Ecological causes and consequences of bird orientation

T. Alerstam

Department of Ecology, University of Lund, Ecology Building, S-223 62 Lund (Sweden)

Summary. An advanced orientation capability offers possibilities for birds to optimize movement patterns in a wide variety of ecological situations. The adaptive significance of different patterns of angular dispersion and of orientation responses to topography and sociality are elucidated. The orientation capacity is characterized by flexibility, exemplified by reorientation promoting safety and restoration of fat reserves during migration. There are also limitations to the orientation process, leading to costs of migration through mis- or disorientation, and to constraints on the evolution of routes and timing of migratory flights. Young migrants may acquire an erroneous compass sense, and misorient several thousands of kilometers off their normal course. Widespread and dense fog of long duration causes disorientation and mortality among land birds migrating over the sea. Orientational constraints in the evolution of migration routes may be most easily disclosed at high geographic and magnetic latitudes. Here the birds are faced with special difficulties in using their celestial as well as their magnetic compasses. The sun compass could be used for great circle orientation, but observed spring flight trajectories of high arctic shorebirds and geese seem to conform with rhumbline routes.

Key words. Bird migration; orientation; angular dispersion; leading-lines; flocking; reorientation; misorientation; disorientation; great circle routes; timing of flight.

Introduction

Orientation is a part of all types of bird movement; domestic movements in a local familiar area, dispersal and exploration, migration, homing and compensation for displacement. There are also other well-oriented movements, the meaning of which is less well understood, like escape orientation by ducks[20,56,76,77] and penguins[39,87] (fig. 1). In the latter case, it is believed that the adaptive significance of the penguins' northward orientation is to guide them out of ice entrapment to offshore feeding grounds. The easterly component of their orientation may represent a compensation for a westward ice drift by coastal Antarctic currents[39,87]. This serves to illustrate the fundamental fact that ecological premises are decisive for a correct interpretation of adaptive values of orientation behaviour.

Birds have an advanced compass sense, based on celestial and geomagnetic cues[40]. Within the home range, landmark recognition seems to be integrated within a compass frame. Hence, the sun compass plays an important role for pigeon orientation also over very familiar terrain close to the lofts[47,53], and for seed-cache relocation by scrub jays[127]. With the compass framework serving to align as yet unknown mosaic or gradient cues extending beyond the home range also, birds may navigate home from unfamiliar sites, as do homing pigeons.

Migratory orientation is not only determined by the birds' celestial or magnetic compass systems, but is also directly influenced by environmental, social and physiological factors. Among environmental factors, wind is of paramount importance (cf. review by Richardson), but topography, weather, and ecological barriers are also of great significance. How and why is the orientation affected by these proximate ecological factors?

The orientation capability has its limitations, and birds sometimes misorient or completely lose their orientation. How does this come about, and do the risks for mis- or disorientation represent a significant cost of migration? What do these phenomena tell us about the function of the birds' complex orientation systems? Orientational constraints may have important effects on the evolution of migratory habits. To what extent are routes and timing of migratory flights determined by factors related to orientation?

These and similar questions will be addressed in this review of ecological causes and consequences of orientation.

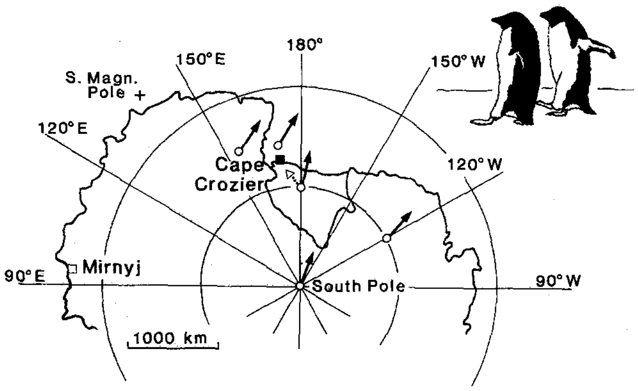

Figure 1. Mean orientation of Adelie penguins *Pygoscelis adeliae* transported from their home rookery at Cape Crozier and released on featureless snow-ice surfaces at various Antarctic localities. The birds used a time-compensated sun compass, with their internal clocks remaining in phase with local home time, to orient consistently towards NNE/NE with respect to their home longitude. Birds from a rookery at Mirnyj, released at long. 180°, also oriented NE in relation to their home longitude (dotted short arrow). After their circadian rhythms were reset to the solar cycle at the new longitude, they changed to the same orientation as the Cape Crozier birds. In addition to this fixed escape orientation response, Adelie penguins have a navigation system allowing them to return home after considerable longitudinal and latitudinal displacement[39,87].

Angular dispersion

In figure 2 ringing data are used to exemplify different patterns of orientation with respect to the angular dispersion.

A more or less random or uniform circular distribution is typical of dispersal orientation. Dispersal occurs widely among young birds, soon after independence, in resident as well as migratory species[83]. This behaviour is important for exploration (for example for possible future breeding opportunities), competition avoidance and, possibly, inbreeding avoidance[18, 54, 84]. Griffin[55] presented a theoretical analysis of exploration, and discussed optimal search patterns. Movement and orientation strategies adopted by birds during their dispersal phase remain to be investigated in the light of this theory.

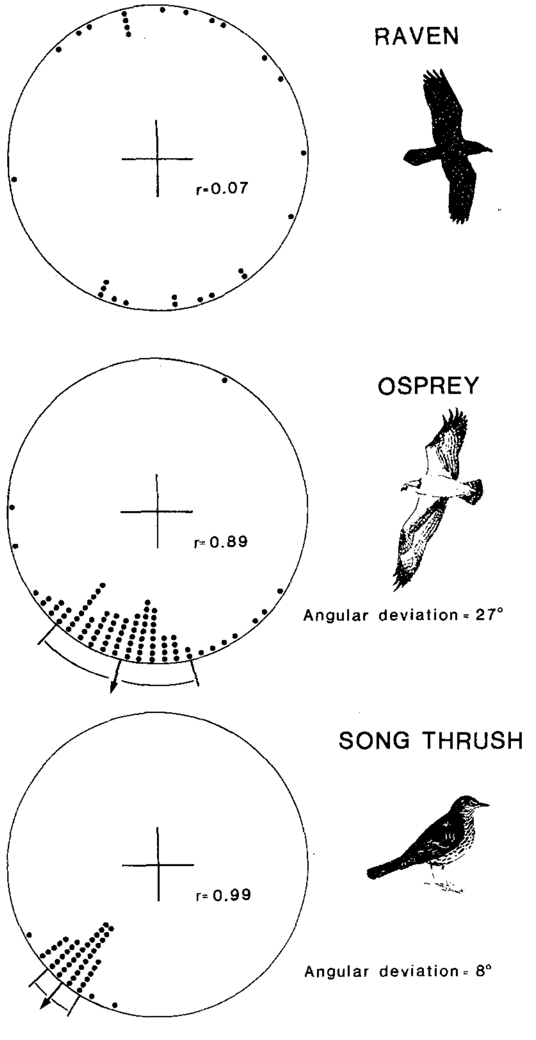

Figure 2. Angular distribution of ringing recoveries of raven *Corvus corax* (resident species), osprey *Pandion haliaetus* (migrant to Africa), and song thrush *Turdus philomelos* (migrant to SW Europe) from Sweden. Mean vectors and angular deviations are calculated according to Batschelet[19]. The data refer to birds ringed as nestlings and recovered > 100 km away, during their first year of life (raven, n = 27), during the first autumn migration in Sept. and Oct. (osprey, n = 84) or during the first autumn migration and winter season Sept.–March (song thrush, n = 42). Based on annual reports 1972–1984 from Bird Ringing Centre, Swedish Museum of Natural History.

There is an indication of an axial orientation for the long-distance dispersal of Swedish ravens in figure 2 ($r_2 = 0.46$, $p < 0.01$)[19], presumably an effect of the topography of the Scandinavian peninsula. In a more extensive analysis of movements by Finnish ravens, no important deviations from a random scatter were found[109]. Quite a different pattern of post-breeding movement, 'Zwischenzug', is found in juvenile starlings *Sturnus vulgaris*[45]. Before the summer moult they travel 100 km or more. In some populations the orientation is close to the normal migratory direction later in autumn, while other populations show an orientation distinctly divergent from the autumn migratory direction, sometimes almost reversed. Still other populations exhibit widely scattered movements, influenced by topography in mountain regions.

