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Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic North Pole

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The Earth’s magnetic field and celestial cues provide animals with compass information during migration. Inherited magnetic compass courses are selected based on the angle of inclination, making it difficult to orient in the near vertical fields found at high geomagnetic latitudes. Orientation cage experiments were performed at different sites in high Arctic Canada with adult and young white-crowned sparrows (Zonotrichia leucophrys gambelii) in order to investigate birds’ ability to use the Earth’s magnetic field and celestial cues for orientation in naturally very steep magnetic fields at and close to the magnetic North Pole. Experiments were performed during the natural period of migration at night in the local geomagnetic field under natural clear skies and under simulated total overcast conditions. The experimental birds failed to select a meaningful magnetic compass course under overcast conditions at the magnetic North Pole, but could do so in geomagnetic fields deviating less than 3° from the vertical. Migratory orientation was successful at all sites when celestial cues were available.

Keywords: orientation; migratory birds; magnetic compass; magnetic North Pole; white-crowned sparrow; Zonotrichia leucophrys gambelii

1. INTRODUCTION

Migratory songbirds are able to use geomagnetic information and celestial cues based on information from the Sun, the pattern of skylight polarization and the stars for orientation (Emlen 1975; Able 1980; Wiltschko & Wiltschko 1995). Birds and other animals have been shown to possess an inherited magnetic compass based on the angle of inclination and not the polarity of the Earth’s magnetic field (Wiltschko & Wiltschko 1972; Phillips 1986; Lohmann & Lohmann 1994). However, at high geographical and geomagnetic latitudes orientation is problematic (Alerstam et al. 1990; Alerstam & Gudmundsson 1999) as the midnight Sun makes orientation by the stars impossible for large parts of the polar summer and the geomagnetic field lines are very steep (Skiles 1985). Furthermore, geomagnetic declination exhibits large variation between nearby sites, the position of the magnetic North Pole is gradually shifting due to secular variation and diurnal variation of the geomagnetic field parameters can sometimes be substantial during so-called magnetic storms (Skiles 1985). That migrating birds can use the geomagnetic field for orientation in areas close to the geomagnetic poles has therefore been questioned (Alerstam et al. 1990; Alerstam & Gudmundsson 1999) and it has recently been shown that a time-compensated Sun compass may be used by Arctic waders departing from breeding areas in the high Arctic on long-distance migration flights (Alerstam et al. 2001). However, it still remains a mystery as to what cue(s) tell birds breeding at high geomagnetic and geographical latitudes their inherited migratory direction in the first place.

We displaced a group of white-crowned sparrows (Zonotrichia leucophrys gambelii) from their breeding area in northwestern Canada and recorded their orientation at different sites along a northeasterly route to the magnetic North Pole. The experiments were analysed with respect to the birds’ ability to orient with the aid of celestial cues as compared to a situation with geomagnetic field information alone. In particular, we investigated at what angles of inclination the birds were able to use geomagnetic field information for orientation.

2. METHODS

(a) Study species

A group of 62 young and adult white-crowned sparrows identified according to Pyle et al. (1987) were captured with mist-nets near Inuvik, Northwest Territories, Canada (68.4°N, 133.7°W) (site 1 in figure 1), at the end of the breeding period (15 July–10 August 1999). Thirty of these birds were transported by the Canadian icebreaker Louis S. St-Laurent along a northeasterly route to eight sites on the tundra, including the magnetic North Pole located on Ellef Ringnes Island (79.0°N, 105.1°W) (table 1 and figure 1) where 13 cage experiments were performed in order to record the birds’ migratory orientation (for the method see Åkesson et al. 1995). We were able to record the birds’ orientation under both clear and overcast sky conditions at times of the day when white-crowned sparrows naturally migrate (table 1) at two sites with similar angles of declination as the breeding area (sites 3 and 4) and at the magnetic North Pole (site 5) and those experiments are reported here. This paper is concerned with orientation capabilities in relation to magnetic inclination. However, the birds experienced large shifts in geomagnetic declination at sites 6–9 and these data are reported elsewhere (S. Åkesson, U. Ottosson, J. Morin and R. Muheim, unpublished data). During transport the displaced birds were fed and kept in separate cages (200 mm x 200 mm x 400 mm) inside a container located on the front deck of the expedition vessel, with a window allowing the birds to record the local light regime, but not to see any specific visual
outdoor cues. The birds were transported to the field sites by helicopter, where they were kept in cages in a tent for 1–2 days. We used 32 white-crowned sparrows that were kept indoors under similar conditions at the Aurora Research Institute in Inuvik as controls. Both groups of experimental birds were fed with a food mixture for insectivorous birds: mealworms and water with vitamins.

