OIKOS 103: 341–349, 2003

Compass orientation and possible migration routes of passerine birds at high arctic latitudes

Rachel Muheim, Susanne Åkesson and Thomas Alerstam

Muheim, R., Åkesson, S. and Alerstam, T. 2003. Compass orientation and possible migration routes of passerine birds at high arctic latitudes. – Oikos 103: 341–349.

The use of celestial or geomagnetic orientation cues can lead migratory birds along different migration routes during the migratory journeys, e.g. great circle routes (approximate), geographic or magnetic loxodromes. Orientation cage experiments have indicated that migrating birds are capable of detecting magnetic compass information at high northern latitudes even at very steep angles of inclination. However, starting a migratory journey at high latitudes and following a constant magnetic course often leads towards the North Magnetic Pole, which means that the usefulness of magnetic compass orientation at high latitudes may be questioned. Here, we compare possible long-distance migration routes of three species of passerine migrants breeding at high northern latitudes. The initial directions were based on orientation cage experiments performed under clear skies and simulated overcast and from release experiments under natural overcast skies. For each species we simulated possible migration routes (geographic loxodrome, magnetic loxodrome and sun compass route) by extrapolating from the initial directions and assessing a fixed orientation according to different compass mechanisms in order to investigate what orientation cues the birds most likely use when migrating southward in autumn. Our calculations show that none of the compass mechanisms (assuming fixed orientation) can explain the migration routes followed by night-migrating birds from their high Nearctic breeding areas to the wintering sites further south. This demonstrates that orientation along the migratory routes of arctic birds (and possibly other birds as well) must be a complex process, involving different orientation mechanisms as well as changing compass courses. We propose that birds use a combination of several compass mechanisms during a migratory journey with each of them being of a greater or smaller importance in different parts of the journey, depending on environmental conditions. We discuss reasons why birds developed the capability to use magnetic compass information at high northern latitudes even though following these magnetic courses for any longer distance will lead them along totally wrong routes. Frequent changes and recalibrations of the magnetic compass direction during the migratory journey are suggested as a possible solution.

R. Muheim, S. Åkesson and T. Alerstam, Dept of Animal Ecology, Lund Univ., Ecology Building, SE-223 62 Lund, Sweden (rachel.muheim@zooekol.lu.se).

Migratory birds can use various orientation cues during the migratory journeys, which can lead them along different migration routes depending on the cues they rely on (Sandberg and Holmquist 1998, Alerstam and Gudmundsson 1999a, b). Orientation experiments with wild-caught and hand-raised birds have shown that migrating birds use celestial and geomagnetic information for orientation (reviewed by Wiltschko and Wiltschko 1995). The sun compass allows them to identify the azimuth of the sun during the day in association with local time, measured by their internal clock (reviewed by Schmidt-Koenig 1990). As long as the birds do not compensate for the change in local time when traveling across longitudes, a sun compass directs birds along migration routes that are similar to great circle routes or orthodromes at high latitudes

Accepted 14 February 2003

ISSN 0030-1299

(Alerstam and Pettersson 1991). Compensating for the longitudinal shift in time and thereby resetting the internal clock regularly, leads the birds along a geographic loxodrome when following the sun compass (Alerstam and Pettersson 1991). The other known celestial compass system is the star compass that provides the birds with geographic north-south information by observing the rotation center of the starry sky (Emlen 1970, Weindler et al. 1997). A migration route following a star compass will thereby lead the birds along a constant geographic route, a geographic loxodrome. The geomagnetic field is another orientation cue used by migrating birds (Merkel and Wiltschko 1965, Wiltschko and Wiltschko 1972). Birds use the inclination angle of the geomagnetic field lines, presumably relative to gravity, which give them information about the axis of the field lines as well as the direction towards the magnetic pole or equator (reviewed by Wiltschko and Wiltschko 1995). A migratory route based alone on geomagnetic orientation will lead birds along a constant magnetic course, a magnetic loxodrome (Alerstam and Gudmundsson 1999a) or possibly along so-called magnetoclinic routes, assuming the birds follow an apparent angle of inclination, a constant angle between the direction of the field lines and the heading of the bird (Kiepenheuer 1984). Birds can thus end up at sites quite far apart when starting their migration from the same location into the same direction, depending on which compass mechanisms and cues they use for orientation.

