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Evaluation of Long-Distance Orientation in Birds on the Basis of Migration Routes Recorded by Radar and Satellite Tracking

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Predicted flight trajectories differ depending on which orientation cues are used by migrating birds. Results from radar and satellite tracking of migrating birds can be used to test which of the predicted trajectories shows the best fit with observed flight routes, supporting the use of the associated orientation mechanism. Radar studies of bird migration at the Northeast Passage and the Northwest Passage support the occurrence of migration along sun compass routes in these polar regions. In contrast, satellite tracking of Brent geese (*Branta bernicla*) migrating from Iceland across Greenland and from Northwest Europe to Siberia show routes that conform most closely with geographic loxodromes, but which are also profoundly influenced by large-scale topography. These evaluations are discussed in relation to the adaptive values of different routes in different parts of the world. Sun compass routes are favourable mainly for east-west migration at high latitudes. For east-west migration at mid and high latitudes magnetic loxodromes are more favourable than geographic loxodromes in certain regions while the reverse holds in other regions. The geometry of migration routes, as recorded by radar and satellite tracking, may be important for understanding the evolution of the complexity of birds' orientation systems, and for providing clues about the orientation mechanisms guiding the birds on their global journeys.

KEY WORDS

1. Animal Navigation. 2. Migration. 3. Orientation.

1. THE GEOMETRY OF BIRD MIGRATION ROUTES. Migrating birds have a complex orientation system, based on multiple cues such as the sun, stars, geomagnetic field, skylight polarisation pattern and sunset/sunrise directions (Berthold, 1991). Different orientation principles are expected to lead the birds along at least three different types of trajectory:

(a) Birds orienting by time-independent celestial rotation cues (like the star compass; cf. Emlen, 1975) will travel along geographic loxodromes (rhumb-lines) maintaining their geographic course constant (Able and Able, 1995).
(b) Birds using the magnetic compass (Wiltschko and Wiltschko, 1995) will follow magnetic loxodromes maintaining their magnetic course constant.
(c) The sun compass involves time compensation by the birds' internal circadian clock for the apparent motion of the sun during the day (Kramer, 1957). By using this time-compensated sun compass, a bird should be able to select the appropriate departure direction at any site when the sun is visible. As soon as the bird starts migrating in either easterly or westerly directions and thereby

traverses longitudes, its internal clock gets out of phase with local time. As a consequence of this natural time shift associated with movements across longitudes, birds will orient along routes with gradually changing courses (as long as the birds' internal clock is not reset in phase with local time).

In addition, orientation in relation to topographical cues and to wind as well as programmed changes in preferred compass courses will affect the resulting migratory routes.

Analysing the geometry of bird migration routes in the light of orientation mechanisms serves to investigate to what extent the mechanisms and responses that have been demonstrated by orientation cage experiments and release experiments (mainly homing pigeons) can explain long-distance orientation by birds on actual migration (cf. Wehner, 1998 and 2001). Such an approach has until now been adopted in only rather few studies, using more general faunistic data about migration routes (Kiepenheuer, 1984) or using the distribution of ringing recoveries (focused on exploring the effects of migration by vector summation; Rabøl, 1978; Mouritsen, 1998; Thorup and Rabøl, 2001) or analysing directions and routes recorded by radar and satellite tracking (Alerstam, 1996). In this contribution, I wish to stress two main points about the possible importance of considering migration routes in orientation research:

(a) The geometry of flight paths and migration routes, as recorded by, for example radar or satellite tracking, can be used to test which cues and principles the birds are likely to use for their orientation on actual migration. This will also bring into focus the requirements imposed on the birds' orientation performance under different environmental conditions at different seasons and in different parts of the world.
(b) Flight paths and migration routes can be regarded not only as proximate consequences of the birds' orientation behaviour but also as ultimate causes of how the birds' integrated orientation systems have evolved in different situations. One may expect that the orientation behaviour has evolved to meet the requirements for efficient travel along the most favourable routes (as determined by ecological factors like energy, time and risk costs). That would mean that the birds' routes are not primarily constrained by the orientation capacity but rather that the orientation behaviour varies in an adaptive way with respect to, for example, the primary cues used and the intercalibration hierarchy between different compass mechanisms depending on the environmental conditions associated with different flight paths.

