COMMENTARY

Migratory navigation in birds: new opportunities in an era of fast-developing tracking technology

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Summary

Birds have remained the dominant model for studying the mechanisms of animal navigation for decades, with much of what has been discovered coming from laboratory studies or model systems. The miniaturisation of tracking technology in recent years now promises opportunities for studying navigation during migration itself (migratory navigation) on an unprecedented scale. Even if migration tracking studies are principally being designed for other purposes, we argue that attention to salient environmental variables during the design or analysis of a study may enable a host of navigational questions to be addressed, greatly enriching the field. We explore candidate variables in the form of a series of contrasts (e.g. land *vs* ocean or night *vs* day migration), which may vary naturally between migratory species, populations or even within the life span of a migrating individual. We discuss how these contrasts might help address questions of sensory mechanisms, spatiotemporal representational strategies and adaptive variation in navigational ability. We suggest that this comparative approach may help enrich our knowledge about the natural history of migratory navigation in birds.

Key words: bird, migration, navigation, telemetry, tracking.

Introduction

There is an ornithological revolution underway. Rapid and sustained miniaturisation of biologging technologies and increased affordability are triggering an explosion of tracking studies of wild bird species across the whole of their annual cycle. The result is an accelerating increase in data on the migratory routes of a growing number of wild species. These studies are often motivated by questions unrelated to the outstanding questions of animal navigation, which have largely been tackled within the laboratory or with a restricted set of model species. We start from the premise that the impending explosion in avian migration tracking offers unprecedented opportunity for understanding navigation within the context of migration. We observe that, despite considerable accumulated knowledge of the mechanisms and capabilities of avian navigation, much less is known about the processes of navigation during active migration itself (which we term 'migratory navigation'). We aim to consider ways in which new studies involving the tracking of migrants, perhaps set up for quite different reasons, might address questions of navigational interest by helping to describe the natural history of migratory navigation or by involving natural factors that might reveal navigational mechanisms. We do this largely by exploring a set of contrasts (see Table 1), where the natural availability of a potential navigational cue or presumed appropriateness of a potential navigational

strategy differ during or between flights, and illustrating how analyzing the birds' responses during migration across such contrasts might potentially contribute to the study of migratory navigation, an approach that might easily be extended to other migratory animal groups.

New technologies, tools and capabilities

Historically, it has been a major challenge to study the behaviour of birds throughout a natural migration with any accuracy, but recent rapid advances in biotelemetry are changing this (reviewed in Robinson et al., 2010; Bridge et al., 2011). Although specialist technologies are becoming available for recording a range of physiological, motion-related or environmental variables in flight (Bowlin et al., 2005; Wilson et al., 2008), information about position is probably most important for studying migratory navigation. The simplest and smallest available tag (0.3 g devices exist) produces a radio pulse, detected by a VHF receiver, providing the animal's direction of movement or, by triangulation, its location. Because radio tags must be actively located for each fix, they are most suitable only for animals with short-scale movements, or for recording departure directions. Long-distance tracking is only possible with tremendous effort (Bridge et al., 2011), and to date no migratory songbird has been tracked on its complete path from breeding to wintering ground using a VHF tag

(Holland et al., 2007), although partial tracks covering hundreds to over a thousand kilometres have been achieved by actively following migrants by car (e.g. Cochran, 1987; Cochran et al., 2004) or aircraft (Thorup et al., 2007; Holland et al., 2009).