Birds starting their migratory journey at high northern latitudes are challenged by several difficulties. The stars cannot be used for orientation during the initial part of migration because they are not visible during the light nights of the polar summers. It can be difficult to use a sun compass because of the rapid longitudinal time shifts birds will experience during long-distance migratory flights (reviewed by Alerstam 1990). Magnetic compass orientation has also been considered problematic. Since the magnetic field lines cross the surface of the Earth at very steep angles of inclination close to the geomagnetic poles (Skiles 1985), the detection of magnetic compass information at high latitudes might be difficult (Wiltschko and Wiltschko 1995), and the birds might have problems to translate inclination compass information into a migratory direction. Furthermore, the birds will be exposed to rapid and large changes in declination during flights at high latitudes, and studies simulating migration routes have shown that a constant magnetic course north of 270° and 90° will lead the birds towards the North Magnetic Pole (Alerstam and Gudmundsson 1999a, Alerstam et al. 2001). However, despite of all objections, several orientation cage experiments have indicated that migrating birds are capable of detecting magnetic compass information at high northern latitudes even at very steep angles of inclination (Sandberg et al. 1991, 1998, Åkesson et al. 1995, 2001, Gudmundsson and Sandberg 2000, Muheim and Åkesson 2002). Åkesson et al. (2001) showed that white-crowned sparrows, *Zonotrichia leucophrys*, could select a magnetic compass course in geomagnetic fields where the inclination angles deviated less than 2° from the vertical. This requires a very accurate magnetic compass receptor and the ability to transfer the information to a migration course.

In this study we compare possible long-distance migration routes of three species of passerine migrants living at high northern latitudes in order to analyse where the directions chosen in orientation cages would lead the birds when orienting in a fixed way by the same compass mechanism over several thousands of kilometers. The initial directions are taken from orientation cage experiments and one release experiment performed at high Nearctic sites under natural clear or overcast skies or under simulated overcast. Hence, the directions chosen for the calculations of routes represent actual migration directions selected in situations where the birds could use celestial information for orientation, as for example the polarization pattern of the sky at sunset (Able 1989, Phillips and Moore 1992), or where the birds did not have access to celestial cues (experiments under simulated overcast or complete natural overcast). For each species we calculated possible migration routes (geographic loxodrome or rhumbline route, magnetic loxodrome or constant magnetic course and sun compass route) and evaluated to what extent the different routes, based on different orientation principles and cues, would be realistic and useful for the birds' autumn migration.

Methods

Simulation program

We developed a program written in Turbo Pascal (Borland Pascal, Version 7.0) to simulate migration routes starting from any location on Earth into a chosen direction. The migration directions were recalculated after each step of 20 km, assuming one of the following orientation mechanisms: (1) sun compass with compensation for longitudinal time-shift or star compass leading along a geographic loxodrome (rhumbline route that follows a constant geographic course), (2) magnetic compass following a magnetic loxodrome (constant magnetic course) or (3) sun compass without compensation for the time-shift associated with longitudinal displacement (closely matching a great circle route). The magnetic loxodrome route was calculated by progressively adding steps of 20 km and using the changing magnetic declination to translate the fixed magnetic course to a geographic direction for each new step. For each species and start position, we created a grid from the geomagnetic reference field models for a date approximately in the middle of the respective experimental periods (see Table 1). The sun compass route was calculated according to Alerstam and Pettersson (1991) assuming that the birds used this compass at sunset times only. This is reasonable, since all three species are night migrants and probably make decisions about their migratory direction during this time of day. Magnetoclinic routes as proposed by Kiepenheuer (1984) are not shown since they could not be applied in any of the three species (cf. Kiepenheuer about special high-latitude situations not fulfilling the requirements for ideal magnetoclinic orientation). ArcView GIS Version 3.1 with a Mercator projection was used for illustrating the results for geographic loxodromes and sun compass routes and a polar gnomonic projection for the magnetic loxodromes (for the use of map projections see Gudmundsson and Alerstam 1998).

Species and start parameters

We selected start positions and directions for our simulations from three orientation cage studies that were performed at high northern latitudes, in areas with an inclination of more than 80° (Table 1). They include three species of passerine migrants, Savannah sparrow, *Passerculus sandwichensis*, white-crowned sparrow and snow bunting, *Plectrophenax nivalis (*Sandberg et al. 1998, Åkesson et al. 2001, Muheim and Åkesson 2002). In these studies, both Savannah sparrows and snow buntings were tested at the same site as they were caught (Sandberg et al. 1998, Muheim and Åkesson 2002), the white-crowned sparrows were all caught in the area of Inuvik and displaced eastward by an ice breaker to Banks and Melville Island (Åkesson et al. 2001). The start directions used for calculating the geographic loxodrome and sun compass routes were taken from orientation cage experiments performed under clear sky conditions (geographic compass course), start directions for the magnetic loxodrome routes from simulated overcast experiments and one release experiment performed under natural overcast (magnetic compass course; Table 1). In two cases did the birds show axial orientation in the cage experiments, under clear skies in Muheim and Åkesson (2002) and under simulated overcast in Sandberg et al. (1998). Here, we used only the southerly directions of the axes for the simulations. Since the geomagnetic field models used in this study do not agree with the models used in the original studies, with the exception of Savannah sparrows in Inuvik, we had to adjust the geographic and magnetic compass courses as follows: for all sites except Inuvik we used the geographic direction published in the original papers, since north was identified by geographic means (landmarks with known positions or GPS positions), and calculated magnetic north using the declination according to the geomagnetic field models used in this study (Table 1); for the white-crowned sparrows in Inuvik we used magnetic north from the original paper, since north was identified using a magnetic compass, and calculated geographic North using the declination according to the model used in this study.

