

THE GEOGRAPHICAL SCALE FACTOR IN ORIENTATION OF MIGRATING BIRDS

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Summary

Migration routes of birds throw light on orientation performance at different geographic scales, over distances ranging from a few kilometres to more than 10^4 km. Detailed knowledge about the flight routes may be used to test predictions about optimal orientation according to theoretical principles and about the use of compasses based on celestial or magnetic cues. Ringing recoveries demonstrate that the migratory journey of many species, such as the wheatear and willow warbler, is divided into successive legs with different main orientation. Autumn and spring migration routes are often different, sometimes diverging on a continental scale. Aerial radiotracking of whooping cranes in North America and satellite tracking of brent geese migrating from Iceland across the Greenland ice cap point to the significant role of large-scale topography for the shaping of migration routes. Compass and position control are also required, e.g. during long passages across featureless sea or ice, but how these elements are integrated into the birds' orientation system

remains unclear. Radar studies from the Arctic Ocean illustrate the importance of map projections for interpreting flight paths and suggest that birds accomplish approximate great circle orientation. Gradual course changes shown by migrating knots monitored by radar in Scandinavia are at variance with expected changes if the birds were to use a star, sun or magnetic compass over longer distances. Accurate recording of short flight segments shows how flying birds respond to visual, audible and electromagnetic cues, and also documents orientation precision and capacity to integrate rapidly shifting courses into a consistent resulting orientation. Analyses of flight patterns are crucial for understanding how birds find and follow their migration routes over different ranges of geographical scale.

Key words: bird migration, orientation, flight routes, satellite tracking, radar tracking, map projection.

Introduction

The capacity of birds to find their way on wide-ranging migratory journeys arouses our fascination at the power and precision that can be achieved by a biological orientation system.

In spite of extensive knowledge about birds' compass systems, based on cage and homing experiments (e.g. Wiltschko and Wiltschko, 1988; see reviews in Berthold, 1991), we have little understanding how they actually orient when travelling on migration. We cannot tell whether migratory birds flying past us steer according to a celestial or magnetic compass and how they take into account topographical features and wind. On a larger scale, we do not know whether birds use any means of orienting along the shortest great circle routes, and we are uncertain whether a 'vector-orientation' mechanism (an inherited orientation programme based on a succession of vectors with directions and lengths as defined by constant compass courses in force for different seasonal periods according to an endogenous circannual clock, cf. Gwinner and Wiltschko, 1978, 1980) is sufficient to guide the birds between breeding and winter quarters (Kiepenheuer, 1984). Are elements of coordinate determination or goal area navigation (Rabøl, 1978, 1985)

involved in the migratory orientation, perhaps playing different roles for adult and juvenile birds (see Perdeck, 1958)?

In order to unravel the possible mechanisms by which birds find and follow their migration routes, it is important to approach the questions addressed above from two different perspectives: (1) to analyse, on the basis of the travel routes, the requirements imposed on the birds' orientation performance, and (2) to examine flight paths critically in the light of various predictions, based on different possible orientation mechanisms, about courses and course changes. Flight routes may be particularly revealing in, for example, equatorial and polar regions where the birds meet accentuated difficulties of orientation. It is important to realize that different principles of orientation probably come into play to guide migratory birds over different ranges of geographical scale, from local to global.

In this paper, I will review some examples of migration and flight routes over different geographical dimensions with regard to possible implications for the birds' orientation performance. There are as yet only few studies where route data have been used for the purpose of analysing orientation principles. I think that it is important that more studies

involving, for example, satellite and radar registrations be planned with this purpose in mind, because such analyses of the routes followed by free-flying migrants form a necessary complement to cage experiments if we are to understand more fully the function of the orientation and navigation systems of migratory birds.

Registration of flight routes at different geographical scales

There are a variety of methods suitable for registering flight routes of migratory birds at different geographical scales, throwing light on orientation performance over at least five orders of magnitude of distance (Table 1). These different methods are to a large degree complementary with respect to range and precision.

Distribution data about breeding, stopover and winter ranges for specific populations, as well as ringing results, primarily serve to display the broad migratory patterns on global and continental scales. With the new techniques in molecular biology, DNA markers may be identified for narrowly defined populations, allowing a more detailed mapping of migration patterns (Avisé, 1994).

Satellite-based radiotelemetry provides excellent opportunities to clarify orientation capacity by registering travel routes of individual birds over periods of weeks or months, or even a full year. This technique allows a positioning accuracy of about ± 1 km, with average intervals between successive fixes of about an hour. With existing transmitters and batteries, however, the possibility of satellite tracking is, at present, restricted to birds with body masses of about 1 kg or more (Nowak and Berthold, 1991; ARGOS, 1994).

Large birds, such as cranes, storks, raptors and swans, may also be tracked visually from aircraft (e.g. Pennycuick, 1972; Pennycuick *et al.* 1979; Kuyt, 1992), with positions being determined from maps or by the use of a geographical positioning system (GPS).

With miniature transmitters that can be carried even by small passerine birds, radiotelemetry based on a combination of

signal registration from the ground, cars and aircraft has provided highly impressive tracking results about successive flights of individual birds covering more than 1000 km (Cochran 1972, 1987; Cochran and Kjos, 1985).

Another interesting technique is to equip the bird with a 'direction recorder' (Bramanti *et al.* 1988; Ioalè *et al.* 1994), storing information about the bird's heading at regular time intervals. The stored data can be used to reconstruct the flight route on the basis of various assumptions about the bird's flight speed and the wind. Because the recorder with its stored information must be retrieved, this method is useful mainly in homing experiments and to monitor central-place foraging flights, but not for following migrating birds. In the future, the satellite-based GPS technology may allow the construction of a 'position recorder' that is sufficiently small to be carried by a bird throughout its entire migration and that will be retrieved at the bird's return to its home site with stored information about position and height for the full annual journey.