Satellites have provided one solution for tracking long-distance migrants, with the first systems using ARGOS satellites to estimate position from the Doppler shift of a signal transmitted from the animal. Position data are delivered without device retrieval, a huge advantage for studying many species, but accuracy is variable – from 100 m to 100 km (Bridge et al., 2011). For more accurate locations (approximately 4 m error) and increased temporal resolution and control, a GPS device can be carried and the data relayed *via* the ARGOS satellite in a combined device. In many respects, satellite-based tracking is ideal for studying migratory navigation, particularly when high-resolution GPS tracks are obtained, but a problem with both ARGOS and GPS/ARGOS is size. The smallest currently available ARGOS transmitter is 5 g and the smallest GPS/ARGOS is 22 g. Generally, biologists have applied a 5% rule to the mass a bird can carry without adversely affecting its behaviour (Brander and Cochran, 1969), and this has been adopted by some advisory bodies as best practice (Fair et al., 2010), although it remains largely untested and arbitrary (Barron et al., 2010). Five per cent makes 400 g the lightest bird that could carry a device with GPS and satellite download capability, and 1 g the largest load acceptable for a small 20 g songbird, such as those used in many laboratory studies of migratory orientation mechanisms. In some avian groups, even smaller relative payloads have been shown to have negative impacts [albatrosses and petrels (Phillips et al., 2003); penguins (Saraux et al., 2011)], and where aerodynamic (or hydrodynamic) drag is crucial, the shape and positioning of the device may be more important than its mass (Bowlin et al., 2010). These constraints have allowed satellite tracking of larger migratory birds such as albatrosses, raptors or waterbirds (Jouventin and Weimerskirch, 1990; Thorup et al., 2003a; Thorup et al., 2003b; Thorup et al., 2006; Vardanis et al., 2011), but are currently too restrictive for songbirds.

If animals return to a predictable location and can be recaptured, data may be stored on board without the need for power-hungry transmission technology. Thus, archival GPS devices as light as 2.5 g are now available from specialist manufacturers and 15 g devices are cheaply available as consumer products. As recovery probability drops, however, data concerning navigational decisions become biased because only successfully returning animals can provide tracks. The addition of wireless data download to GPS devices [for example using UHF or global system for mobile (GSM) communication] can circumvent this problem in many situations, although devices are still relatively heavy: 27 g for GSM (Bridge et al., 2011) and 15 g for UHF (R. Freeman, personal communication).

Archival light loggers, known as 'geolocators', can provide an alternative lightweight technology for tracking individual movements throughout migration. Geolocators, now as small as <1 g, are being employed widely in studies of migration on progressively smaller avian species from albatrosses to songbirds (Croxall et al., 2005; Egevang et al., 2010; Guilford et al., 2009; Shaffer et al., 2006; Stutchbury et al., 2009). However, the calculation of location estimates from time-stamped archival light intensity data is inherently error prone (position accuracy is rarely better than 150 km) (Phillips et al., 2004) and, although noise can sometimes be reduced using additional data streams (such as temperature), the resultant accuracy is generally too low to answer many questions about detailed navigational mechanisms.

Nevertheless, not all navigational questions require high spatial accuracy. For example, geolocators have been sufficient to reveal that a highly dispersive migration in the Atlantic puffin (*Fratercula arctica*) is combined with strong individual route fidelity across multiple years (Guilford et al., 2011). This pattern is not easily explained by current models of navigational control, and implies a major role for individual exploration in determining migratory destinations. Where tracking across a contrast might reveal such a major difference in spatial behaviour, navigational questions may well be resolvable without the need for high-precision tracks.

It is clear from our discussion of available technology that device size is an important constraint, and leads to trade-offs with spatio-temporal resolution even for migrants large enough to be tracked at all. But technology continues to advance. The main limiting factor in reducing mass is power consumption (and therefore battery size). Solar panels are helping, with a 2 g ARGOS Doppler shift transmitter on the drawing board (P. Howey, Microwave Telemetry, personal communication) and 5 g devices already in production (Meyburg et al., 2011). GPS loggers weighing 2.5 g are becoming available. Solar powering has allowed a surface-based wireless-data-transmitting 18 g GPS device to provide 0.3 Hz fixes for 1 month (Shamoun-Baranes et al., 2011). Perhaps most exciting of all is the announcement that the European Space Agency plans to launch the International Cooperation for Animal Research Using Space (ICARUS) project in 2014. This aims to deploy a satellite-based sensor system for receiving signals from transmitters as small as 1 g (Bridge et al., 2011). Thus, although the ideal tag for tracking the full migratory path of a songbird (lightweight, high spatio-temporal resolution, longevity and remote download) may not currently exist, it should be available in the foreseeable future.