Wide-angle orientation is illustrated in figure 2 by recoveries of ospreys ringed in Sweden. Juveniles as well as adults fan out widely across Europe on a broad-front migration to African winter quarters. Österlöf[85] found that environmental rather than hereditary influences are responsible for this wide scatter. Siblings show as large angular differences in migratory bearings as do young from neighbouring broods.

Narrow-angle orientation is exemplified by the song thrush migrating from Sweden to winter quarters in SW Europe (fig. 2). Similar narrow-angle orientation has been reported, on the basis of ringing recoveries, for, e.g., spotted flycatcher *Muscicapa striata* (angular deviation 8–18° for ad., 13–23° for juv.)[46], willow warbler *Phylloscopus trochilus* (from Finland; ang. dev. 9° for ad., 21° for juv.)[61], ortolan bunting *Emberiza hortulana* (ang. dev. 5–8°)[117] and honey buzzard *Pernis apivorus* (ang. dev. about 8° for ad., 12° for juv.)[116].

Which factors determine the angular concentration of migratory orientation? Within species there is often an important difference between age groups, with young and inexperienced migrants showing a wider orientation scatter than adults (cf. above). Stabilizing selection may operate to maintain the orientation within narrow limits[95]. On the basis of experiments with Savannah sparrows *Passerculus sandwichensis*, Moore[80] demonstrated a greater within-individual variability in migratory orientation, both between and within test nights, for juveniles (first autumn) as compared to adults. In contrast, between-individual variability was larger among adults. With en route experience and stopover and winter site attachment, the orientation capability of adult birds may differ fundamentally from that of naive migrants[80, 89, 95]. Populations at migratory divides show a wide angular scatter of recoveries[61, 108], and analyses of selection pressures on migratory orientation in such transition populations are desirable.

The concentration of orientation can differ markedly between species, even between closely related species. The song thrush can be contrasted with the redwing *Turdus iliacus*; individual redwings may winter as far west as

Britain in one year and in the Middle East or Soviet Georgia the next[6]. A similar contrast holds between the chaffinch *Fringilla coelebs*, which leaves Scandinavia for winter quarters towards the southwest, and the brambling *Fringilla montifringilla*, which spreads during the winter over a much wider sector in Europe. Such wide-angle migration is characteristic of several temperate-zone migrants from northerly latitudes. Due to their late breeding season, these species rank lowest in the temperate-zone winter competition hierarchy. The evolution of wide-angle migration with between- and within-year winter nomadism may be associated with a release from this competition pressure. These species are to a large extent adapted to using as winter resources a supply of seeds or fruit from woody plants which varies a great deal, both geographically and yearly[7]. The reason for the osprey's wide-angle orientation is not at all clear. Intraspecific competition for fishing opportunities along the migration route may be one relevant factor.

Topography and orientation

'Zugstrassen' and 'flyways' designate well-defined and traditional migration corridors used mainly by waterfowl and shorebirds[34, 86]. Generally, these corridors are clearly linked up with topography, favourable habitats and stopover sites. Palmén[86] pointed out that by travelling along littoral migration routes, the birds gain the dual advantage of frequent contact with favourable habitats and access to landmark guidance for their orientation.

Large-scale topography is also of major importance (along with climate and wind) for the evolution of broad-front migration patterns – migratory divides and changes in standard direction having evolved to reduce or prevent hazardous flight paths across sea, desert and mountain areas[26, 49]. In addition, competition for breeding and wintering space, early arrival, and distance and speed of migration along the diverging routes, presumably belong to the complex set of factors determining the evolution of migratory divides.

Geyr von Schweppenburg[50] introduced the term 'Leitlinie' or leading-line for longish topographical features, which influence migrating birds to change their orientation and to fly along them. This frequently happens at coastlines, but also at mountain ranges and other habitat borders. At least three types of adaptive value have been suggested for leading-line migration. 1) Refraining from crossing ecological barriers reduces mortality risks to an extent that more than compensates for the detour flight costs. Many landbirds are exposed to significant risks of predation, not least by gulls[25], and fatal disorientation over the sea[9]. Birds with small fat reserves should be particularly inclined to avoid or shorten passages across inhospitable habitats. 2) Orientation by landmarks will be facilitated. Eiders *Somateria mollissima*, migrating to the Baltic Sea in spring, show a prominent change in direction upon reaching the southeast coast of Sweden. With widespread low-level fog, probably preventing the birds flying above the fog from seeing landmarks, radar observations showed that the eiders failed to change their course properly[10]. Rabøl[93] interpreted low-altitude coastal migration into the wind as a correction movement for wind drift incurred by the diurnal migrants during preceding high-altitude flights over land. Topographical leading-lines also make it easier for nocturnal migrants to compensate for wind drift, as suggested for birds flying low over ridges in the Alps[27] and along the conspicuously lighted Hudson River in New York[23]. 3) Birds can save energy and time by detour migration via coastlines. At low altitude along the coast, migrants may gain protection from head/crosswinds[4]. Assuming that birds are subjected to wind drift to a higher degree over sea than over land, coasting rather than departing directly across the sea towards the destination is preferable under certain wind conditions[14].

The energetic advantage of thermal soaring migration in relation to powered flight is positively correlated with the bird's mass and inversely correlated with wing span[88]. This advantage will decide how long a detour of soaring migration over land will be favourable in comparison with flapping flight along the direct oversea route[6]. Rudebeck[104] demonstrated important differences between raptor species in propensity for soaring migration, and Kerlinger[66] found a positive relationship between the aspect ratio of different raptor species and their readiness to abandon soaring migration in order to cross a water body by flapping flight.

If time saving is more important than energy saving, the advantages of detour soaring migration over land become somewhat less[13]. The honey buzzard shows less propensity for soaring and coasting than does the common buzzard *Buteo buteo*, possibly due to marked differences between these species in migration distances and associated demands on speed and timing[104]. Common buzzards change their orientation to circumfly the Alps, to an increasing degree in the course of the autumn season, as soaring conditions deteriorate significantly[110].

Swifts *Apus apus* and ocean birds lead a roaming and pelagic life in the airspace and over the open sea, respectively. Both are exposed to strong winds and poor weather in cyclonic weather systems. Presumably, as an adaptation to avoid unfavourable weather, these birds perform circuitous movements away from approaching cyclones[24, 70, 118]. The movements often involve massive leading-line migration along coastlines, possibly providing guidance for orientation and checking excessive wind displacement.

Sociality and orientation

In some species, old and young birds migrate together in flocks. Juveniles of these species are not entirely dependent on the adults for orientation but show an appropriate innate directional preference, as indicated by experiments where young birds have been held in the breeding area until all others of their species have departed[76]. Still, social influence may be of overriding importance, as demonstrated by experiments on the white stork *Ciconia ciconia* reported by Schüz[111]. Young storks from eastern Europe, that were transported west of the migratory divide, and released after all local storks had departed, migrated in their typical SSE direction. In contrast, when transported and released earlier, most young storks obviously joined flocks of local conspecifics, and the majority of recoveries were reported in the SW sector, i.e., along the migration route for storks breeding west of the migratory divide[111].

A dominating parental influence on the migration route has been used in an interesting attempt to alter drastically the migration pattern of lesser white-fronted geese *Anser erythropus*, from Scandinavia[43]. Originally, this species travelled to winter quarters in SE Europe and the Middle East. In recent decades, the population has declined to the verge of extinction. In the current re-introduction project, young are released before fledging, with their barnacle goose *Branta leucopsis* foster parents, in suitable breeding regions in the Scandinavian mountains, for breeding site imprinting. They subsequently follow their foster parents to winter quarters in Holland. Several of the young have, after independence, successfully returned to the Scandinavian breeding region as well as to the winter quarters in Holland. At least one female raised under this scheme has already bred successfully and brought her brood and male to the new winter quarters (v. Essen[43], and unpubl. results).