The known wintering areas of Savannah sparrows of the subspecies *P. s. anthinus* breeding in the area of Inuvik are located along coastal western United States from southwestern British Columbia south to northern and western Mexico (Byers et al. 1995). White-crowned sparrows that breed in the area of Inuvik (subspecies *Z. l. gambelli*) spend the winter in the southwestern United States (Chilton et al. 1995). Snow buntings of the nominate subspecies *P. n. nivalis* breed across arctic Canada and winter in the central plains and in the eastern agricultural land of North America (Lyon and Montgomerie 1995).

Results

Migration routes along both geographic loxodromes and magnetic compass courses do not guide the birds to the expected wintering areas, with two exceptions (Fig. 1). Following a constant geographic course (Fig. 1, upper row) directs both Savannah and white-crowned sparrows towards the Atlantic Ocean (with the exception of adult white-crowned sparrows) and the snow buntings towards the Pacific Ocean. The magnetic compass route eventually leads all three species northwards (except for snow buntings in the release experiment), ending up spiraling around the North Magnetic Pole because of the changing declinations along the flight route (Fig. 1, lower row). The sun compass routes best describe the expected migration routes, leading the birds closest to the expected wintering areas (Fig. 1, upper row).

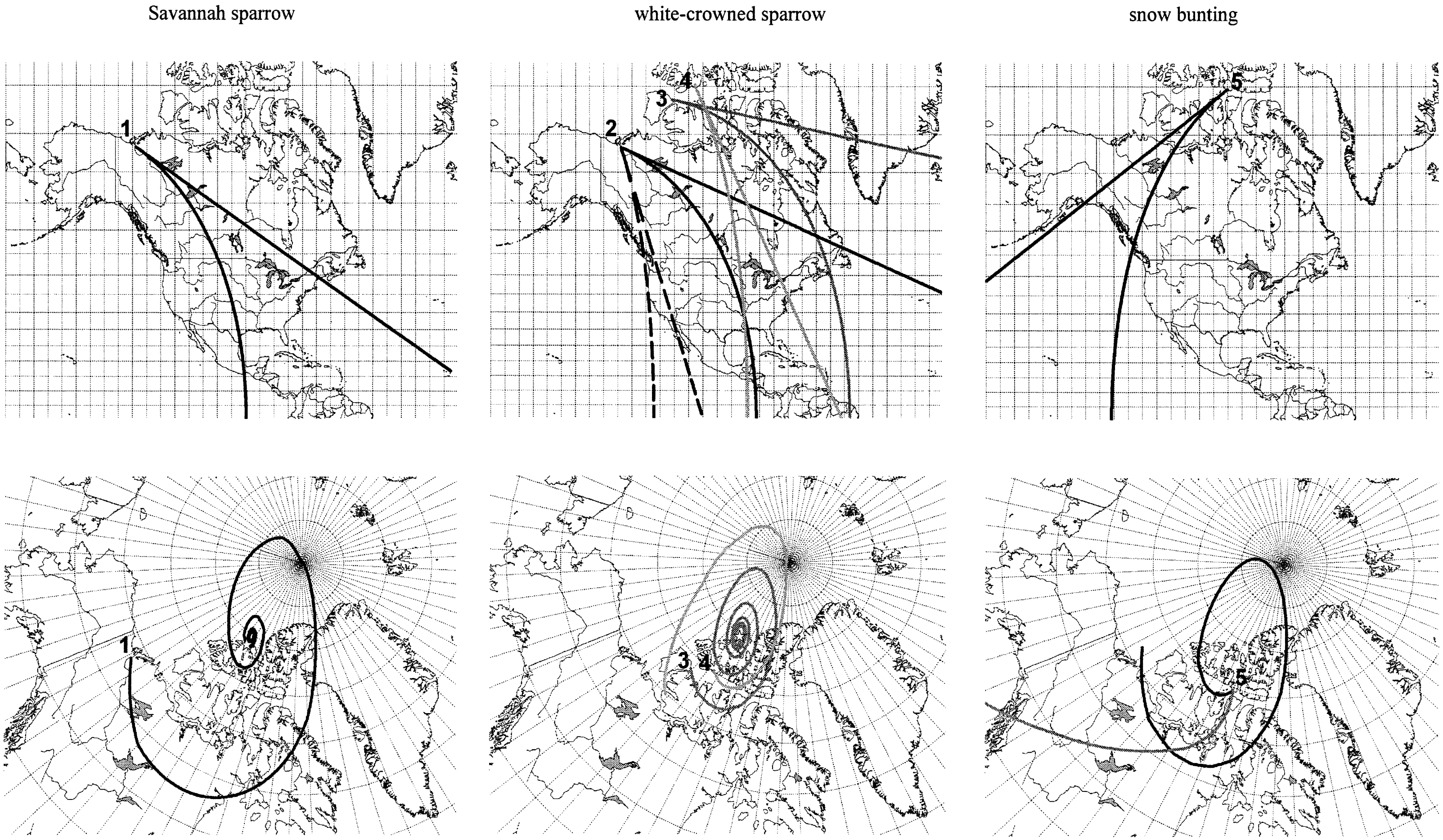
Savannah sparrows starting from Inuvik into the southeasterly geographic direction of 125° and resetting their flight direction every 20 km according to the sun compass migrate close to the known wintering area (Fig. 1, upper row, exp. 1). Following a constant geographic course of 125° on the other hand leads the birds to the eastern United States and towards the Atlantic Ocean. The magnetic compass route with a start direction of 79° (geographic direction 113°) spirals towards the North Magnetic Pole (Fig. 1, lower row, exp. 1).

