Bird orientation at high latitudes: flight routes between Siberia and North America across the Arctic Ocean

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Bird migration and orientation at high latitudes are of special interest because of the difficulties associated with different compass systems in polar areas and because of the considerable differences between flight routes conforming to loxodromes (rhumb lines) or orthodromes (great circle routes). Regular and widespread east-north-east migration of birds from the northern tundra of Siberia towards North America across the Arctic Ocean (without landmark influences) were recorded by ship-based tracking radar studies in July and August. Field observations indicated that waders, including species such as *Phalaropus fulicarius* and *Calidris melanotos*, dominated, but also terns and skuas may have been involved. Analysis of flight directions in relation to the wind showed that these movements are not caused by wind drift. Assuming possible orientation principles based on celestial or geomagnetic cues, different flight trajectories across the Arctic Ocean were calculated: geographical loxodromes, sun compass routes, magnetic loxodromes and magnetoclinic routes. The probabilities of these four alternatives are evaluated on the basis of both the availability of required orientation cues and the predicted flight paths. This evaluation supports orientation along sun compass routes. Because of the longitudinal time displacement sun compass routes show gradually changing compass courses in close agreement with orthodromes. It is suggested that an important migration link between Siberia and North American stopover sites 1000–2500 km apart across the Arctic Ocean has evolved based on sun compass orientation along orthodrome-like routes.

Keywords: bird orientation; bird migration; bird flight routes; sun compass; magnetic compass; great circle orientation

1. INTRODUCTION

The orientation of migrating birds is based on celestial (the sun, skylight polarization patterns and the stars) and geomagnetic cues, as demonstrated by many experiments with birds in orientation cages (Berthold 1991; Wiltschko & Wiltschko 1995). However, it is still unknown how birds use their compass systems on actual migratory flights.

Orientation at high latitudes (in this paper we adopt a Northern Hemisphere perspective, but the general reasoning is equally relevant for polar latitudes in the Southern Hemisphere) presents special difficulties (Alerstam 1990). Stars are not readily visible during the light nights in the polar summer season which is when most bird migration takes place in these regions. The time-compensated sun compass is sensitive to the time-shift associated with longitudinal displacement (as long as the internal clock is not reset to the new local time) and such displacement may be substantial during migratory flights at high latitudes where distances between longitudes are small. Orientation by the birds' magnetic compass will be affected by rapid changes in the magnetic

declination at high latitudes as well as by a very steep angle of inclination close to the magnetic pole.

Flight routes at high latitudes are of special interest for yet another reason. It is at these latitudes that great circle routes (orthodromes) bring the most substantial reductions in distance and, thus, have a distinct selective advantage relative to rhumb line routes (loxodromes; cf. Gudmundsson & Alerstam 1998a; Alerstam 1999). Great circle orientation involves continuously changing compass courses as successive lines of longitudes are intersected, while loxodromes are associated with constant compass courses.

We used tracking radar on board an expedition ship moving along the North-East Passage to record the post-breeding migration pattern during July and August 1994 of tundra birds along the Eurasian coast of the Arctic Ocean. The general results are presented in Alerstam & Gudmundsson (1999). In this analysis we focus on departures from the Siberian tundra with geographical directions in the sector between north and east (mainly between 60 and 90°). Such movements were of wide-ranging and regular occurrence in a vast longitudinal sector 113–170° E over the Laptev and East Siberian Seas (at latitude 70–76° N).

The majority of migrants recorded along the North-East Passage, east of the Taymyr Peninsula, travelled on

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east-south-east courses broadly in parallel with the north Siberian coast. Hence, these migrants may have been influenced by the topography for their orientation (Alerstam & Gudmundsson 1999). In contrast, the movements evaluated in this study were heading far out over the Arctic Ocean where it is reasonable to assume that the birds are guided by compass systems without landmark influences. Field observations indicated that the grey phalarope *Phalaropus fulicarius* and pectoral sandpiper *Calidris melanotos* were among the species taking part in the east-north-east migration from Siberia. It is likely that additional wader species and possibly also terns and skuas participated in these movements (Alerstam & Gudmundsson 1999).