Radar registrations and optical measurements (by range-finder used as an 'ornithodolite'; cf. Pennycuick, 1982a) give the highest precision, at the cost of reduced tracking range. Still, surveillance radar may record flight paths of specific flocks over several hundreds of kilometres. By tracking radar, the flight of individual birds or flocks may be recorded over several kilometres, sometimes more than 10–20 km, providing precise information about height and position (± 20 m) every few seconds (Eastwood, 1967; Richardson, 1979; Alerstam, 1985a).

Optimal orientation and different compass systems

Information about the birds' migration and flight routes over different ranges should be analysed in the light of predictions about flight course control according to different theoretical orientation principles and according to the use of different types of compass based on celestial or magnetic cues.

Theoretically, the optimal path between two places on the Earth's surface is the great circle route (Fredga and Fredga, 1962; Kern, 1962; Imboden and Imboden, 1972). Great circle orientation implies continuously changing courses as successive longitudes are intersected. The great circle routes (orthodromes) differ most markedly from rhumbline routes (with a constant compass course; loxodromes) when considering movements between places in east–west directions at polar latitudes, where the great circle distance may be up to 36% shorter than the rhumbline distance. Two different possible ways of approximate great circle orientation by birds have been proposed, based on a magnetoclinic compass mechanism (Kiepenheuer, 1984) and on a time-compensated celestial compass sense (Alerstam and Pettersson, 1991). Predictions about exact course changes differ between the two models (being most pronounced in certain polar regions) because of diverging effects related to the Earth's magnetic and rotational axes.

Considering the effect of wind on birds' flight courses, strategies for optimal orientation have been predicted (1) for

Table 1. *Examples of methods used to register and analyse flight routes and orientation performance of migrating birds at different geographical scales*

Basis of analysis	Geographical scale (km)				
	10 ⁴	10 ³	10 ²	10	1
Distribution data	x	x			
Ringing recoveries	x	x	x		
Radiotelemetry, satellite-based	x	x	x		
Aerial tracking		x	x		
Radiotelemetry		x	x	x	
Extrapolation from radar/optical registrations		x	x	x	
Surveillance radar registration			x	x	
Tracking radar registration				x	x
Optical tracking					x

differing wind compensatory ability over sea and land (Alerstam and Pettersson, 1977), (2) for different altitudinal wind patterns (Alerstam, 1979a), and (3) for wind variability between the different flights of the migratory journey (Alerstam, 1979b, 1990; see review by Richardson, 1991).

Exact flight paths are expected to differ depending on whether birds steer according to a star, sun or magnetic compass. With a star compass, which is dependent on the rotational centre of the sky (no time compensation involved; see Emlen, 1975), migrants will maintain a constant geographic bearing irrespective of their longitudinal movement.

In contrast, the time-compensated sun compass (Kramer, 1950; Schmidt-Koenig *et al.* 1991) is affected by the longitudinal time shift (Penney and Emlen, 1967; Matthews, 1968), which will bring about course changes that accumulate with increasing time displacement until the birds have reset their internal daily clock in phase with the new local conditions (Alerstam and Pettersson, 1991). It is near the poles, where the longitudes (and time zones) are most densely spaced, that the migrants become exposed to the most dramatic time shifts.

The global pattern of geomagnetic declination or variation (i.e. the angular difference between geomagnetic and geographic north) will cause geographic course changes for birds orienting along constant magnetic bearings. A map of geomagnetic declination must be consulted for predicting these course changes in different regions. Of course, the magnetic declination changes most markedly over short distances near the magnetic and geographic poles. The north magnetic pole is presently situated at about 78° N, 103° W in northernmost Canada (Queen Elizabeth Islands), and the south magnetic pole is at 65° S, 139° E (at the coast of the Antarctic continent at Wilkes Land). In wide regions around these poles, the horizontal component of the magnetic field is very small and the magnetic inclination angle extremely steep, making magnetic orientation highly difficult and liable to disturbances (Alerstam *et al.* 1990). It would be surprising if birds could accomplish magnetic orientation in these regions, where the magnetic compass instrument is too unreliable to be used in human technical navigation.

The significance of map projections

Projecting the rounded surface of the Earth onto a two-dimensional map causes inevitable distortions, which are important to bear in mind when charting and analysing migration routes of birds. The classical Mercator projection (a cylindrical projection) is very useful because it represents routes with constant geographic courses (rhumblines or loxodromes) as straight lines. This type of projection has been traditionally used for nautical charts. However, the scale varies with latitude, so that polar distances and areas are grossly exaggerated in comparison with equatorial conditions.

On a gnomonic projection (a central azimuthal projection), great circles are depicted as straight lines. Different tangent points on the Earth's surface must be selected for gnomonic

maps covering various parts of the globe. Particularly useful are central polar projections, giving a satisfactory correspondence with the true global geography around the poles and at the same time showing great circles as straight lines. It should be noted that in other types of polar projections, such as the stereographic or orthographic projection, great circle routes will show some deviation from linearity. Gnomonic maps are not equidistant and do not reflect the true area proportions. Map projections satisfying these latter criteria are less useful for considering aspects of orientation, because neither rhumblines nor great circles are displayed as straight lines.