The southeasterly migration routes of the white-crowned sparrows migrating from Inuvik, Banks and Melville Island resemble the ones found in the Savannah sparrow from Inuvik (Fig. 1, upper row, exp. 2, 3, 4). Following geographic loxodromes leads the birds eastwards from Inuvik and Banks Island towards the Atlantic Ocean. One exception are the adult white-

Table 1. Selection of orientation and release experiments performed with birds at high northern latitudes used for simulating migration routes (Fig. 1). The start directions used for the magnetic compass courses were taken from simulated overcast experiments and release experiments under natural overcast performed in the field, the start directions for the geographic loxodrome and sun compass routes were taken from clear sky experiments. The dates given refer to the middle of each experimental period and were used to create the geomagnetic field grid. Inclination (Incl.) and declination (Decl.) are calculated from the respective geomagnetic field model at the given dates. IGRF = International Geomagnetic Reference Field, DGRF = Definitive Geomagnetic Reference Field (IAGA Division V 1995). mN = magnetic North, gN = geographic North. For magnetic compass courses both magnetic and geographic start directions are given, since the geographic directions are visible on the maps.

Exp.	Species	Experimental site	Geographic coordinates	Geomagnetic field model	Date	Incl.	Decl.	Magnetic compass course (mN = 0°) (overcast experiments)	Type of experiment (magnetic compass course)	Geographic compass course (gN = 0°) (clear-sky experiments)	Study
1	Savannah sparrow	Inuvik	68° 21′N, 133° 43′W	IGRF 95	1 Sept 99	+82°	+34°	79° (113° gN)	Simulated overcast	125°	(Muheim and Åkesson 2002)
2	White-crowned sparrow	Inuvik	68° 21′N, 133° 43′W	IGRF 95	1 Sept 99	+82°	+34°	– #	– #	114° (ad+juv) 163° (ad only)	(Åkesson et al. 2001)
3	White-crowned sparrow	Banks Island	73° 39′N, 115° 39′W	IGRF 95	11 Aug 99	+87°	+42°	81° (123° gN)	Simulated overcast	102°	(Åkesson et al. 2001)
4	White-crowned sparrow	Melville Island	75° 07′N, 107° 41′W	IGRF 95	13 Aug 99	+89°	+32°	93° (125° gN)	Simulated overcast	156°	(Åkesson et al. 2001)
5	Snow bunting	Resolute	74° 41′N, 94° 54′W	DGRF 90	20 Aug 92	+89°	−51°	264° (213° gN) 216° (165° gN)	Simulated overcast Release experiment under natural overcast (8/8)	232° (fat birds only)	(Sandberg et al. 1998)

no overcast experiments at this site.



Savannah sparrow

white-crowned sparrow

snow bunting

Fig. 1. Migration routes of Savannah sparrows, white-crowned sparrows and snow buntings following constant geographic courses and sun compass routes (upper row) and constant magnetic courses (lower row), as specified in Table 1. Migration routes are presented on Mercator map projections (upper row) and Polar Gnomonic map projection (ns; lower row), respectively. The stars indicate the position of the North Magnetic Pole calculated from the geomagnetic field models at the dates according to Table 1. White-crowned sparrows at site 2 (upper row): dashed lines refer to adult birds only, solid lines refer to juvenile and adult birds; snow bunting (lower row): grey route refers to release experiment, black route to orientation cage experiment.

crowned sparrows that chose more southerly directions in the funnel experiments and therefore migrate over the continent towards California (Fig. 1, upper row, exp. 2, dashed line). Since the migratory directions recorded at Melville Island were directed more to the south compared to Inuvik and Banks Island, the birds are led towards southeastern United States. The sun compass directs the birds along more southerly routes, but, with the exception of adult white-crowned sparrows, still does not guide them to the expected wintering sites in the southwestern United States (Fig. 1, upper row, exp. 2, 3, 4). Adult white-crowned sparrows using a sun compass closely follow the Pacific coast, but drift out into the Pacific Ocean before reaching southern California (Fig. 1, upper row, exp. 2, dashed line). Birds from Banks and Melville Island following a constant magnetic course based on the directions they chose in orientation cages under simulated overcast conditions are directed northwards, spiraling towards the North Magnetic Pole (Fig. 1, lower row, exp. 3, 4).