Our objective in this study was to extrapolate the observed directions from Siberia and calculate the predicted flight trajectories across the Arctic Ocean assuming the use of different compass mechanisms by the birds. Hence, we will consider predicted flight routes if the birds travel on constant celestial or magnetic compass courses along geographical or magnetic loxodromes, respectively. We will also consider the celestial and magnetic compass mechanisms that have been suggested to allow birds to travel along orthodrome-like routes—sun compass orientation without compensation for the longitudinal time-shift (Alerstam & Pettersson 1991) and orientation along ‘magnetoclinic’ routes with a constant apparent angle of magnetic inclination (Kiepenheuer 1984).

In this paper we will first demonstrate the occurrence of migration in the north-east sector, as recorded by tracking radar off the north coast of Siberia and analyse these movements in relation to the wind. We will then proceed to evaluate and compare predicted flight trajectories mapped on Mercator and gnomonic projections (Gudmundsson & Alerstam 1998a) in order to draw conclusions about the most likely routes and orientation principles used by the birds on their long-distance flights across the Arctic Ocean from Siberia towards North America.

2. METHODS AND STUDY AREA

Migratory flights of birds were recorded along the Eurasian coast of the Arctic Ocean between 40 and 170° E by a tracking radar on board the ship *Akademik Fedorov* during the Swedish–Russian Tundra Ecology-Expedition-94 (Grönlund & Melander 1995). The radar was operated only when the ship was stationary, normally in pack ice 10–100 km off the nearest tundra shores. The position of the target was recorded (and stored by computer) every 2 s by the radar (3 cm wavelength, 200 kW peak power, 0.5 μ s pulse duration and 1.65° nominal pencil beam width) which was operated in automatic tracking mode. Flocks of migrating birds were tracked between 30 s and 20 min, on average 3–4 min, within 10–12 km range from the radar. The wind direction and speed at the altitudes where the birds were flying were measured by radar tracking of helium balloons with aluminium foil reflectors. The heading direction and air speed were calculated by subtraction of the wind vector from the target’s track vector (track direction and ground speed). Further information about radar tracking and evaluation methods are given in Alerstam & Gudmundsson (1999).

The means and scatters of the directional data were calculated as mean vectors and angular deviations according to

Batschelet (1981). We used the Mercator and gnomonic map projections to plot the predicted flight trajectories with calculation of the coordinates as described by Gudmundsson & Alerstam (1998a).

In this paper we consider radar observations from the ten different sites that were situated east of longitude 110° E. The place names, coordinates and dates are given in table 1 (see also the map in Alerstam & Gudmundsson (1999)). Post-breeding migration of tundra birds was also recorded by radar at five sites to the west of 110° E, but no significant north-eastward migration over the Arctic Ocean took place at these sites (Alerstam & Gudmundsson 1999).

3. EAST-NORTH-EAST MIGRATION FROM SIBERIA

Tracks in the north-east sector (0–90°) were recorded at nine out of the ten radar sites and their numbers and directional distribution are shown in table 1. A total of 177 tracks in the north-east sector comprised 22% of the grand total of 803 radar tracks recorded at the ten sites. The majority of all tracks were directed in the south-east sector (69%), while only 9% were in the south-west and north-west quadrants (Alerstam & Gudmundsson 1999). As seen from table 1, north-east migration made up a substantial fraction (24–41%) of the total migration at seven of the ten sites. There were only a few scattered tracks in the 0–50° sector, while migration towards 50–90° was of a more widespread and regular occurrence (table 1). Below, we have calculated the predicted trajectories for three directions (60, 75 and 90°) within this latter sector.

