Commentary

The bird GPS – long-range navigation in migrants

Kasper Thorup[1],* and Richard A. Holland[2]

[1]Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark and [2]Max Planck Institute for Ornithology, Department for Migration and Immuno-ecology, Schlossallee 2, Radolfzell 78315, Germany

*Author for correspondence (kthorup@snm.ku.dk)

Summary

Nowadays few people consider finding their way in unfamiliar areas a problem as a GPS (Global Positioning System) combined with some simple map software can easily tell you how to get from A to B. Although this opportunity has only become available during the last decade, recent experiments show that long-distance migrating animals had already solved this problem. Even after displacement over thousands of kilometres to previously unknown areas, experienced but not first time migrant birds quickly adjust their course toward their destination, proving the existence of an experience-based GPS in these birds. Determining latitude is a relatively simple task, even for humans, whereas longitude poses much larger problems. Birds and other animals however have found a way to achieve this, although we do not yet know how. Possible ways of determining longitude includes using celestial cues in combination with an internal clock, geomagnetic cues such as magnetic intensity or perhaps even olfactory cues. Presently, there is not enough evidence to rule out any of these, and years of studying birds in a laboratory setting have yielded partly contradictory results. We suggest that a concerted effort, where the study of animals in a natural setting goes hand-in-hand with lab-based study, may be necessary to fully understand the mechanism underlying the long-distance navigation system of birds. As such, researchers must remain receptive to alternative interpretations and bear in mind that animal navigation may not necessarily be similar to the human system, and that we know from many years of investigation of long-distance navigation in birds that at least some birds do have a GPS – but we are uncertain how it works.

Key words: navigation, orientation, long-range, birds, stellar, magnetic, olfactory.

Introduction

Navigation is an essential part of the life of most mobile animals. Often they have to find their way back to a nest, a burrow or some other feature on which they are dependent. Such navigation tasks range from a few metres, e.g. as in the case of ants, up to thousands of kilometres, e.g. as in the case of foraging albatrosses. The scale of these tasks varies enormously and thus different systems probably come into play. Even though the simplest navigation tasks may rely on retracing a route or simple recognition of landscape features, most species have other means of ensuring a safe return. In desert ants and many mammals, the outbound path is recorded and integrated to allow the calculation of the direction back to the origin. Such systems are probably too unreliable over longer ranges, because errors in distance measurements are compounded. Rather than relying on path integration, other animals are capable of true navigation, originally described as type III homing by Griffin: 'the ability to choose approximately the correct direction to its goal when carried in a new and unaccustomed direction' (Griffin, 1952).

Although an ability for true navigation is thought to exist in many species, it has actually only been shown in a few cases, especially over longer distances (Table 1). In general, evidence for an ability to use true navigation comes from displacement experiments. If an animal is able to return home from unfamiliar territory after being translocated without access to any cues during the displacement this is evidence for such an ability. Displacement experiments have been performed in a number of animals (for a review of bird displacement, see Åkesson, 2003), notably albatrosses (Kenyon and Rice, 1958) and shearwaters (Mazzeo, 1953), over thousands of kilometres and the ability is well known in pigeons that fly back to their home lofts (Wallraff, 2005) (Table 1). Other more indirect evidence for true navigation comes from studies of migratory species in which individuals tend to converge along some travel pathway, indicating the ability to diverge and come back (Table 1).

However, the question of how animals perform these tasks has been a subject of intense research and debate for decades. Human navigators, having existed long before the advent of modern GPS systems, have generally considered the two axes: latitude and longitude. Both can be determined from the position and movement of celestial bodies; however, determining longitude is far more difficult than latitude (Gould, 2008). Effective determination of longitude requires access to a clock, which is independent of the celestial bodies, and this problem was first solved in the 18th century (Gould, 2008). Even though birds have obviously solved the problem of true navigation, we still have limited knowledge about how this is done. This is especially the case over longer distances far beyond the tasks performed within the normal home range as seen in most sedentary species, e.g. homing pigeons (Gould, 2008). Long-range navigation, performed by billions of migrants each year finding the way as they return to familiar breeding sites in spring and wintering sites in autumn, will be the focus of this commentary.