The snow buntings chose southwesterly directions in the orientation cage experiments performed at Resolute on Cornwallis Island under both clear skies and simulated overcast and directions almost due south in the release experiment under complete overcast (Sandberg et al. 1998). The constant geographic course of 232° guides the birds towards northwestern Canada and out into the Gulf of Alaska. The sun compass route gradually redirects the birds towards a more southerly course and guides them towards British Columbia (Fig. 1, upper row, exp. 5). The magnetic loxodrome leads the birds northward around the North Magnetic Pole (Fig. 1, lower row, exp. 5), with the exception of the birds released under complete overcast, that showed a compass course of 216° relative to magnetic north, following a route towards the Gulf of Alaska.

Discussion

Our simulations clearly show that none of the compass courses alone can explain the migration routes followed by night-migrating passerines from their high Nearctic breeding areas to the wintering sites further south. Provided that the results of the orientation experiments (Table 1) reflect the departure orientation of the arctic passerine migrants in a reliable way, we can therefore draw the conclusion that their orientation along the migration routes must be a more complex process than assumed in our analysis. We believe that this complexity is associated with two main factors, namely that successful long-distance orientation requires (1) that the birds use different compass mechanisms depending on environmental conditions and (2) that they change their preferred orientation (changes possibly triggered by endogenous program or external cues) during the course of migration. This concept of multiple compass use (involving calibration between the different compass mechanisms) and changing rather than fixed orientation is certainly not new (Wiltschko and Wiltschko 1995, Able 1996). However, the arctic species in our analysis seem to require a level of complexity in their migratory orientation, with regard to both compass mechanisms and course changes, that clearly exceeds what has been suggested for e.g. passerines migrating from Europe to Africa (Gwinner and Wiltschko 1978, Wiltschko and Wiltschko 1995, Mouritsen 1998, but see Thorup and Rabøl 2001).

Following one single compass for orientation during the complete migratory journey does not only lead the birds along unfavourable routes as shown for most geographic and magnetic loxodromes, but is also unrealistic because the different orientation cues are not always available along the migration route. The star compass is unavailable during the initial part of migration because stars are not visible during the light polar summer when birds depart from their breeding grounds. The sun, on the other hand, is readily available at high northern latitudes and might act as primary orientation cue during the initial part of the migratory journey (Muheim and Åkesson 2002, Åkesson et al. 2002). With the nights becoming longer in more southern regions the stars might gain importance as orientation cue whereas sun compass orientation becomes more difficult because the sun is below the horizon during large parts of the nocturnal flights. The magnetic compass will be easier to use with increasing distance from the North Magnetic Pole, because the geomagnetic field will be less steep and more homogenous (smaller changes in declination; Skiles 1985). Therefore, we propose that birds use a combination of several compass mechanisms during a migratory journey with each of them being of a greater or smaller importance in different parts of the journey, depending on environmental condition.

It seems paradoxical that birds can orient at places with steep angles of inclination by using a magnetic compass, when the outcome of following these magnetic courses for any longer distance is to lead them along totally wrong routes. The magnetic compass directions that the birds chose in orientation funnels under simulated overcast at high arctic sites do not lead them to their population-specific wintering sites, but around the North Magnetic Pole. However, the same orientation studies clearly show that birds are able to orient without access to celestial cues (Sandberg et al. 1991, 1998, Åkesson et al. 1995, 2001, Gudmundsson and Sandberg 2000, Muheim and Åkesson 2002). They seem to be able to derive a compass course using magnetic cues only, even though the magnetic field lines are almost vertical. This indicates that the magnetoreceptor must be extremely sensitive to small changes in the angle of inclination and that the vestibular system provides them with very accurate information about the