The mean altitude of north-east migration was 1222 m (s.d. = 756 m and $n=177$), with the highest altitude at 4106 m. Fifty per cent of the tracks were recorded at altitudes of 0–1 km, 34% at 1–2 km, 14% at 2–3 km and 2% above 3 km.

The mean vertical speed (V_z) was $+0.15 \text{ m s}^{-1}$ (s.d. = 0.37 m s^{-1} and $n=146$) and more flocks were recorded in climbing flight (69%) than in descending flight (31%). However, the majority of flights (75%) were close to level with a V_z of between -0.4 and 0.4 m s^{-1} . In 19% of cases the birds were climbing at $V_z > 0.4 \text{ m s}^{-1}$ (maximum 1.34 m s^{-1}) and in 6% of cases they were descending at $V_z < -0.4 \text{ m s}^{-1}$ (minimum -1.06 m s^{-1}).

The distribution of the air speeds shows a well-defined peak, with 85% in the range of 8–18 m s^{-1} and an overall mean at 13.5 m s^{-1} (s.d. = 3.5 m s^{-1} and $n=161$). In comparison, the distribution of the ground speeds shows a wider scatter (with 91% in the range of 12–32 m s^{-1}) and a larger mean at 20.6 m s^{-1} (s.d. = 6.6 m s^{-1} and $n=177$). This difference between the mean ground and air speeds ($+7.1 \text{ m s}^{-1}$) reflects the free gain in speed that the migrants obtained from the winds, because they were most often flying in following winds. In fact, 81% of all recorded flocks benefited from the wind with ground speeds exceeding air speeds, while wind reduced the resulting speed in the remaining 19% of cases. The migrants generally experienced wind speeds in the range of 2–20 m s^{-1} (91%), with an overall mean wind speed at 10.2 m s^{-1} (s.d. = 6.2 m s^{-1} and $n=161$).

The means and scatters of the track, heading and wind directions are given in table 2 for the total sample of north-east migration, as well as for the subsamples with winds blowing from the left (with track minus heading

Table 1. *Number of tracks of birds migrating with directions in the north-east sector (0–90°) as recorded by a ship-based tracking radar at ten sites along the North-East Passage in eastern Siberia during July and August 1994*

(The study sites are listed according to their longitudinal position from west to east. The proportion (%) of tracks in the north-east sector in relation to the total number of tracks recorded at each study site is also given.)

site	latitude (°N)	longitude (°E)	date	number of tracks in north-east sector				
				0–30°	30–60°	60–90°	total north-east	% north-east
East Taymyr	76.5	113.5	10–12 August	—	2	9	11	27
South-East Taymyr	74.7	115.6	4–5 July	—	—	2	2	3
Olenyoksi Bay	74.4	119.9	6–8 July	—	2	6	8	24
New Siberian Islands, Kotelyny	74.7	137.8	31 July–2 August	1	6	21	28	24
Yana	72.4	138.9	3–6 August	3	7	25	35	33
New Siberian Islands, Novaya Sibir	75.7	147.3	11 July	—	1	11	12	41
Indigirka	72.3	152.3	14–15 July	—	—	6	6	6
Kolyma	70.8	162.9	18 July	—	—	28	28	39
Ayon Island	70.3	168.4	20 July	—	—	—	0	—
Cape Shelagski	70.3	170.5	22–26 July	—	12	35	47	29
all sites	—	—	—	4	30	143	177	22

Table 2. *Means and scatters of track, heading and wind directions for migration in the north-east sector (0–90°) as recorded by radar along the North-East Passage in Siberia*

	all winds ($n = 161^a$)		winds from left ($n = 58$)		winds from right ($n = 103$)	
	mean vector	angular deviation	mean vector	angular deviation	mean vector	angular deviation
track direction	72°	16°	67°	20°	74°	12°
heading direction	79°	30°	51°	31°	92°	18°
wind direction	239°	43°	275°	39°	221°	36°

^a For track direction, $n = 177$.