Orientation perspectives on the basis of ringing results

Wheatears *Oenanthe o. leucorrhoa* breeding in Iceland, Greenland and northeasternmost Canada have their winter quarters in West Africa (Cramp, 1988). The migration route is illustrated in Fig. 1, based on recoveries during both autumn

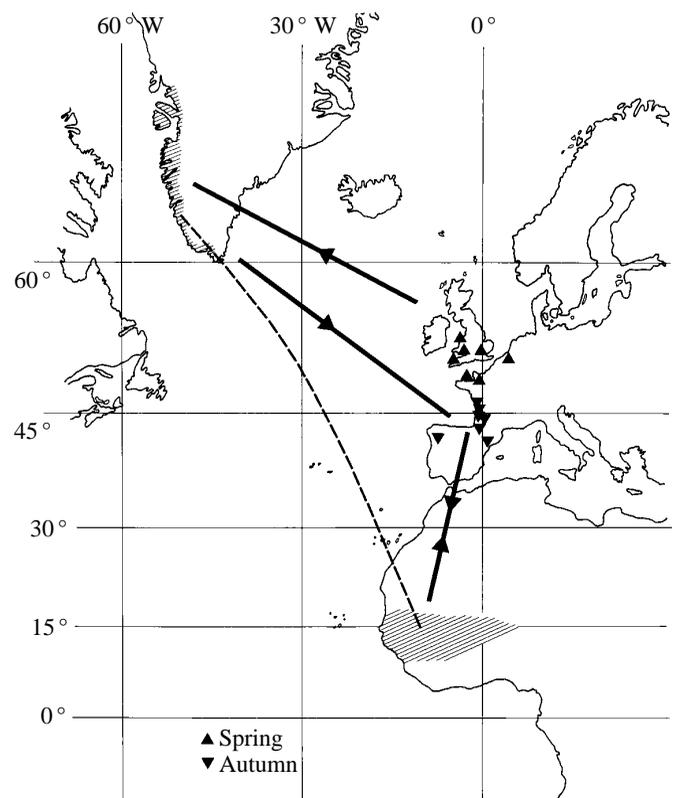


Fig. 1. Recoveries during autumn and spring migration of wheatears *Oenanthe o. leucorrhoa* ringed at breeding places in west Greenland (hatched area). The winter range is in tropical west Africa as indicated. The ringing recoveries suggest that the birds do not follow the direct route between breeding and winter ranges (indicated by the broken-line great circle route), but divide the journey into successive legs with different main orientation. All recoveries during spring migration (end of April, May) stem from more northerly regions in western Europe than the autumn (September, October) recoveries. Ringing data by courtesy of the Zoological Museum, University of Copenhagen, through Kaj Kampp. The map is a Mercator projection.

and spring migration of birds ringed in West Greenland (between 60 and 72° N). These recoveries immediately indicate two complications about the migration route. (1) The journey does not go directly between departure and destination areas, neither along the rhumbline nor along the great circle route, but is divided into at least two legs involving radically different orientation. (2) The autumn and spring migration routes are different; the wheatears cross the Atlantic Ocean at more northerly latitudes in spring than in autumn. This difference is also supported by observations of wheatears from ships in the Atlantic (Snow, 1953).

The two legs of the autumn migration route are of similar length – the first between western Greenland and the Biscay region embraces about 3800 km, and the succeeding leg to western Africa, almost perpendicular to the first, covers about 3400 km. On the first leg, the wheatears must fly at least 3000 km across the Atlantic Ocean, and the second leg involves another long-distance passage across the Sahara desert. It is possible that the autumn migration in reality consists of two main long non-stop flights, preceded by extensive fuel deposition in western Greenland (Ottosson *et al.* 1990) and at a stopover region in southwest Europe, as indicated by the ringing recoveries.

During the spring migration, the leg from west Africa to the British Isles may approach 5000 km in length, while the remaining crossing of the ocean and the Greenland ice cap extends over approximately 2500 km.

These autumn and spring migration routes represent significant detours in comparison with the direct great circle route (plotted in Fig. 1), which covers 6400 km. To fly such a long distance in one stage is not completely beyond the theoretical scope for a bird with maximal fuel reserves assisted by fair tailwinds. It cannot be entirely excluded that such wind assistance allows some wheatears to accomplish direct flights in autumn (but hardly in spring), although the ringing results strongly indicate a regular detour *via* Europe.

The wheatears' transoceanic passages, taking place in different latitudinal zones in autumn and spring, have probably evolved as an adaptation to prevailing wind and barometric pressure patterns (Salomonsen, 1967). Depressions regularly move eastwards south of Iceland, and in autumn the birds may depart across the Atlantic with NW–W winds behind and to the south of such a low-pressure centre. In contrast, easterly winds that could assist the birds on their spring passage are most likely to occur ahead and to the north of an approaching depression.

How the wheatears actually orient on their impressive transoceanic flights is a matter of speculation. Depending on whether they use the time-compensated sun compass or maintain a constant magnetic orientation (see Sandberg *et al.* 1991), the routes will be curved (if plotted on a Mercator map projection as in Fig. 1) according to the shift in time or magnetic declination, respectively, between Greenland and western Europe. Using any of these two compass mechanisms, the birds would in fact travel in rough agreement with a great circle. Magnetoclinic courses, as drawn by Kiepenheuer

(1984), also curve in a broadly similar way, but are difficult to reconcile with the ringing recovery locations. If the wheatears orient by the stars, they may follow a route closer to a rhumbline route.

The transoceanic flight paths will be determined not only by compass mechanisms of this kind but also, and perhaps most decisively, by the birds' responses to wind and weather conditions.

The breeding range of the wheatear is almost circumpolar, extending across Eurasia to eastern Siberia and Alaska (Cramp, 1988; Conder, 1989). Birds breeding in Alaska are thought to winter in East Africa and these birds would be expected to fly across the Arctic Ocean close to the North Pole if they are to follow the shortest migration route! A quite different main route would be predicted if they flew with a fixed apparent angle of magnetic inclination (Kiepenheuer, 1984). Also, for wheatears breeding in East Siberia, the scope of their orientation capacity has strong implications for the migration pattern (Åkesson *et al.* 1995). Should technical innovations be made that allow us to monitor in more detail the journey of the individual wheatear, be it from Greenland, Alaska or Siberia, there is, no doubt, much to be learned about orientation principles.

