g. Granger et al. [2020]). Moreover, the magnetic field can potentially provide animals with both directional and positional information (Lohmann et al., 2007). Indeed, humans have used the geomagnetic field as a simple but powerful source of directional information for centuries.

The pervasiveness and reliability of Earth's magnetic field leads to an interesting paradox. Specifically, given that the geomagnetic field is a ubiquitous sensory cue that is potentially available for all animals to exploit in orientation and navigation, why do so few species appear to rely exclusively or even primarily on magnetic cues for guiding their movements? In addition, why is it often difficult to reliably produce magnetic orientation and navigation responses under laboratory conditions?

Three examples illustrate the essence of the enigma. The desert ant *Cataglyphis*, a famous insect navigator, begins its adult life with a functional magnetic compass sense that is used as it transitions from underground life to foraging above ground (Fleischmann et al., 2018). Nevertheless, older adult ants undertaking foraging trips orient their movements relative to a celestial compass instead of the geomagnetic field (Wehner et al., 1996). Why do ants switch from using a magnetic compass to using a celestial compass despite the fact that the geomagnetic field is constantly available?

Similarly, studies have revealed that several birds, including homing pigeons, appear to use a combination of input from multiple compasses to select a direction instead of relying on the magnetic compass alone (Munro and Wiltschko, 1993; Wiltschko and Wiltschko, 2001). Why is deriving input from multiple compasses in these birds advantageous relative to relying exclusively on the magnetic compass?

Finally, loggerhead sea turtles have a well-developed magnetic sense that provides both directional and positional information (Lohmann, 1991; Lohmann and Lohmann, 2012; 2019). Yet hatchling turtles, when leaving the beach and swimming offshore, guide themselves seaward by swimming into ocean waves (Lohmann and Lohmann, 1992), even though the offshore migration could be guided by magnetic cues instead.

In this Commentary, we explore the question of why magnetic field information, although potentially available to all animals, often seems to be used either as a 'backup' cue or as one of several different sources of information. For simplicity we will focus primarily on the ability of animals to maintain directional headings relative to Earth's field, or what is often called the 'magnetic compass sense', as this represents the simplest use of magnetic information by animals (see Box). We propose a novel hypothesis: that the magnetic compass sense of animals is 'noisy', meaning that magnetic receptors are unable to instantaneously acquire magnetic information that is highly precise or accurate because the magnetic signal is small relative to thermal and receptor noise. As a simple analogy, imagine a human-built compass in which the needle does not point unerringly toward the north; instead, the needle points north *on average*, swinging erratically among a variety of directions, so that the reading at any specific instant is unreliable. Such a compass can still be used in orientation, but extracting a useful signal requires some kind of processing -- for example, averaging a series of readings over time -- that might make the magnetic compass harder to use and inefficient relative to alternative cues that can be detected instantly. We argue that a scenario similar to this is consistent with some of the most persistently mysterious aspects of magnetic orientation behavior.

Magnetic orientation responses in the laboratory

Despite the pervasive and reliable nature of the geomagnetic field, behavioral responses of animals in magnetic orientation experiments are typically weak. Informally, the data have a large spread around the mean angle of orientation resulting from different individual animals selecting a wide range of directions. More formally, the confidence interval of the mean angle can be large relative to that seen in studies of orientation to other cues (e.g. Figure 1). This dispersion results in low statistical power when comparing orientation data from different magnetic treatments, which in turn creates several problems for the researcher. For example, unless large numbers of individuals are used, an effect can easily be missed.

The relatively weak responses also make it difficult to use magnetic behavior in a single individual as an assay, unlike, for example, vision, where one can illuminate the retina of one individual and get a repeatable response that can then be used to examine the effects of various manipulations (e.g. measurement of a spectral sensitivity curve). Indeed, there is currently no species that has a magnetic response so robust that it can easily be used as a model system to study the underlying physiological, biophysical and genetic basis of the sense. Additionally, there is no species in which magnetoreception is definitively known not to exist, making it difficult to establish negative control species for comparative studies. Again, this contrasts with vision, in which blind species are well known and usually easy to identify. Within a magnetoreceptive species, nulled magnetic fields can of course be used as an experimental control, but we do not currently have the ability to say that magnetorception has been evolutionarily lost in a given environment, the way we can – for example – say that vision has been lost in certain cave-dwelling species.

Another unusual aspect of magnetoreception, found in both behavioral studies and neurobiological assays in certain species, is that the responses to changes in the magnetic field sometimes have a long time-constant (Figure 2). Although species vary significantly in the speed at which they interact with the environment, ranging from darting swifts to lumbering sea slugs, the rate of response within a species tends to be relatively independent of the sensory modality cuing the response (though of course there are exceptions). However, an insect or lobster that may respond within milliseconds to a visual stimulus may take several minutes to respond to an altered magnetic field (Lohmann et al., 1995; Vácha, 2006; Dreyer et al., 2018). Similarly, in the marine mollusc *Tritonia*, one of the few neurobiological model systems for magnetoreception, several identified neurons respond with enhanced electrical activity to changes in Earth-strength magnetic fields, but only after a latency of several minutes (Lohmann et al., 1991; Popescu and Willows, 1999; Wang et al., 2003; 2004). Similarly long latencies from a change in the magnetic field to the onset of an electrophysiological response have been reported in several other animals (e.g. Semm et al., 1980; Semm, 1983; Korall and Martin, 1987), although it should be noted that shorter latencies have also been observed (Semm and Beason, 1990; Walker et al., 1997; Wu and Dickman, 2012).

Together the weakness and, in some cases, slowness of the magnetic response have contributed to the challenge of determining the sensor involved. Given the lack of an identified magnetoreceptor that can be studied directly, most of the evidence for and against different hypothesized sensor mechanisms has been behavioral. Thus, the fact that the behavioral data are sometimes difficult to interpret has complicated efforts to determine the physiological basis of the magnetic sense.

