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Dramatic Orientation Shift of White-Crowned Sparrows Displaced across Longitudes in the High Arctic

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Summary

Advanced spatial-learning adaptations have been shown for migratory songbirds [1], but it is not well known how the simple genetic program encoding migratory distance and direction in young birds [2–4] translates to a navigation mechanism used by adults [2, 4–6]. A number of convenient cues are available to define latitude on the basis of geomagnetic and celestial information [7–15], but very few are useful to defining longitude [12–15]. To investigate the effects of displacements across longitudes on orientation, we recorded orientation of adult and juvenile migratory white-crowned sparrows, *Zonotrichia leucophrys gambelii*, after passive longitudinal displacements, by ship, of 266–2862 km across high-arctic North America. After eastward displacement to the magnetic North Pole and then across the 0° declination line, adults and juveniles abruptly shifted their orientation from the migratory direction to a direction that would lead back to the breeding area or to the normal migratory route, suggesting that the birds began compensating for the displacement by using geomagnetic cues alone or together with solar cues. In contrast to predictions by a simple genetic migration program, our experiments suggest that both adults and juveniles possess a navigation system based on a combination of celestial and geomagnetic information, possibly declination, to correct for eastward longitudinal displacements.

Results and Discussion

By performing repeated cage experiments under clear and simulated overcast skies with displaced songbirds, we investigated the ability of young and adult white-crowned sparrows to use natural celestial and geomagnetic cues for orientation in high-arctic North America. At high geographic and geomagnetic latitudes, orientation by both celestial and geomagnetic cues is problematic because the midnight sun makes star navigation impossible during much of the polar summer, the geomagnetic field lines are very steep [9], the declination (the angular difference between magnetic and geographic north) shows large variation between nearby sites (Figure 1A), and the position of the magnetic North Pole is gradually shifting as a result of secular variation [9]. We expected the displaced juvenile white-crowned sparrows to express a simple compass mechanism, possibly with compass calibrations, and adults were expected to show course corrections and navigation [2, 4, 16] (Figure 2; see the Supplemental Data available with this article online).

Under clear-sky conditions, both control and displaced white-crowned sparrows showed significant mean orientations toward east to southeast relative to geographic north at sites 1 (controls) and 2–4 (west; Figure 3). The mean orientation of adult birds (161°) did not differ from the expected initial great circle (GC; i.e., the shortest distance between two locations) of 135° or rhumbline (RL) routes (i.e., constant geographic course) of 151° (95% confidence interval [CI] $p > 0.05$, Figure 2) [17], as calculated from the breeding area in Inuvik to the center of the presumed population-specific wintering area in western Texas and eastern Arizona [18]. Juvenile white-crowned sparrows in the breeding area showed more-easterly directions, significantly different from a GC route (95% CI, $p < 0.05$, Figure 3H), but not from a RL route ($p > 0.05$), both of which lead from the site of capture to the expected wintering area. At sites 2–4, west of the magnetic North Pole, the displaced juveniles selected courses toward southeast not different from courses toward the wintering area (95% CI, $p > 0.05$ for both GC and RL, Figure 3I). We found no difference in mean orientation under clear-sky conditions between the displaced white-crowned sparrows at the sites west of the magnetic North Pole (site 5) and that of birds recorded in the breeding area (adults, $F_{1,18} = 0.097$, $p > 0.05$; juveniles, $F_{1,52} = 2.43$, $p > 0.05$; Mardia's one-way classification test; Figure 3) [19]. However, at the eastern sites (6–9) the white-crowned sparrows shifted their orientation to west (adults) and northwest (juveniles) under clear-sky conditions, thereby deviating greatly from the geographic courses selected in the breeding area (adults, $F_{1,18} = 17.53$, $p < 0.001$; juveniles, $F_{1,51} = 10.90$, $p < 0.005$; Figure 3) and from those recorded at the western sites (adults, $F_{1,28} = 14.98$, $p < 0.001$; juveniles, $F_{1,27} = 23.43$, $p < 0.001$; Figure 3). A similar pattern was found for adult white-crowned sparrows under simulated overcast skies, with the mean angle of orientation shifted to the west at the eastern sites, an orientation different from that recorded at the western sites ($F_{1,27} = 37.19$, $p < 0.001$, Figure 3). The mean orientation at eastern sites (6–9) did not differ from the westward to northwestward courses leading back to the site of capture (95% CI, $p > 0.05$ in all cases, Figure 3, Table 1). For juvenile white-crowned sparrows at the eastern sites, the mean orientation relative to geographic north under overcast skies was nonsignificant ($p = 0.13$, statistics given in Figure 3L), but the mean orientation differed from those of courses selected at the western sites ($U^2 = 0.06$, $p < 0.05$, Watson's U^2 test) [17]. There were large differences in orientation relative to magnetic north under overcast skies for both adult ($F_{1,27} = 28.47$, $p < 0.001$; Figures 3F and 3G) and juvenile white-crowned spar-