We recorded the birds’ body mass to the nearest 0.1 g with a Pesola spring balance (30 and 60 g) and classified their fat levels according to a 10-graded visual scale for fat classification (Pettersson & Hasselquist 1983) extended by three grades) at capture and immediately before the cage experiments were performed. These visually classified fat levels were used for identifying when the birds started to accumulate fuel for migration, i.e. the period when they were migratory active.

White-crowned sparrows are solitary nocturnal migrants that breed in northern Canada and winter in the southern USA (Chilton et al. 1995). The population of white-crowned sparrows breeding in the area of Inuvik spends the winter in the southwestern USA (Chilton et al. 1995), thereby resulting in an expected autumn migration course along an initial great circle route towards geographical south to southeast (ca. 135°) and a rhumb line route of ca. 151° (Imboden & Imboden 1972), as calculated from Inuvik to an approximate central position of the wintering area in southwestern Texas. During the last week of August and the beginning of September, all white-crowned sparrows departed from the natural breeding area in Inuvik (authors’ observations).

(b) Experimental procedure and statistics

The migratory orientation of individual birds was repeatedly recorded in circular cages, i.e. so-called Emlen funnels (Emlen & Emlen 1966) (lined with Tipp-Ex paper), thereby allowing the birds to see ca. 140° of the sky at zenith. The experiments were performed outdoors during the autumn migration period at different sites on the Canadian tundra (figure 1 and table 1) (for the method see Åkesson et al. 1996). The mean angle of orientation of individual birds was recorded for 1 (natural clear skies) or 2 h (simulated overcast conditions, i.e. the top of the cage was covered with a 2 mm diffusing Plexiglas sheet) once per experimental condition at each site at times when the Sun had reached its lowest position during the night (table 1). The mean orientation of the control birds was repeatedly recorded two times per individual between 21 and 30 August for juveniles and six times for adults between 9 and 29 August using the same experimental procedure under natural clear and partly covered skies (0–6/8 = cloud cover, 0/8 = cloudless and 8/8 = completely covered skies).

We calculated the mean angle of orientation relative to geographical north by using vector addition (Batschelet 1981) based on the birds activity in the cage as recorded by claw marks in the pigment of the Tipp-Ex paper (minimum set to 40 registrations). Experiments for which the mean orientation of an individual was not significantly different from random (p > 0.05 according to the Rayleigh test) (Batschelet 1981) were not included in further analyses. The numbers of experiments classified as inactive, disoriented and included are given in table 1. We

Figure 1. Sites where the experimental birds were captured in the breeding area (site 1) and the birds’ migratory orientation were recorded in circular orientation cages during autumn migration (sites 1–9). In 1999 the magnetic North Pole was located on Ellesf Ringnes Island (site 5). The distributions of locations with the same angles of inclination are indicated by different shades of grey. The program GEOMAGIX (Interplex Limited, Golden, CO, USA) was used for calculating the angles of inclination based on the IGRF-95 model (IAGA Division V, Working Group 8 1995). The map is given as a Mercator projection.
Table 1. Locations of the experimental sites, geomagnetic and celestial conditions, total number of cage experiments and number of experiments classified as inactive, disoriented or included.

(The locations of the experimental sites where cage experiments were performed with adult and young white-crowned sparrows captured in the breeding area in Inuvik, Northwest Territories, Canada (site 1). The experiments were performed at different tundra sites under natural clear and simulated overcast conditions in autumn 1999. The geomagnetic field parameters, total field intensity, angle of inclination and declination (Canadian Geomagnetic Reference Field 2000) and Sun elevations in the middle of the experiment are given for respective dates of the experiment. The starting times of the experiments are given relative to the local time. The total number of experiments and the number of experiments classified as inactive, disoriented and included are given. See §2 for the selection criteria.)