Contrasts

Short- to medium-range tracking of migrant birds with respect to navigational ability (Chernetsov et al., 2004; Thorup et al., 2007; Thorup et al., 2011) and sensory mechanisms (e.g. Bonadonna et al., 2003; Cochran et al., 2004; Mouritsen et al., 2003) has already hinted at the potential power of tracking studies. In our view, future long-range tracking studies might contribute further to understanding migratory navigation when they allow a comparison of movement behaviour over one or more informative 'contrasts'. We define a contrast as a natural situation in which our expectations about navigational behaviour may differ because of some underlying difference in the availability of a potential navigational cue, or presumed appropriateness of a potential navigational strategy. Such a difference might involve the availability of useful magnetic field information at different latitudes or stable visual landmarks over different terrain types, and further examples are developed below. Comparisons are most likely to involve flight-path data, which might consist of spatial parameters (such as orientation within tracks or route similarity amongst multiple tracks), movement parameters (such as flight tortuosity or speed) or phenology (the timing of migratory movements at different scales). Comparisons might be between flight path patterns of species differing across a contrast, paths of different individuals within a species undergoing different migration routes, or path segments within an individual's migration during periods or over terrains that differ in the contrast. The argument essentially is that if the availability of a navigational cue, for example, varies across a contrast that is encountered by migrants, either within or between species and/or within or between migrations, then correlated changes in movement behaviour (or their absence) can indicate whether the navigational cue is salient. Table 1 summarises a

Table 1. Example contrasts over which the tracks of migrant birds might be compared, with examples of the type of navigational questions the comparison might inform and the type of track differences to look for

Contrast	Example navigational interest	What to look for
1. First *vs* subsequent migrations	Role of experience in influencing navigational ability and strategy	Experiential changes in route or site fidelity
2. Short *vs* long migrations	Do longer migrations require more navigational systems?	Different track characteristics at different migratory stages
3. Nocturnal *vs* diurnal migration	Role of complex visual landscape cues in wind-drift correction	Track variability less wind dependent in diurnal migrants
4. Land *vs* open-water migration	Dependence on stable visual landmark guidance	Track variability greater over open water
5. Wind	Role of wind in track directions and route selection	Wind drift and compensation events between flight segments
6. Magnetic disturbance	Dependence on magnetic cues for either map or compass navigation	Increased route tortuosity, or variability, at places (anomalies) and times (storms) of magnetic disturbance
7. Polar latitudes	Role of sun compass cues in migratory movements	Difficulty of solar time compensation leads to track curvature at higher latitudes (see Alerstam et al., 2001)
8. Equatorial latitudes	How do migrants cope with deteriorating magnetic compass ability with the diminishing angle of magnetic dip (inclination) near the equator?	Change in track characteristics, such as prevailing direction, or use of leading lines or alternative compasses
9. Longitude	Potential magnetic map components are less distinctive with E–W movements	Less goal or route fidelity in migrations with more dominant E–W component
10. Stopover fidelity	Stopover constraints select for greater navigational ability	Better corrective re-orientation after displacement in habitat-constrained species
11. Social migration	Culturally inherited route information buffers against error in innate vector navigation	Fewer atypical routes in social migrants

candidate list of 11 contrasts, their relevance to questions of migratory navigation and what might be looked for in the migratory tracks. If researchers are unsure about how to analyse their tracking data to study migratory navigation, further information can be obtained by contacting the corresponding author.

How might identifying contrasts help guide research? As an illustrative example contrast, consider comparing the flight paths of birds migrating at night *versus* during the day. First, if birds depend on the complex visual landscape features visible only during daylight for correcting for wind drift, then diurnal birds may show less path variability, and a lower likelihood of displacement, in response to unfavourable winds. However, if birds require only simplified features, such as leading lines or point sources, then the artificial landscape of man-made lighting visible at night may be sufficient to execute drift compensation (it may even be preferable). In the latter case, we may instead expect to see a difference in track structure over populated *versus* unpopulated terrain in nocturnal migrants (Bingman et al., 1982). Second, once aloft, nocturnal migrants are likely to be more dependent on a magnetic compass (Cochran et al., 2004) whereas diurnal migrants are likely to primarily rely on a sun compass (Kramer, 1957). Therefore, disrupted flight paths (e.g. greater variability, increased tortuosity) during magnetic storms or close to magnetic anomalies may be more prevalent during night migration. However, in the case of the magnetic compass it has been argued that birds may be able to compensate quickly for intensity changes if the underlying directional information remains consistent (Wiltschko and Wiltschko, 1995; Wiltschko et al., 2006), so magnetic storms or anomalies may affect magnetic compass orientation in unforeseen ways. This does not make the comparison meaningless, but the predictions more subtle. Thus, a difference in track characteristics across a contrast may reveal the use of an underlying navigational mechanism. However, predictions are unlikely always to be robust and simple, and it will be crucial to consider subtleties and alternative explanations (as with any comparative method).