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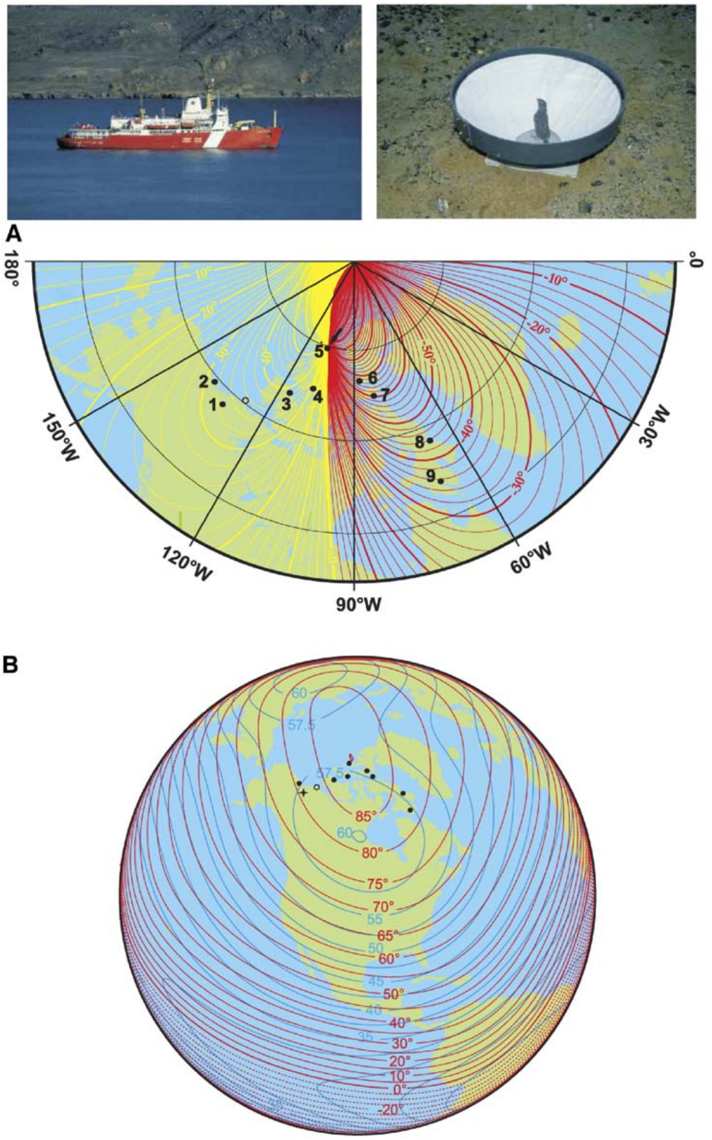

Figure 1. Sites Where Orientation Cage Experiments with White-Crowned Sparrows Were Performed in Autumn, 1999

The birds were captured in the breeding area (site 1), and their orientation was recorded in circular cages at sites 1–9. At one site (open circle), the birds were transported to the tundra, but no experiments were performed because of high wind speeds. In 1999, the geomagnetic North Pole was located at Ellef Ringnes Island (site 5, arrow in [A]).

(A) The map is a polar stereographic projection and gives the magnetic declinations in accordance with the World Magnetic Model/Chart, Epoch 2000. Declination isolines in yellow denote positive (deviations to the east of geographic north) and red negative (deviations to the west) values, respectively.