Table 2. Mean masses and fat classes for experimental birds recorded at capture and before the experiments were performed at different sites in the Canadian high Arctic.

(Dates are given for the periods of capture and for the experiments. The sites refer to the locations given in table 1. The mean masses and fat classes are given for the number of experimental birds displaced \( n \) and for birds recorded prior to each control experiment \( n = \text{number of tests} \) performed in the breeding area (site 1).)

\[ \text{Table 2. Mean masses and fat classes for experimental birds recorded at capture and before the experiments were performed at different sites in the Canadian high Arctic.} \]

\[ \text{(Dates are given for the periods of capture and for the experiments. The sites refer to the locations given in table 1. The mean masses and fat classes are given for the number of experimental birds displaced \( (n) \) and for birds recorded prior to each control experiment \( (n = \text{number of tests}) \) performed in the breeding area (site 1).)} \]
Table 3. Results from the orientation cage experiments with adult and juvenile white-crowned sparrows in high Arctic North America.

(The number of experiments \((n)\) and mean angles of orientation \((\bar{\alpha})\) given relative to geographical north \((gN)\) and magnetic north \((mN)\). The mean vector length \((r)\) is a measure of the scatter of the circular distribution, ranging between zero and one (Batschelet 1981). The 95\% confidence interval \((95\% CI)\) and significance levels \((p)\) according to the Rayleigh test are given (Batschelet 1981). The significance levels for the 95\% CI \((p < 0.05\) and n.s. \(p > 0.05\)) indicate whether the observed mean orientation is significantly different from the expected migratory direction along a great circle route \((GC = 135^\circ)\) or a rhumb line route \((RL = 151^\circ)\) leading from the breeding area in Inuvik (site 1) to the likely wintering area in the southwestern USA (cf. Chilton et al. 1985). Test statistics \((U^2)\) and significance levels \((p)\) are given according to Watson’s \(U^2\)-test (Batschelet 1981) and indicate whether the mean orientations recorded for adult and juvenile white-crowned sparrows differ for the respective experimental category and site.)

<table>
<thead>
<tr>
<th>site condition</th>
<th>experimental category</th>
<th>mean vector length ((r))</th>
<th>(\bar{\alpha} ) ((mN))</th>
<th>(\bar{\alpha} ) ((gN))</th>
<th>(n)</th>
<th>95% CI</th>
<th>test statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 clear skies all</td>
<td>77 0.22 0.05 (\pm 60^\circ) (n.s. and n.s.)</td>
<td>114 78</td>
<td>(U^2 = 0.32) and (p &lt; 0.002)</td>
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<tr>
<td>clear skies adult</td>
<td>24 0.50 0.003 (\pm 47^\circ) (n.s. and n.s.)</td>
<td>163 130</td>
<td></td>
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<td></td>
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<tr>
<td>clear skies juvenile</td>
<td>53 0.25 0.04 (\pm 54^\circ) (and*)</td>
<td>66 33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 clear skies all</td>
<td>30 0.32 0.04 (\pm 52^\circ) (n.s. and n.s.)</td>
<td>102 63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clear skies adult</td>
<td>15 0.25 0.39 —</td>
<td>140 100</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clear skies juvenile</td>
<td>15 0.47 0.03 (\pm 48^\circ) (and*)</td>
<td>83 44</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>3 overcast all</td>
<td>26 0.38 0.02 (\pm 44^\circ) (n.s. and n.s.)</td>
<td>123 84</td>
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<tr>
<td>overcast adult</td>
<td>12 0.52 0.04 (\pm 49^\circ) (n.s. and n.s.)</td>
<td>154 114</td>
<td></td>
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<tr>
<td>overcast juvenile</td>
<td>14 0.40 0.11 —</td>
<td>87 48</td>
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<tr>
<td>4 clear skies all</td>
<td>28 0.36 0.02 (\pm 37^\circ) (n.s. and n.s.)</td>
<td>156 127</td>
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<tr>
<td>clear skies adult</td>
<td>14 0.41 0.10 —</td>
<td>158 129</td>
<td></td>
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<tr>
<td>clear skies juvenile</td>
<td>14 0.32 0.24 —</td>
<td>154 125</td>
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<tr>
<td>4 overcast all</td>
<td>26 0.37 0.05 (\pm 49^\circ) (n.s. and n.s.)</td>
<td>125 96</td>
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<tr>
<td>overcast adult</td>
<td>13 0.20 0.59 —</td>
<td>115 86</td>
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<tr>
<td>overcast juvenile</td>
<td>13 0.54 0.02 (\pm 44^\circ) (n.s. and n.s.)</td>
<td>128 99</td>
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<tr>
<td>5 clear skies all</td>
<td>28 0.44 0.004 (\pm 35^\circ) (n.s. and n.s.)</td>
<td>143 —</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>clear skies adult</td>
<td>14 0.41 0.10 —</td>
<td>175 —</td>
<td></td>
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<td></td>
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<tr>
<td>clear skies juvenile</td>
<td>14 0.58 0.008 (\pm 47^\circ) (n.s. and n.s.)</td>
<td>122 —</td>
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<td></td>
<td></td>
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<tr>
<td>5 overcast all</td>
<td>26 0.017 0.99 —</td>
<td>58 —</td>
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<td></td>
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<tr>
<td>overcast adult</td>
<td>13 0.29 0.32 —</td>
<td>68 —</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>overcast juvenile</td>
<td>13 0.26 0.41 —</td>
<td>250 —</td>
<td></td>
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</tr>
</tbody>
</table>