Low signal relative to noise as a potential explanation

Most human experience of magnetic field detection is based on observing the steady needle of a handheld compass, but an interesting possibility is that biological magnetoreceptors do not yield the same consistent and reliable signal. Instead, as mentioned above, the ‘needle’ of the biological compass may move rapidly and seemingly randomly over large angles about the correct direction. In engineering terms, the signal-to-noise ratio (SNR) of the compass may be low. This term is relatively uncommon in much of biology, but is critically important for understanding sensory processes such as vision under low light, a research area for two of the authors. For example, although visual scenes under daylight appear smooth and continuous to the human eye or a camera, those under starlight appear grainy and coarse. This reduction in detail is due to the signal being smaller relative to the noise; the signal decreases because the scene is darker, and the noise – which arises from receptor noise and the random arrival of photons – remains constant. In this situation, one cannot simply increase the brightness of the image to recover the lost detail; doing so only results in a brighter but still coarse image. Instead, visual systems and cameras must sample the scene for a longer period of time, and it is well-known that the temporal resolution (i.e. the ‘speed of the shutter’) of many animal visual systems decreases as the illumination level decreases, meaning that the scene is sampled for longer periods (Warrant 1999).

The hypothesis that magnetoreceptors have a low SNR appears plausible for several reasons. First, the geomagnetic field at the earth’s surface is weak, much as light levels are low at night or in the deep sea. More importantly, the interaction of magnetic fields with biological tissue is extraordinarily weak. For example, although magnetic fields can split the energy states of atomic orbitals (known as Zeeman splitting), the energy resulting from this is only one five-millionth that of the thermal noise at human body temperature. In other words, any magnetic compass composed of standard biological molecules would be buffeted about by thermal forces that are many orders of magnitude larger.. The only materials that interact strongly with magnetic fields are the elements iron, nickel, cobalt, gadolinium and dysprosium, , and some of their compounds. Ferromagnetic materials, in particular the mineral magnetite (Fe_3O_4), have been proposed as a possible basis of magnetoreception, but an important constraint is that animals do not appear to have the ability to magnetize macroscopic amounts of these materials. Instead, they must use crystals that are either of single-domain size (~50 nm diameter) or smaller, but such small crystals are again vulnerable to the randomizing effects of thermal noise (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985; Yorke, 1985). Magnetotactic bacteria and other single-cell organisms that move along magnetic field lines (Bellini, 1963; Blakemore, 1975) partly overcome this limitation by forming chains of single-domain magnetite crystals, but the general situation in metazoans appears to be one of nano-scale objects being influenced by weak magnetic fields in the presence of relatively large amounts of Brownian motion.

Magnetoreception mediated by chemical reactions (known as the ‘radical pair’ hypothesis) faces similar or perhaps even larger hurdles because this mechanism does not have the advantage of the unusually large coupling between ferromagnetic minerals and magnetic fields. Nevertheless, analyses suggest that chemical magnetoreception is viable from a theoretical standpoint and that high sensitivity with such a system might be possible (Weaver et al., 2000; Ritz et al., 2000). Of course, receptors in many sensory modalities detect quite small stimuli; for example, photoreceptors respond to individual photons. However, many sensory receptors have focusing/amplifying structures (lenses, outer ears, nostrils) and signal amplification pathways, both of which function to significantly improve signal-to-noise ratio. For the magnetic sense, mechanisms for focusing or amplifying magnetic signals have not been discovered; moreover, they appear unlikely due to the weak interaction between biological tissue and magnetic fields.

In sum, an animal magnetic compass (whatever its form) might oscillate significantly and randomly around the correct bearing angle due to the presence of levels of thermal and receptor noise that are high relative to the magnetic signal itself. This in turn might contribute to the large dispersion in directional responses often observed in orientation studies. It might also explain the slow responses to changes in the magnetic field, because the animal may have to integrate the signal over a long time course to increase the reliability of the signal, much as eyes integrate over longer periods under dim light. A reliable compass reading, possibly acquired through integration, is necessary for an efficient path of travel (Figure 3).

In the context of this discussion, a distinction should perhaps be drawn among three separate time courses: (1) the time required for the transduction process itself; (2) the time required for the nervous system to integrate and analyze the signal, which depends in part on SNR; and (3) the time needed for a behavioral response, which depends on context, motivation and navigational task. At present, both theoretical and empirical studies suggest that the transduction process itself is likely to require only fractions of a second (e.g. Johnsen and Lohmann, 2008; Slaby et al., 2018). Nevertheless, whether an animal can detect the new direction of the ambient field the instant that it changes, or instead must average signals over time to extract compass information, remains unclear. To our knowledge, no experimental results exist in which a change in the direction of the ambient magnetic field results in a nearly instantaneous change in the heading of an animal. Indeed, experiments with lobsters and moths have revealed a latency of more than a minute between the time that the field direction is changed and the time that the animal changes its direction of travel (Figures 2 and 4).

It is also important to note that a magnetoreceptor may not itself be any noisier than receptors for other sensory modalities, inasmuch as thermal and receptor noise are common to all biological receptors. Instead, the central challenge with the magnetic sense might be that the signal is weak, due to the weakness of the geomagnetic field and the limited interaction of biological materials with magnetic fields. Thus, the magnetic sense might be operating under challenging signal-to-noise circumstances, much like the eyes of deep-sea fish or nocturnal moths.

Low signal-to-noise and navigational strategies

If receptor and thermal noise in magnetoreception are indeed high relative to the signal then this might influence how the sense is used. Specifically, if the magnetic sense does not provide a continuous and rapid source of information, then it might be easier for animals to use other cues for orientation whenever a choice exists. In this context it is worth noting that pigeons, juvenile sea turtles and young salmon can all maintain headings using both magnetic and celestial compasses, but celestial compasses are often used when both cues are available (Keeton, 1971; Quinn, 1980; Avens and Lohmann, 2003; Mott and Salmon, 2011).