Table 1. Examples of studies documenting ability of long-distance navigation (>1000 km)

Type of study	Taxa	Description	Reference
(A) Displacements			
Return to breeding sites after displacement (marine species)	Laysan albatrosses	Displacement up to 6630 km from Midway Atoll to the Philippine Islands (returning in 32 days)	Kenyon and Rice, 1958
	Manx shearwater	Displacement up to 5150 km from Wales, UK, to Boston, MA, USA (returning in 12.5 days)	Mazzeo, 1953
	Herring gull	Displacement up to 5150 km from Penikese Island, MA, USA, to Savannah	Griffin, 1943
	Sooty tern and brown noddy	Displacement up to 1368 km from Tortugas, FL, USA, to Cape Hatteras, NC, USA	Watson and Lashley, 1915
(Terrestrial species)	White stork	Displacement up to 2269 km from Butyny, Poland to Lydda, Palestine (returning in 19 days)	Wodzicki et al., 1938
	Alpine swift	Displacement up to 1641 km from Switzerland to Portugal (returning in 3 days)	Schifferli, 1942
	Wryneck	Displacement up to 1500 km from Berlin to Saloniki, Greece (returning in 12 days)	Rüppell, 1937
	Barn swallow	Displacement up to 1850 km from Berlin, Germany, to Madrid, Spain (returning in 7 days)	Rüppell, 1937
	Red-backed shrike	Displacement up to 1200 km from Berlin, Germany, to Marseille, France (returning in 11–13 days)	Rüppell, 1937
	Starling	Displacement up to 1850 km from Berlin, Germany, to Madrid, Spain	Rüppell, 1937
Return to wintering grounds	White-crowned and golden-crowned sparrows	Displacement of 2900 km from California to Louisiana, USA	Mewalt, 1964
	White-crowned and golden-crowned sparrows	Displacement of 3860 km from California to Maryland	Mewalt, 1964
Migration redirected towards winter grounds	White-crowned sparrows	Displacement of 3700 km during migration, from Seattle, WA, USA, to Princeton, NJ, USA	Thorup et al., 2007
	Starlings	Displacement of 570 km during migration, from The Netherlands to Switzerland	Perdeck, 1958
Orientation redirected towards breeding grounds	Reed warblers	Displacement of 1000 km during migration, from Rybachy to Zvenigorod, Russia.	Chernetsov et al., 2008
(B) Diverging/converging routes			
Winter grounds much more restricted than general migration route	Barred warbler	Diameter of winter grounds of 1200 km and migration distance of 6100 km, inferred from observations	Thorup and Rabøl, 2001
	Eleonora's falcons	Diameter of winter grounds of 1500 km and migration distance of 8000 km, inferred from satellite tracking	Gschweng et al., 2008
Migration goals much more restricted than general migration route	Hobbies	Width of migration goal of 67 km and migration distance of 6500 km, inferred from satellite tracking	Strandberg et al., 2009
	Marsh warbler	Width of migration goal in East Africa of 100–200 km and migration distance of 6800 km, inferred from observations and ring recoveries	Thorup and Rabøl, 2001
	Spotted flycatcher	Width of migration goal in Central Africa of 1400 km and migration distance of 7300 km, inferred from ring recoveries	Thorup and Rabøl, 2001
Stopover areas of satellite tracked birds much more restricted than general migration route	Ospreys	Individual visiting the same stopover areas of 50×50 km^2 on repeated journeys of 6000 km, inferred from satellite tracking	Alerstam et al., 2006
Straight courses over long distances	Albatrosses	Approaching home island from >500 km distance along a straight course even with crosswinds	Papi and Luschi, 1996
	Sea turtles	1616 km with a straightness index of 0.93	Luschi et al., 1996
	Sea turtles	475 km direct to the goal with constant speed and direction both night and day	Papi et al., 1995

Two categories of studies are included: (A) displacements that can directly show navigation and (B) studies with diverging/converging routes, where navigation is indirectly inferred from the observation that most birds are able to return to a narrow species-specific route after having been spread out over large areas. Some studies included several different translocation sites and in these the maximum performance (i.e. longest distance) documented is described (i.e. distance and duration of fastest returning individual).

Homing *vs* migration

Homing is the process of finding a known location. Homing can be an important part in migratory orientation, but at least in first-time migrants the 'goal' (e.g. the species-specific winter grounds) cannot be known and thus homing cannot be involved in first-time migration. While adult birds of most species in general return to the same overall breeding and wintering areas that they have previously visited, little is known about the degree to which navigation to these areas is based on homing or whether they rely on the inherited migration programme that originally guided them to previously unvisited wintering grounds. However, it is most likely that at least part of the migration process in experienced birds can be considered a homing process (e.g. Alerstam et al., 2006).