A division of the migratory journey into distinct legs, each with a different main orientation, and with disparate autumn and spring configurations, is by no means restricted to the wheatear. Another good example is the willow warbler *Phylloscopus trochilus*, for which ringing data show different broad annual migration trajectories for populations breeding in southern and western Scandinavia (Roos, 1984) and in northern Scandinavia and Finland, respectively, as schematically drawn in Fig. 2 (Hedenström and Pettersson, 1987). Bird migration atlases compiled on the basis of ringing results (Zink, 1973–1995; Zink and Bairlein, 1995) provide evidence of several similar cases and constitute a most valuable source demonstrating differential migration patterns between populations and seasons.

On a truly global scale, numerous ringing recoveries of Arctic terns *Sterna paradisaea* demonstrate that birds from western Greenland travel along the eastern Atlantic seaboard towards their Antarctic winter range. In contrast, for the return journey there are no valid recoveries along this route but, instead, two recoveries from South America (Salomonsen, 1967; Alerstam, 1985*b*). Adding recent radar observations of Arctic tern migration at the Antarctic Peninsula (suggesting possible circumnavigation of the Antarctic continent; Gudmundsson *et al.* 1992) to this picture gives an idea of their supreme orientation capacity, allowing terns (as well as many ocean birds and some waders; Alerstam, 1990) to reach their high-latitude destinations in either hemisphere by shifting between autumn and spring routes that may run oceans or continents apart.

Aerial radiotracking of whooping cranes

Migration routes of whooping cranes *Grus americana*

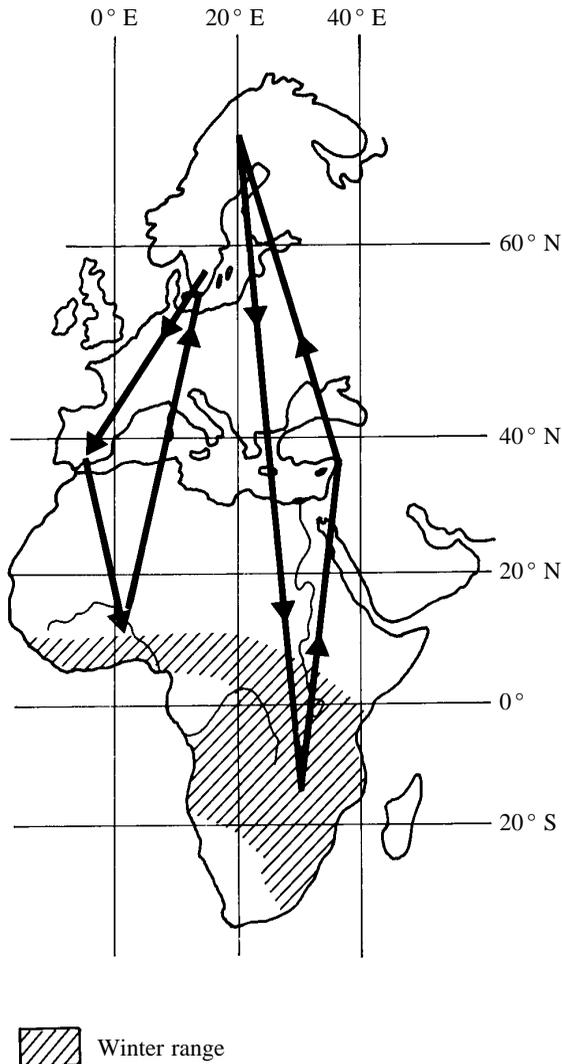


Fig. 2. Schematic main routes and orientation of two populations of Fenoscandian willow warblers *Phylloscopus trochilus*. Based on an analysis of ringing results by Hedenström and Pettersson (1987). The map is a Mercator projection.

between their breeding sites in Canada and winter area in Texas have been mapped in detail by tracking birds equipped with radio transmitters from aircraft during a number of autumn and spring seasons (Kuyt, 1992). The cranes migrate mainly in families, pairs or small groups of subadults, and nine and five such flocks were monitored throughout the autumn and spring migration, respectively. The migration corridors within which the flocks covered their 4000 km journey are shown in Fig. 3. The mean width of the corridor was about 200 km (varying between 80 and 300 km) in autumn and about 125 km in spring.

As seen from Fig. 3, there is a negligible difference between the rhumbline (with geographic compass course 161°/341°) and great circle routes connecting the cranes' departure and destination sites. Although the cranes travel on fairly direct routes to their goals, their migration corridors deviate significantly from the ideal routes. The main course