Among waterfowl, pair formation typically takes place during the non-breeding season. Spring migration is led by the female of the pair. Females show a high degree of site fidelity, benefiting from being in familiar terrain because of their full responsibility for nest site selection and brood rearing[54, 78]. In contrast, males are not philopatric, and wide-ranging emigration to new breeding regions is a recurrent phenomenon (abmigration)[112].

Migration in flocks may improve the accuracy of orientation, either because flock direction represents the average of the individuals' directional tendencies, or because flock orientation is determined by the most competent leaders[21, 58, 124]. This is supported by some field observations[96, 122], and an experiment comparing the orientation of single homing pigeons and small flocks[120]. An earlier similar experiment failed to demonstrate a significant effect of flocking on orientation performance[65]. It has been proposed that nocturnal migrants improve their orientation by responding to flight calls, and possibly the associated Doppler shifts, from surrounding conspecifics[121].

Reorientation

Retreat migration in spring is a well-known case of reorientation. Early spring migrants reverse their flight direction in response to cold spells, with northerly winds and snow[119]. Svärdson[119] suspected that retreat migration involving insectivorous night-migrants, also occurs later in spring, and such movements have been documented in late May by radar studies in Canada, typically in association with northerly winds[100].

Spring retreat migration is closely related to 'hard-weather' winter movements, such as those described from the southern North Sea[36, 72] and Scandinavia[15]. In the former region, westward and southward departures take place during cold spells with easterly and northerly winds, respectively. Return flights follow almost immediately after the weather ameliorates and the wind changes back to the west or south. The birds may soon set out again in a subsequent spell of hard weather[72].

More complicated to explain is the reorientation of land birds which migrate over the eastern and western Atlantic Ocean in autumn, as recorded by radar and analysed by Myres[81] and Richardson[101], respectively. Over the Norwegian and the North Sea, nocturnal migrants from Scandinavia, which are over the sea at dawn, ascend to considerable heights (after having descended to fly low over the sea during the later part of the night) and reorient from SW to SE courses. Only birds within 16–24 km of the coast fly directly towards the nearest land after dawn[81]. Nocturnal migrants travelling SW off Nova Scotia ascend, aggregate, and reorient towards the NW at dawn. Reorientation mainly occurs in unfavourable cross/headwinds, while the birds often continue their offshore migration towards the SW on days with northerly winds[101]. Both authors concluded that most birds use cues other than landmarks for their reorientation perpendicular to the principal migratory direction. This behaviour has presumably evolved in populations migrating at the seaboard, as an adaptation for safely regaining contact with land when the birds find themselves over the open sea at dawn, not yet within close reach of the British Isles[81], or in winds unsuitable for a long southwesterly overwater flight[101].

To what extent the above-mentioned reorientation also serves to compensate for wind displacement is uncertain[16, 25, 101]. Orientation cage experiments on both sides of the Atlantic Ocean have been interpreted in favour of such wind compensation reorientation[1, 44]. Displacement experiments have demonstrated that adult but not juvenile starlings detected the removal and reoriented towards the original destination area[89]. There are some indications that juvenile night-migrating passerines also may show compensatory reorientation after artificial displacement[40, 92].

Two examples of reverse autumn migration in figure 3 show responses by land birds when confronted with a sea passage after having travelled a considerable distance over land in the normal SW migratory direction. The jay is an irruptive species, typically migrating slowly with very small fat deposits[13]. That jays and other irruptive species, like tits *Parus* spp., show extreme reluctance to

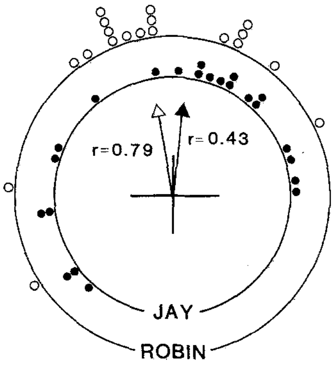

Figure 3. Circular distribution of recoveries of jay *Garrulus glandarius* and robin *Erithacus rubecula* ringed during autumn migration at Falsterbo, the southwesternmost point of Sweden. Data for the jay include autumn and winter recoveries, within approx. 4 months after ringing. Range of recovery distance was 23–645 km, with median 66 km[103]. Data for the robin include short-distance recoveries (< 300 km) a few days after ringing in Sept. and Oct. Range of recovery distance was 21–295 km, with median 36 km[103, 106]. Mean vectors show a significant reverse autumn orientation in both species ($p < 0.01$)[19].

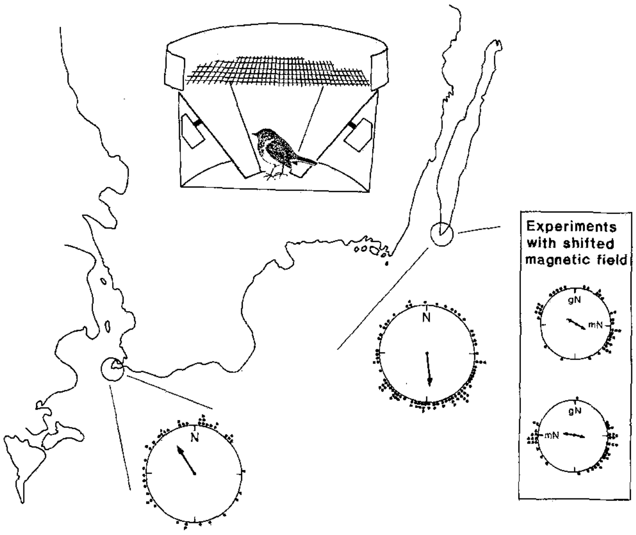

Figure 4. Autumn orientation, as demonstrated by orientation cage experiments, differed significantly between migrating robins captured at two nearby stopover sites (Falsterbo to the left, Ottenby to the right). Circular diagrams show mean headings of a large number of individuals tested shortly after sunset under simulated total overcast. Only at Ottenby did the robins clearly change their orientation with shifted magnetic fields. Based on Sandberg et al.[106, 107].

continue across even short sea passages, and that many return north to seek wintering opportunities in the adjoining hinterland may well be adaptive[103].

Also regular migrants among land birds frequently reorient before a sea passage[5]. In southern Sweden, chaffinches and bramblings fly NE from the coast and inland, i.e., opposite to the normal autumn migration direction[75]. The daily peak of reoriented finch migration at inland sites 20–40 km from the coast is on average 3.5 h later than the early morning departure in the normal migratory direction, and 1 h later than peak migration at the coast. Reoriented finches have smaller fat reserves than finches proceeding across the sea in the normal direction. By returning inland, lean birds can find suitable stopover sites for restoring fat reserves, and can avoid strong predation pressure and competition close to the coastline[75].

Orientation cage experiments revealed a marked difference in behaviour between robins captured during autumn migration at two nearby stopover sites in southern Sweden (fig. 4)[106]. Birds at both sites are on their way to the same winter region in SW Europe. Orientation behaviour as well as short-distance recoveries, one or only a few days after ringing, indicate that robins grounded at Falsterbo had temporarily reoriented towards northerly directions when confronted with the Baltic Sea after southwestward overland migration in southern Sweden (figs 3, 4). In contrast, most robins arrive at Ottenby by extensive flights across the Baltic Sea and rapidly continue their sea crossing in the normal migratory directions[106], responding to shifted magnetic fields (fig. 4)[107]. Ottenby robins had, on average, larger fat reserves than Falsterbo birds, and fat-weight relationships differed between the two groups[63].

Further explanations for reverse autumn migration have been reviewed by Richardson[102], including exploration[18], redetermined migration after overshooting, and downwind orientation. In addition, regaining of social bonds has been suggested as an explanation for reverse autumn migration by immature geese[99], and aerodynamic stability in upwind flight for reverse movements by gliding birds like swallows, swifts and raptors[98].

Misorientation

Rare migrant birds have aroused fascination among bird-watchers for more than a hundred years[48]. Most vagrants are juveniles on their first autumn migration, and many are encountered on isolated islands on the fringes of continents, like Helgoland[48] and many parts of the British Isles, not least Fair Isle[113, 114], in Northwest Europe; Nova Scotian Islands (Sable Island)[79] in East Canada; Farallon Islands[31], California; and Aleutian Islands[51], Alaska.