Another possible way to accommodate a low-SNR magnetic compass is to use it as one cue in a set of multimodal cues. An interesting example consistent with this possibility comes from recent studies with the Bogong moth (*Agrotis infusa*), a nocturnal Australian moth that migrates long distances between summer and winter habitats (Warrant et al., 2016, Dreyer et al., 2018). In initial studies, moths were tested in a flight arena with a largely unobstructed view of the sky; under these conditions, rotating the ambient magnetic field had little or no apparent effect on orientation. By contrast, when a conspicuous visual cue was deliberately placed into the arena as a visual landmark, it emerged that moths changed orientation when the field and landmark were moved together, but became disoriented after 2–3 minutes when either the magnetic field or the visual landmark was shifted alone (Dreyer et al., 2018; Figure 4). These findings suggest that, for Bogong moths, magnetic orientation is one component of a multimodal navigational strategy that also involves visual landmarks. An intriguing possibility is that moths periodically consult their magnetic compasses to ensure that they are moving in the right general direction, but prefer to use visual cues for moment-to-moment maintenance of headings, in much the same way that humans hiking through forests intermittently consult a compass but then, rather than continually peering at the compass as they walk, use visual landmarks to maintain the chosen course.

Such a multimodal navigational strategy might actually be the preferred strategy in situations when all available compass cues have low SNR, as might occur in the dimly lit nocturnal habitats of migratory birds or moths or in the murky underwater habitats of sea turtles. In this case, an optimal integration of these low-SNR multimodal cues could be performed to maximize the reliability of the combined information; indeed, by knowing the uncertainty inherent in each compass, such integration can be used to estimate the optimal steering direction (Collett 2012; Ernst and Banks, 2002; Hoinville and Wehner, 2018). Interestingly, homing pigeons have been proposed to simultaneously use a sun compass and magnetic compass under some conditions (Wiltschko and Wiltschko, 2001); indeed, mathematical models have suggested that avian navigation is a complex process that relies on simultaneous use of at least four or five different factors (Schiffner et al., 2011).

High-precision magnetic maps?

In addition to having a magnetic compass, some animals also have a ‘magnetic map’, defined as an ability to derive positional information from Earth’s magnetic field (Lohmann et al., 2007). Magnetic maps can be used for a variety of purposes, from changing migratory direction at an appropriate location (Lohmann et al., 2001; 2012; Putman et al., 2014; Naisbett-Jones et al., 2017) to navigating toward a specific home area (Lohmann et al., 2004).

The concept of a low-SNR magnetic compass might, at first glance, seem inconsistent with findings suggesting that a few animals can use magnetic information to determine their geographic position when displaced relatively short distances from a home area. For example, lobsters and newts displaced short distances (12 to 45 km) from a home area were able to orient in the homeward direction, apparently by using magnetic cues (Phillips et al., 1995; Fischer et al., 2001; Boles and Lohmann, 2003). If magnetic maps do indeed function over such small distances, then animals presumably can detect the very small differences in the magnetic fields that exist at nearby locations, implying high-precision sensing.

An important distinction must be drawn, however, between the precision of a system and the speed with which the precision is achieved. In homing experiments with newts and lobsters, animals remained in the magnetic field of the location to which they had been moved either overnight (lobsters; Boles and Lohmann, 2003) or for several days (newts; Phillips et al., 1995) prior to testing. In principle, this extended duration in the local field might have provided an opportunity for the animals to repeatedly sample the field and, perhaps, average the results. To our knowledge, all demonstrations that animals derive positional or 'map' information from Earth's field (e.g., Lohmann et al., 2001; Putman et al., 2014) have involved experiments in which animals had a period of at least several minutes in which to assess the field. Thus, we caution that an ability to detect magnetic fields with high precision does not, by itself, preclude the possibility that the magnetic sense is noisy; it might mean only that an animal has a mechanism that enables it to extract a high-quality signal through averaging or other means.

Implications for the performance of magnetoreception research

If the magnetic compass does indeed have a low SNR, and especially if it is used in combination with other cues, then one practical lesson for experimentalists might be that the standard practice of testing for magnetic orientation in the absence of other sensory cues may not be optimal. As with the Bogong moth, removing 'competing' cues may inadvertently create an environment in which animals are less likely, rather than more likely, to express magnetic orientation behavior. Instead, treating the magnetic field as one part of a multi-modal orientation system, and designing experiments that combine magnetic cues with others in a conflict/concordance design, may prove productive.

Another suggestion is to undertake experiments with significantly longer time courses, allowing the animal time to assess the field and any changes in it. This may improve the odds of finding a species that has a repeatable response that can be used as an assay to probe the underlying mechanisms.

An additional issue is that the SNR of the magnetoreceptor is likely to be under natural selection. Diurnal, terrestrial species that always (or usually) have access to multiple directional cues (e.g. birds) may be under less selective pressure to have a reliable magnetic compass than those that have access to fewer navigational cues, such as nocturnal species or those that inhabit subsurface ocean habitats (e.g. sea turtles, lobsters). Therefore, it would be interesting to study whether the confidence intervals in aquatic and nocturnal species (for example) are smaller than those in terrestrial and diurnal species, although differences in experimental protocols may make such a comparison difficult.

Conclusions

From uncertain beginnings, the study of magnetoreception has developed into a vibrant field with the potential to unearth a sensor with a completely novel design. Despite advances, however, progress has been hindered by the complexities and inconsistencies of the behavioral data. We suggest that this complexity may not be a failing of the research, but might instead reflect the natural behavioral output of a sensory system with an unusually low level of signal relative to receptor and thermal noise.