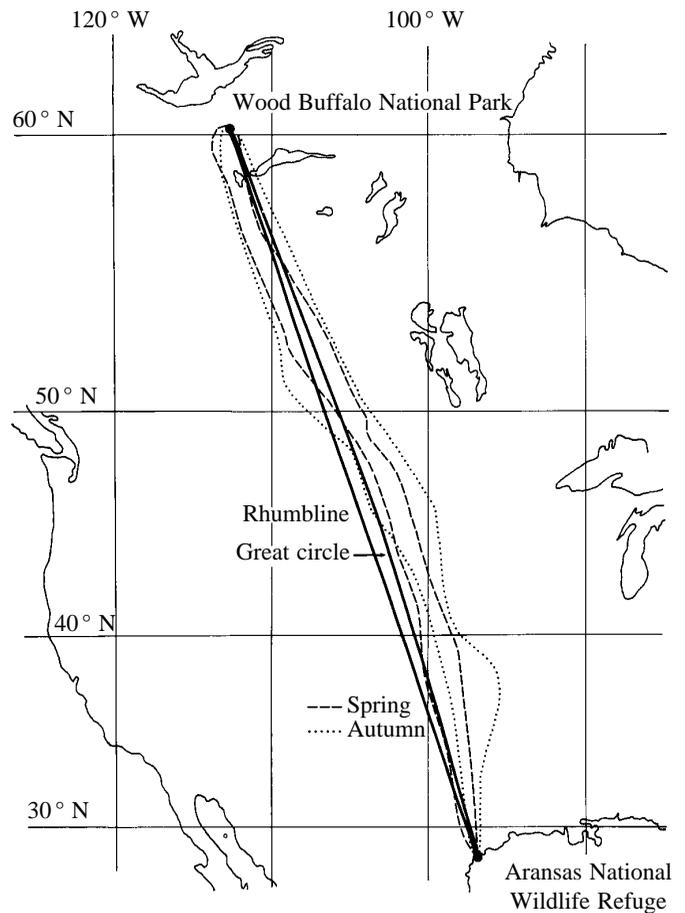


Fig. 3. Spring and autumn migration corridors of whooping cranes *Grus americana*, as determined by aerial radiotracking between breeding and winter places. Based on Kuyt (1992). The map is a Mercator projection.

deviations occur in the region of 50° N, where the principal axis of migration is about 150°/330°, and in Texas, where it is about 170°/350°. Even though these bearings do not diverge more than 10° from the constant bearing along the rhumbline route, the consistent patterns among flocks and between seasons (see maps in Kuyt, 1992) suggest that these course deviations are not accidental aberrations due to, for example, wind drift.

These deviations indicate that the cranes' orientation is not solely governed by a celestial or magnetic compass in any simple way. In fact, the magnetic declination differs by more than 20° between the points of departure and destination, in such a way that the cranes would travel along a route curving to the west of the rhumbline if they were to follow a constant magnetic course.

Kuyt (1992) pointed out the possible influence of the continental height relief on the cranes' migration corridors. By deviating from the rhumbline route, the cranes' flyway remains east of the 1000 m contour line, away from the higher parts of the Great Plains. Even if the cranes did not follow distinct landmarks for longer distances, situations were recorded when they responded to rivers and valleys as if they used such

features for temporary visual guidance when suitably aligned in the preferred migratory direction.

Furthermore, the cranes sometimes made drastic course changes when approaching staging localities, to which they returned after visits in previous years, as if they had recognized landscape features and responded to familiar landmarks. Of course, learning traditional routes, staging sites and goals is probably important for birds such as cranes and geese where the young accompany their parents on their first journey.

The whooping cranes' orientation system seems to accommodate elements of both short-distance responses to landscape features and long-distance general guidance in relation to large-scale topography. How compass and position control are integrated into this system remains unclear.

Satellite tracking of geese on arctic journeys

A surprising case of a profound topographical influence on birds' orientation was revealed by satellite tracking of brent geese *Branta bernicla hrota* departing from spring stopover sites in Iceland towards their breeding range in High Arctic Canada (Gudmundsson *et al.* 1995). Satellite tracking was conducted in two spring seasons involving ten different geese. The transmitters were active for about 3 weeks before the batteries were exhausted, and this was sufficient for tracking eight of the geese successfully to East Greenland, and five of them further across the ice cap to West Greenland, a total distance of 1500–1900 km.

The flight routes turned out to be very different from steady

extrapolations of the departure courses from Iceland (Fig. 4). The average departure direction when the geese flew out low over the sea from Iceland was 295° , which is in good agreement with earlier visual measurements (Alerstam *et al.* 1990). When reaching the pack-ice zone off the steep eastern Greenland coast, the geese paused repeatedly (apparently resting on the ice or water surface) and veered towards westsouthwest. They stopped for 2–7 days at east Greenland before continuing across the ice cap. It is noteworthy that they all passed a delimited area, at about 65° N, 38° W, close to the coast in southeast Greenland.

The mean orientation across the Greenland ice cap, rising to 2500–2850 m above sea level where the geese migrated, was 297° . This is similar to the orientation at Iceland and does not agree with the course changes that are predicted to occur between Greenland and Iceland if the birds were to use a sun compass affected by the longitudinal time shift or if they were to orient on a constant magnetic course affected by the shift in magnetic declination. In both cases, the orientation over Greenland is expected to become shifted counterclockwise from that at Iceland (Gudmundsson *et al.* 1995).

However, the geese might retain the same geographical course across Greenland as at Iceland by using their sun compass, if they were capable of resetting their internal clock from local Icelandic to Greenland time. Indeed, one cannot exclude the possibility that the temporary halt of migration at east Greenland at least partly serves the purpose of compass recalibration, although awaiting suitable weather for the transglacial flight is probably important as well. Alternatively,