Vagrants have often misoriented thousands of kilometres, sometimes as much as 5000–7000 km, away from their normal migration route. The seasonal timing of their appearance strongly suggests that some have travelled in the wrong direction for a month or more at about the normal speed of migration during the regular migration period. In these cases, their appearance cannot be the result of accidental displacement by strong winds or disorientation in poor weather, but suggests consistent misorientation. Successful progress along the aberrant route is favoured by anticyclonic weather and frequent tailwinds[17, 62, 125]. American land birds appearing as vagrants in western Europe have certainly been carried by strong westerly winds across the Atlantic Ocean. Still, the time factor suggests that many of these transoceanic vagrants are misoriented, having flown actively towards the east[38, 82].

Misorientation may arise for physiological or genetic reasons, or because of environmental influences. Three types of internal mechanisms causing different patterns of misorientation have been suggested. Young birds often show a comparatively wide scatter of orientation, perhaps reflecting genetic variation in directional preferences, counteracted by stabilizing selection (cf. above). Genetically determined misorientation promotes rapid evolution of new migration patterns in response to changing environmental conditions[22]. Small angles of inherited compass deviations are expected to be much more frequent than large angles of misorientation. Ralph[97] estimated that 1–10% of juvenile passerine migrants in the coastal United States may perish because of offshore misorientation.

Reverse misorientation has been suggested by Rabøl[94] to occur as a result of reverse compass orientation or reverse great circle or biocoordinate navigation. 180°-misorientation may be related to polarity errors and axial orientation sometimes found in orientation cage experiments[3, 107], or to endogenous spring/autumn ambiguity.

In mirror-image misorientation, proposed by DeSante[30], the birds take the correct bearing with respect to the north-south axis, but select the wrong east-west (right-left) sense of that angle. Such an error may be linked to physiological impairment in left-right discrimination[32]. Rudebeck[105] pointed out SW/SE ambivalence in relation to migratory divides and the evolution of migration patterns.

The suggestions of reverse or mirror-image misorientation stem from the observation that in certain situations, specific large-angle misorientations seem more frequent than small or intermediate deviations from the normal migration course.

Environmentally induced misorientation has been suggested by Alerstam and Högstedt (unpubl.) on the basis of the magnetic calibration hypothesis[129] and an experiment showing differences in orientation between juvenile pied flycatchers *Ficedula hypoleuca* from nest-boxes with different regimes of horizontal magnetic direction[12]. According to this hypothesis, birds growing up where there is an anomalous magnetic declination learn an erroneous compass that will lead them astray during the forthcoming migration season. We compared vagrancy to Britain and Ireland[113, 114] of passerine species from easterly breeding ranges enclosing different areas of magnetic anomalies in the Soviet Union. The Soviet magnetic anomaly map shows important anomaly regions in the Ural Mountains, Central Siberian Plateau, SE Siberia and, most pronounced, in the Central Russian Uplands around the city of Kursk. The latter region constitutes one of the Earth's greatest anomalies; along strips of 250 km length, total magnetic field intensity is everywhere above normal, up to 190 μT (normal about 50 μT)[115]. We found a broad agreement between incidence of vagrancy and estimated magnetic anomaly indices for the species' breeding ranges.

Magnetic miscalibration may also occur close to the North Magnetic Pole (NMP) in Canada, where the horizontal field intensity is very weak and the magnetic compass erratic or useless. Indeed, Nearctic wader species with breeding ranges extending close to NMP, where horizontal magnetic field intensity is less than 1 μT (viz. *Pluvialis dominica*, *Calidris bairdii*, *C. fuscicollis*, *C. melanotos*, *Tryngites subruficollis*)[52], show a remarkable pattern of globe-trotting vagrancy (including a large number of records in northwest Europe)[113, 114], in contrast to most wader species from other parts of Canada. One might expect, on the basis of this hypothesis, that the risk for misorientation due to strong magnetic anomalies or the NMP would lead to a local reduction in breeding abundance of migratory birds in these areas. However, detailed inspection of air magnetic maps from an extensive region in northern Scandinavia with several strong magnetic anomalies reveals that magnetic declination diverges strongly from normal over at most 1/1000 of the area. Hence, the risk is very small, although on a continental scale a multitude of migrants may be affected. Proposed explanations for misorientation, as discussed above, remain speculative.

Disorientation

Many studies show that migrating birds are able to maintain an accurate orientation under a complete overcast sky[2, 40]. However, experimental releases have indicated that selection of the appropriate orientation may be seriously hampered by overcast conditions[76]. Adelie penguins rely on the sun for their orientation on featureless ice in Antarctica (fig. 1). When the sun was obscured by clouds, the penguins' departure bearings were scattered in all directions[39]. White-throated sparrows *Zonotrichia albicollis* released aloft and tracked by radar behaved differently depending on whether they were released under totally overcast or under clear starry skies. In the latter circumstances they rapidly selected departure bearings along straight tracks in the normal migration direction, whereas orientation ability deteriorated under overcast skies and the birds flew slowly along winding tracks[42].

Observations of free-flying diurnal as well as nocturnal migrants indicate that the scatter of orientation increases, approaching serious disorientation, during prolonged periods with the sky permanently overcast. Orientation improves again as soon as the sun or sunset becomes visible, even if only during a short period[41, 60, 123]. It remains to be clarified how these findings should be reconciled with the fact that homing pigeons can be trained to orient properly under completely overcast conditions, using a magnetic compass, and that an innate magnetic compass sense, allowing orientation in the migratory direction in the absence of visual cues, is widespread among birds[128].

Birds are capable of climbing or descending through clouds, and of flying some distance in or between cloud layers, without losing their orientation[57]. However, tracking radar studies have also revealed disoriented migrants in cloud[2, 57], indicating that birds fail to maintain their orientation for long in this situation. King[69] observed migrating land birds from a ship in fog. The birds flew towards the ship but soon departed in the normal migratory sector (99%) as long as visibility was about 1 km (no land or sky could be seen). During the first half hour after the fog closed down to about 150 m, 97% of the birds still departed in the same sector. However, during the succeeding 90 min, when the fog remained dense, the birds became completely disoriented. Only after the ship approached within 5 km of the nearest land were the migrants again able to orient accurately (towards land), in spite of the fact that the fog still remained as dense as before.

Widespread disorientation, with birds flying in random directions, their courses changing irregularly in zig-zags or circles, has been observed by radar in both Europe and North America[35, 36, 71]. These observations, mainly referring to land birds migrating over the sea, are typically associated with total cloud, fog, rain, stationary fronts and falls of migrants at the coast. Such disoriented movements occur on about 3.5% of September mornings and evenings and 11% of October mornings and evenings, according to four years of radar studies by Lack[71] in eastern England.

Disorientation may lead to catastrophic mortality, as exemplified by two recent occurrences in the southern Baltic Sea, where large numbers of victims were washed ashore (table)[9]. Estimates indicate that at least 20,000 migrants perished during the first instance of fatal disorientation in spring 1985, and the number of victims was probably of similar magnitude in autumn 1988. Surveillance radar films revealed echoes from disoriented migrants during these occurrences, although these movements were not prominent, presumably because disoriented birds descended to low altitudes over the sea and moved at slow speeds (unpubl.). Dead birds washed ashore represent only a fraction of all victims – small-sized species were probably grossly underrepresented because of consumption by gulls at sea[9].

A wide variety of diurnal as well as nocturnal migrants suffered from the catastrophic mortality over the Baltic Sea, and the fatal weather conditions (geomagnetic disturbance was small on both occasions) are of special interest (ref. 9 and unpubl.): 24–26 March 1985. Widespread fog, often dense with 100–200 m visibility, lasted almost permanently during three days, when warm and moist air from the west penetrated over the cold and icy waters of the Baltic Sea. Coastal weather stations reported weak winds at low latitude. Radiosonde data indicated fog/cloud up to about 400 m altitude in the southwestern part of the region, extending up to 1000 m further to the northeast. Simultaneously with disoriented movements,

Percent distribution of different species of migrating land birds washed ashore after fatal disorientation over the S Baltic Sea at two occasions during spring and autumn migration, respectively. In 1985 a total number of 288 dead land bird migrants were identified and counted at seven shoreline localitites, with mean density 35 inds/km (range 10–93 inds/km), and in 1988 59 victims were recorded at two localities with mean density 27 inds/km (17–37 inds/km). Single individuals (0.3%) in the 1985 sample are indicated by plus signs (based on Alerstam[9] and unpubl.)