direction positive) and right (with track minus heading direction negative) of the flight direction, respectively. The comparison of directions with winds from the left and right serves to investigate whether the migrants are liable to wind drift (as indicated by constant heading direction in left and right winds and track direction shifted with the wind) or whether they compensate for wind drift (as indicated by constant track direction in left and right winds and heading direction shifted into the wind). As seen from table 2, the average track direction is very similar in winds from the left and right (median test $\chi^2 = 3.38$, d.f. = 1 and $p > 0.05$), and the small difference between the two subsamples is in the opposite direction to that expected with wind drift. In contrast, the mean heading direction is clearly different between the two subsamples (median test $\chi^2 = 69.1$, d.f. = 1 and $p < 0.001$) and shifted into the wind as expected with compensation for wind drift. This pattern of compensation for wind drift is confirmed by relating the track and heading directions to the angle between the track and heading direction and calculating the regression slopes b and $b - 1$, respectively, as described in Alerstam & Gudmundsson (1999). The expected result is $b = 0$ for complete compensation and $b = 1$ for full wind drift. The coefficient b is -0.06 for north-east migration (s.e. = 0.06, 95% confidence interval -0.17 to 0.05 and $n = 156$ considering

track minus heading angles of between -60 and $+60^\circ$), which conforms with complete compensation for wind drift but is significantly different from the expected value with full drift.

North-east migration usually took place in fine weather with sunshine, only partial cloudiness and excellent visibility. On some occasions the birds were migrating above low-level fog, which was, however, seldom compact. Hence, they usually had access to a good view of the pack-ice pattern in the Arctic Ocean, possibly facilitating compensation for wind drift.

4. PREDICTED FLIGHT TRAJECTORIES WITH DIFFERENT ORIENTATION PRINCIPLES

The predicted flight trajectories are illustrated for four different cases of orientation principles in figures 1*a,b* and 2*a,b*, respectively. Trajectories have been extrapolated for three different geographical courses of 60, 75 and 90° (for only two courses in figure 2*b*) from a position at 76° N, 150° E, which is close to one of the study sites, just north of the New Siberian Islands (cf. table 1).

The Mercator projection used in these illustrations shows correct geographical course angles relative to the latitude–longitude grid, but is greatly distorted with respect to distance and area (Gudmundsson & Alerstam

Figure 1. Flight trajectories extrapolated from 76° N, 150° E in Siberia (for three initial geographical compass courses at 60, 75 and 90°) according to possible orientation principles by celestial cues on a Mercator map projection. (a) Geographical loxodromes. (b) Sun compass routes.

1998a). Isolines showing the magnetic declination and inclination (Peddie 1993) are included in the illustrations of routes based on orientation by geomagnetic cues (figure 2a,b).

(a) *Geographical loxodromes*

Birds may maintain constant geographical courses and orientate along geographical loxodromes by their star compass (Emlen 1975) or by their sun compass if they compensate for the longitudinal time-shift (e.g. on the basis of the rate of change of sun altitude, as suggested by Sandberg & Holmquist (1998)). Flights along geographical loxodromes would lead the birds towards the most northerly high Arctic islands of Canada or even north of Canada and Greenland (figure 1a) in a spiral towards the North Pole. These routes are highly unlikely. Furthermore, daylight prevailed throughout the Arctic summer days when east-north-east migration from Siberia took place, making the use of a star compass (stars were never visible to the human eye) highly improbable.

(b) *Sun compass routes*

Using the time-compensated sun compass without adjusting for the longitudinal time-shift would lead birds along courses that change by, on average, 1° for each degree of longitude transected. At high latitudes this rate of course change would be very steady, with negligible daily and seasonal variation. However, below latitude 50–60° this variation will be significant (Alerstam & Pettersson 1991).