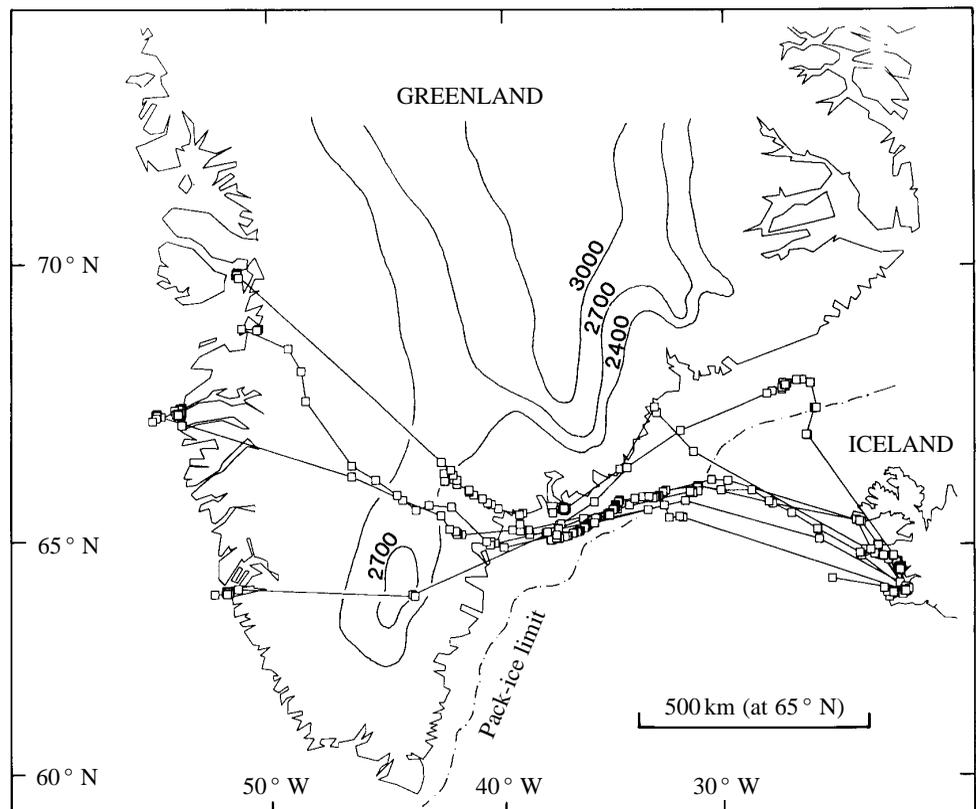


Fig. 4. Pattern of brent goose migration from Iceland in spring, as registered by satellite-based radio-telemetry. Open squares show high-precision locations from tracks of ten different geese. Based on Gudmundsson *et al.* (1995). Map and plotting by courtesy of G. A. Gudmundsson. The map is a Mercator projection.

the possible resetting of their internal clock may be an effect rather than a cause of the halt at east Greenland.

The circuitous migration routes of these brent geese may have a higher adaptive value than the direct path to the destination. The geese travel on routes that minimize flight distance over open sea and avoid the steepest and widest parts of the Greenland ice cap (a serious obstacle for the geese which, because of heavy fuel loads, have a much reduced climbing capacity; see Gudmundsson *et al.* 1995). The geese presumably rely on a compass that is independent of landmarks when departing over featureless sea at Iceland and over the Greenland ice cap. At other places, such as in east Greenland, large-scale topographical guidance is probably of overriding importance. The convergence of the flight routes on a delimited area in southeast Greenland may reflect the involvement of a position control system in the migratory process.

Satellite tracking of albatrosses has provided fascinating accounts of complex flights over vast expanses of open ocean (Jouventin and Weimerskirch, 1990; Prince *et al.* 1992; Weimerskirch *et al.* 1993), where the birds' performance seems to indicate that they have a positioning system at their disposal. Another pattern holds for the flight paths registered by satellite tracking of white storks, which are thermal migrants performing marked directional shifts at specific geographic locations (Berthold *et al.* 1992, 1995).

Polar flight routes

In order to throw light on polar migration patterns, which are of unique interest from the point of view of bird orientation, we have recently conducted studies using a tracking radar onboard an expedition ship sailing along the Northeast Passage in the Arctic Ocean (Alerstam *et al.* 1995; T. Alerstam, G. A. Gudmundsson and B. Larsson, in preparation). Flocks of migrating birds were tracked by radar for 3–8 min and samples of migration patterns, with respect to direction, speed and height, were obtained from 18 different sites on days and nights when the ship was stationary. About 7% of all targets tracked by the radar could be identified to species through telescopes aligned with the radar beam. Winds were measured by radar tracking of ascending helium balloons.

A sample of radar trackings from one of the most northerly sites, when the ship was situated 20 km north of one of the New Siberian Islands at 76°N, 147°E, is presented in Fig. 5. On this occasion, the sun was shining from an almost cloudless sky, visibility was excellent and the winds were weak and had little impact on the birds' flight direction. Birds were tracked when migrating at heights between 700 and 3200 m above sea level on easterly geographic courses between 55° and 144° (median 90°, $N=31$), heading out over vast expanses of pack ice in the Arctic Ocean.

The track directions recorded have been extrapolated in Fig. 5 as straight lines on a Mercator projection (Fig. 5A) and a gnomonic polar projection (Fig. 5B) to show the birds' routes if they were to maintain their geographic courses constant or