The approach we suggest is necessarily correlational, so it suffers from inherent inferential weaknesses. For example, differences across a contrast might in fact be due to a hidden third variable. Nevertheless, such shortcomings are common to comparative

methods in general (Harvey and Pagel, 1991), so some of the solutions developed in other disciplines might be applicable here too. For example, susceptibility to the influence of hidden third variables is reduced if the comparison is within a species or between very closely related species (sister groups), or if multiple independent evolutionary dichotomies are used. Our approach can never be a substitute for experiments, which allow explicit manipulation of the relevant factors (e.g. in orientation cages) in well-studied model species, but it could at the very least suggest where best to target experiments. For the same reason, tracking should eventually be combined with experimental manipulation (Bonadonna et al., 2003; Cochran et al., 2004; Chernetsov et al., 2004; Holland et al., 2009; Mouritsen et al., 2003; Thorup et al., 2007). Furthermore, the choice of potential future model experimental species might benefit from such comparative considerations, and could make use of the natural variation in navigational mechanisms that life history contrasts may promote (Helbig, 1991; Berthold et al., 1992).

Navigational ability and spatiotemporal representational strategies

Perhaps the most fundamental questions of navigation have concerned the extent and variation in animals' navigational ability, the kinds of spatiotemporal representational strategies used to accomplish feats of navigation, and the underlying sensory mechanisms that control them. First we consider how modern tracking studies might help contribute to our understanding of navigational abilities and spatiotemporal representational strategies.

Adult migratory birds (and perhaps other life stages) display a stunning ability to return to the same breeding, overwintering and even stopover sites during repeated migrations (Moreau, 1972; Mouritsen, 2003), and more importantly, they can do so (or at least start to do so) following both passive and experimental displacements from familiar routes or locations (Chernetsov et al., 2008; Mewaldt, 1964; Perdeck, 1958; Thorup et al., 2007). This capacity is usually explained as the result of true navigation (*sensu* Griffin, 1952). However, there are only a few experimental studies that infer or track movements of migrants in free-flight following

experimental displacement, such as the band-recapture studies of starlings [*Sturnus vulgaris* (Perdeck, 1958)] and white-crowned sparrows [*Zonotrichia leucophrys* (Mewaldt, 1964)], the satellite tracking of white storks [*Ciconia ciconia* (Chernetsov et al., 2004)] and the short-range transmitter tracking of white-crowned sparrows (Thorup et al., 2007).

Envisioning a future that will enable the long-range tracking of migrant songbirds over the course of a complete migration cycle, including experimental displacements, offers unparalleled opportunities for understanding the properties, capacity and limits of migrant navigational ability. In addition to the obvious question of how widespread true navigation may be across species, analyses of flight paths (Alerstam et al., 2001; Hake et al., 2003; Chernetsov et al., 2004), comparisons between flight paths and predictions from specific migration strategy models (Mouritsen, 1998; Mouritsen and Mouritsen, 2000; Thorup et al., 2003a) can reveal much about the spatiotemporal orientation and navigation representational strategies used by different birds of different ages (Alerstam et al., 2001; Chernetsov et al., 2004; Hake et al., 2003; Thorup et al., 2003b). For example, do the routes taken by displaced (whether naturally or experimentally) migrants demonstrate a capacity to carry out goal-directed re-orientation immediately or do displaced birds engage in something like 'search behaviour' before re-orienting? The answers will need to be based on detailed route reconstructions, a challenge for tracking technology development. If one could document different stages in the corrective navigation phenology, this could inform researchers about possible limits in the range of true navigation and possibly suggest something about the underlying sensory mechanism (see below). In summary, we know little about the extended flight paths of migrant birds following displacement during migration itself. As such, because our knowledge of the natural history of true navigation is so limited, researchers are hindered in field-testing questions about mechanisms and the influence of evolutionary and ecological constraints on migratory routes and spatiotemporal navigation strategies.