Because magnetoreceptors have not yet been identified with certainty in any animal, it is not yet possible to test this hypothesis directly using cellular recording techniques. However, it may be possible to test the hypothesis indirectly using behavioral assays similar to those that have been used to measure temporal resolution in vision. For example, certain three-color light emitting diodes consist of both a red and green light emitting circuit, wired in opposite polarity, such that DC current in one direction creates red light, DC current in the opposite direction creates green light. Thus, a 60 Hz AC current creates an amber mixture because the alternating flashing of the red and green circuits is above the temporal resolution of the human eye. One can then use these LEDs run at different AC frequencies in a forced choice conditioning trial to assess temporal resolution behaviorally. An analog experiment using alternating magnetic fields may be possible, and is currently under development by the authors.

The concept of a low SNR magnetic compass represents a possible unifying explanation for a variety of peculiarities in magnetoreception research, including consistently weak magnetic orientation behavior, long time courses for behavioral responses and the finding that few if any animals rely solely on magnetic orientation when alternative cues are present. Considering this possibility may provide new insights into the conditions under which animals use their magnetic sense and the ways in which magnetoreception can most effectively be studied.

BOX: **A Quick Guide to Magnetoreception**

Earth's magnetic field provides two types of information that can be exploited by animals in orientation and navigation. Animals that use the geomagnetic field as a source of *directional* information, for example to maintain headings to the north or south, are said to have a 'magnetic compass'. By contrast, animals that derive *positional* information from Earth's magnetic field are said to have a 'magnetic map' (Lohmann et al., 2007). Magnetic maps can be used by animals to change direction at appropriate locations along migratory routes (e.g., Lohmann et al., 2001; 2012; Putman et al., 2014) or to navigate to specific locations (e.g., Lohmann et al., 2004; Kishkinev et al., 2015).

Despite abundant behavioral evidence that animals sense magnetic fields, little is known about how they do so. More than one mechanism may exist, perhaps even in the same animal (Lohmann et al., 2010). Most research has focused on three possibilities.

Electromagnetic Induction: When an electrically conductive object such as a fish moves through Earth's magnetic field, negatively and positively charged particles migrate to opposite sides of the object, resulting in a constant voltage determined by speed and direction relative to the magnetic field. This might provide the basis for a magnetic sense in elasmobranch fish (e.g., sharks), which have highly sensitive electroreceptors (Kalmijn 1974; 1984; Johnsen and Lohmann, 2008). Electromagnetic induction might also underlie magnetoreception in birds, with the crucial detection process occurring in the fluid-filled inner ear (Nimpf et al., 2019).

Magnetite: The magnetite hypothesis proposes that particles of magnetite (Fe_3O_4) underlie magnetoreception. Single-domain magnetite crystals act as tiny magnets that twist into alignment with the Earth's magnetic field if allowed to rotate freely. In principle, such crystals might transduce magnetic information to the nervous system by exerting torque or pressure on secondary receptors (such as stretch receptors, hair cells, or mechanoreceptors) or by opening ion channels directly if, for example, cytoskeletal filaments connect the crystals to the channels (e.g., Kirschvink et al. 2001; Johnsen and Lohmann 2005; Walker 2008).

Chemical Magnetoreception: Another hypothesis is that magnetoreception involves unusual chemical reactions that are influenced by Earth's magnetic field. Because the proposed reactions involve pairs of free radicals as short-lived intermediates, this idea is sometimes referred to as the radical pairs hypothesis. Details are complex and have been described elsewhere (e.g., Ritz et al., 2010; Hore and Mouritsen, 2016). Many of the best-known radical-pair reactions begin with electron transfers that are induced by the absorption of light; thus, chemical magnetoreceptors might also be photoreceptors and magnetoreception might be tied to the visual system. Photoreceptive proteins known as cryptochromes have been proposed as a possible magnetoreceptive substrate (Ritz et al., 2000).

LITERATURE CITED

Avens, L., and Lohmann, K. J. (2003). Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta. J. Exp Biol.* **206**, 4317-4325.

Bellini, S. (1963). *Su di un particolare comportamento di batteri d'acqua dolce*. Institute of Microbiology, University of Pavia.

Blakemore, R. (1975). Magnetotactic bacteria. *Science* **190**, 377–379.

Boles, L.C. and Lohmann, K.J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature*, **421**, 60-63.

Collett, M. (2012). How navigational guidance systems are combined in a desert ant. *Curr. Biol.* **22**, 927–932.

Dreyer, D., Frost, B., Mouritsen, H., Günther, A., Green, K., Whitehouse, M., Johnsen, S., Heinze, S., and Warrant, E. J. (2018). The Earth's magnetic field and visual landmarks steer migration in a nocturnal moth. *Curr. Biol.* **28**, 2160-2166.

Ernst, M. O., and Banks, M. (2002) Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* **415**, 429–433.

Fischer, J. H., Freake, M. J., Borland, S. C. and Phillips, J. B. (2001). Evidence for the use of magnetic map information by an amphibian. *Animal behaviour*, **62**, 1-10.

Granger, J. N., Fitak, R. R., Walkowicz, L., and Johnsen, S. (2020). Gray whales strand more often on days with increased levels of atmospheric radio-frequency radiation. *Curr. Biol.* **30**, R155-R156.

Hoinville, T., and Wehner, R. (2018). Optimal multiguidance integration in insect navigation. *PNAS* **115**, 2824-2829.

Hore, P. J., and Mouritsen, H. (2016). The radical-pair mechanism of magnetoreception. *Ann. Rev. Biophys.* **45**, 299-344.

Irwin, W. P. and Lohmann, K. J. (2005). Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. *J. Comp. Physiol. A* **191**, 475-480.