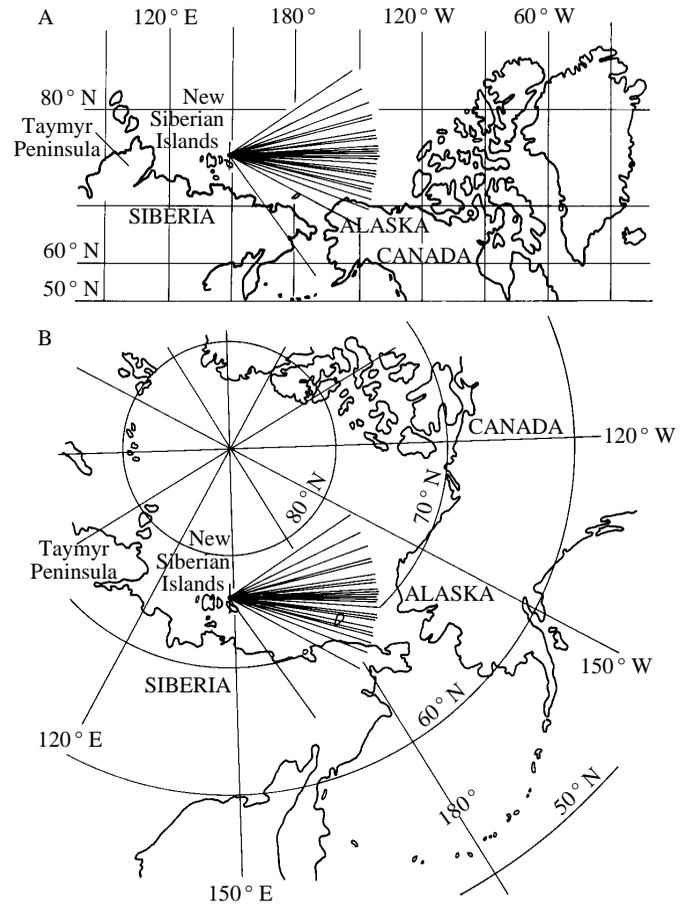


Fig. 5. Extrapolated track directions of high-altitude wader migration, registered on 11 July 1994 by tracking radar from a ship at the New Siberian Islands. Linear extrapolations are presented on (A) a Mercator projection and (B) a gnomonic polar projection, illustrating the substantial differences between rhumbline and great circle orientation in polar regions. Based on Alerstam *et al.* (1995).

if they were to change their courses according to great circle routes, respectively.

The most likely species involved in the flights were, according to field observations from the tundra as well as the ship, grey phalarope *Phalaropus fulicarius* and pectoral sandpiper *Calidris melanotos*, and additional wader species probably also participated. A likely first postbreeding halt on the global journeys of the relevant wader species (the two above-mentioned species are destined for winter quarters in South America) is Alaska (see Gill and Handel, 1990; Johnson and Herter, 1990), in good agreement with the case in Fig. 5B. There seem to be no grounds to suspect that birds migrate from Siberia to northernmost Canada (as in Fig. 5A).

Even if more intensive migration was recorded at observation sites closer to the Siberian coast, the radar registrations at the New Siberian Islands strongly support the existence of approximate great circle orientation by birds travelling 2000–3000 km directly across the Arctic Ocean between Siberia and Alaska. To accomplish this, the birds must change their geographic flight courses as they fly. One

possibility is that they orient by their time-compensated sun compass (the sun remains above the horizon throughout the 24 h of the polar summer day). While flying across the time zones without resetting their internal clock, the birds' flight bearings would continuously change in close accordance with great circles. If the birds were to travel on constant magnetic courses, the changing magnetic declination would also result in a gradual shift in geographic flight courses as they moved eastwards from the New Siberian Islands, but to a smaller extent than with the sun compass. However, the course shift over the relevant region of the Arctic Ocean would again be more pronounced if the birds were to adopt a magnetoclinic compass mechanism as proposed by Kiepenheuer (1984). Clearly, polar orientation is a key issue for further analysis and study.

Surveying gradual course changes by radar

If flight paths of migrating birds can be plotted in detail over long enough distances, it becomes possible to evaluate gradual course changes in relation to different predictions depending on whether the birds orient by a sun, star or magnetic compass. Gudmundsson (1994) used this approach to analyse the flight paths of flocks of knot *Calidris canutus* during their spring passage in June over southern Scandinavia. By time-lapse filming of a high-power surveillance radar it was possible to plot the trajectories of radar echoes from individual flocks over distances up to 400 km, spanning 5° of longitude (Fig. 6).

The migratory passage through the study area mainly took place from the time of sunset and onwards during the night, with a peak around midnight. The elevation of the sun was never below -10° , making it possible for the birds to decide the position of the sun from the horizon glow throughout clear nights and at the same time to see the stars.

If the knots orient by stars at the rotation centre of the sky,

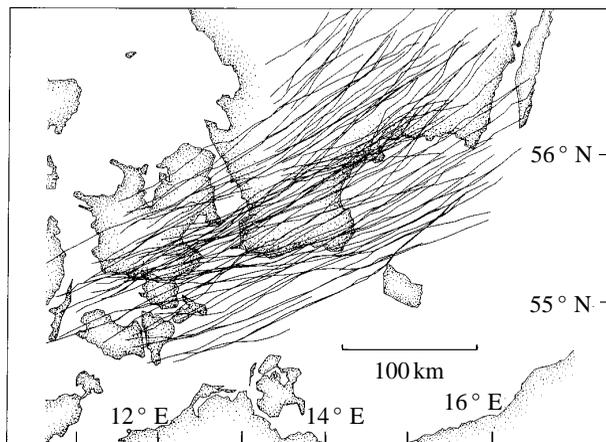


Fig. 6. Geographic migration pattern of knots *Calidris canutus* passing south Scandinavia in spring. Tracks of radar echoes from flocks of migrating birds are illustrated for one selected season. The tracks were plotted on the basis of registrations from a high-power surveillance radar in south Sweden. From Gudmundsson (1994), reprinted with permission.

they would be expected to maintain their geographic courses precisely. If they rely on the sun or magnetic compass, their courses would be expected to change gradually in a clockwise direction by about 4 and 2.5° , respectively, as the migrants become exposed to a shift in time and magnetic declination along the observed segment of their route. Contrary to these predictions, the knots changed their courses in the opposite (anticlockwise) direction by about 6° , especially in the eastern part of the study region (Fig. 6).

Because the knots were affected by wind drift only to a minor degree, and the registrations are from many different occasions, it seems implausible that the rather consistent pattern of course changes was due to wind or other weather influences. Rather, the knots' flight paths seem to be related to the overall topography of the south Scandinavian region. This possible association with topography must be on a very general and large-scale level because, as seen from Fig. 6, the birds migrated on a fairly broad front and they seemed to ignore the fine-scale topography of specific coastlines and islands.