In this paper, I will briefly review four case studies of orientation of arctic birds based on migration routes recorded by radar and satellite tracking. In a final section, I will exemplify the possibility of adaptive differences in the use of compass systems depending on the environmental conditions in different migratory regions.

2. MIGRATION BETWEEN SIBERIA AND NORTH AMERICA ACROSS THE ARCTIC OCEAN.

In a radar study of post-breeding migration (July and August) of mainly waders, skuas and terns at the Northeast Passage in Siberia (icebreaker expedition in 1994), regular departures towards geographic courses 60–90° over the Arctic Ocean were discovered (Alerstam and Gudmundsson, 1999a and b). Migration towards the NE sector was recorded at 9 out of 10 radar sites in

eastern Siberia (between longitudes 113°E and 171°E) and comprised 22% of all migratory movements recorded at the ten sites. These observations indicate a regular migration link between Siberia and North America, extending 1000–2500 km directly across the Arctic Ocean, for birds that have their final winter quarters in South America (e.g. pectoral sandpiper, *Calidris melanotos*) and in the waters off South America and in the southern Pacific Ocean (e.g. grey phalarope, *Phalaropus fulicarius*; pomarine skua, *Stercorarius pomarinus*) or even further to the south (arctic tern, *Sterna paradisaea*).

Extrapolations of a course towards 075° from the New Siberian Islands according to different orientation principles guiding the birds along (1) a geographic loxodrome, (2) a magnetic loxodrome and (3) a sun compass route, are illustrated in Figure 1. The

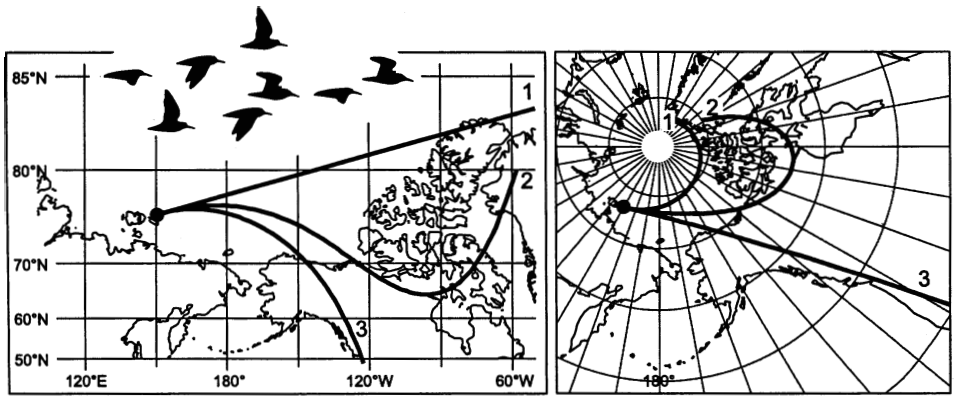

Figure 1. Flight trajectories extrapolated from New Siberian Islands, for an initial geographic compass course of 75°, according to (1) a geographic loxodrome, (2) magnetic loxodrome and (3) sun compass route. Trajectories are shown on a Mercator (left) and gnomonic (right) map projection. Based on Alerstam and Gudmundsson, 1999a.

three trajectories are shown on a Mercator map projection (showing geographic loxodromes as straight lines) as well as on a gnomonic map projection (showing orthodromes as straight lines; cf. Gudmundsson and Alerstam, 1998). The predicted trajectory associated with 'magnetoclinic' orientation, as suggested by Kiepenheuer (1984), was refuted because of invalid magnetic conditions for this mechanism (see Alerstam and Gudmundsson, 1999a).

It was concluded from this evaluation that orientation towards constant geographic courses was highly implausible while both the magnetic and sun compass would guide the birds across the Arctic Ocean along gradually changing courses towards Alaska and surrounding regions of arctic North America (Alerstam and Gudmundsson, 1999a). At northerly latitudes, sun compass routes are very similar to great circle routes, and they are thereby advantageous from the point of view of saving flight distance (Alerstam and Pettersson, 1991). The following circumstances seem to be compatible with the possibility of long-distance sun compass orientation in this case:

(a) daylight prevailed throughout the 24 hours of the polar summer days,
(b) migration typically took place in weather with the sun readily visible,
(c) the birds were flying high (mean altitude 1200 m above sea level) without access to topographical landmarks, and

(d) the migrants probably often cross the Arctic Ocean in a single non-stop flight, making it unlikely that they re-synchronise their internal clock in phase with local time.