Homing has been intensively studied in pigeons. These animals are able to return to a home loft from distances as far as 700 km away or even further and this can be achieved without access to any cues during the outward journey (Wallraff, 2005). However,

whereas in some regions the range of an individual's navigation system probably covers more than a thousand kilometres, in many others it is likely to cover several hundred kilometres only (Wallraff, 2005). Given that migratory birds make journeys of as far as 15,000 km, one way, in the 10 g willow warbler and 19,000 km, almost from pole to pole, in the arctic tern (Alerstam et al., 2003), this suggests that there may be differences in the process of homing in a central place foraging bird such as a pigeon and a migrating bird.

Two recent studies (Thorup et al., 2007; Chernetsov et al., 2008) highlight the extraordinary ability of experienced migratory birds to home toward their normal wintering and breeding grounds, respectively (Fig. 1B,C). The study by Thorup et al. was carried out in the wild by following radio-tagged birds, which had been translocated more than 3000 km, in a small aircraft (Thorup et al., 2007). The adult birds took a direction straight towards their normal wintering grounds, showing the global nature of their navigational
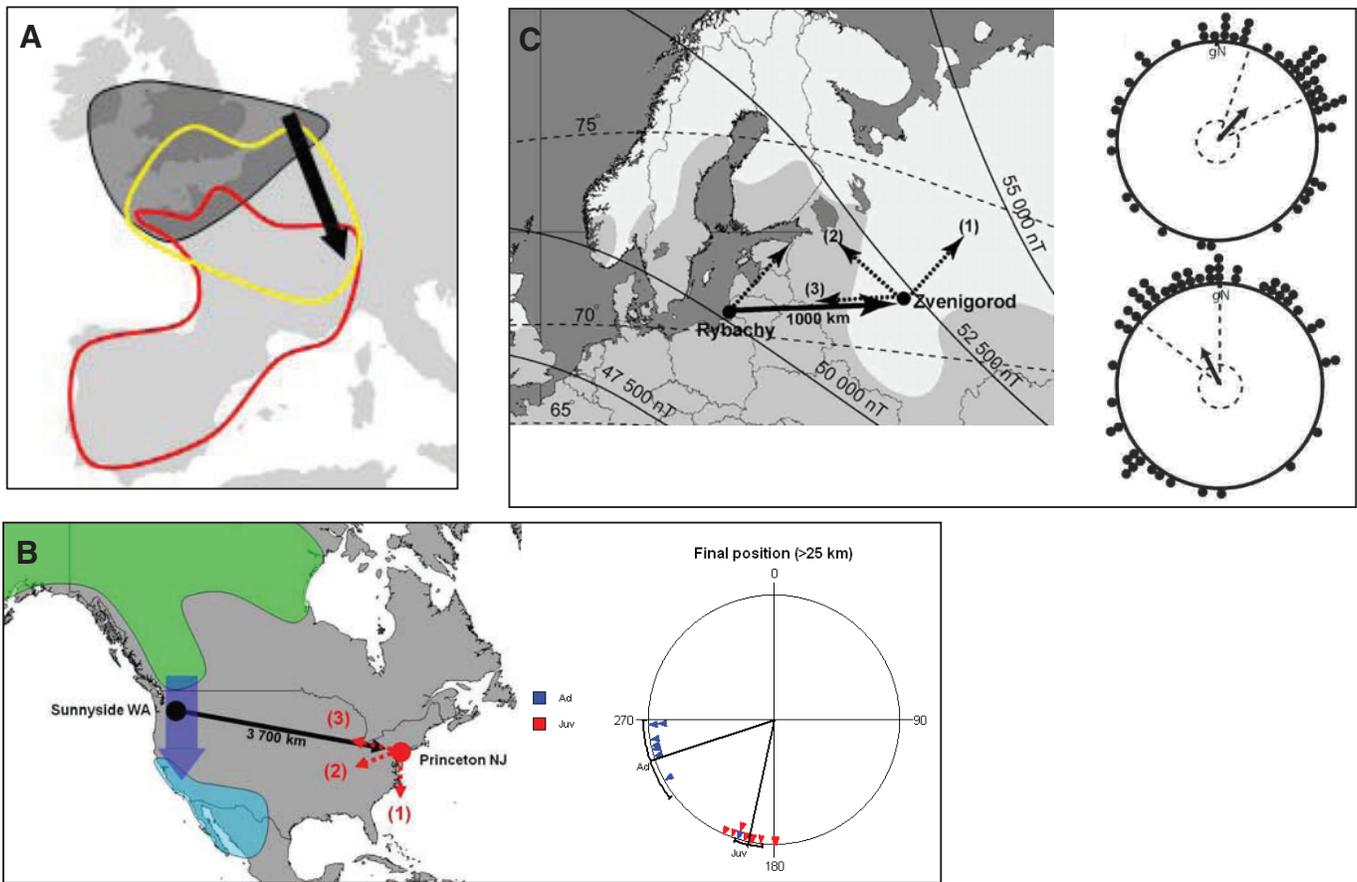