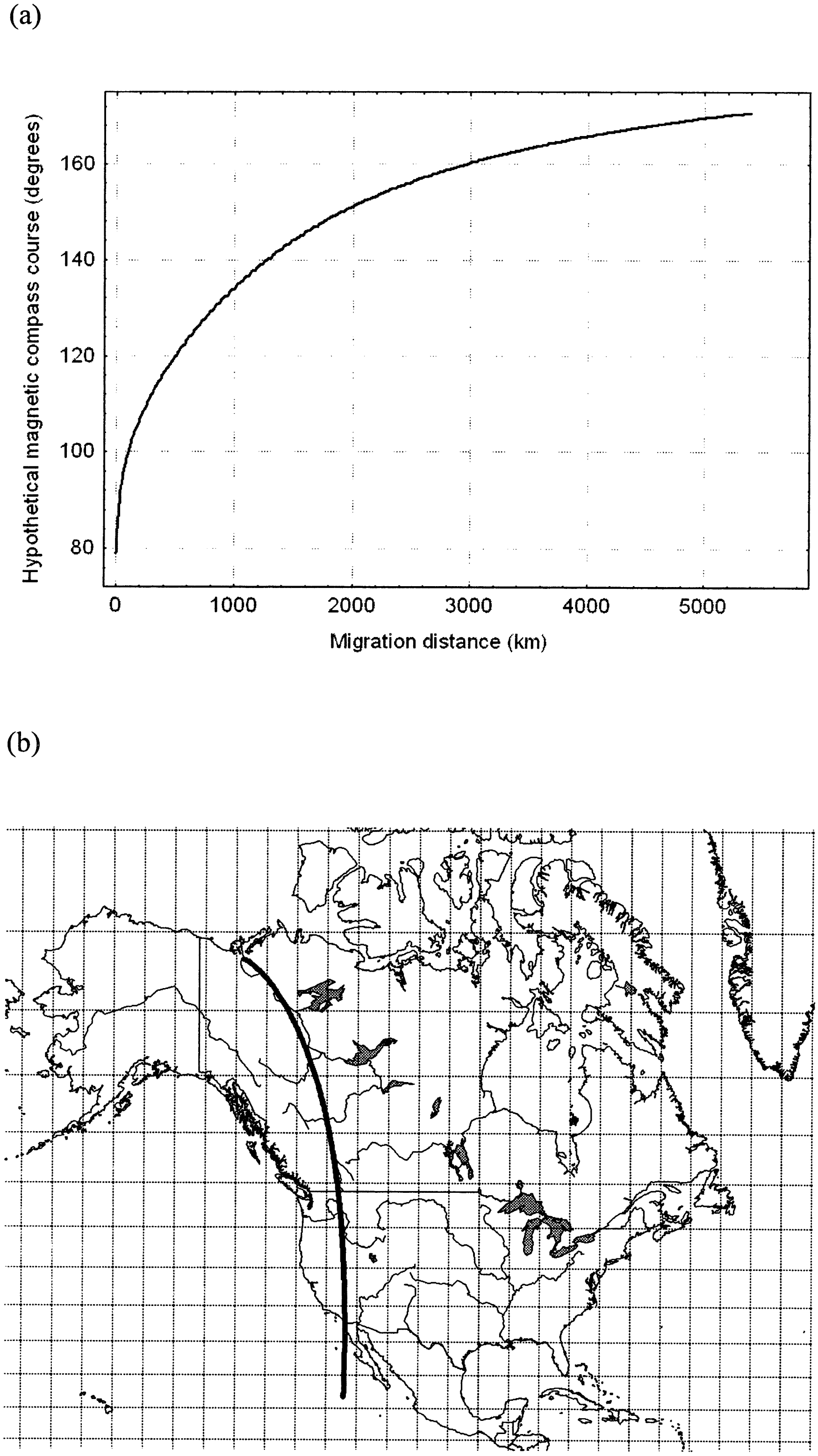


Fig. 2. (a) Hypothetical magnetic compass course a Savannah sparrow has to follow in order to reach the species-specific wintering area, assuming that it starts its migration from Inuvik with a magnetic compass course of 79° (corresponding to the geographic course of 113°) and follows a route as shown in (b).

position of the head relative to gravity. Following a constant magnetic course leads birds along a magnetic loxodrome where the geographic direction changes because of changing declinations along the migration route. It has been shown also by Alerstam and Gudmundsson (1999a) and Alerstam et al. (2001) that a constant magnetic course between 270° and 90°, as was recorded by radar observation for many arctic waders and skuas migrating in northern Siberia and Canada, will lead the birds towards the North Magnetic Pole instead of southwards towards their wintering sites.

We can only speculate about the reasons why birds developed the capability to perceive magnetic compass information at high northern latitudes with such precision that they can use the information to derive a magnetic compass course. Magnetic field intensity is up to two times stronger at high latitudes close to the geomagnetic poles compared to areas close to the geomagnetic equator (Skiles 1985). This might lead to a stronger signal from the magnetoreceptor at high latitudes and a higher accuracy because of biophysical reasons. Thus, the magnetoreceptor might have evolved to a sensitivity level necessary for magnetoreception at lower latitudes and the high sensitivity at high latitudes might be a by-product with no extra cost involved in developing such a sensitive magnetic compass receptor. A functional magnetic compass at high latitudes might also be useful as a backup system for overcast days when celestial orientation is not applicable.