Because the gradual course change resulting from the increasing lag between the birds' internal clock and local time brings the benefit of an orthodromic flight route, one should in actual fact expect the birds to suppress any such resetting of their internal clock.

3. MIGRATION ACROSS HIGH ARCTIC NORTH AMERICA. In order to further test the possible orientation principles used by birds in the Arctic, the migration patterns of waders, skuas and terns were recorded by tracking radar at several sites at the Northwest Passage during July and August (icebreaker expedition in 1999; Alerstam *et al*., 2001; Gudmundsson *et al*., in press). In this region, the differences between magnetic loxodromes and sun compass routes are extreme because of the proximity to the North Magnetic Pole.

The most intensive migration was registered at three sites in the southeastern Beaufort Sea, where the overall mean direction was 096°. Climbing birds, which presumably were recorded soon after departure, showed a mean track direction of 085° while descending flocks (which in some cases may have been arrivals after crossing the Arctic Ocean from Siberia) had a mean direction of 105° (Gudmundsson *et al*., in press).

Extrapolations of a course towards 090° from the mean Beaufort position according to the orientation principles for (1) a geographic loxodrome, (2) a magnetic loxodrome, and (3) a sun compass route, are illustrated in Figure 2 on Mercator and

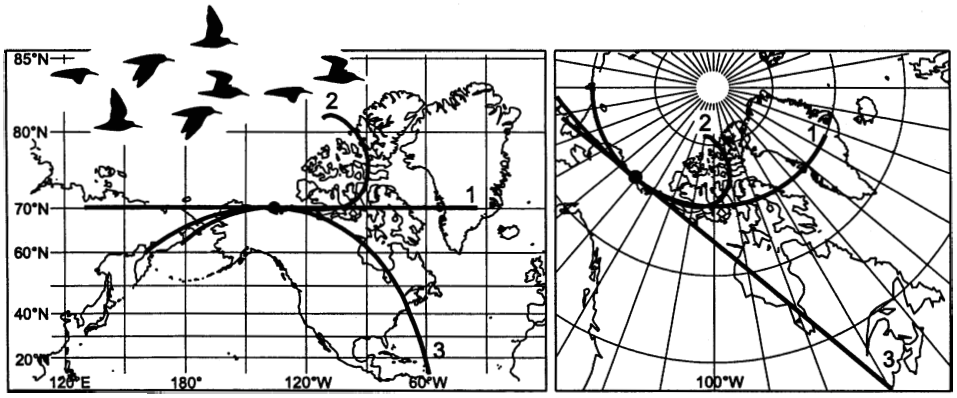

Figure 2. Flight trajectories extrapolated from the Beaufort Sea, for an initial geographic compass course of 90°, according to (1) a geographic loxodrome, (2) magnetic loxodrome and (3) sun compass route. Trajectories are shown on a Mercator (left) and gnomonic (right) map projection. Based on Alerstam *et al*., 2001.

gnomonic map projections. The birds, which were mainly waders such as semipalmated sandpiper, *Calidris pusilla*; white-rumped sandpiper, *C. fuscicollis*; American golden plover, *Pluvialis dominica*, pectoral sandpiper and others, are expected to migrate towards the Atlantic coast of North America (from Labrador/St.

Lawrence/Nova Scotia and further south; cf. Morrison, 1984). From these coastal areas they embark on transoceanic flights to South America (Williams and Williams, 1990).

Figure 2 shows that in this case not only the geographic but also the magnetic loxodrome can be ruled out as both are unrealistic. Magnetic orientation is extremely complicated at the Northwest Passage with magnetic declination changing strongly over small distances and magnetic inclination being excessively steep. Only the sun compass route is in agreement with expectation. Further support for sun compass routes is provided by track directions at other sites (Alerstam *et al*., 2001).