Fig. 1. Three long-distance displacement experiments, two showing a difference in orientation between experienced and inexperienced birds and one showing a change in orientation after displacement in spring. (A) Recoveries of 11,000 starlings displaced from The Netherlands to Switzerland. The normal wintering area of starlings captured in The Netherlands is shaded dark. Areas with recoveries in the winter following replacement are shown for juveniles (red) and adults (yellow). The juveniles generally continued in the normal migration direction whereas adults flew back toward their normal wintering ground in The Netherlands (dark shading). After Perdeck (Perdeck, 1958). (B) White-crowned sparrows displaced from Seattle, WA, USA, to Princeton, NJ, USA. The map to the left shows the displacement and breeding area (green), wintering area (cyan) and normal migration route (blue) as well as possible migration routes [red arrows: (1) normal migration direction, (2) toward normal winter grounds and (3) toward capture site] after release at New Jersey. The circle to the right shows the directions with the mean and confidence interval indicated in which adults (blue) and juveniles (red) flew after being released in New Jersey. Adults flew in the direction toward their normal wintering grounds whereas juveniles continued in their normal migration direction. After Thorup et al. (Thorup et al., 2007). (C) Reed warblers displaced from Rybachi to Zvenigorod, Russia. The map to the left shows the displacement and possible orientation responses after displacement [dotted arrows: (1) normal migration direction, (2) toward normal breeding grounds and (3) toward capture site]. The circles to the right show the observed orientation with mean and confidence interval indicated before (upper) and after (lower) displacement. The birds clearly correct for the eastward displacement and turn their orientation to the west. Reprinted from Chernetsov et al. (Chernetsov et al., 2008) with permission from Elsevier.

Table 2. Studies testing the nature of an experience-based long-range map

Taxa	Description of study	Reference
Evidence for latitude determination based on magnetic cues		
Silvereyes	Change in magnetic inclination signalled end of directed migration	Fisher et al., 2003
Indirect evidence for a magnetic map		
Silvereyes	Magnetic pulses affect adults but not juveniles	Munro et al., 1997
Silvereyes	Magnetic pulses changes directional choice relative to magnetic north. Assuming a magnetite-based map and a light-dependent compass, the result indicates that the compass is not affected by the pulse and is thus assumed to affect the map	Wiltschko et al., 2006
Inherited magnetic signposts		
Thrush nightingale	Fattening initiated by magnetic cues	Fransson et al., 2001
Pied flycatchers	Directional changes induced by changes in the magnetic field	Beck and Wiltschko, 1982; Beck and Wiltschko, 1988
Negative 'evidence' for a magnetic map		
Albatrosses	Birds with moving magnets homed successfully	Bonadonna et al., 2005; Mouritsen et al., 2003
Negative 'evidence' for a celestial map		
	Clock shift, indicating no sun navigation in migrants	Able and Cherry, 1986
Sun and olfactory navigation have not been tested over long distances.		

task. The birds flew individually and were certainly well beyond the area that they had known previously. In the study by Chernetsov et al., experienced migrants corrected their orientation in cages after being displaced approximately 1000 km (Chernetsov et al., 2008).

How navigation works

For practical reasons we will define navigation and orientation as two separate processes (Åkesson, 2003). To successfully home from unfamiliar territory one needs to navigate whereas orientation involves only the ability to take up a particular direction. Thus, navigation allows correction for displacements whereas the latter does not. This distinction is crucial in animal orientation/navigation studies. That animals are able to follow a chosen direction has been convincingly shown, with different studies showing that animals are able to use both the sun (Kramer, 1953), stars (Emlen, 1967) and the geomagnetic field (Wiltschko and Wiltschko, 1972) as compasses for orientation.

