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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 × 200 mm × 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

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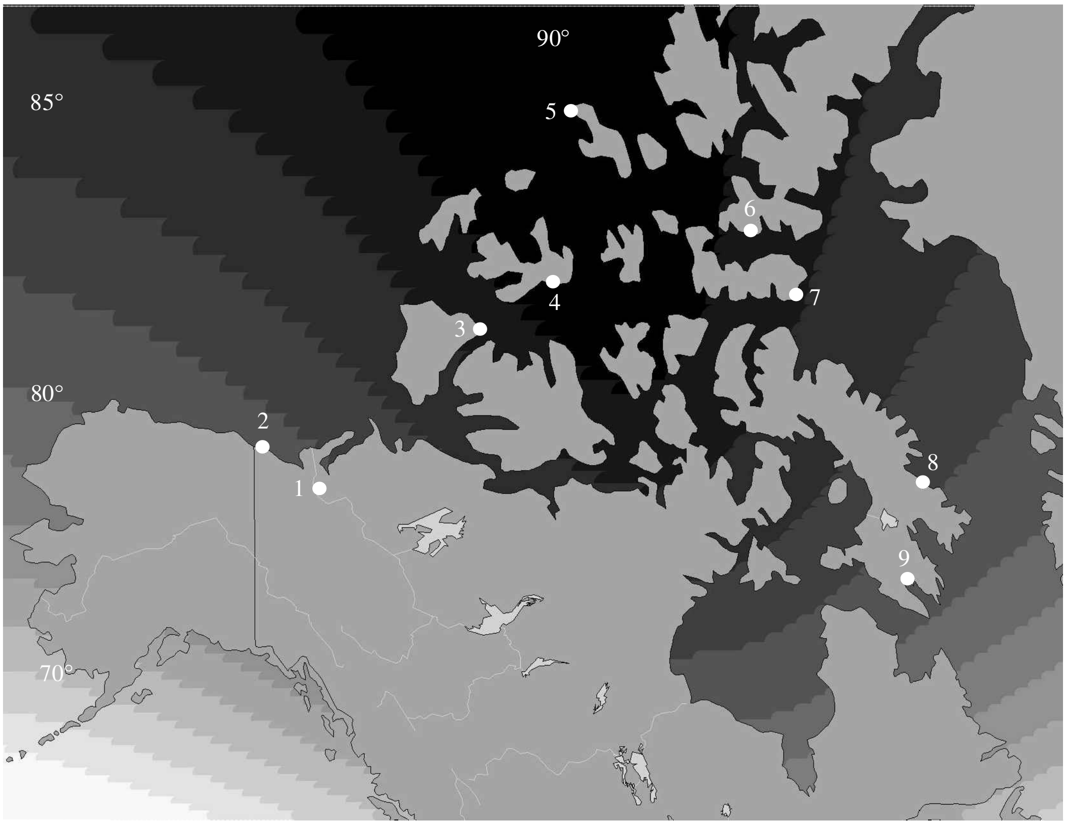

Figure 1. Sites where the experimental birds were captured in the breeding area (site 1) and the birds' migratory orientation were recorded in circular orientation cages during autumn migration (sites 1–9). In 1999 the magnetic North Pole was located on Ellef Ringnes Island (site 5). The distributions 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.

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 (1985) 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 westernmost 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 bird's 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

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.)

site	location	dates	experimental start (h)	total intensity (nT)	inclination (°)	declination (°)	Sun elevation (°)	experimental condition	inactive (adult/juvenile)	disoriented (adult/juvenile)	included (adult/juvenile)	total (adult/juvenile)
1	68.4° N, 134.7° W	18 August[a]	—	58 477	81.8	32.8 E	−1/−9	clear skies	2/1	4/1	24/53	30/55
3	73.7° N, 115.6° W	11 August	01.35	58 387	87.1	39.5 E	0	clear skies	0/0	0/0	15/15	15/15
3	73.7° N, 115.6° W	12 August	00.00	58 387	87.1	39.5 E	0	overcast	2/1	1/0	12/14	15/15
4	75.1° N, 107.7° W	13 August	01.45	58 099	88.6	28.8 E	1	clear skies	1/0	0/0	14/14	15/14
4	75.1° N, 107.7° W	14 August	00.40	58 099	88.6	28.8 E	0	overcast	2/1	0/0	13/13	15/14
5	79.0° N, 105.1° W[b]	18 August	00.50	57 266	89.7	—	2	clear skies	0/0	1/0	14/14	15/14
5	79.0° N 105.1° W[b]	19 August	00.20	57 266	89.7	—	2	overcast	1/0	1/1	13/13	15/14

[a]Geomagnetic field information according to the Canadian Geomagnetic Reference Field 2000 is given for the middle of the experimental period in Inuvik.
[b]Experiments performed at the magnetic North Pole in 1999. The position of the magnetic North Pole at that time was calculated to be located at 79.7° N, 106.5° W based on measurements collected during spring 1999 (L. Newitt, personal communication).