Richardson (1979) recorded an overall mean track direction of 134° (with a large variation in daily means of 110–170°) for waders departing over the Atlantic Ocean in the region of Nova Scotia (about 64°W) during autumn. Assuming that this departure direction reflects the course along sun compass routes from the high arctic breeding grounds (a speculative assumption because the birds have in many cases spent a longer stopover period in eastern North America before their departure over the Atlantic Ocean), this course at Nova Scotia translates into a sun compass course of 069° at the Beaufort Sea (133°W). This latter course falls in the northerly flank but still within the recorded range of track directions at this site (Gudmundsson *et al*., in press; see extrapolation of 075° course in Alerstam *et al*., 2001).

As for the Siberian case, the use of the sun compass is facilitated at the northerly latitudes of arctic North America where:

(a) the position of the sun is visible throughout the light polar summer days (except in poor weather when bird migration normally comes to a halt) and
(b) sun compass routes will be very similar to great circle routes, minimising travel distances.

Hence it will be favourable for the migrants to incur a time lag as they move across the time zones and to postpone resetting of their internal clock in phase with local time until reaching temperate latitudes.

One cannot rule out the possibility that the birds rather than migrating on fixed sun compass courses divide their journey into two or more differently programmed orientation steps to accomplish the course changes needed to reach their destinations. This alternative possibility applies to the flights between Siberia and North America as well as to the flights across arctic North America towards the Atlantic coast. In the case of migration at the Northwest Passage, there are opportunities for topographical guidance, although the migrants were normally flying rather high, with a mean altitude at 800 m above sea level, sometimes above extensive low-level cloud or fog. However, it is difficult to propose an alternative complex orientation program that accounts for both the Siberian and North American cases with their different environmental conditions.

Once transmitters for satellite telemetry or GPS-loggers have been reduced in size and mass to the extent that they can be carried by, for example, a pectoral sandpiper from Siberia or an American golden plover from northernmost Alaska, the full story about the course changes and flight trajectories of single individuals will be revealed.

4. MIGRATION OF BRENT GEESE ACROSS GREENLAND. A population of light-bellied Brent geese (*Branta bernicla hrota*) migrates from their main winter quarters in Ireland via Iceland, where they make a stopover during spring, to

breeding grounds in high arctic Canada. Ten of these geese were equipped with radio transmitters for satellite tracking in Iceland. Their subsequent departures from Iceland and crossings of the Greenland ice cap were recorded according to Figure 3

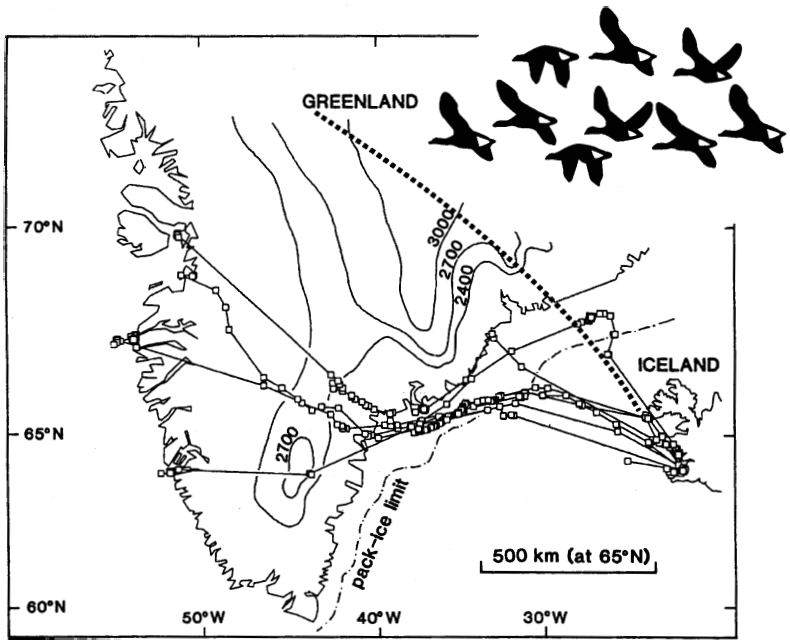

Figure 3. Pattern of Brent goose migration from Iceland in spring, as recorded by satellite tracking. Open squares show high-precision locations for tracks of ten different geese. The predicted great circle route to the breeding destination is indicated by the dotted line. Altitudes (m above sea level) of the Greenland ice cap as well as the limit of the East Greenland pack ice zone are indicated. The map is a Mercator projection. Based on Gudmundsson *et al.*, 1995.