The navigational process represents an ability to locate ones position with respect to a goal. It has been defined by Griffin (Griffin, 1952) and more recently by Able (Able, 2001) as taking a number of forms but is most simply reduced to the ability to find a goal from a familiar area or an unfamiliar area. In a familiar area, it is presumed that cues recognised at the site of displacement from previous visits indicate the direction to home (Holland, 2003). In the case of unfamiliar area navigation, while it is thought that the animal also uses cues detected at the site of displacement, it has never experienced the particular conditions or combinations of cues at the unfamiliar site before. How and what cues animals use for unfamiliar area navigation remain the most controversial aspect of the field and while there are a number of theoretical constructs as to how they might be used, so far, the way in which animals navigate from an unfamiliar area remains to be solved.

Experienced-based navigation

In contrast to the navigational mechanisms found in experienced birds, the principal guiding mechanisms used by first-time migrants is most probably a simple form of orientation, where the bird reaches its wintering grounds by flying in certain directions for certain periods of time (known as vector navigation). Evidence for an experienced-based navigation system in migratory birds comes from an impressive experiment carried out on starlings by Perdeck (Perdeck, 1958). In that study, more than 11,000 starlings caught on migration in The Netherlands were transported to Switzerland and ringed. After release, recoveries of the adult birds were in a north-westerly direction from the release site on the way toward their normal wintering grounds in the south of England and in northwest France whereas juveniles were recovered in south-westerly directions corresponding to the normal direction of migration through The Netherlands (Fig. 1A). The obvious conclusion was that experienced birds homed toward their previously visited winter grounds whereas the young, inexperienced migrants relied on an innate one-direction compass programme.

However, the starling is a short-distance, social, diurnal migrant in which juveniles could easily be thought to follow the migration route of local starlings. Repeating the starling experiment on a true long-distance, individually migrating bird did not seem feasible for many years due to the difficulties of tracking wild birds. Finally, the experiment was 'repeated' in 2007 when Thorup et al. (Thorup et al., 2007) found a similar difference between adult and juveniles in their study as the one found by Perdeck in white-crowned sparrows, a long-distance, nocturnal, solitary songbird migrant (Perdeck, 1958) (Fig. 1B).

It is worth noting that a few studies testing the orientation in cages indicate that the distinction may not be that clear-cut: some juvenile migrants do tend to show compensatory behaviour after displacement when tested in cages (Åkesson et al., 2005; Thorup and Rabøl, 2007), and in some species migrations undertaken by juveniles spread out over large areas and later converge into narrowly defined routes, the latter also hinting at an ability to navigate in juveniles [e.g. marsh warblers (Thorup and Rabøl, 2001); Eleonora's falcons (Gschweng et al., 2008)]. Additionally, the experimental series by Lohmann and Lohmann (Lohmann and Lohmann, 1994; Lohmann and Lohmann, 1996a, Lohmann and Lohmann, 1996b) show changes in preferred directions as an innate response to experimental changes in the geomagnetic field by juvenile sea turtles, which could serve a navigational purpose in keeping inexperienced animals within a goal area. Hence, at present

at least, it cannot be fully ruled out that juveniles have some sort of innate ability for navigation toward an unknown goal. Nevertheless, it appears safe to conclude that there is now good evidence that an experience-based navigation system is important for guiding at least adult birds to previously experienced wintering and breeding grounds.

Navigation and bi-coordinate maps in migrating animals
The big mystery in our understanding of animal navigation systems still lies in what the learned navigational system is based upon. GPS and map location in humans is based on the latitude/longitude coordinate systems. The current theory of animal navigation is based on a similar system, assuming extrapolation of familiar gradients to unfamiliar areas (Fig. 2). If an animal assumes that a cue with the properties of a gradient (i.e. monotone changes with distance) varies in the same way outside the home range, such extrapolation beyond the area in which it is known can be used for navigation.