We think that birds frequently change their magnetic compass direction during migration. It is very unlikely that birds follow a constant magnetic course in situations as shown in our simulations. The changes in magnetic course direction required to follow a reasonable and favourable route towards the winter quarters are substantial as shown in Fig. 2. Frequent and large changes are especially necessary at higher latitudes, where the changes in declination between nearby areas are large. Such changes can be preprogrammed and regulated by endogenous factors, like the innate time program (Gwinner and Wiltschko 1978, Helbig et al. 1989, Munro et al. 1993) or they can be triggered by exogenous factors, as demonstrated for geomagnetic field information as initiating behavioural and physiological changes in migrating birds (Beck and Wiltschko 1988, Fransson et al. 2001). Generally, magnetic loxodromes are less favourable (longer distance) as migration routes than geographic loxodromes in North America, while the reverse holds in e.g. Europe (Alerstam 2001). This will make it particularly favourable to recalibrate the magnetic compass in relation to celestial cues in the former region. Cue-conflict experiments during ontogeny have shown that young birds can calibrate their magnetic compass by visual cues, especially when reared in large magnetic declinations (reviewed by Able and Able 1999). Visual cues used for calibrations have been shown to include celestial rotation of the stars (Able and Able 1990) and the daytime pattern of polarized skylight (Able and Able 1993, 1995b, Weindler et al. 1998). Savannah sparrows, for example, recalibrated their magnetic compass in orientation experiments, when artificially exposed to large declinations for several days, using celestial cues as reference also during migration long after their initial learning phase during ontogeny (Able and Able 1995a, 1999). These recalibrations are very advantageous in areas with large changes in declination (in arctic North America), allowing the birds to make magnetic and celestial compasses compatible and to maintain a migration course similar to a geographic loxodrome if stars are used to calibrate the magnetic compass or to follow great circle routes if sun factors are the reference and the internal clock is not reset. Hence, a magnetic compass fully functioning along the whole migration route can be very advantageous for migrating birds, assuming that birds frequently change their magnetic compass direction en route.

Acknowledgements – We are grateful for logistic support during fieldwork from Swedish Polar Research Secretariat, the Aurora Research Institute in Inuvik, North-Western Territories, Polar Continental Shelf Project, and Martin D. Male, Inuvialuit Development Corporation, Canada. This project was performed as a Polar Continental Shelf Project (no. 704-99 and publication no. 00403). Permissions to work within Nunavut and North-Western Territories were kindly given by Canadian Wildlife Service, the local Hunters and Trappers Associations and the Ethical Committee in Canada. The project was performed according to the guidelines given for research on experimental animals in Canada. We would like to thank Jens Morin and Ulf Ottosson for their help during fieldwork. This project was financed by grants from the Swedish Science Research Council, Stiftelsen Olle Engkvist Byggmästare, Kungliga Fysiografiska Sällskapet i Lund (all to S.Å.), Lund University (to U.O.) and a grant from the Swedish Institute (to R.M.).

References

Able, K. P. 1989. Skylight polarization patterns and the orientation of migratory birds. – J. Exp. Biol. 141: 241–256.

Able, K. P. 1996. The flexible migratory orientation system of the Savannah sparrow, *Passerculus sandwichensis*. – J. Exp. Biol. 199: 3–8.

Able, K. P. and Able, M. A. 1990. Calibration of the magnetic compass of a migratory bird by celestial rotation. – Nature 347: 378–380.

Able, K. P. and Able, M. A. 1993. Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarization. – Nature 364: 523–525.

Able, K. P. and Able, M. A. 1995a. Interactions in the flexible orientation system of a migratory bird. – Nature 375: 230–232.

Able, K. P. and Able, M. A. 1995b. Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird. – J. Comp. Physiol. A. 177: 351–356.

Able, K. P. and Able, M. A. 1999. Evidence for calibration of magnetic migratory orientation in Savannah sparrows reared in the field. – Proc. R. Soc. Lond. B 266: 1477–1481.

Åkesson, S., Ottosson, U. and Sandberg, R. 1995. Bird orientation: displacement experiments with young autumn migrating wheatears, *Oenanthe oenanthe*, along the Arctic coast of Russia. – Proc. R. Soc. Lond. B 262: 189–195.

Åkesson, S., Morin, J., Muheim, R. and Ottosson, U. 2001. Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic North Pole. – Proc. R. Soc. Lond. B 268: 1907–1913.

Åkesson, S., Morin, J., Muheim, R. and Ottosson, U. 2002. Avian orientation: effects of cue-conflict experiments with young migratory songbirds in the high Arctic. – Anim. Behav. 64: 469–475.

Alerstam, T. 1990. Ecological causes and consequences of bird orientation. – Experientia 46: 405–415.

Alerstam, T. 2001. Evaluation of long-distance orientation in birds on the basis of migration routes recorded by radar and satellite tracking. – J. Navig. 54: 393–403.

Alerstam, T. and Pettersson, S. G. 1991. Orientation along great circles by migratory birds using a sun compass. – J. Theor. Biol. 152: 191–202.

Alerstam, T. and Gudmundsson, G. A. 1999a. Bird orientation at high latitudes: flight routes between Siberia and North America across the Arctic Ocean. – Proc. R. Soc. Lond. B 266: 2499–2505.

Alerstam, T. and Gudmundsson, G. A. 1999b. Migration patterns of tundra birds: tracking radar observations along the Northeast passage. – Arctic 52: 346–371.

Alerstam, T., Gudmundsson, G. A., Green, M. and Hedenström, A. 2001. Migration along orthodromic sun compass routes by arctic birds. – Science 291: 300–303.