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 = number of tests) performed in the breeding area (site 1).)

			juveniles			adults		
site	category	date	n	mean fat class ± s.d.	mean mass ± s.d. (g)	n	mean fat class ± s.d.	mean mass ± s.d. (g)
1	controls at capture	19 July–10 August	27	1.7 ± 0.8	26.8 ± 1.9	5	1.2 ± 0.4	25.4 ± 1.9
1	displaced birds at capture	19–29 July	15	2.3 ± 0.8	27.3 ± 1.9	15	2.4 ± 0.9	26.4 ± 2.3
1	controls, experiment	15–30 August[a] 9–29 August[b]	55	4.9 ± 0.7	27.3 ± 2.1	30	3.7 ± 0.8	24.3 ± 1.9
3	displaced birds, experiment	11 August	15	4.5 ± 0.5	26.3 ± 1.2	15	3.9 ± 0.8	24.9 ± 1.7
3	displaced birds, experiment	12 August	15	4.9 ± 0.4	26.7 ± 1.2	15	3.9 ± 0.8	24.8 ± 1.8
4	displaced birds, experiment	13 August	14	4.7 ± 0.7	26.0 ± 1.3	15	3.80 ± 0.5	24.2 ± 1.8
4	displaced birds, experiment	14 August	14	4.7 ± 0.7	26.6 ± 1.2	15	4.1 ± 0.8	25.3 ± 1.9
5	displaced birds, experiment	18 August	14	4.8 ± 0.6	26.4 ± 1.3	15	4.3 ± 0.7	24.9 ± 2.1
5	displaced birds, experiment	19 August	14	5.1 ± 0.7	26.7 ± 1.2	15	4.7 ± 0.7	25.2 ± 4.7

[a]Juveniles.
[b]Adults.

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 (α) 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°) or a rhumb line route (RL = 151°) 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.)

site	experimental condition	experimental category	α (gN) (°)	α (mN) (°)	n	mean vector length (r)	p	95% CI (GC and RL)	test statistics
1	clear skies	all	114	78	77	0.22	0.03	± 60° (n.s. and n.s.)	$U^2 = 0.32$ and $p < 0.002$
	clear skies	adult[a]	163	130	24	0.50	0.003	± 47° (n.s. and n.s.)	—
	clear skies	juvenile	66	33	53	0.25	0.04	± 54° (*and*)	—
3	clear skies	all	102	63	30	0.32	0.04	± 52° (n.s. and n.s.)	$U^2 = 0.18$ and $p > 0.05$
	clear skies	adult	140	100	15	0.25	0.39	—	—
	clear skies	juvenile	83	44	15	0.47	0.03	± 48° (*and*)	—
3	overcast	all	123	84	26	0.38	0.02	± 44° (n.s. and n.s.)	$U^2 = 0.17$ and $p > 0.05$
	overcast	adult	154	114	12	0.52	0.04	± 49° (n.s. and n.s.)	—
	overcast	juvenile	87	48	14	0.40	0.11	—	—
4	clear skies	all	156	127	28	0.36	0.02	± 37° (n.s. and n.s.)	$U^2 = 0.027$ and $p > 0.05$
	clear skies	adult	158	129	14	0.41	0.10	—	—
	clear skies	juvenile	154	125	14	0.32	0.24	—	—
4	overcast	all	125	96	26	0.37	0.03	± 49° (n.s. and n.s.)	$U^2 = 0.087$ and $p > 0.05$
	overcast	adult	115	86	13	0.20	0.59	—	—
	overcast	juvenile	128	99	13	0.54	0.02	± 44° (n.s. and n.s.)	—
5	clear skies	all	143	—	28	0.44	0.004	± 35° (n.s. and n.s.)	$U^2 = 0.081$ and $p > 0.05$
	clear skies	adult	175	—	14	0.41	0.10	—	—
	clear skies	juvenile	122	—	14	0.58	0.008	± 47° (n.s. and n.s.)	—
5	overcast	all	58	—	26	0.017	0.99	—	$U^2 = 0.13$ and $p > 0.05$
	overcast	adult	68	—	13	0.29	0.32	—	—
	overcast	juvenile	250	—	13	0.26	0.41	—	—

[a]The circular statistics for adults as calculated for the second-order individual mean orientations were α(mN) = 127°, $n = 5$, $r = 0.82$ 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 *ca*. 0.2° for angles of inclination, with 200 nT for the horizontal component and 280 nT for the vertical component (L. Newitt, personal communication, Geological Survey of Canada). The temporal variations in the geomagnetic field parameters x (north–south component) and y (east–west component) were calculated for 1 h during experiments based on measurements at the Magnetic Observatory at Resolute Bay (75.3° N, 94.9° W) (Geological Survey of Canada), resulting in only small variations during the experiments (minimum − maximum difference, $x = 8.8 - 126.0$ nT and $y = 13.3 - 114.6$ nT). 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