Species		Mainly nocturnal/ diurnal migration	Spring migration 1985 (%)	Autumn migration 1988 (%)
Sparrowhawk	*Accipiter nisus*	D	1	–
Rough-legged buzzard	*Bueto lagopus*	D	–	5
Lapwing	*Vanellus vanellus*	D	3	–
Woodcock	*Scolopax rusticola*	N	2	–
Stock dove	*Columba oenas*	D	+	–
Wood pigeon	*Columba palumbus*	D	4	5
Tawny owl	*Strix aluco*	N	+	–
Long-eared owl	*Asio otus*	N	1	–
Short-eared owl	*Asio flammeus*	N	+	–
Sky lark	*Alauda arvensis*	D	5	3
Meadow pipit	*Anthus pratensis*	D	+	–
Robin	*Erithacus rubecula*	N	+	3
Blackbird	*Turdus merula*	N	1	17
Fieldfare	*Turdus pilaris*	D	1	5
Song thrush	*Turdus philomelos*	N	1	34
Redwing	*Turdus iliacus*	N	+	9
Mistle thrush	*Turdus viscivorus*	N	–	2
Jackdaw	*Corvus monedula*	D	4	3
Rook	*Corvus frugilegus*	D	66	12
Starling	*Sturnus vulgaris*	D	2	2
Chaffinch	*Fringilla coelebs*	D	6	–
Siskin	*Carduelis spinus*	D	+	–
			100	100

radar revealed well-directed ENE migration across the Baltic Sea, presumably taking place above the fog.

14–18 October 1988. Completely overcast conditions lasted throughout the period, with widespread, dense fog during a large fraction of the time. Low altitude winds were weak. Fog/cloud often extended up to 500 m, maximally all the way up to 4000 m altitude in the southwestern part of the area on one day, when rain or drizzle occurred in addition to the fog. Massive falls of nocturnal passerines were recorded at bird observatories in the area[64].

These observations indicate that mortality of disoriented birds may represent a significant cost of migration, especially for early spring and late autumn migrants. Although not migrating long distances, these land birds make sea crossings when there is a particularly grave risk of encountering widespread fog of long duration, and precipitation. Perhaps weak winds contribute to make orientation in fog extra difficult by preventing reference to sea waves or wind direction per se. Obviously, birds cannot orient effectively by the magnetic compass sense in these situations. Poor visibility in cloud or haze is also a critical factor when birds lose their orientation in the artificial illumination from lighthouses, gas flares, ceilometer lamps etc., as shown by circular radar tracks of birds flying near a lighted tower in cloud[74]. Magnetic disturbances, during magnetic storms or at locations of magnetic anomalies, may affect the orientation of homing pigeons as well as of migrating birds[128]. Whether such disturbances contribute to serious disorientation among departing migrants or migrants in flight remains to be demonstrated.

Importance of orientation for flight routes and timing

Migratory habits and pathways of different species and populations have evolved in relation to various environmental factors – where and when the migrants can find suitable living resources and flight conditions, and avoid hazards, predation and competition. Is the orientation capacity of birds flexible enough to allow flight routes and timing to be fully optimized, with respect to time, energy and safety, in relation to environmental factors alone? Or are there limitations in the orientation mechanisms that impose important constraints in this evolutionary process?

Kiepenheuer[68] suggested that migration routes with shifting course directions may be a direct consequence of the orientation mechanism. He proposed a special type of magnetic compass, by which flying birds orient at a constant apparent angle of inclination, i.e., the inclination of the magnetic field vector as projected on a plane orthogonal to the bird's trajectory or body axis. As a result, birds travel along curved magnetoclinic routes, characterized by a fixed angle of apparent inclination. However, according to a recent evaluation, this hypothesis fails to explain changing orientation by a thrush followed for 1500 km by radiotelemetry[28], responses by birds migrating across a strong magnetic anomaly[8], and flight routes of high arctic waders and geese[11].

Migration routes in the Arctic and Antarctic are of unique interest from the point of view of bird orientation and navigation. At high geographic and magnetic latitudes, the birds are faced with difficulties in using the sun compass (problems of time compensation during rapid longitudinal displacement) or star compass (stars not visible during the polar summer season) as well as the magnetic compass (an excessive declination and inclination make the geomagnetic field unreliable for orientation purposes within a wide region around the North and South Magnetic Poles).

Shorebirds, notably knots *Calidris canutus*, and brent geese *Branta bernicla* make long spring flights virtually non-stop from staging sites in Iceland to breeding areas on the Queen Elizabeth Islands[11], and from the Wadden Sea to breeding sites at Taimyr[33, 90, 91] (fig. 5). In both cases the birds travel rather close to the rhumbline route, with a constant geographic compass course, and not along the shortest great circle route. This is intriguing

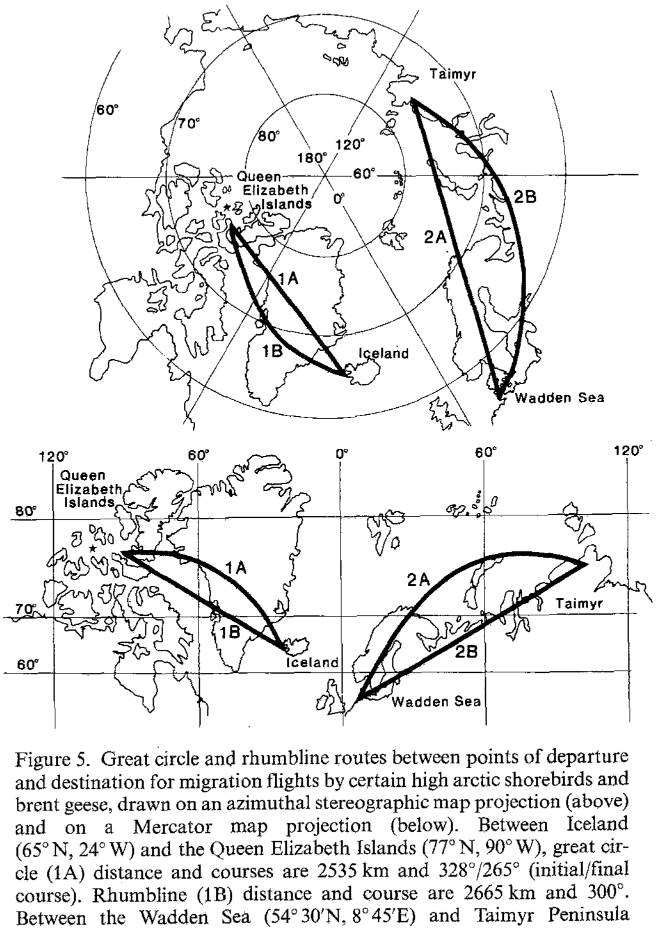

Figure 5. Great circle and rhumbline routes between points of departure and destination for migration flights by certain high arctic shorebirds and brent geese, drawn on an azimuthal stereographic map projection (above) and on a Mercator map projection (below). Between Iceland (65° N, 24° W) and the Queen Elizabeth Islands (77° N, 90° W), great circle (1A) distance and courses are 2535 km and 328°/265° (initial/final course). Rhumbline (1B) distance and course are 2665 km and 300°. Between the Wadden Sea (54° 30'N, 8° 45'E) and Taimyr Peninsula (76° N, 100° E), great circle (2A) distance and courses are 4234 km and 23°/110° (initial/final course). Rhumbline (2B) distance and course are 4634 km and 59°. Spring flight routes by the high arctic migrants are in agreement with rhumbline but not with great circle routes[11, 33, 90, 91]. The position of the North Magnetic Pole is indicated by a star.

since the great circle would seem to be the easiest option from an orientational point of view. At latitudes close to the north or south poles it holds as a good approximation that course changes along great circles are almost equal to the associated longitudinal displacements. Hence, birds could follow great circles by using their time-compensated sun compass, maintaining their internal clocks in phase with the time at the place of departure[11]. Adelie penguins use their sun compass with the internal circadian rhythm in phase with the time at the home longitude for their escape orientation (fig. 1)[39, 87].