The circular statistics for adults as calculated for the second-order individual mean orientations were \(\bar{\alpha}\) \((mN)\) = 127\^°, \(r = 5\), \(r = 0.82\) and \(p < 0.05\).

used only the side of the axis with the majority of the registrations for further statistical analyses for individuals with a significant axial mean orientation (35 out of 168 experiments). We used circular statistics for calculating the mean orientation of a group of birds recorded for each site and the Rayleigh test for analysing whether the mean orientation differed from a random distribution (Batschelet 1981). Differences between groups were compared with Watson’s \(U^2\)-test (Batschelet 1981). We used the 95\% confidence interval \((95\% CI)\) (Batschelet 1981) for analysing whether the mean orientation differed from the expected migratory directions along an initial great circle route or a rhumb line route leading from the breeding area in Inuvik to the likely wintering area in the southwestern USA (Chilton et al. 1995).

(c) The Earth’s magnetic field and the Sun’s azimuth

The geomagnetic parameters, i.e., the total field intensity, inclination and declination, were calculated for each site and date of experiment based on the model for the Canadian Geomagnetic Reference Field (CGRF) 2000 by the Geological Survey of Canada (table 1). The precision of this model is \(0.13 \, \text{nT}\) for angles of inclination, with 200 \text{nT} for the horizontal component and 280 \text{nT} for the vertical component (L. Newitt, personal communication, Geological Survey of Canada). The temporal variations in the geomagnetic field parameters can be expected to covary between nearby areas in the western high Canadian Arctic (L. Newitt, personal communication) (see also Skiles 1985). At sites where the Earth’s magnetic field was unreliable for using a hand-held magnetic compass for measuring
magnetic north, we used a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site and a hand-held Global Positioning System for measuring the location of the experimental site.

3. RESULTS

The experimental birds carried relatively large fat reserves at the time of the experiment compared to at capture (table 2). Thus, the birds had started to accumulate fat for use as fuel for migration during the experimental period.

(a) Orientation under natural clear skies

Both the displaced (sites 3–5) and control (site 1) birds showed east to southeasterly mean orientations relative to geographical north under clear sky conditions (table 3 and figure 2a–c). The birds’ mean orientation did not differ from the expected migratory directions along an initial great circle route of 135° or a rhumb line route of 151° (Imboden & Imboden 1972) leading from Inuvik to the likely wintering area in the southwestern USA (Mewaldt 1964; Chilton et al. 1995) except for juvenile birds at sites 1 and 3. The mean orientation of all birds only differed significantly from the expected migratory direction along a rhumb line route in the breeding area (p < 0.05) (table 3) due to a more easterly orientation in juvenile birds. The mean orientation of adult white-crowned sparrows at this site differed from the orientation recorded for juvenile birds (statistics given in table 3), whereas there were no differences in orientation recorded for adult and juvenile birds at the other sites. We found no or only small differences in mean orientation under clear sky conditions for the displaced birds as compared to birds recorded in the breeding area (Watson’s U^2-test, site 3 U^2 = 0.019 and p > 0.05, site 4 U^2 = 0.19 and p < 0.05 and site 5 U^2 = 0.098 and p > 0.05).