Beck, W. and Wiltschko, W. 1988. Magnetic factors control the migratory direction of pied flycatchers, *Ficedula hypoleuca*. – In: Quellet, H. (ed.), Acta XIX Congr Int Ornithol. Univ. of Ottawa Press, Ottawa, pp. 1955–1962.

Byers, C., Olsson, U. and Curson, J. 1985. Buntings and sparrows: a guide to the buntings and North American sparrows. – Pica Press.

Chilton, G., Baker, M. C., Barrentine, C. D. and Cunningham, M. A. 1995. White-crowned sparrow, *Zonotrichia leucyphrys*. The birds of North America, Philadelphia.

Emlen, S. T. 1970. Celestial rotation: its importance in the development of migratory orientation. – Science 170: 1198–1201.

Fransson, T., Jakobsson, S., Johansson, P. et al. 2001. Magnetic cues trigger extensive refuelling. – Nature 414: 35–36.

Gudmundsson, G. A. and Alerstam, T. 1998. Optimal map projections for analysing long-distance migration routes. – J. Avian Biol. 29: 597–605.

Gudmundsson, G. A. and Sandberg, R. 2000. Sanderlings, *Calidris alba*, have a magnetic compass: orientation experiments during spring migration in Iceland. – J. Exp. Biol. 203: 3137–3144.

Gwinner, E. and Wiltschko, W. 1978. Endogenously controlled changes in the migratory direction of garden warbler, *Sylvia borin*. – J. Comp. Physiol. 125: 267–273.

Helbig, A. J., Berthold, P. and Wiltschko, W. 1989. Migratory orientation of blackcaps, *Sylvia atricapilla*: population-specific shifts of direction during the autumn. – Ethology 82: 307–315.

IAGA Division V, W. G. 1995. International geomagnetic reference field, 1995 Revision. – Geomag. Geoelectr. 47: 1257–1261.

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

Lyon, B. and Montgomerie, R. 1995. Snow bunting, *Plectrophenax nivalis*. The birds of North America, Philadelphia.

Merkel, F. W. and Wiltschko, W. 1965. Magnetismus und Richtungsfinden zugunruhiger Rotkehlchen, *Erithacus rubecula*. – Die Vogelwarte 23: 71–77.

Mouritsen, H. 1998. Migrating young pied flycatcher, *Ficedula hypoleuca*, do not compensate for geographical displacement. – J. Exp. Biol. 201: 2927–2934.

Muheim, R. and Åkesson, S. 2002. Clock-shift experiments with Savannah sparrows, *Passerculus sandwichensis*, at high northern latitudes. – Behav. Ecol. Sociobiol. 51: 394–401.

Munro, U., Wiltschko, W. and Ford, H. 1993. Changes in the migratory direction of yellow-faced honeyeaters, *Lichenostomus chrysops*, during autumn migration. – Emu 93: 59–62.

Phillips, J. B. and Moore, F. R. 1992. Calibration of the sun compass by sunset polarized light patterns in a migratory bird. – Behav. Ecol. Sociobiol. 31: 189–193.

Sandberg, R. and Holmquist, B. 1998. Orientation and long-distance migration routes: an attempt to evaluate compass cue limitations and required precision. – J. Avian Biol. 29: 626–636.

Sandberg, R., Ottosson, U. and Pettersson, J. 1991. Magnetic orientation of migratory wheatears, *Oenanthe oenanthe*, in Sweden and Greenland. – J. Exp. Biol. 155: 51–64.

Sandberg, R., Bäckman, J. and Ottosson, U. 1998. Orientation of snow buntings, *Plectrophenax nivalis*, close to the magnetic north pole. – J. Exp. Biol. 201: 1859–1870.

Schmidt-Koenig, K. 1990. The sun compass. – Experientia 46: 336–342.

Skiles, D. D. 1985. The geomagnetic field: its nature, history, and biological relevance. – In: Kirschvink, J. L., Jones, D. S. and McFadden, P. L. (eds), Biomineralization and magnetoreception in organisms: a new biomagnetism. Plenum Press, pp. 43–102.

Thorup, K. and Rabøl, J. 2001. The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. – J. Avian Biol. 32: 111–119.

Weindler, P., Baumetz, M. and Wiltschko, W. 1997. The direction of celestial rotation influences the development of stellar orientation in young garden warblers, *Sylvia borin*. – J. Exp. Biol. 200: 2107–2113.

Weindler, P., Böhme, F., Liepa, V. and Wiltschko, W. 1998. The role of daytime cues in the development of magnetic orientation in a night-migrating bird. – Behav. Ecol. Sociobiol. 42: 289–294.

Wiltschko, R. and Wiltschko, W. 1995. Magnetic orientation in animals. – Springer-Verlag.

Wiltschko, W. and Wiltschko, R. 1972. Magnetic compass of European robins. – Science 176: 62–64.