(Gudmundsson *et al.*, 1995). Nine geese were tracked when departing from Iceland, and five of them (two migrating together) were recorded across Greenland before the batteries were exhausted.

The mean departure direction from Iceland was 295°, which agrees well with earlier visual measurements of mean departure courses of 290° and 313° at two sites on the west coast of Iceland (Alerstam *et al.*, 1990). The Brent geese seem to depart along loxodromes (predicted course about 300° to their breeding destinations) rather than along orthodromes (with expected departure course about 328°; cf. Alerstam *et al.*, 1990).

However, the satellite results show that the routes were much more roundabout than direct loxodromes, being heavily influenced by topography. After crossing the open sea and reaching the pack ice zone off the steep East Greenland coast, the geese paused repeatedly and veered towards west-southwest. They all passed an area about 65°N 38°W at southeastern Greenland. After 2–7 days they crossed the ice cap where the ice slope was shallower and the top height was lower (2550–2850 m above sea level) than further north (Figure 3). The geese were probably severely restricted with respect to climbing capacity because of their heavy fuel reserves. This was indicated

by their very slow movement up the ice slope (Gudmundsson *et al*., 1995). The mean course of the four tracks across the Greenland ice cap was 297°, which is similar to the departure direction from Iceland. One of the geese crossed the ice cap on a course that was 54° counterclockwise of its departure direction at Iceland, while the other three tracks showed 3–12° clockwise course shifts over the ice-slope in comparison with the directions at Iceland.

On the basis of the differences in longitude and magnetic declination between southeastern Greenland and West Iceland, one would expect a course across Greenland that was shifted counterclockwise by at least 15–20° or 10–15° if the geese used a fixed course according to the sun compass (without resetting their internal clock) or magnetic compass, respectively. The tracking results do not support such constant sun or magnetic compass orientation. However, sun compass orientation cannot be excluded, since the geese may have reset their internal clock from local Icelandic to Greenland time during the interval (2–7 days) between their flights from Iceland and across Greenland, respectively.

By their indirect flight paths the Brent geese minimise flight distance over the open sea (flying the shortest distance to the East Greenland pack ice) and also avoid the steepest and widest parts of the Greenland ice cap. This may represent important adaptive benefits especially for a large-sized bird which, because of heavy fuel reserves, is exposed to size-dependent power constraints (Gudmundsson *et al*., 1995). Orientation seems to be based on topographical guidance to a large degree, involving compass control independently of landmarks only when the geese depart over the sea from Iceland and over the Greenland ice cap.

5. MIGRATION OF BRENT GEESE TO SIBERIA. Satellite tracking indicates that also dark-bellied Brent geese (*Branta b. bernicla*) migrating to Siberia to a large extent rely on topographical guidance for their orientation (Green *et al*., in press). The overall pattern, as shown in Figure 4, is that the geese follow close to a geographic loxodrome with a mean geographic course at 055° between their spring staging areas at the Wadden Sea and the breeding grounds at Taymyr in Siberia. Their main flight route deviates markedly from both an orthodrome and a magnetic loxodrome.

A closer inspection reveals that the orientation of the geese is much more variable and complex than flying on a single constant preferred geographic course. The geese frequently deviate from the mean course, for example, when crossing southernmost Sweden on courses about 085° (radar studies; Green, 1998) continuing across the Baltic Sea along directions close to 045°. The satellite tracks in Figure 4 show several examples of such course variations along the entire route. It seems that there is a strong element of course control in relation to large-scale topographical features. The geese show individual patterns in their use of different stopover sites at the White Sea and along the tundra coast of the Arctic Ocean.

It seems reasonable to assume that the geese must rely on compass orientation in many situations, for example, when making passages across sea or ice at low altitudes without access to landmarks. These compass courses may however be temporary and local, and perhaps frequently changed according to a fixed scheme. Major topographical features may have an important role as external cues for keeping track of the migratory progress and regulating course shifts according to such a compass scheme.