What cues could be used as gradients? Celestial and magnetic cues have repeatedly been shown to be important in orientation but their role in bird navigation remains equivocal despite the fact that both the sun's azimuth and the strength of the magnetic field are obvious cues to latitude (Wallraff, 2005). To further complicate matters, in homing pigeons, evidence indicates that olfactory cues are necessary for homing from unfamiliar areas (Gagliardo et al., 2006; Gagliardo et al., 2008; Wallraff, 2005). However, neither current atmospheric models nor navigational map theories explain how olfactory cues present in Seattle could be detected or used in New Jersey over 3000 km away, as would need to be the case if
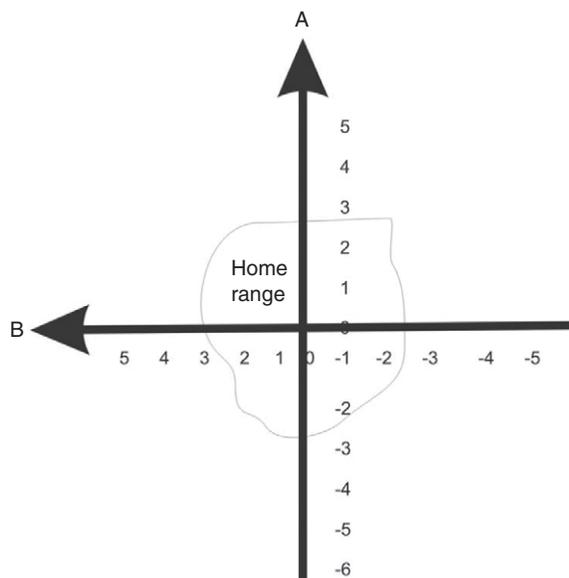

Fig. 2. In a bi-coordinate gradient map animals learn that at least two cues, ideally intersecting at 90 deg., vary in strength within the home range, and the animal assumes by extrapolation that they continue to vary in this way outside the home range. In the case of many long distance migrants, these cues would need to vary consistently on a global scale, but at the very least on the basis of current evidence, on a continental scale. In the schematic shown, if the animal finds itself at A5, B5, then even though it has never encountered these values in its home range, they are both increasing values. As gradient A increases northward and gradient B increases westward within the home range, this means that it is north and west of its home range and must fly south east to return.

they were to explain the results of Thorup et al. (Thorup et al., 2007).

If determining latitude is a relatively easy task, as it is for humans, it seems reasonable to assume that this is also the case in animals. Indeed, a number of studies have indicated how animals can recognise latitudinal displacements. The best evidence for latitudinal cues used in navigation comes not from migrating birds but from newts, juvenile turtles and lobsters (Boles and Lohmann, 2003; Fischer et al., 2001; Lohmann et al., 2004); all three studies have indicated that changing the intensity and inclination of the magnetic field to a value far outside the natural one at the site of testing results in the animal perceiving its location as latitudinally displaced. Whether this represents the use of a gradient map to allow determination of precise latitudinal displacement or a simpler system in which the animal relies on a rule of thumb to the effect of 'when the magnetic field is greater than the goal, orient southward until it matches the home value' has not yet been determined as these have not been combined with longitudinal displacements. More curious is that the distances over which these animals would normally be required to home are in the region of 10–30 km or less. Because of local variation in the magnetic field, it has been proposed that a magnetic map is inoperative or, at best, highly inaccurate over these distances (Bingman and Cheng, 2006; Phillips et al., 2006).

Most of the studies on latitudinal displacements refer to species that normally perform smaller-scale 'within home-range' navigation (Gould, 2004), and we still lack indications that the mechanisms are the same over longer distances (thousands of kilometres). Nevertheless, these smaller-scale systems could provide insights into what could be a possible solution when extending navigation over longer distances. Due to the general difficulties in performing these experiments over longer distances, experimenters have often adhered to very simple designs (and a lack of replication) studying reactions to single treatments only, which complicates extrapolating the interpretations of behaviours and increases the chances of misinterpreting behaviours arising from changes in motivational state for example.

As mentioned previously, the use of a clock, which is independent of local time, in conjunction with the stars finally allowed humans to solve the longitude problem. A role of stars in bird orientation was demonstrated early but whether the stars or the sun are involved in navigation are not well established. The classic experiment demonstrating a role of the stars in bird orientation overall indicated the use of stars as a compass in juvenile birds in that the birds reacted to the axis of celestial rotation, not rotation in itself (Emlen, 1967), and studies failing to show compensatory changes of direction over time, which are not expected if the birds use the stars to navigate, have mostly tested juveniles in their first migration (Mouritsen and Larsen, 2001). And so we can make no conclusion about the role of experience-based maps from them. Like the stars, the sun can be used to determine longitude, in conjunction with a clock. When the sunset position has been manipulated by advancing or delaying the night/day regime (so-called clock shift), birds in general change direction according to the use of a time-compensated sun compass, where birds determine a certain compass direction by compensating for the sun's movement across the sky during the day. In the only sunset test involving experienced, clock-shifted birds, the birds on northward migration in spring changed their direction 51 deg. counter-clockwise as a response to a three hour delayed sunset, approximately in accordance with the 45 deg. counter-clockwise shift expected from its use as a compass (Able and Cherry, 1986),

and quite different from the clockwise directional change expected if the birds perceived the delayed timing as a westward displacement and compensated for it.