Waders and geese travelling from Iceland to the Queen Elizabeth Islands have another possibility of orienting close to the great circle – by flying on a constant magnetic compass course close to north, i.e. towards the North Magnetic Pole, which is situated in the destination area[11]. Whether birds can use their magnetic compass under the extreme geomagnetic conditions close to the magnetic poles is an open question, but several studies indicate an acute degree of magnetic sensitivity in birds[128]. It remains unknown how birds orient along rhumblines at northerly latitudes, and whether orientation premises are important for the evolution of polar migration patterns.

There are several examples of long-distance migratory pathways which are, at least broadly, in agreement with great circle routes[6, 68]. Such pathways are advantageous, since the shortest route between two points on our globe is always along the great circle. Great circle orientation may seem complicated, because the birds must continuously change their courses. However, as pointed out above, at high latitudes birds will automatically travel close to great circles routes if they orient by their time-compensated sun compass, without resetting their internal clock in accordance with the time shift associated with longitudinal displacement. Actually, birds could use their sun compass in the same way for approximate great circle orientation at all latitudes if their internal time compensation mechanism takes into account the different rates of angular change of the sun's azimuth during the day[126], and if the birds migrate and orient mainly during the hours around sunset and sunrise.

Many birds do indeed depart on migration around sunset or sunrise, during transition periods between daylight and darkness that may be of critical importance for the integration of multiple orientation cues[41]. The departure of nocturnal passerine migrants is prominent on radar screens, starting on average 28–45 min after sunset, according to studies in North America and Europe[101]. Visual ceilometer observations showed that the first nocturnal passerines departed on average 38 min after sunset from a wooded island in Louisiana, with a peak of exodus 40–45 min after sunset[59]. Hence, departure occurred shortly after the end of local civil twilight (sun 6° below the horizon), about 30 min after sunset. On the basis of radiotelemetry data, Cochran[28] reported that on six nights a Swainson's thrush *Catharus ustulata* began migration 9–13 min after civil twilight, always after having perched high in a tree during the preceding twilight period. Initiation of migratory flights by thrushes also takes place at later hours, sometimes several hours after sunset, mainly depending on weather conditions[29].

Some species of nocturnal migrants which travel in flocks, like many shorebirds, terns and diving ducks, regularly initiate night migration during the hours preceding sunset[37]. The departure may be modified by feeding and roosting conditions according to the tidal cycle; waders prefer to depart during rising or high tide[11, 73]. Foraging possibilities, flight behaviour and atmospheric structure have been suggested as primary selection forces in the evolution of daily time schedules of migration[67].

In spite of the vast literature in the field of bird orientation, little is known about how and when free-flying migrants actually select and maintain their orientation. Increased knowledge about the complex and dynamic process of orientation will lead to a better understanding of routes and timing of migratory flights. Conversely, detailed analysis of flight routes under various celestial, weather, and magnetic conditions, and of behaviour and flight initiation by individual birds, is crucial in order to unravel the nature of the birds' orientation systems.

This work was supported by the Swedish Natural Science Research Council. I am grateful to Dr W. John Richardson for valuable comments on the manuscript. I thank Kerstin Persson for drawing the figures and Inga Rudebeck for typing the manuscript.

1 Able, K. P., The orientation of passerine nocturnal migrants following offshore drift. Auk *94* (1977) 320–330.
2 Able, K. P., The effect of overcast skies on the orientation of free-flying nocturnal migrants, in: Avian Navigation, pp. 38–49. Eds F. Papi and H. G. Wallraff. Springer-Verlag, Berlin 1982.
3 Able, K. P., and Bingman, V. P., The development of orientation and navigation behaviour in birds. Q. Rev. Biol. *62* (1987) 1–29.
4 Alerstam, T., Analysis and a theory of visible bird migration. Oikos *30* (1978) 273–349.
5 Alerstam, T., Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? Oikos *30* (1978) 405–408.
6 Alerstam, T., The course and timing of bird migration, in: Animal Migration, pp. 9–54. Ed. D. J. Aidley. Cambridge University Press, 1981.
7 Alerstam, T., Fågelflyttning. Signum, Lund 1982. (Engl. Edn: Bird Migration. Cambridge Univ. Press, in press).
8 Alerstam, T., Bird migration across a strong magnetic anomaly. J. exp. Biol. *130* (1987) 63–86.
9 Alerstam, T., Findings of dead birds drifted ashore reveal catastrophic mortality among early spring migrants, especially Rooks *Corvus frugilegus*, over the southern Baltic Sea (in Swedish with English summary). Anser *27* (1988) 181–218.
10 Alerstam, T., Bauer, C.-A., and Roos, G., Field- and radar studies of the spring migration of the Baltic eider *Somateria mollissima* (in Swedisch with English summary). Vår Fågelvärld *33* (1974) 15–27.
11 Alerstam, T., Gudmundsson, G. A., Jönsson, P. E., Karlsson, J., and Lindström, Å., Orientation, migration routes and flight behaviour of knots, turnstones and brent geese departing from Iceland in Spring. Arctic, in press.
12 Alerstam, T., and Högstedt, G., The role of the geomagnetic field in the development of birds' compass sense. Nature, Lond. *306* (1983) 463–465.
13 Alerstam, T., and Lindström, Å., Optimal bird migration: the relative importance of time, energy and safety, in: Bird Migration: The Physiology and Ecophysiology. Ed. E. Gwinner. Springer-Verlag, Berlin, in press.

14 Alerstam, T., and Pettersson, S.-G., Why do migrating birds fly along coastlines? J. theor. Biol. *65* (1977) 699–712.

15 Alerstam, T., and Ulfstrand, S., A radar study of winter bird movements in southern Scandinavia. Ornis scand. *5* (1974) 13–23.

16 Baird, J., and Nisbet, I. C. T., Northward fall migration on the Atlantic coast and its relation to offshore drift. Auk *77* (1960) 119–149.

17 Baker, K., Westward vagrancy of Siberian passerines in autumn 1975. Bird Study *24* (1977) 233–242.

18 Baker, R. R., The Evolutionary Ecology of Animal Migration. Hodder and Stoughton, London 1978.

19 Batschelet, E., Circular Statistics in Biology. Academic Press, London 1981.

20 Bellrose, F. C., Orientation behaviour of four species of waterfowl. Auk *80* (1963) 257–289.

21 Bergman, G., and Donner, K. O., An analysis of the spring migration of the common scoter and long-tailed duck in Southern Finland. Acta zool. fenn. *105* (1964) 1–59.

22 Berthold, P., Evolutionary aspects of migratory behavior in European warblers. J. evol. Biol. *1* (1988) 195–209.

23 Bingman, V. P., Able, K. P., and Kerlinger, P., Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. Anim. Behav. *30* (1982) 49–53.

24 Blomqvist, S., and Peterz, M., Cyclones and pelagic seabird movements. Mar. Ecol. Prog. Ser. *20* (1984) 85–92.

25 Bourne, W. R. P., The midnight descent, dawn ascent and re-orientation of land birds migrating across the North Sea in autumn. Ibis *122* (1980) 536–540.

26 Bruderer, B., Radar data on the orientation of migratory birds in Europe, in: Acta 17th Int. Orn. Congr., pp. 547–552. Ed. R. Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin 1980.

27 Bruderer, B., and Jenni, L., Strategies of bird migration in the area of the Alps, in: Acta 19th Int. Orn. Congr., pp. 2150–2161. Ed. H. Quellet. University of Ottawa Press, Ottawa 1988.

28 Cochran, W. W., Orientation and other migratory behaviours of a Swainson's thrush followed for 1500 km. Anim. Behav. *35* (1987) 927–929.

29 Cochran, W. W., Montgomery, G. G., and Graber, R. R., Migratory flights of *Hylocichla* thrushes in spring: a radiotelemetry study. Living Bird *6* (1967) 213–225.