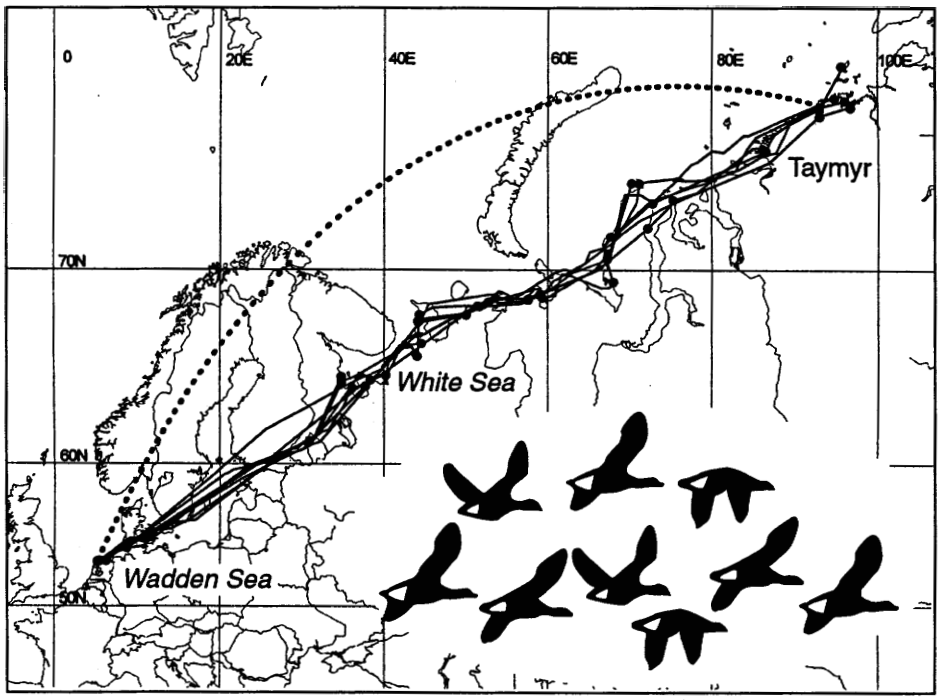

Figure 4. Pattern of Brent goose migration during spring between the Wadden Sea and the Taymyr Peninsula in Siberia, as recorded by satellite tracking. Tracks of eight different geese are shown, with filled dots indicating sites where the geese stopped for more than two days. The great circle route between departure and destination localities is shown by the dotted line. The map is a Mercator projection. Based on Green *et al.*, in press.

Even if the route used by the Brent geese is significantly longer than the great circle route it is probably still the most favourable from the point of view of energy and time economy. By being able to deposit fuel at stopover sites along the route, the birds will avoid energy (and time) costs associated with the carrying of extra heavy fuel burdens necessary for travelling along the great circle route (where there are no suitable stopover sites; Green *et al.*, in press).

6. ADAPTIVE ROUTES AND ORIENTATION. The above case studies indicate different types of route and ways of orientation in different birds, depending on environmental conditions and also on such issues as flight constraints related to the size and morphology of the birds. Migrating birds may show adaptations in their use of celestial, geomagnetic or topographical cues, as well as in their wind response, to varying conditions in different regions and seasons.

Are there any general patterns to be expected regarding the possibility of differential use of compass systems in different parts of the world? Some speculations are possible concerning the adaptive values of geographic and magnetic loxodromes, and of sun compass routes, in different geographic regions. Considering migratory movements with an important east-west component, sun compass routes may be favourable at high latitudes, north of lat 50–60°N or south of lat 50–60°S, for several reasons:

(a) Sun compass routes will be similar to orthodromes, minimising travel distance (Alerstam and Pettersson, 1991).
(b) The reduction in distance along orthodromes compared with loxodromes is largest at high latitudes (Alerstam, 2000).
(c) If migration takes place in the polar summer season the sun will be visible during most or all hours of the day (except in overcast weather).

At temperate and tropical latitudes, the sun compass will be less useful for long-distance orientation because of the daily and seasonal variation in the rate of change in sun azimuth, and resulting routes will deviate from orthodromes except under special conditions (Alerstam and Pettersson, 1991).