Because young birds are thought to be unable to correct for displacements during their first autumn migration (Perdeck, 1958; Mouritsen and Larsen, 1998; Mouritsen, 2003; Thorup et al., 2007), the dominating opinion at the moment suggests that only experienced migrants are capable of true navigation, whereas young birds on their first autumn migration rely on an inherited program of direction and distance, so-called vector navigation or clock-and-compass orientation, to arrive at their overwintering site (Perdeck, 1958; Berthold, 1991; Mouritsen, 2003; Thorup et al., 2007) (but see Rabøl, 1978; Thorup et al., 2011). Young birds on their first spring migration already seem to have gained true navigational abilities (Chernetsov et al., 2008). Long-range tracking of experienced and first-time migrants is necessary to test the validity of this proposition. For example, in some pelagic seabirds, the role of innate migratory programmes may be strongly reduced (Guilford et al., 2011).

Regardless of whether first-time migrants are vector navigators, most migratory birds are likely to go through changes in navigational strategy both within and between migratory journeys as their experience with environmental features increases. Studies tracking a single migratory journey, multiple migratory journeys and, specifically, studies contrasting first-time and subsequent migrations, may uncover strategy switches along with their timing and development (Mouritsen, 2003). More telling would be studies that include some type of experimental displacement of migrants while en route.

Taking the lead from homing pigeon studies, it has been speculated that different points along the migratory journey may be reached by using different sensory mechanisms and representational strategies. For example, a gradient map (based on extrapolated experience of how two or more environmental cues vary over a large scale), coupled to a compass-based mechanism, may guide navigation when a bird is distant from its goal location, whereas a mosaic map (based on a network of known locations) or a map based on familiar landmarks and/or landscape features may guide navigation closer to the goal (Wallraff, 2005; Bingman and Cheng, 2006; Gagliardo et al., 2007). The hypothesis of changing navigational-representational strategies would be supported by changes in flight behaviour, detected by tracking, occurring at appropriate points in the migratory journey.

Sensory mechanisms

Perhaps the most contentious issue in migratory navigation is its underlying sensory basis. It is widely accepted that birds probably use a two-step system for navigation: first fixing their position relative to the goal using a map, and then selecting and maintaining an appropriate compass direction towards the goal (Griffin, 1952; Kramer, 1957). Studies on captive birds are likely to remain an important tool for studying fundamental avian sensory capabilities, which birds can potentially use for finding their way during migration, because it will be hard to control rigidly potential sensory cues during a free-flight experiment. Likewise, laboratory-based experiments (Bingman et al., 1999; Möller et al., 2004; Zapka et al., 2009; Heyers et al., 2010) will remain essential for understanding the molecular, neurobiological and cognitive mechanisms used by birds to sense the cues they use to find their way. Nevertheless, although captive bird studies have provided a rich understanding of compass and/or orientation mechanisms employed by migrants, they have provided little insight into the sensory mechanisms of map-like navigation (but see Fischer et al., 2003).

One vigorously debated sensory map cue for the long-distance navigation ability of migrants is the predictable variation in various parameters of the earth's magnetic field (Fischer et al., 2003; Freake et al., 2006). In our view, experimental tracking studies, in combination with laboratory-based approaches, could help resolve this issue. For example, and relying on experimental strategies already applied to the study of homing pigeons (e.g. Wiltschko et al., 2010), it could be informative if changes in flight behaviour during migration were found to co-occur with geomagnetic features (e.g. magnetic anomalies) or events (e.g. magnetic storms), or whether courses taken by birds follow better a constant direction relative to magnetic North or geographic North (Thorup et al., 2006). Are flight paths different near the geomagnetic equator where inclination is horizontal, or near the geomagnetic poles where inclination is vertical (Alerstam et al., 2001; Åkesson et al., 2005)? Of course, natural magnetic disturbances might impact either compass-based or putative map-based information or both (but see above for why map-based effects may be more likely), and disentangling their effects might be difficult using correlation alone. Nevertheless, this kind of opportunistic approach might prompt complementary experimental studies like that of Cochran et al. (Cochran et al., 2004). For example, disrupting the capacity of migrant birds to detect the earth's magnetic field, as has been done in homing pigeons (Gagliardo et al., 2006; Gagliardo et al., 2008, Gagliardo et al., 2009), would be expected to result in changes in flight behaviour indicative of compromised navigational ability that might, with the appropriate experimental manipulations,

be dissociated from a compass orientation effect. There are of course legitimate ethical concerns that must be considered before one carries out sensory manipulation on a free-flying migrant bird. As such, the best kind of sensory manipulation and/or deprivation is one that is transient and reversible, and the manipulation should occur at a point that would be most informative with respect to navigation.