There is also very little direct evidence that magnetic cues are used by birds to determine latitude in a bi-coordinate map system (Table 2). Indeed, there are more reviews published on the subject than there are experiments providing evidence for the hypothesis at present (reviews by Bingman and Cheng, 2006; Freake et al., 2006; Phillips, 1996; Wiltschko and Wiltschko, 2006; Phillips et al., 2006; Lohmann et al., 2007). A few studies have dealt with theoretical aspects of whether it is possible to use the geomagnetic field for navigation (e.g. Åkesson and Alerstam, 1998) but apart from that there are few studies dealing with potential coordinates of a map. According to the review by Freake et al. (Freake et al., 2006), there is only one direct test of the use of magnetic cues to determine latitude in migratory birds: a study of Australian silvereyes (Fisher et al., 2003) showed northward orientation (towards wintering grounds) when the birds were exposed to a field with magnetic inclination and intensity corresponding to a location south of the winter range but when the birds where exposed to magnetic conditions corresponding to those on the wintering grounds the birds were not significantly oriented. However, as with the experiments on newts, turtles and lobsters, the interpretation of the results is still not clear. It could be the result of recognition of a gradient as part of a map or as a magnetic 'waypoint', i.e. stop migrating when this intensity/inclination is reached. In another study, involving sea turtles (Luschi et al., 2007), individuals with moving magnets attached to their heads showed longer homing paths than controls, indicating that the birds had to switch to other means of navigation when the geomagnetic field could not be perceived, but it was not possible to distinguish between its use in a map or a compass in this experiment.

Indirect evidence that the magnetic field plays a role in the map of migratory birds is argued on the basis of the different response between adults and juveniles in experiments in which a magnetic pulse is administered (Wiltschko and Wiltschko, 2006). Strong magnetic pulses disrupt magnetite, thought to be involved in magnetoreception, and it has been demonstrated that adult but not juvenile birds are affected by these pulses, responding in an orientation cage by shifting their heading (Munro et al., 1997). The birds are still able to orient by a magnetic compass mechanism independent of the magnetite-based sensory system (Wiltschko et al., 2006), further suggesting that it could well be a map that is being affected. However, a property of the pulse experiments may indicate that the interpretation is only indirect: in some cases birds on both northward and southward migrations showed eastward migration afterwards (Wiltschko et al., 1994). Identical reactions in northward and southward migrations are expected if the birds perceive the treatment as a displacement but not if the bird's map is somehow turned (i.e. the direction of a gradient relative to magnetic north). Recent evidence has indicated that birds also have a magnetite-based fixed directional response (Stapput et al., 2008; Wiltschko et al., 2008) and so further experiments are needed to confirm that the pulses did not affect this behaviour.

In contrast to the studies indicating the magnetic field to be part of the navigational map, two studies on albatrosses aimed at testing whether magnetic cues are involved in navigation failed to find an effect: homing albatrosses with magnets attached to their heads behaved similarly to control birds without magnets (Bonadonna et al., 2007; Mouritsen et al., 2003). However, failure to demonstrate an effect of a sensory manipulation does not represent evidence for rejection of that sense as a navigational cue (Freake et al., 2006)

and so what such studies mean is unclear, although they certainly demonstrate that magnetic cues do not represent the only means by which long-distance navigators can determine position. On this note, despite a large body of evidence that indicates that olfactory cues play a role in the successful homing of pigeons (Papi, 2001; Wallraff, 2005), little attention has been given as to what role, if any, olfactory cues might play in migratory navigation. The instability of the atmosphere over terrestrial locations would seem to make it unlikely that olfaction would play any role in a global scale bi-coordinate map, either as a longitudinal or latitudinal cue (Bingman and Cheng, 2006), but it has been proposed that it may play a role, in conjunction with the inherited migratory direction, in successful migration (Wallraff, 2005). In a marine environment, large stable odour plumes made up from dimethylsulphide (DMS) make it possible that olfactory cues could play a role in a map (Nevitt and Bonadonna, 2005). These hypotheses have not so far been tested however.