30 DeSante, D. F., Vagrants: when orientation or navigation goes wrong. Point Reyes Bird Observ. Newsletter No. *61* (1983) 12–16.

31 DeSante, D. F., and Ainley, D. G., The avifauna of the South Farallon Islands, California. Studies in Avian Biol. No. 4 (1980) 104 pp.

32 Diamond, J. R., Mirror-image navigational errors in migrating birds. Nature, Lond. *295* (1982) 277–278.

33 Dick, W. J. A., Piersma, T., and Prokosch, P., Spring migration of the Siberian knot *Calidris canutus canutus*: results of a co-operative Wader Study Group project. Ornis scand. *18* (1987) 5–16.

34 Dorst, J., The Migrations of Birds. Heinemann, London 1962.

35 Drury, W. H., and Nisbet, I. C. T., Radar studies of orientation of songbird migrants in southeastern New England. Bird-Banding *35* (1964) 69–119.

36 Eastwood, E., Radar Ornithology. Methuen, London 1967.

37 Edelstam, C., The Visible Migration of Birds at Ottenby, Sweden. Vår Fågelvärld, Suppl. 7, Stockholm 1972.

38 Elkins, N., Nearctic landbirds in Britain and Iceland: a meteorological analysis. Br. Birds *72* (1979) 417–433.

39 Emlen, J. T., and Penney, R. L., Distance navigation in the Adelie penguin. Ibis *106* (1964) 417–431.

40 Emlen, S. T., Migration: orientation and navigation, in: Avian Biology, vol. 5, pp. 129–219. Eds D. S. Farner and J. R. King. Academic Press, New York 1975.

41 Emlen, S. T., Decision making by nocturnal bird migrants: the integration of multiple cues, in: Acta 17th Int. Orn. Congr., pp. 553–560. Ed. R. Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin 1980.

42 Emlen, S. T., and Demong, N. J., Orientation strategies used by free-flying bird migrants: a radar tracking study, in: Animal Migration, Navigation and Homing, pp. 283–293. Eds K. Schmidt-Koenig and W. T. Keeton. Springer-Verlag, Berlin 1978.

43 Essen, L. von, An effort to reintroduce the lesser white-fronted goose (*Anser erythropus*) into the Scandinavian mountains. Aquila *89* (1982) 103–105.

44 Evans, P. R., Reorientation of passerine night migrants after displacement by the wind. Br. Birds *61* (1968) 281–303.

45 Fliege, G., Das Zugverhalten des Stars (*Sturnus vulgaris*) in Europa: Eine Analyse der Ringfunde. J. Orn. *125* (1984) 393–446.

46 Fransson, T., The migration and wintering area of Nordic spotted flycatcher (in Swedish with English summary). Vår Fågelvärld *45* (1986) 5–18.

47 Füller, E., Kowalski, U., and Wiltschko, R., Orientation of homing pigeons: compass orientation vs piloting by familiar landmarks. J. comp. Physiol. A. *153* (1983) 55–58.

48 Gätke, H., Heligoland as an Ornithological Observatory. David Douglas, Edinburgh 1895.

49 Gauthreaux, S. A. Jr, The influence of global climatological factors on the evolution of bird migratory pathways, in: Acta 17th Int. Orn. Congr., pp. 517–525. Ed. R. Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin 1980.

50 Geyr von Schweppenburg, H., Zur Theorie der Leitlinie. Ardea *22* (1933) 83–92.

51 Gibson, D. D., Migrant birds at Shemya Island, Aleutian Islands, Alaska. Condor *83* (1981) 65–77.

52 Godfrey, W. E., The Birds of Canada. National Museums of Canada, Ottawa 1986.

53 Graue, L. C., The effect of phase shifts in the day-night cycle on pigeon homing at distances of less than one mile. Ohio J. Sci. *63* (1963) 214–217.

54 Greenwood, P. J., Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. *28* (1980) 1140–1162.

55 Griffin, D. R., Bird navigation. Biol. Rev. *27* (1952) 359–393.

56 Griffin, D. R., Bird Migration. Doubleday & Co., New York 1964.

57 Griffin, D. R., Oriented bird migration in or between opaque cloud layers. Proc. Am. phil. Soc. *117* (1973) 117–141.

58 Hamilton, W. J., Social aspects of bird orientation mechanisms, in: Animal Orientation and Navigation, pp. 57–71. Ed. R. M. Storm. Oregon State Univ. Press, Corvallis 1967.

59 Hebrard, J. J., The nightly initiation of passerine migration in spring: a direct visual study. Ibis *113* (1971) 8–18.

60 Hebrard, J. J., Fall nocturnal migration during two successive overcast days. Condor *74* (1972) 106–107.

61 Hedenström, A., and Pettersson, J., Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* ringed in Fennoscandia. Ornis fenn. *64* (1987) 137–143.

62 Howey, D. H., and Bell, M., Pallas's warblers and other migrants in Britain and Ireland in October 1982. Br. Birds *78* (1985) 381–392.

63 Karlsson, L., Persson, K., Pettersson, J., and Walinder, G., Fat-weight relationships and migratory strategies in the robin *Erithacus rubecula* at two stop-over sites in south Sweden. Ringing and Migration *9* (1988) 160–168.

64 Karlsson, L., Persson, K., and Walinder, G., The ringing at Falsterbo Bird Observatory in 1988 (in Swedish with English summary). Anser *28* (1989) 133–152.

65 Keeton, W. T., Comparative orientational and homing performances of single pigeons and small flocks. Auk *87* (1970) 797–799.

66 Kerlinger, P., Water-crossing behavior of raptors during migration. Wilson Bull. *97* (1985) 109–113.

67 Kerlinger, P., and Moore, F., Atmospheric structure and avian migration, in: Current Ornithology, vol. 6, pp. 109–142. Ed. D. M. Power. Plenum Publ. Corp., New York 1989.

68 Kiepenheuer, J., The magnetic compass mechanism of birds and its possible association with the shifting course directions of migrants. Behav. Ecol. Sociobiol. *14* (1984) 81–99.

69 King, J. M. B., Orientation of migrants over sea in fog. Br. Birds *52* (1959) 125–126.

70 Koskimies, J., The life of the swift, *Micropus apus*, in relation to the weather. Ann. Acad. Sci. Fenn. Series A, No. 15 (1950) 152 pp.

71 Lack, D., Radar evidence on migratory orientation. Br. Birds *55* (1962) 139–158.

72 Lack, D., Migration across the southern North Sea studied by radar. Part 5. Ibis *105* (1963) 461–492.

73 Lank, D. B., Why fly by night? Inferences from tidally-induced migratory departures of sandpipers. J. Field Orn. *60* (1989) 154–161.

74 Larkin, R. P., and Frase, B. A., Circular paths of birds flying near a broadcasting tower in cloud. J. comp. Psychol. *102* (1988) 90–93.

75 Lindström, Å., and Alerstam, T., The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. Behav. Ecol. Sociobiol. *19* (1986) 417–424.

76 Matthews, G. V. T., Bird Navigation. 2nd edn. Cambridge Univ. Press, 1968.

77 Matthews, G. V. T., 'Nonsense' orientation in mallard; a resumé and an investigation of the mechanism of a sun-compass. Wildfowl *35* (1984) 81–92.

78 McKinney, F., Ecological factors influencing the social systems of migratory dabbling ducks, in: Ecological Aspects of Social Evolution, pp. 153–171. Eds D. I. Rubenstein and R. W. Wrangham. Princeton Univ. Press 1986.

79 McLaren, I. A., The incidence of vagrant landbirds on Nova Scotian Islands. Auk *98* (1981) 243–257.

80 Moore, F. R., Age-dependent variability in the migratory orientation of the savannah sparrow (*Passerculus sandwichensis*). Auk *101* (1984) 875–880.

81 Myres, M. T., Dawn ascent and re-orientation of Scandinavian thrushes (*Turdus* spp.) migrating at night over the northeastern Atlantic Ocean in autumn. Ibis *106* (1964) 7–51.