So far, we have emphasised the earth's magnetic field, but it should be clear that the same approach could apply to any sensory modality of interest. For example, olfaction is also a serious contender for the sensory control of position fixing during navigation in birds (Gagliardo et al., 2006; Gagliardo et al., 2008, Gagliardo et al., 2009; Papi et al., 1972; Wallraff, 2005). As with the earth's magnetic field, the availability or reliability of olfactory information may vary along the migratory route, perhaps in relation to geography, climate or weather. Detailed understanding of how migratory routes are affected (correlationally) by such factors might help to pinpoint a role for olfaction, or lack of it, in different situations.

Indeed, in the spirit of what we envision, a recent short-range tracking study (Holland et al., 2009) examined the effects of experimental magnetic and olfactory disruption on the flight behaviour of migratory catbirds (*Dumetella carolinessis*), revealing unexpectedly that an intact olfactory sense was necessary for experience-based adult migration, both on the normal migratory route and after displacement. In line with the discussion on spatiotemporal representational strategies above, we would not be surprised if sensory control co-varied with stage of the migratory journey as well as the developmental stage and/or experience of a bird.

Geography

The earth's geography provides not only a natural laboratory of contrasts for considering the classic questions of navigation, but also generates its own fundamental questions of migratory navigation. Large-scale geographic features can provide opportunities and challenges (Alerstam, 1996), which may assist or interfere with migratory navigational systems. The topographical outline at different geographic scales and the availability of sensory information, e.g. the geomagnetic field, may vary greatly between geographical areas (Lohmann and Lohmann, 1996; Åkesson and Alerstam, 1998; Muheim et al., 2003; Lohmann et al., 2004; Freake et al., 2006) and continents. The boundary properties of the continents are likely to have played an important role in the evolution of migration systems, including the routes flown by birds. Range expansions, as the precursors to migration, and the subsequent evolution of migratory populations are likely to have proceeded in directions channelled by local topography and the location of environmental barriers (Alerstam et al., 2001; Zehtindjiev et al., 2010). Physiological adaptations, locomotor skills and sensory capabilities exploited to extract navigational information are thought to have evolved in concert with range expansion, the use of new and more remote breeding areas, and associated migratory behaviour (Åkesson and Hedenström, 2007; Förschler and Bairlein, 2011). However, it remains an open question whether sensory limitations on navigational systems are due in part to historic range expansions. Large-scale comparative experiments using high-resolution tracking devices could be helpful in unravelling the complex relationships between geography, the evolution of migratory systems and the sensory basis of navigational mechanisms (López-López et al., 2009; Battley et al., 2011). On more regional and local scales, topography

and barriers have been shown to have a major influence on orientation decisions in migratory birds (e.g. Åkesson, 1993). Local movements performed both by young and adult birds during migration are influenced by body condition (Muhkin et al., 2005; Sandberg, 2003) and have navigational consequences that are poorly understood in both first-time and experienced migrants.

At high latitudes, migratory birds face extreme navigational challenges similar to those encountered by human navigators. Solar longitudinal progression occurs over short distances, and the orientation behaviour of at least some migrants seems to be guided by a time-uncompensated sun compass set at the starting location and does not correct for the time shift met during a migratory flight (Alerstam et al., 2001). In fact, the problem of longitudinal solar progression for use of the time-compensated sun compass is encountered at all latitudes during migrations with an east–west component, but it is especially acute closer to the poles. Along these lines, future tracking studies may also be able to test whether some bird species use differences in time zones as part of a 'double-clock' or 'jetlag' mechanism to determine their east–west position (Kishkinev et al., 2010). Also, at high latitudes, stellar cues are largely unavailable during the summer months when naïve birds grow up and begin their first migratory journey. Also, at high latitudes migrants face problems using the steep geomagnetic field lines as well as stellar and solar cues (Åkesson et al., 2001; Alerstam et al., 2001; Muheim et al., 2003) for orientation and/or navigation.