(b) Orientation under simulated total overcast conditions

The experiments performed under the simulated total overcast conditions at sites 3 and 4 (including 87.1 and 88.6°, respectively) resulted in mean orientations towards the southeast (figure 2d,e), in agreement with the expected migratory directions (p < 0.05) (table 3). There was no difference in mean orientation under the
simulated overcast conditions between adult and juvenile birds at sites 3–5 (statistics given in table 3) and, therefore, the experiments from both age categories were pooled. We found no difference in mean orientation between clear sky experiments and those performed under simulated overcast conditions at sites 3 (Watson’s $U^2$-test, $U^2 = 0.092$ and $p > 0.05$) (Batschelet 1981) and 4 (Watson’s $U^2$-test, $U^2 = 0.092$ and $p > 0.05$). The mean orientation under simulated overcast conditions at site 5, which was located at the magnetic North Pole (inclination 89.7°), was highly scattered and differed significantly from the birds’ orientation under clear sky conditions at the same site (Watson’s $U^2$-test, $U^2 = 0.41$ and $p < 0.001$) (table 3 and figure 2c).

4. DISCUSSION

The experiments performed under overcast conditions demonstrate the birds’ ability to use very steep angles of inclination for meaningful orientation (sites 3 and 4), while they fail to orient in a natural vertical magnetic field (site 5). Celestial cues can be used for orientation at all sites, including the magnetic North Pole. These results are intriguing, because white-crowned sparrows do not naturally breed at these high geographical latitudes (inclination 81.8° in the breeding area) (Chilton et al. 1995). Thus, our data suggest that displaced migratory sparrows have an inborn ability to adjust to and use steep inclination angles of the Earth’s magnetic field despite no prior experience. Our observation of migratory orientation in near vertical geomagnetic fields is supported by the finding that young migratory snow buntings ($Plectrophenax nivalis$) breeding and tested at Resolute (74.7° N, 94.9° W) situated on Cornwallis Island, Canada, were able to select meaningful migratory courses presumably on the basis of magnetic field information alone (inclination 88.9°) (Sandberg et al. 1998).

Disorientation in artificial vertical magnetic fields is known from experiments with several species of nocturnal passerine migrants (for reviews see Åkesson 1994; Witschko & Witschko 1995) demonstrating increased scatter in mean orientation under overcast and natural clear sunset skies, suggesting that a combination of both celestial and magnetic compass information are important for selecting a meaningful course during migration (Åkesson 1994). Experiments with long-distance migratory songbirds have demonstrated the importance of exposure to both celestial rotation and geomagnetic field information during the ontogenetic phase in the development of a functional migratory compass (Weidler et al. 1996). Our experiments in manipulated magnetic fields at the site of capture (site 1) showed that white-crowned sparrows possess a magnetic compass and that compass course transfer occurs between magnetic and visual cues after cue–conflict exposures (S. Åkesson, J. Morin, R. Muheim and U. Ottosson, unpublished data). A mechanism by which birds might overcome the potential difficulty caused by geographical variations in the Earth’s magnetic field parameters might be by calibrating the inherited magnetic compass course relative to celestial cues (Able & Able 1990, 1993, 1995; see also Witschko et al. 1998 for a review) and relying on celestial cues for orientation during migration flights. The use of a time-compensated Sun compass mechanism for orientation during migratory flights has recently been proposed for migrating Arctic waders (Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999; Alerstam et al. 2001) and compass calibrations have been shown to occur in several species of North American passerine migrants (Able & Able 1990, 1993, 1995; Sandberg et al. 2000; S. Åkesson, J. Morin, R. Muheim and U. Ottosson, unpublished data). In conclusion, we show that an inherited magnetic compass may also serve as a basic compass in areas close to the magnetic North Pole, thereby providing meaningful migratory directions and that the migratory course can also be selected by using a celestial compass, which can even be used at the magnetic North Pole.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.