Johnsen, S., and Lohmann, K. J. (2005). The physics and neurobiology of magnetoreception. *Nature Rev. Neurosci.* **6**, 703-712.

Johnsen, S., and Lohmann, K. J. (2008). Magnetoreception in animals. *Phys. Today* **61**, 29-35.

Keeton, W. T. (1971). Magnets interfere with pigeon homing. *PNAS* **68**, 102-106.

Kirschvink, J. L. and Gould, J. L. (1981). Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems* **13**, 181-201.

Kirschvink, J. L., and Walker, M. M. (1985). Particle-size considerations for magnetite-based magnetoreceptors. In *Magnetite biomineralization and magnetoreception in organisms* (pp. 243-254). Springer, Boston, MA.

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., and Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Curr. Biol.* **25**, R822-R824.

Korall, H. and Martin, H. (1987). Response of bristle-field sensilla in *Apis mellifica* to geomagnetic and astrophysical fields. *J. Comp. Physiol. A* **161**, 1-22.

Lohmann., K. J. (2010). Q&A: Animal behaviour: Magnetic-field perception. *Nature* **464**, 1140-1142.

Lohmann, K. J. and Lohmann, C. M. F. (1992). Orientation to oceanic waves by green turtle hatchlings. *J. Exp. Biol.* **171**, 1-13.

Lohmann, K. J., and Lohmann, C. M. F. (1994). Acquisition of magnetic directional preference in hatchling loggerhead sea turtles. *J. Exp. Biol.* **190**, 1-8.

Lohmann, K. J., and Lohmann, C. M. (2019). There and back again: natal homing by magnetic navigation in sea turtles and salmon. *J. Exp. Biol.*, **222**, jeb184077.

Lohmann, K. J., Lohmann, C. M. F., and Putman, N. F. (2007). Magnetic maps in animals: Nature's GPS. *J. Exp. Biol.* **210**, 3697-3705.

Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G., Zimmer-Faust, R. K., Jarrard, H. E., and Boles, L. C. (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J. Exp. Biol.* **198**, 2041-2048.

Lohmann, K. J., Willows, A. O. D., and Pinter, R. B. (1991). An identifiable molluscan neuron responds to changes in earth-strength magnetic fields. *J. Exp. Biol.* **161**, 1-24.

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

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

Lohmann, K. J., Putman, N. F., and Lohmann, C. M. (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342.

Lucas, M., Salmon, M., Fritz, E., and Wyneken, J. (1992). Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour* **122**, 56-77.

Moore, B. R. (1980). A modification of the Rayleigh test for vector data. *Biometrika* **67**, 175-180.

Mott, C. R., and Salmon, M. (2011). Sun compass orientation by juvenile green sea turtles (*Chelonia mydas*). *Chelon. Conserv. Biol.* **10**, 73-81.

Mouritsen, H. (2013) The magnetic senses. In *Neurosciences - From Molecule to Behavior: a university textbook* by G. Galizia and P.M. Lledo (Eds.) (Springer 2013), pp. 427-443.

Munro, U. R., and Wiltschko, R. O. (1993). Clock-shift experiments with migratory yellow-faced honeyeaters, *Lichenostomus chrysops* (Meliphagidae), an Australian day-migrating bird. *J. Exp. Biol.* **181**, 233-44.

Naisbett-Jones, L.C., Putman, N.F., Stephenson, J.F., Ladak, S. and Young, K.A. (2017). A magnetic map leads juvenile European eels to the Gulf Stream. *Curr. Biol.* **27**, 1236-1240.

Nimpf, S., Nordmann, G. C., Kagerbauer, D., Malkemper, E. P., Landler, L., Papadaki-Anastasopoulou, A., ... and Lendl, T. (2019). A putative mechanism for magnetoreception by electromagnetic induction in the pigeon inner ear. *Curr. Biol.* **29**, 4052-4059.

Nordmann, G. C., Hochstoeger, T., and Keays, D. A. (2017). Magnetoreception—a sense without a receptor. *PLoS Biol.* **15**, e2003234.

Phillips, J.B., Adler, K. and Borland, S.C. (1995). True navigation by an amphibian. *Anim. Behav.* **50**, 855-858.

Popescu, I. R., and Willows, A. O. D. (1999). Sources of magnetic sensory input to identified neurons active during crawling in the marine mollusk *Tritonia diomedea*. *J. Exp. Biol.* **202**, 3029–3036.

Putman, N. F., Scanlan, M. M., Billman, E. J., O'Neil, J. P., Couture, R. B., Quinn, T. P., ... and Noakes, D. L. (2014). An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr. Biol.* **24**, 446-450.

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Phys. A* **137**, 243-248.

Ritz, T., Adem, S., and Schulten, K. (2000). A model for photoreceptor-based magnetoreception in birds. *Biophys. J.* **78**, 707-718.

Schiffner, I., Baumeister, J. and Wiltschko, R. (2011). Mathematical analysis of the navigational process in homing pigeons. *J. Exp. Biol.* **291**, 42-46.

Semm, P., Schneider, T. and Vollrath, L. (1980). Effects of an earth-strength magnetic field on electrical activity of pineal cells. *Nature* **288**, 607-608.

Semm, P. (1983). Neurobiological investigations on the magnetic sensitivity of the pineal gland in rodents and pigeons. *Comp. Biochem. Physiol.* **76A**, 683-689.

Semm, P. and Beason, R. C. (1990). Responses to small magnetic variations by the trigeminal system of the bobolink. *Brain Res. Bull.* **25**, 735-740.

Skiles, D. D. (1985). The geomagnetic field: Its nature, history, and biological relevance**.** In *Magnetite Biomineralization and Magnetoreception in Organisms* (pp. 43-102). Springer, Boston, MA.