Another relevant issue is the surface properties that migrants fly over. For example, land and ocean potentially provide different opportunities for birds to make navigational corrections for wind drift, with a greater prospect for compensation expected for flights over land. However, in the tracking study of Cochran et al. (Cochran et al., 2004), birds kept a constant heading in mid-air, and their heading was not influenced by the prevailing wind. Instead, the birds flew longer when the winds were favourable with respect to their preferred heading compared with when the winds were disadvantageous (Cochran et al., 2004). Selective flight departures associated with favourable wind conditions have been observed in radio-tracked songbirds departing from stopover sites on migration flights across the sea (Åkesson and Hedenström, 2000). Migration altitude (Bruderer and Liechti, 1998) might also offer different possibilities for compensation for wind drift depending on the visibility of the land below.

Comparing diurnal and nocturnal migratory flight paths at the same location (Bruderer and Liechti, 1998) might be one way to gain insight into this issue, and one could even compare flights at night and day in the same individual migrant using new tracking technology. Migration over ocean and land may also differ in the availability of navigational cues, such as detectable stable visual landmarks. Tracking studies across different types of topography will enable researchers to relate corrective navigation following wind (Klaassen et al., 2010) or any natural displacement to surface features below, environmental barriers as well as wind speeds (Gauthreaux et al., 2003; Gauthreaux et al., 2006). Detailed knowledge of wind conditions at sample locations and flight altitudes may be needed for these analyses. Migratory paths that cross geographic boundaries between ocean and land, as well as migratory routes that are adjusted to follow other prominent topographical features (Bingman et al., 1982; Åkesson, 1993; Gauthreaux et al., 2003; Gauthreaux et al., 2006), may reveal changes in migratory route structure and underlying navigation mechanisms. We are optimistic about the possibility of using tracking devices to examine variations in migratory behaviour

associated with large-scale differences between continents, smaller-scale differences in local topography, and the availability of sensory information, all of which can influence navigational behaviour and underlying mechanisms.

Natural history

As we discover ever more about the natural history of migration, a process greatly facilitated by new technologies, additional life-history contrasts may become useful tools for investigating questions of migratory navigation. Differences in the life and natural history of migratory species may have led to adaptive specialisations in navigational mechanisms. For example, the use of discrete stopover sites may not only require greater navigational control, and in some cases more accurate timing [e.g. timing of arrival during peak occurrence of a food source (Beekman et al., 2002; Drent et al., 2003; Bauer et al., 2006)], but, for first-time migrants, also an innate knowledge of where to find or at least recognise favourable stopover sites, i.e. information that goes beyond a simple vector of time and direction. Systematic observations of the site-faithful stopover of individual birds during consecutive years, such as the incredible 25% recapture probability observed for several small passerines at a stopover site in Spain (Cantos and Tellería, 1994), may not be exceptional and could turn out to be routine once we are in a position to track an individual over several migration seasons. The remarkable accuracy with which some migrants are known to home to the same breeding area [for examples, see Mouritsen (Mouritsen 2003)] may not only apply to their terminal destination, but to a number of stopover sites along the entire migratory route. In contrast, some species with less spatially restricted habitat requirements, such as the highly pelagic Manx shearwater, *Puffinus puffinus* (Guilford et al., 2009), may use much more diffuse stopover areas that require less stringent navigational control. Might the navigational abilities, and even the underlying representational strategies, sensory cues or navigational mechanisms, differ in response to such different life history demands? We might predict that corrective re-orientation following displacement would be most pronounced in species with the most restrictive stopover requirements, implying a higher resolution navigational system.

Dependence on specific habitat that is only patchily distributed along a migration route (e.g. reed beds, lakes and oases) could provide selective pressure on the type of navigational system that migrants employ. Locating and recognizing suitable patchy habitat would require some knowledge of how to find and recognise these sites, and differences between experienced and inexperienced migrants could be particularly informative. Here, it would be interesting to study small-scale movements of birds before migration (Muhkin et al., 2005) as well as shortly before, during and shortly after a migratory flight. Once migrating, are birds able to pinpoint the goal habitat already from the air during their migratory descent (which may be easier for diurnal than for nocturnal migrants if they are depending on visual landmarks), or does finding suitable habitat involve search strategies, which could occur after the migratory descent?