The average flight direction over south Sweden was 63° , which is slightly to the right of the predicted rhumbline bearing (57°) towards destinations on the Taymyr Peninsula in Siberia, whereas the predicted great circle route from the Wadden Sea to the same destination would not pass south Sweden at all (Gudmundsson, 1994). By veering to the left, as observed in the radar studies, the birds will regain contact with the rhumbline route over the Baltic Sea. One may envisage a situation where the knots travel within a slightly winding flight corridor in broad harmony with the large-scale topography, via the Baltic Sea, the Gulf of Finland and parts of the White Sea and tundra coasts of the Arctic Ocean to their destinations.

How the knots use their compass sense during these long flights is not at all clear – the radar study indicated that they did not maintain fixed star, or sun or magnetic compass headings for very long distances.

Short flight segments and orientation

Recording flight tracks of birds with a high degree of accuracy over short distances will help to reveal orientation precision at the finer end of the scale spectrum.

Analyses of the straightness of flight paths, as measured by tracking radar over some kilometres, have demonstrated that birds show more small-scale turns, zigzags or other irregular movements when flying within or between cloud layers than in other situations (Griffin, 1973; Able, 1982). White-throated sparrows, carried aloft in balloons and released under clear as well as overcast night skies, showed more sinusoidal or zigzag flight paths under the latter conditions (Emlen and Demong, 1978). In contrast, Able (1982) found no differences in the straightness of tracks when comparing nocturnal migration under clear conditions with situations when the birds were flying beneath solid clouds.

Further studies of small-scale changes in flight paths have demonstrated responses by flying birds to light and aircraft (Larkin *et al.* 1975), to sounds (Larkin, 1978) and to changing

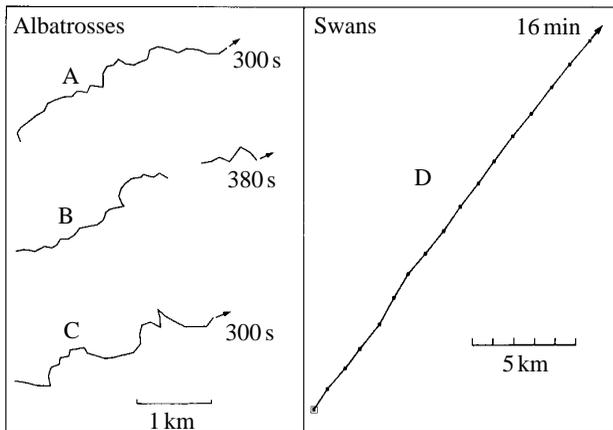


Fig. 7. Flight paths of albatrosses and swans recorded by tracking radar while the birds flew over the sea. (A) A black-browed albatross *Diomedea melanophris*, and (B,C) two grey-headed albatrosses *Diomedea chrysostoma* soaring over large swells in the open ocean under near calm conditions. The time interval between successive position measurements is 10 s, and the total radar tracking time is indicated (from Alerstam *et al.* 1993). (D) A flock of six whooper swans *Cygnus cygnus* on spring migration across the Baltic Sea in moderate tailwinds, with positions shown every minute over a distance of more than 22 km.

electromagnetic fields (Larkin and Sutherland, 1977). Birds migrating across a strong local magnetic anomaly maintained straight tracks, but showed temporary changes in altitude as they passed the anomalous area (Alerstam, 1987).

Clear examples of wind drift have been revealed from curving flight paths, shown by migrating terns when climbing through altitudinal strata with changing wind conditions (Alerstam, 1985b).

The straightness of birds' tracks also depends on their flight behaviour. Contrasting examples of characteristic flight paths are illustrated for albatrosses and swans in Fig. 7. Albatrosses use a technique of dynamic soaring and sweeping flight, making frequent turns, pull-ups and descents in relation to wind, waves and swells (Pennycuik, 1982b). The examples of flight tracks in Fig. 7 (recorded by tracking radar) are typically irregular as the albatrosses twisted and turned within a width of 300–500 m laterally from their overall direction of movement (Alerstam *et al.* 1993). The directions at 10 s intervals vary within a range of approximately $\pm 90^\circ$ from the mean resulting direction (angular deviation about $\pm 45^\circ$). It is highly impressive how the albatrosses integrate their constantly and widely changing flight vectors into a very consistent resulting orientation over a few kilometres distance (Fig. 7) and sometimes over thousands of kilometres (Jouventin and Weimerskirch, 1990; Prince *et al.* 1992).

In contrast to albatrosses, swans migrate by flapping flight in flock formations, maintaining their tracks very precisely when flying over land as well as sea. In the example shown in Fig. 7, the directions at 1 min intervals keep within $\pm 6^\circ$ from the mean course. Radar tracks of swans and geese with 10 s time resolution reveal similarly small variations in flight

direction (angular deviation may be as low as $\pm 3^\circ$). Considering the fact that part of this variation must be due to radar measurement errors, it is not an exaggeration to say that swan and goose formations have the capacity to orient as straight as an arrow.

Large- and small-scale perspectives on bird orientation

Varying the magnification and the field of view from global to local when considering birds' migration patterns and flight routes provides a great deal of fundamental information about orientation performance. It seems surprising that orientation research has built on analyses of this type of route data to such a small extent. However, no clearcut interpretations about how the birds actually use their different compass systems have emerged from the rather few studies that have attempted such an approach.

Why does the comparison between findings from orientation cage experiments and analyses of birds' actual orientation performance on their migratory journeys provide such limited information? One possible reason is the complexity of the situation in 'uncontrolled' nature, with flexibility in the migrants' behaviour and the effects of wind and topography obscuring the picture. However, this alleged complexity may to some extent be an illusion, reflecting our ignorance about what might be elegant, but as yet undiscovered, principles that govern the birds' orientation over different ranges of geographical scale.

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