Courses along ideal great circle routes do not change quite so much with longitudinal displacement as do courses along the predicted sun compass routes, but at

Figure 2. Flight trajectories extrapolated from 76° N, 150° E in Siberia (for three initial geographical compass courses at 60, 75 and 90°) according to possible orientation principles by geomagnetic cues on a Mercator map projection.

(a) Magnetic loxodromes. (b) Magnetoclinic routes according to Kiepenheuer's (1984) model. Isomagnetics for declination and inclination (Peddie 1993) are also indicated in (a) and (b), respectively.

high latitudes this difference is negligible (Alerstam & Pettersson 1991). This means that the trajectories in figure 1b are very similar to great circle routes, giving the shortest distance between points of departure and arrival on the spherical surface of the Earth.

As seen from figure 1b, sun compass routes with geographical courses of 60–90° at the New Siberian Islands lead towards the southern shores of the Beaufort Sea. These routes seem to be entirely feasible for a safe and efficient migration step directly from Siberia to North America. Ideal great circle routes all the way from Siberia to the winter quarters of grey phalaropes and pectoral sandpipers in South America are associated with departure directions from Siberia at around 60 and 36°, respectively. This means that if these species use the sun compass routes in figure 1b for a first migratory step from Siberia to North America, they generally travel a bit to the south of ideal great circle routes to their final destinations (possibly for stopover or safety reasons) and they must adjust their preferred orientation accordingly at some later stage during migration.

As pointed out above, the sun was generally available as a cue for the migrants during their flights across the Arctic Ocean. The distances from the New Siberian Islands to the coast of North America along the routes in figure 1b are 1500–2500 km, which would be covered by the birds in 20–35 h if they flew non-stop by the average ground speed recorded in this study. It is highly unlikely that birds could reset their internal clock to new local times as they move across the longitudes during such a

flight. Resetting the internal clock to a new daily cycle is a process which takes three to six days to accomplish experimentally in starlings and homing pigeons (Hoffman 1954; Schmidt-Koenig 1958), but this resynchronization time may be shorter for smaller differences between the clock and ambient time and for birds in a hormonal status associated with migratory restlessness (Gwinner 1996). If birds stop along the route and reset their internal clock in phase with the new local time, the original geographical course will be restored on their sun compass (if the preferred orientation remains unchanged). To avoid this and to continue along the same sun compass routes after such a resetting of the internal clock, the migrants must temporarily transfer the local course angle at the stopover locality from the sun compass to other cue systems as described by Alerstam & Pettersson (1991). The possibilities for birds to continue along orthodrome-like routes at more southerly latitudes (below latitude 50–60°) by time-compensated celestial (sun and star) compass orientation have been demonstrated by Alerstam & Pettersson (1991).

(c) *Magnetic loxodromes*

If the birds maintain constant magnetic compass courses according to their inclination compass (Wiltschko & Wiltschko 1995) they are expected to travel along magnetic loxodromes as shown in figure 2a. The magnetic declination at the starting position for the trajectories plotted in figures 1 and 2 is 10.5° W, meaning that the geographical compass courses 60, 75 and 90° correspond to magnetic compass courses of 70.5, 85.5 and 100.5°, respectively.

The magnetic loxodromes lead across the Arctic Ocean towards the south-easterly coasts of the Beaufort Sea, i.e. towards more easterly and northerly Nearctic regions in comparison with the sun compass routes (figure 2a). As long as declination increases towards the east, the magnetic loxodromes curve in a distance-saving manner (but less efficiently than the sun compass routes; cf. figure 3). However, east of longitude 135–120° W, where declination changes in the opposite direction as one moves towards the east, the magnetic loxodromes curve in a highly unfavourable way with the two northerly trajectories spiralling towards the magnetic North Pole (which is situated at ca. 78° N, 104° W). Consequently, orientation along magnetic loxodromes may serve to guide the migrants across the Arctic Ocean, but only as far as the very shores of the Beaufort Sea, where the migrants must abolish these routes and change their orientation.