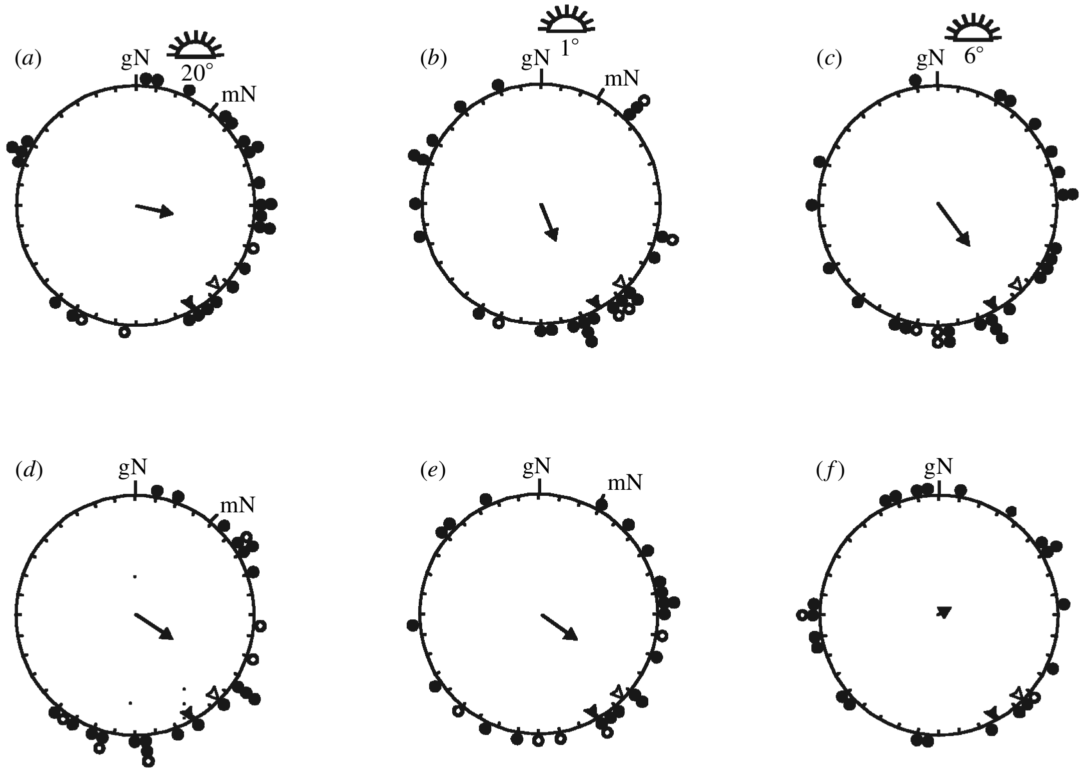

Figure 2. The orientation of autumn migrating white-crowned sparrows recorded in outdoor cage experiments at three sites in Arctic Canada close to (*a*,*d*) site 3 Banks island and (*b*,*e*) site 4 Melville's Islands and at the magnetic North Pole (*c*,*f*) site 5 Ellef Ringnes Island. The birds' migratory orientation was recorded under (*a*–*c*) natural clear and (*d*–*f*) simulated overcast skies in the local geomagnetic field. The symbols on the periphery of the circles indicate the mean orientations of individual birds. Open symbols indicate individuals with axial mean orientations. Directions towards geographical north (gN) and magnetic north (mN) are given. The Sun's azimuth positions are given for the middle of the experimental period (under the symbol of the Sun) and the expected initial directions of migration along a great circle (open arrowhead) and rhumb line route (filled arrowhead) are indicated. Arrows indicate the mean angles of orientation and the length of the arrow is a measure of the scatter of the circular distribution ranging between zero and one, being inversely related to scatter (Batschelet 1981). For further information see table 3.

magnetic north, we used a hand-held Global Positioning System for measuring the location of the experimental site and a distant landmark (or the expedition vessel) in order to align the cages. The orientation of the cages was also checked with reference to the position of the Sun. The altitude and position of the Sun in the middle of the test hour was calculated relative to geographical north for each experimental site. Experiments at sites 3–5 were performed at night during periods when the Sun was located close to the horizon (table 1) and stars were not yet visible (cf. Åkesson *et al.* 1996).

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 2*a*–*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 2*d*,*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 2*c*).

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; Wiltschko & Wiltschko 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 (Weindler *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 Wiltschko *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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