For movements with a strong east-west component, magnetic loxodromes will be more favourable (giving a shorter distance) than geographic loxodromes in certain regions, while the reverse holds in other regions, depending on the pattern of magnetic declination as illustrated in Figure 5. Hence, magnetic loxodromes will be

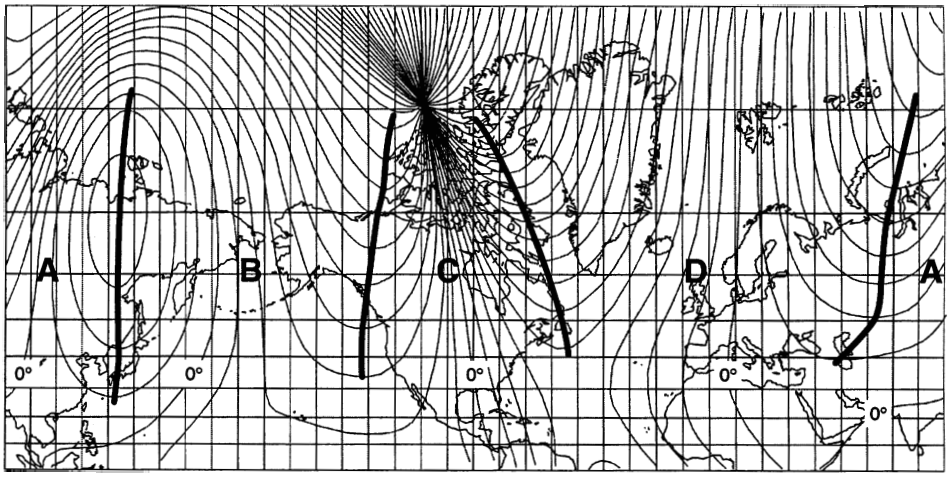

Figure 5. Map of magnetic declination showing regions where, for east-west movements, magnetic loxodromes are associated with a shorter distance between two points than geographic loxodromes (regions B and D), and where magnetic loxodromes are longer than geographic loxodromes (regions A and C). The declination map (5° isoline interval) is based on the model WMM-2000 (software by J. M. Quinn at http://geomag.usgs.gov).

associated with a shorter distance than geographic loxodromes (for east-west movements) in region B and D, while magnetic loxodromes will be less favourable (longer distance) than geographic loxodromes in regions A and C. This effect arises as a consequence of the change in magnetic declination when moving east-west, making magnetic loxodromes curve in a favourable (distance-saving) or unfavourable way depending on the direction of shift in declination. This effect is relevant at mid and high latitudes, where declination isolines are rather densely spaced and orthodromic curving gives significant reductions of distance, but not at equatorial latitudes.

Able and Able (1995) reported that savannah sparrows (*Passerculus sandwichensis*), during migration in North America, calibrate their magnetic compass in relation to

celestial rotation cues. The reverse behaviour of calibrating the star compass in relation to the magnetic field has been demonstrated for nocturnal passerine migrants in Europe (Wiltschko and Wiltschko, 1975a and b). Such a difference in response between migrants (with an important east-west component in their migration) in North America and Europe is consistent with the fact that geographic loxodromes (resulting from orientation by celestial rotation cues) are favourable in North America (region C) while magnetic loxodromes are favourable in Europe (region D).

In the Southern Hemisphere, the differential favourability of magnetic and geographic loxodromes (east-west movements) is mostly relevant at the Antarctic coast and pack-ice zone, and over the Southern Ocean (lat 50–70°S). Broadly estimated, magnetic loxodromes are unfavourable in comparison with geographic loxodromes in a sector south of Australia and close to the South Magnetic Pole (c. long 90–170°E), while the situation is rather neutral with respect to these two alternatives over the southernmost Pacific Ocean (long 170°E–120°W). In the remaining sector of the Antarctic Peninsula, southernmost South America and Atlantic Ocean (long 120°W–90°E), magnetic loxodromes curve in a distance-saving way. For north-south migration that is more or less parallel with declination isolines, and for migration where isolines are widely spaced, magnetic and geographic loxodromes will of course be equivalent.

These considerations are very speculative, and differences between alternative routes are in many cases small, only a few percent. It is a fascinating task to investigate to what degree migratory birds in their orientation adapt the use of the sun, celestial rotation cues, geomagnetic field, topography and wind to changing conditions in different parts of the world and during different seasons. Further analyses of the geometry of migration routes will be of crucial importance for understanding the ultimate causes in the evolution of the complexity of birds' orientation systems, and for explaining how the birds actually use different orientation cues on migration.

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