Another possible problem with orientation along magnetic loxodromes across the Arctic Ocean is the steep angle of magnetic inclination (82–86°) in this area (cf. figure 2b). It is not known for certain whether birds can use their magnetic compass under such extreme conditions (cf. Sandberg *et al.* 1991, 1998; Åkesson *et al.* 1995), although indications of proper orientation without access to celestial cues have been demonstrated for snow buntings (*Plectrophenax nivalis*) in cage experiments at a site 400 km from the magnetic North Pole, with an inclination angle of 89° (Sandberg *et al.* 1998).

(d) *Magnetoclinic routes*

Kiepenheuer (1984) suggested that migrating birds may orientate along magnetoclinic routes with a constant

Figure 3. Flight trajectories along geographical loxodromes (blue), magnetic loxodromes (green) and sun compass routes (red) extrapolated from 76° N, 150° E in Siberia (with the same three initial geographical compass courses at 60, 75 and 90°, respectively) on a gnomonic map projection.

apparent angle of inclination (the angle of magnetic inclination projected on a plane perpendicular to the bird's flight direction). This suggestion is purely hypothetical, since there are no experimental data to indicate that birds are sensitive to the apparent angle of inclination. However, the proposed compass mechanism affords a possible explanation for orientation along orthodrome-like routes for a number of bird species and populations (Kiepenheuer 1984).

The apparent angle of geomagnetic inclination is a function of both the magnetic inclination and the magnetic compass direction. With an angle of inclination at 83.6° and a declination at 10.5° W at the New Siberian Islands (figure 2), the apparent angles of inclination are 83.96, 83.62 and 83.71° for the three geographical courses 60, 75 and 90°, respectively. The predicted trajectories of the first two routes, with initial magnetic courses slightly north of east, are very similar and only the case with 75° initial geographical direction is shown in figure 2b. Birds following this route will become 'trapped' into travelling on easterly magnetic courses (or only marginally north of east) until this leads to an invalid situation with the actual angle of inclination exceeding the apparent angle. In contrast, for the case with an initial magnetic course south of east, the migrants will respond by veering right to maintain their apparent angle of inclination constant and the predicted route will curve very rapidly towards the south as shown in figure 2b.

Consequently, for migratory departures from Siberia, Kiepenheuer's (1984) model produces invalid routes and disruptions between the predicted trajectories depending on minor differences in the magnetic compass courses. Kiepenheuer (1984) noted the potential inadequacy of his model for certain migration patterns of Arctic birds and he pointed out that some further mechanism is called for to initiate changes from due easterly or westerly magnetic directions.

5. CONCLUSIONS

The widespread departures of migrating birds from the northern tundra of Siberia towards the sector 60–90° across the Arctic Ocean, as documented by tracking radar studies, present a challenging problem with respect to the orientation mechanisms and routes used by the birds. We have shown that, in all probability, these movements are not caused by wind drift. We also consider it highly unlikely that these movements are temporary and random deviations from an intended orientation in the east-south-east sector, reflecting uncertainty and variability in the accuracy of the birds' orientation system (see Rabøl (1978), Mouritsen (1998) and Alerstam (1999) for details about varying courses in migration by vector summation). The trajectories of the migrants, as recorded by radar over 3–10 km distances, were generally very straight, showing no signs of important short-term directional variability.

It seems most reasonable to assume that large numbers of Siberian tundra birds depart east-north-east across the Arctic Ocean in a regular and well-controlled migration system towards North America. This is not to say that this is necessarily a wholly discrete system without overlap with the dominating east-south-east movements. Depending on the starting point and orientation principles, course changes from east-north-east towards east-south-east may already occur along the routes in Siberia (see, for example, figure 4).

Evaluating four possible orientation principles for this migration system, we can judge the probability of each alternative on the basis of (i) the availability of required orientation cues, and (ii) the appropriateness of the associated predicted flight routes across the Arctic Ocean.