As this shows, the evidence for the use of a long-range bi-coordinate map in animals is still rather scant. However, it is not given that animals rely solely on a bi-coordinate map. The map could easily be multi-coordinate, and two studies hint at the possibility of the additional use of inherited magnetic 'signposts': young pied flycatchers changed direction according to shifts in the magnetic field simulating the shifts experienced along the migratory route (Beck and Wiltschko, 1982; Beck and Wiltschko 1988), and fat deposition in young thrush nightingales was similarly affected by changes in the magnetic field (Fransson et al., 2001).

The way forward?

In conclusion, we have a number of exciting experiments pointing to possible ways that long-distance navigation may work but we need many more experiments before we can conclude that a bi- or perhaps multi-coordinate map underlies experience-based long-distance navigation by migratory birds. It is beyond reasonable doubt that many birds are able to locate their direction of displacement precisely and over long distances. This must be achieved by an experience-based system, which appears in some cases at least to have near-global coverage. Likely candidates for this map are celestial, geomagnetic and possibly even olfactory but we cannot be as sure that a bi-coordinate latitude/longitude map is the best model for this system. Very few studies of migratory birds in a natural setting have been performed. While experiments in controlled conditions are necessary to titrate fine scale details of behaviour (Freake et al., 2006), knowledge is almost entirely lacking in the study of bird migration of the nature of the cues essential for navigation in the wild.

We suggest that the way forward is to 'go wild' – extending research on long-distance migratory birds into a natural setting (Wikelski et al., 2007), where it has so far mostly been carried out in cages. However, this must go hand-in-hand with a lab-based effort to study many species and situations to solve this complicated issue. In most laboratory studies, animals move distances of only few decimetres as maximum. Relating this behaviour to the situation in the wild, where conditions change vastly might be difficult. Although a good deal of understanding can no doubt come from field-based research on homing pigeons, we still have hardly explored how animals actually behave over long-distance migrations.

Orientation cage experiments and homing pigeon research have provided a wealth of data, yet several examples demonstrate how field-based research might further or change our understanding of

the results obtained in the laboratory. For example, a recent field tracking study of migrating thrushes demonstrated the sunset as the primary calibration cue (Cochran et al., 2004), in contrast to the many laboratory studies indicating the magnetic compass as the primary calibration cue (Wiltschko and Wiltschko, 1995).

We believe that repeating many of the findings from the laboratory in the wild will provide clues to a deeper understanding of the behaviours observed so far. Additionally, our current inability to track smaller migrants over longer distances has left us somewhat unsure of the true capabilities of wild birds under natural migrations, which might be different to what has been established so far for long-distance migrants, mostly from movements of a few centimetres in a laboratory.

Glossary

Clock shift
Advancing or delaying the night/day regime. If birds are kept indoors in artificial light, the night/day regime is easily advanced or delayed. For example, if the sunrise and sunset positions advanced by three hours compared with the local light regime, the bird's internal clock will be three hours ahead when the bird is exposed to the natural light regime.

Gradient map
A map based on cues, which vary predictably with gradients as shown in Fig. 2. The cues can be used to determine the coordinates in a map and then to calculate the direction toward a goal with known coordinates in the gradient system. Such a direction need not be calculated precisely but could be of the type 'fly southeast', if the experienced cue values are to the north and west of its home. Continuously monitoring the gradient values will ensure returning home even though the path will not be direct.

GPS
Global Positioning System. A satellite system enabling the determination of ones location (latitude, longitude and altitude) with an accuracy in the order of less than 10 m anywhere on earth using a GPS receiver.

Home range navigation
Finding the way in a well-known area, typically the normal home range.

Homing
Homing is the process of returning accurately to a known, previously visited location from a distance. To successfully home from unfamiliar territory one needs to navigate.

Migration
Migration can refer to a more or less permanent movement of an animal away from an area, which the animal is using on a daily basis, for instance the area around a nesting site. Here, we will however mostly be concerned with the seasonal movement of animals back and forth between breeding and wintering grounds.

Navigation
For practical reasons, we will make a clear distinction between navigation and orientation. Navigation is the process of finding a goal whereas orientation involves only the ability to take up a particular direction. Thus, navigation allows correction for displacements whereas the latter does not. This distinction is crucial in animal orientation/navigation studies.

Orientation
The process of orientation concerns the ability to determine a compass direction. Thus, no ability to find a goal is involved. Orientation can also refer to the direction of movement.

Time-compensated sun compass
A time-compensated sun compass uses the azimuth of the sun to determine compass directions, compensating for the sun's movement across the sky during the day, i.e. knowing how fast it moves (approximately 15 deg. per hour).

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