82 Nisbet, I. C. T., American passerines in western Europe, 1951–62. Br. Birds *56* (1963) 204–217.

83 Olsson, V., Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus*. Acta Vertebr. *1* (1958) 91–189.

84 Oring, L. W., Dispersal of juvenile spotted sandpipers: distance, sex bias, and consequences, in: Acta 19th Int. Orn. Congr., pp. 575–584. Ed. H. Quellet. University of Ottawa Press, Ottawa 1988.

85 Österlöf, S., Migration, wintering areas, and site tenacity of the European osprey *Pandion h. haliaetus*. Ornis scand. *8* (1977) 61–78.

86 Palmén, J. A., Om fåglarnas flyttningsvägar. Frenckell & Son. Helsinki 1874. (German translation: Über die Zugstrassen der Vögel. Leipzig 1876).

87 Penney, R. L., and Emlen, J. T., Further experiments on distance navigation in the Adelie penguin *Pygoscelis adeliae*. Ibis *109* (1967) 99–109.

88 Pennycuick, C. J., Fifteen testable predictions about bird flight. Oikos *30* (1978) 165–176.

89 Perdeck, A. C., Two types of orientation in migrating starlings *Sturnus vulgaris* and chaffinches *Fringilla coelebs*, as revealed by displacement experiments. Ardea *46* (1958) 1–37.

90 Prokosch, P., Population, Jahresrhythmus und traditionelle Nahrungsplatzbedingungen der dunkelbäuchigen Ringelgans (*Branta b. bernicla*) im Nordfriesischen Wattenmeer. Ökol. Vögel *6* (1984) 1–99.

91 Prokosch, P., Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet arktischer Watvogelpopulationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*), Knutt (*Calidris canutus*) und Pfuhlschnepfe (*Limosa lapponica*). Corax *12* (1988) 273–442.

92 Rabøl, J., Displacement experiments with night-migrating passerines. Z. Tierpsychol. *30* (1972) 14–25.

93 Rabøl, J., Correlation between coastal and inland migratory movements. Dansk orn. Foren. Tidsskr. *68* (1974) 5–14.

94 Rabøl, J., The orientation of Pallas's leaf warbler *Phylloscopus proregulus* in Europe. Dansk orn. Foren. Tidsskr. *70* (1976) 5–16.

95 Rabøl, J., One-direction orientation versus goal area navigation in migratory birds. Oikos *30* (1978) 216–223.

96 Rabøl, J., and Noer, H., Spring migration in the skylark (*Alauda arvensis*) in Denmark. Vogelwarte *27* (1973) 50–65.

97 Ralph, C. J., Disorientation and possible fate of young passerine coastal migrants. Bird-Banding *49* (1978) 237–247.

98 Ramel, C., The influence of the wind on the migration of swallows, in: Proc. 12th Int. Orn. Congr., pp. 626–630. Eds G. Bergman, K. O. Donner and L. v. Haartman. Tilgmannin Kirjapaino, Helsinki 1960.

99 Raveling, D. G., Migration reversal: a regular phenomenon of Canada geese. Science *193* (1976) 153–154.

100 Richardson, W. J., Spring migration and weather in eastern Canada: a radar study. Am. Birds *25* (1971) 684–690.

101 Richardson, W. J., Reorientation of nocturnal land bird migrants over the Atlantic Ocean near Nova Scotia in autumn. Auk *95* (1978) 717–732.

102 Richardson, W. J., Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. Behav. Ecol. Sociobiol. *10* (1982) 193–206.

103 Roos, G., Migration, wintering and longevity of birds ringed at Falsterbo (1947–1980). (in Swedish with English summary). Anser, Suppl. 13, Lund 1984.

104 Rudebeck, G., Studies on bird migration. Based on field studies in southern Sweden. Vår Fågelvärld, Suppl. 1, Lund 1950.

105 Rudebeck, G., Some aspects on bird migration in the western Palaearctic region, in: Bertil Hanström Zoological Papers, pp. 257–268. Ed. K. G. Wingstrand. Zoological Institute, Lund 1956.

106 Sandberg, R., Pettersson, J., and Alerstam, T., Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? Anim. Behav. *36* (1988) 865–876.

107 Sandberg, R., Pettersson, J., and Alerstam, T., Shifted magnetic fields lead to deflected and axial orientation of migrating robins, *Erithacus rubecula*, at sunset. Anim. Behav. *36* (1988) 877–887.

108 Saurola, P., The migration routes of Finnish Common Buzzards (In Finnish with English summary). Lintumies *12* (1977) 45–53.

109 Saurola, P., Ringing and recoveries of Finnish Ravens, *Corvus corax* (in Finnish with English summary). Lintumies *12* (1977) 118–123.

110 Schmid, H., Steuri, T., and Bruderer, B., Zugverhalten von Mäusebussard *Buteo buteo* und Sperber *Accipiter nisus* im Alpenraum. Orn. Beob. *83* (1986) 111–134.

111 Schüz, E., Überblick über die Orientierungsversuche der Vogelwarte Rossitten (jetzt: Vogelwarte Radolfzell), in: Proc. 10th Int. Orn. Congr., pp. 249–268. Ed. S. Hörstadius. Almqvist & Wiksell, Uppsala 1951.

112 Schüz, E., Grundriss der Vogelzugkunde. Verlag Paul Parey, Berlin 1971.

113 Sharrock, J. T. R., Scarce Migrant Birds in Britain and Ireland. T. & A. D. Poyser, Berkhamsted 1974.

114 Sharrock, J. T. R., and Sharrock, E. M., Rare Birds in Britain and Ireland. T. & A. D. Poyser, Berkhamsted 1976.

115 Skiles, D. D., The geomagnetic field. Its nature, history and biological relevance, in: Magnetite Biomineralization and Magnetoreception in Organisms, pp. 43–102. Eds J. L. Kirschvink, D. S. Jones and B. J. MacFadden. Plenum Press, New York 1985.

116 Søgård, S., and Østerby, G., Autumn migration of honey buzzard, *Pernis apivorus*, at Falsterbo 1977–86 (in Swedish with English summary). Vår Fågelvärld *48* (1989) 191–201.

117 Stolt, B.-O., What is the migratory direction through Europe of ortolan buntings, *Emberiza hortulana*, from Scandinavia and Finland (In Swedish with English summary). Vår Fågelvärld *46* (1987) 48–53.

118 Svärdson, G., Swift (*Apus apus*) movements in summer, in: Proc. 10th Int. Orn. Congr., pp. 335–338. Ed. S. Hörstadius. Almquist & Wiksell, Uppsala 1951.

119 Svärdson, G., Visible migration within Fenno-Scandia. Ibis *95* (1953) 181–211.

120 Tamm, S., Bird orientation: single homing pigeons compared with small flocks. Behav. Ecol. Sociobiol. *7* (1980) 319–322.

121 Thake, M. A., A simple model for the use of Doppler shifted vocalisations by migrating birds. Vogelwarte *32* (1983) 33–39.

122 Thake, M. A., Flock size and orientation accuracy of refuging wagtail (*Motacilla alba*) flocks. Ökol. Vögel *6* (1984) 127–130.

123 Tinbergen, L., Field observations of migration and their significance for the problems of navigation. Ardea *44* (1956) 231–235.

124 Wallraff, H. G., Social interrelations involved in migratory orientation of birds: possible contribution of field studies. Oikos *30* (1978) 401–404.

125 Wheeler, D., The meteorological background to Siberian passerine vagrancy in Northumbria, October 1982. Trans. nat. Hist. Soc. Northumbria *54* (1985) 23–30.

126 Wiltschko, R., Die Sonnenorientierung der Vögel. J. Orn. *121* (1980) 121–143, and *122* (1981) 1–22.

127 Wiltschko, W., and Balda, R. P., Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*) J. comp. Physiol. A. *164* (1989) 717–721.

128 Wiltschko, W., and Wiltschko, R., Magnetic orientation in birds, in: Current Ornithology, vol. 5, pp. 67–121. Ed. R. F. Johnston. Plenum Publ. Corp., New York 1988.

129 Wiltschko, W., Wiltschko, R., Keeton, W. T., and Madden, R., Growing up in an altered magnetic field affects the initial orientation of young homing pigeons. Behav. Ecol. Sociobiol. *12* (1983) 135–142.

0014-4754/90/040405-11$1.50 + 0.20/0