Vácha, M. (2006). Laboratory behavioural assay of insect magnetoreception: magnetosensitivity of *Periplaneta americana*. *J. Exp. Biol.* **209**, 3882-3886.

Wang J. H., Cain S. D., and Lohmann K. J. (2003) Identification of magnetically responsive neurons in the marine mollusk *Tritonia diomedea*. *J. Exp. Biol.* 206, 381–388.

Wang, J. H., Cain, S. D. and Lohmann, K. J. (2004). Identifiable neurons inhibited by Earth-strength magnetic stimuli in the mollusc *Tritonia diomedea*. *J. Exp. Biol.* **207**, 1043-1049.

Warrant, E. J. (1999). Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.* **39**, 1611-1630.

Warrant, E. J., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden A., Brauburger K., and Heinze, S. (2016). The Australian Bogong moth *Agrotis infusa* : A long-distance nocturnal navigator. *Front. Behav. Neurosci.* **10**, doi: 10.3389/fnbeh.2016.00077.

Weaver, J.C., Vaughan, T.E. and Astumian, R.D. (2000). Biological sensing of small field differences by magnetically sensitive chemical reactions. *Nature* **405**, 707-709.

Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.

Wiltschko, R., and Wiltschko, W. (2001). Clock-shift experiments with homing pigeons: a compromise between solar and magnetic information? *Behav. Ecol. Sociobiol.* **49**, 393-400.

Wu, L. Q., and Dickman, J. D. (2012). Neural correlates of a magnetic sense. *Science* **336**, 1054-1057.

Yorke, E. D. (1985). Energetics and sensitivity considerations of ferromagnetic magnetoreceptors. In *Magnetite Biomineralization and Magnetoreception in Organisms* (pp. 233-242). Springer, Boston, MA.

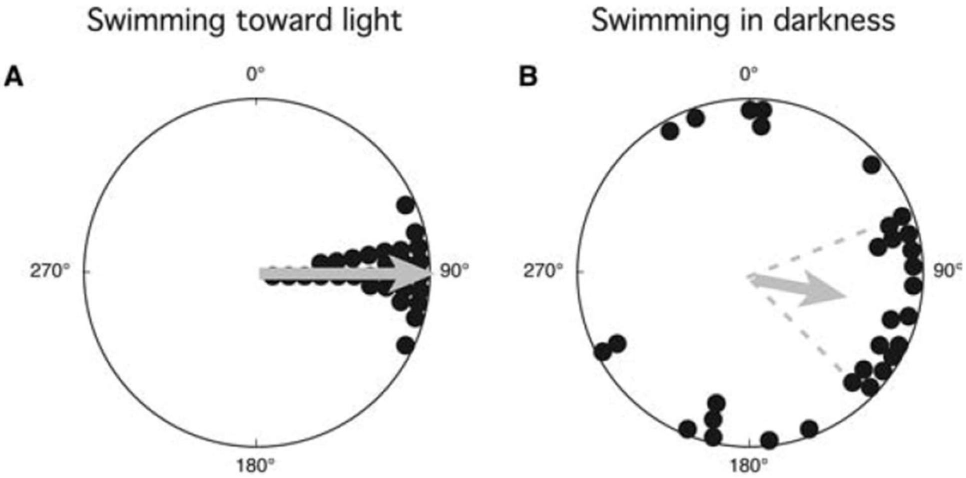

Figure 1: Orientation of hatchling loggerhead sea turtles (*Caretta caretta*) under conditions in which turtles rely on different sensory cues to orient eastward. In both cases, turtles were placed into cloth harnesses and tethered to an electronic tracking device in a circular water-filled arena. (A) Orientation of turtles when dim illumination (a white LED) was present in the east. Under these conditions, turtles are known to use visual cues to swim toward the light; if the ambient magnetic field is reversed while the light is present, turtles do not change direction (KJL, unpublished data), implying either that they do not use their magnetic compass in this situation or, if they do, that visual cues take precedence. (B) Orientation of the same turtles subsequently tested in complete darkness. Turtles tested under these conditions, after exposure to light in the east, are known to orient eastward using Earth's magnetic field (Lohmann, 1991; Light et al., 1993; Lohmann and Lohmann, 1994), but the dispersion of the turtles increases strikingly when they are forced to rely on their magnetic compasses. Data are from Irwin and Lohmann (2005). The comparison between sensory cues is not perfect, inasmuch as it is conceivable that turtles are differentially motivated (for unknown reasons) to swim east under the two conditions, or that having access to magnetic cues and light cues together yields stronger orientation than magnetic cues alone (even though reversing the magnetic field when the light is

present has no effect). These caveats aside, similar comparisons suggest that sea turtles are often more strongly oriented while using visual cues to crawl across the beach (Lucas et al., 1992) or while using wave cues to orient offshore (Lohmann et al., 1990; Lohmann and Lohmann, 1992) than they are while using magnetic compass orientation.