Another question is how social interactions may influence stopover decisions, timing and navigational behaviour. It could be argued that the navigation system of migrants that typically fly alone, e.g. nocturnal songbird species, should be different and perhaps more dependent on innate learning programmes than that of social migrants, where navigational decisions are influenced collectively and where young can directly learn from experienced migrants (Mouritsen, 2003). In species that migrate in flocks, e.g. day-migrating finches, storks, geese, tits and chickadees, a simple backup vector programme of time and direction may be all a first-year migrant needs as long as it stays in a group and follows the more experienced adult conspecifics. Simultaneously tracking of several individual songbirds in a flock may make it possible to study social interactions and their importance for navigational mechanisms. Detailed GPS tracking of pigeons flying in pairs over short distances has already shown that the confidence an individual has in its own route influences leadership decisions during co-navigation (Freeman et al., 2010).

The genetic basis and heritability of migratory behaviour, and hence the underlying control mechanisms, is another exciting avenue where advancements in tracking technology can lead to new insights. The possibility of tracking simultaneously several siblings of a clutch will make it feasible to test hypotheses regarding the genetics of migration, including the flexibility, variation and heritability of migratory navigation (e.g. Ueta and Ryabtsev, 2001). Interbreeding individuals from populations with different population-specific migratory directions and following the offspring during their first migration could provide insights into how genetically 'channelled' migratory behaviour and/or navigation goes beyond what we have gained from the impressive cross-breeding experiments with captive European blackcaps, *Sylvia atricapilla* (Berthold et al., 1992; Helbig, 1991). Investigating the migratory consequences of 'wrong' directional and/or navigational choices in natural settings would provide exciting new information to help estimate the importance of genetic influences and the possible effects on social dynamics that shape the navigational mechanisms used.

Conclusions

Despite what has been learned from laboratory studies, questions about how birds employ navigation systems during migration itself have remained largely inaccessible for logistical reasons. Thus our understanding of the natural history of migratory navigation is comparatively poor. This has meant that rather little is known about how natural selection and/or phylogenetic history have shaped natural variation in navigational mechanisms across species. With the accelerating development of miniature avian tracking systems, the basic data required to address such questions may be coming within reach. To aid research into such questions, we suggest that attention to one or more of a series of contrasts (we outline 11 examples in Table 1, but there are doubtless many more) may allow informative comparisons of different aspects of navigational performance utilising one or more track parameters as dependent variables. Contrasts might also be investigated in combination (or interaction), and could help form the basis of more experimental studies. Care will obviously have to be taken to avoid the evident pitfalls, but comparative methods have been employed with great effectiveness in the study of adaptation in recent decades, and many sophisticated solutions to the methodological problems have already been developed (Harvey and Pagel, 1991). We suggest that paying attention to such contrasts in the planning stages of any tracking study, even if the primary aim is to track migration for other reasons, could greatly enhance the value of such studies for understanding the mechanisms of navigation.

Glossary

Compass orientation
    The capacity to determine and maintain a compass bearing.

Geolocator
Archival light level logging device that allows daily (or twice daily) latitude and longitude estimation.

Global positioning system (GPS)
A satellite-based system enabling the determination of location (latitude, longitude and altitude) with an accuracy of less than 10 m anywhere on the earth using a GPS receiver (Thorup and Holland, 2009).

Migration
The seasonal movements of animals, usually between breeding and wintering areas.

Migratory navigation
The processes of navigation during active migration.

Spatiotemporal representational strategy
A mechanism by which an animal encodes, stores and applies information to execute goal-directed movements through its environment, the properties of which may change depending on the spatial and temporal relationship between an animal's current position and the goal.

Triangulation
The calculating of position from the intersection of at least two independent directional estimates taken from different observation points (especially radio-telemetry).

True navigation
The ability to navigate to a goal location even after displacement to unfamiliar locations outside the range of an animal's previous experience.

Vector navigation
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 or progress towards a migratory goal.

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