Cues for orientation along geographical loxodromes are probably not available (star compass) or remain hypothetical (celestial compass with correction for a longitudinal time-shift). In addition, a magnetic compass based on the apparent angle of inclination is purely hypothetical (Kiepenheuer 1984). In contrast, assuming that the birds orientate by a sun compass, without compensation for the longitudinal time-shift or a magnetic compass rests on firmly established compass functions in birds (Berthold 1991; Wiltschko & Wiltschko 1995). A possible difficulty with the magnetic compass is the very steep angles of inclination along the travel paths over the Arctic Ocean (but see Sandberg *et al.* 1998).

When considering the predicted flight trajectories, the magnetoclinic routes according to Kiepenheuer (1984) may be refuted as invalid and disruptive. The remaining three alternative sets of routes are compared on a gnomonic map projection in figure 3. It is unlikely that the birds fly towards the most northerly and barren parts of Canada and, consequently, geographical loxodromes are least likely, while sun compass routes seem to be the most likely of the three alternatives. Furthermore, sun compass routes conform most closely to orthodromes (which appear as straight lines on a gnomonic projection) and, thus, constitute the most efficient alternative for saving distance. A complication with magnetic loxodromes is the fact that the migrants have to change to a clearly different orientation immediately upon reaching North American shores or they will continue along completely inappropriate

Figure 4. Pattern of sun compass routes (with initial geographical compass directions 60–90°) between Siberia and North America across the Arctic Ocean on a Mercator map projection. Routes are exemplified from a number of sites in the region of Siberia, where east-north-east departures were regular according to radar observations.

routes. We conclude that the availability of orientation cues as well as the probability of predicted trajectories support migration along sun compass routes as the most likely alternative.

This conclusion is in contrast to much recent research in the bird orientation field, where the main focus of attention has been on orientation by geomagnetic cues (Wiltschko & Wiltschko 1995), while sun compass orientation has sometimes been assumed to be of secondary importance because of potentially complicating changing solar conditions along the migration route (Wiltschko & Wiltschko 1990). Furthermore, cue-conflict experiments have indicated that the magnetic compass dominates over celestial cues during the actual migration (but not during the pre-migratory phase) of nocturnal passerine migrants at temperate latitudes (Wiltschko *et al.* 1998). However, in particular at high latitudes, the time-compensated sun compass furnishes the birds with a most useful ability of approximate great circle orientation (Alerstam & Pettersson 1991). In fact, birds could use their sun compass to orientate right across the geographical North Pole. However, radar studies indicate that there exists no regular transpolar bird migration, possibly because such migration may be of little evolutionary advantage considering the geographical configuration of potential stopover and wintering areas for Arctic birds (Gudmundsson & Alerstam 1998b).

Our analysis does not of course exclude the possibility that the birds use a more complex orientation programme than assumed in the four main cases above, e.g. involving changes of preferred compass course or changes between different orientation mechanisms during their passage across the Arctic Ocean. However, such changes are probably more likely to occur between different flight steps (e.g. Gwinner & Wiltschko 1978) rather than during an oceanic passage. Hence, before considering more complex orientation programmes, we have investigated whether any of the celestial or magnetic compass mechanisms described in the literature may lead the birds across the Arctic Ocean in a realistic and favourable way. This seems to be best fulfilled for sun compass orientation, which thus constitutes a primary hypothetical

candidate for further testing in relation to high-latitude bird orientation.

The pattern of sun compass migration from a number of sites in Siberia is illustrated in figure 4 (cf. table 1). According to this pattern, after crossing the Arctic Ocean migrants arrive on east-south-east—south-east courses in the Bering Strait region in western and northern Alaska and north-westernmost Canada. In this general region there are highly important stopover habitats for large numbers of migrating tundra birds (e.g. Gill & Handel 1990; Gill & Senner 1996). We suggest that a migration link between Siberia and North America has evolved according to this pattern, based on sun compass orientation and associated orthodrome-like routes.

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