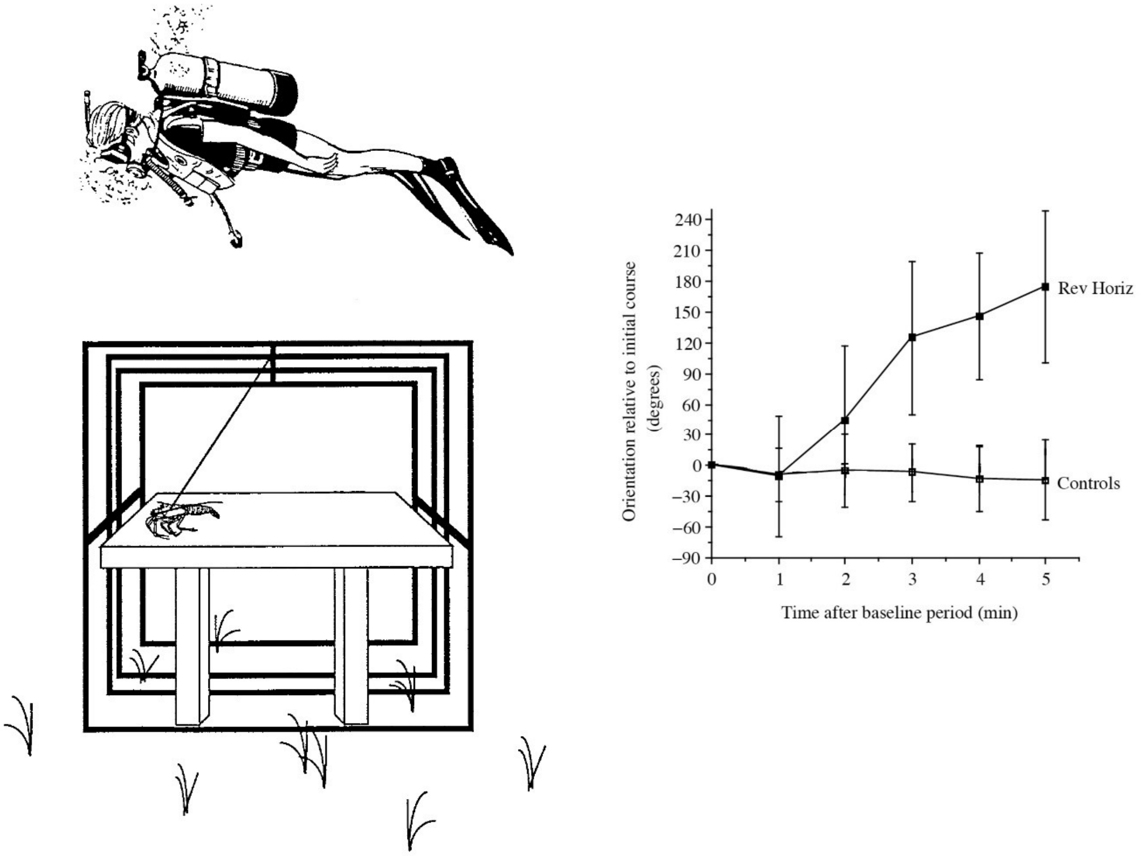

Figure 2: Orientation of Caribbean spiny lobsters (*Panulirus argus*). Diagram on the left shows a lobster walking in place while tethered on a table surrounded by an underwater magnetic coil system (boxlike structure), with a diver monitoring its orientation behavior. After lobsters established consistent headings, the coil was used to reverse the direction of the field in some of the trials; in others, lobsters continued walking in the unaltered local field. In the diagram on the right, time zero on the x-axis is the time at which the field was reversed for half of the lobsters (there was no reversal for the controls). The vertical axis indicates the mean angle of all lobsters in the two groups, with an orientation bearing of zero degrees indicating the previous orientation of the lobsters. Lobsters that were not exposed to a field reversal (n = 14) continued on similar headings with little deviation from their initial courses. By contrast, lobsters exposed to the field reversals (n = 9) began to deviate from their initial headings approximately 1–2 min after the

field reversal and, by 5 min after, were walking in directions approximately opposite to their initial direction. Interestingly, the change in direction did not occur immediately after the field was shifted. Data are from Lohmann et al., 1995.

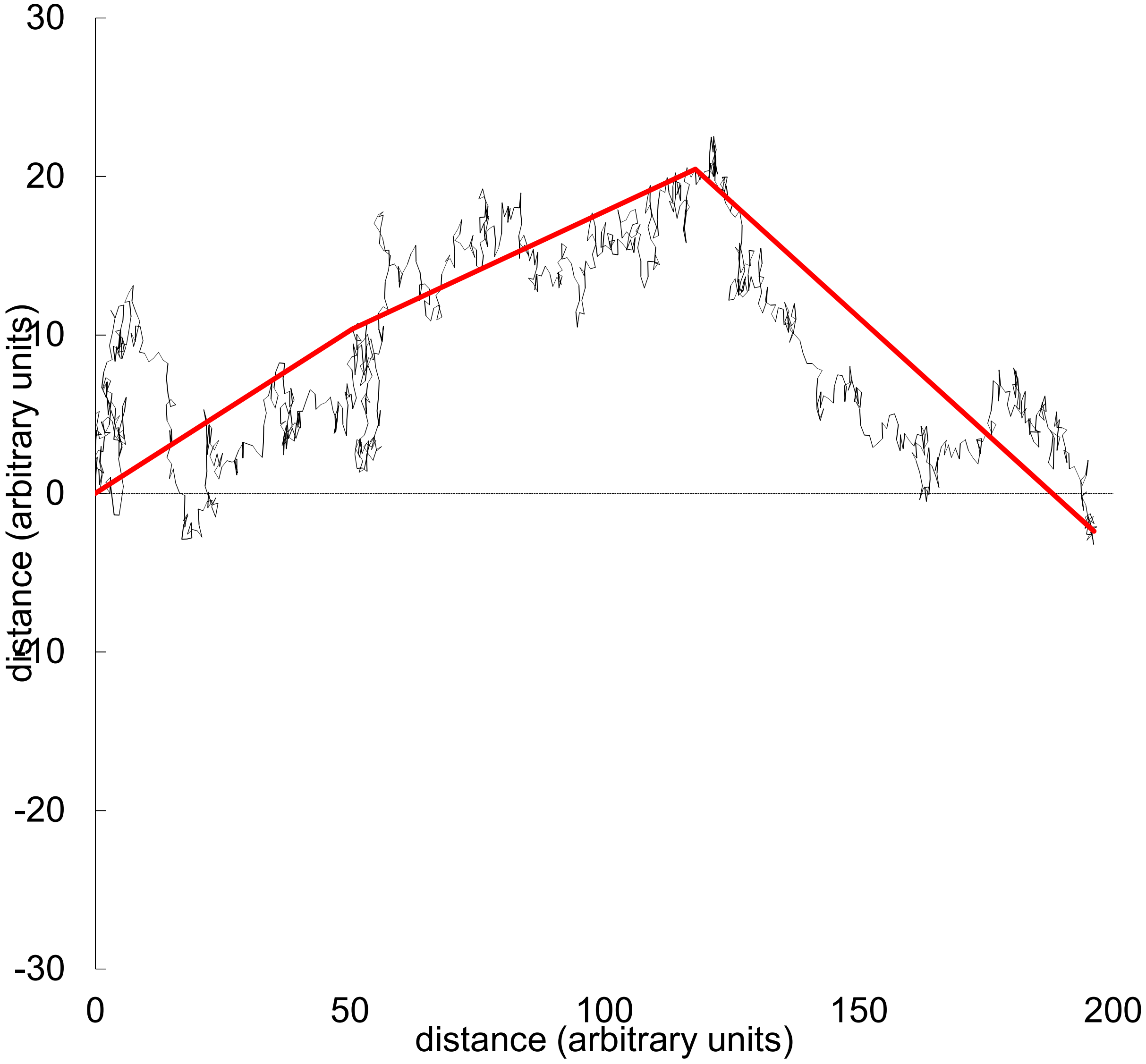

Figure 3: The effects of averaging a noisy signal on the path of an orienting animal. The black line shows the simulated 1200-step path of an animal that is attempting to move directly to the right using a compass whose measurements of a constant field have a normal distribution with a standard deviation of 120 degrees. The red line shows the path of the animal using the same underlying measurements, but averaging the field measurements over 400 steps and then making one large 400-step move. The ratio of the length of the red path to the black path is

approximately 5:1. The ratios for magnetic sensors with standard deviations of 10, 30, 60, 120, and 180 degrees are 1.02±0.01, 1.14±0.02, 1.7±0.04, 4.7±0.26, and 9.6±1.4 respectively (N = 10 simulations for each).

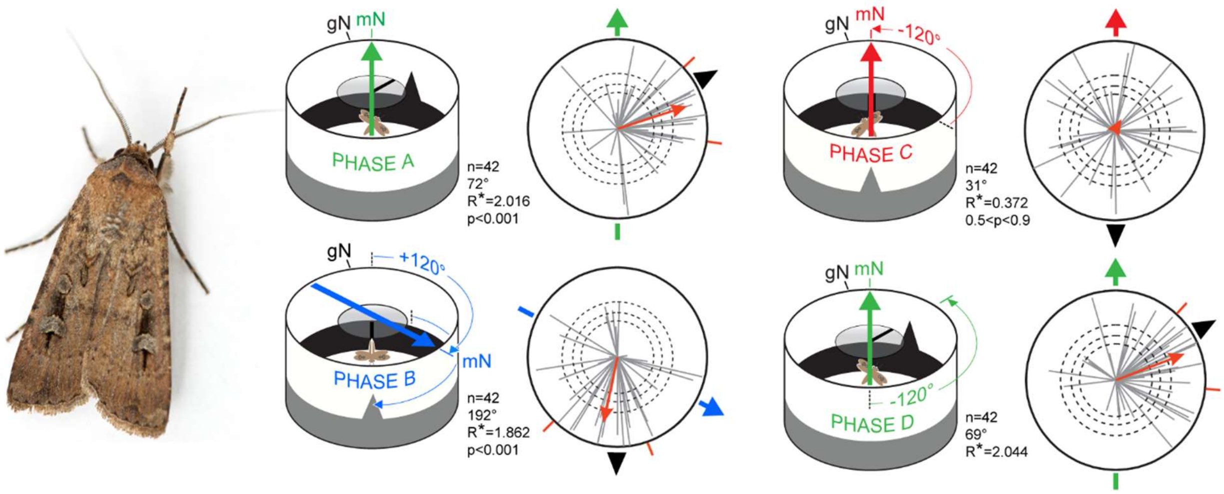

Figure 4. Migratory orientation in Bogong moths is multimodal. Individual moths were tethered at the centre of a cylindrical Perspex flight arena placed vertically on a table outdoors. Moths were then attached to the end of a vertical shaft connected to an encoder that continuously measured the instantaneous orientations of steadily flying moths that were free to turn in any azimuthal direction. Each moth was then subjected to magnetic and visual cues during four 5-minute phases (A to D) and their directions and directedness (orientation and length, respectively, of grey vectors in circular plots) measured. When the positions of the magnetic field (heavy coloured arrows) and visual landmarks (black triangular 'mountain' and dorsal stripe) are correlated and turned together (Phases A, B and D), moths (n=42, grey vectors), the moth population (grey vectors) remains significantly oriented near the landmarks (as indicated by the long (highly directed) red population mean vectors; p<0.001). When the two cues are set in conflict (Phase C), moths become disoriented (as indicated by the short (undirected) red population mean vector; 0.5<p<0.9). The directedness (length) of the population mean vector is given by its R* value: the greater the R* value, the more directed the population of moths it

represents. The R* value also reveals the likelihood that the mean flight direction of a population of moths – where each moth has its own direction and directedness (direction and length of grey vectors) – differs significantly from a random, undirected population (according to the Moore's modified Rayleigh test: Moore, 1980). Dashed circles: required R* value for statistical significance (i.e. the R* value required to reliably distinguish the directedness of the population from a random, undirected population): $p<0.05$, $p<0.01$ and $p<0.001$, respectively for increasing radius. Outer radius of plots: $R^*=2.5$. Red radial dashes: 95% confidence interval. gN, geographic North. mN, magnetic North. Data are from Dreyer et al., 2018.