(B) The map gives isoclinics (geomagnetic inclination) as red (broken) lines and isodynamics (total field intensity, µT) as blue (filled) lines in accordance with the International Geomagnetic Reference Field (IGRF 2000) across the North American continent. The star indicates the site of capture.

rows ($U^2 = 0.19$, $p < 0.05$; Figures 3M and 3N). We found no difference in orientation relative to geographic (gN) and magnetic north (mN) under overcast skies when compared between the age groups for sites west (for gN, $F_{1,27} = 0.28$, $p > 0.05$; for mN, $F_{1,27} = 0.40$, $p > 0.05$) and east (for gN, $U_2 = 0.031$, $p > 0.05$; for mN, $U_2 = 0.015$, $p > 0.05$) of the magnetic North Pole.

There was no difference in orientation relative to geographic north for white-crowned sparrows in the breeding area early (before August 19: Ad, $\alpha = 106.1°$, $r = 0.62$, $p > 0.05$; Juv, $\alpha = 359.4°$, $r = 0.16$, $p > 0.05$) compared to late (after August 20: Ad, $\alpha = 146.5°$, $r = 0.88$, $p < 0.02$; Juv: $\alpha = 62.2°$, $r = 0.27$, $p > 0.05$) in the season (Ad, $U^2 = 0.13$; Juv, $U^2 = 0.085$; $p > 0.05$ in both cases).

Our experiments show that both adult and juvenile migratory white-crowned sparrows displaced westward across longitudes in high-arctic North America selected courses coinciding with the expected migratory directions toward wintering areas. However, after long eastward displacement (>1700 km) and passing of the magnetic North Pole, they shifted their orientation toward west to northwest, directions (either RL or initial GC) that would lead back to the natural migration route and the site of capture (Table 1; Figure 3). Our experiments were performed before and during the early part of the natural migration period (mainly in August; the local population had left the breeding site at the beginning of September, data not shown). Therefore, the white-crowned sparrows might have performed homing orientation rather than heading toward the winter destination, or, alternatively, they might have corrected for longitudinal displacements, perhaps by using the zero declination or the vertical geomagnetic field at the magnetic North Pole as a regional signpost [8, 20]. In contrast to the expectations ([2, 4] cf. [16]), the juvenile birds seemed to have responded to the same external information as the adults—this information was possibly the geomagnetic north's natural shift (i.e., declina-

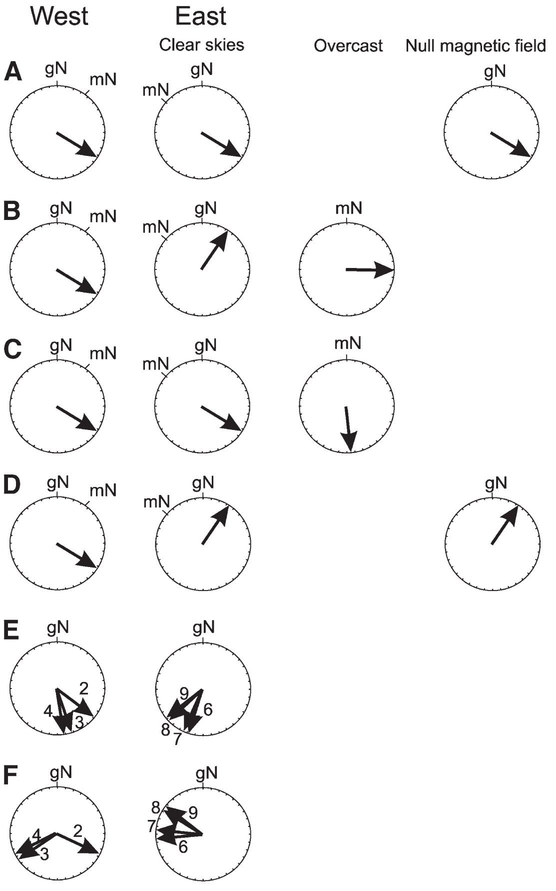

Figure 2. Expected Courses as a Response to Longitudinal Displacement

Expected courses as a response to displacements eastward across longitudes in high-arctic North America to sites east (sites 6–9) of the magnetic North Pole were calculated on the basis of the observed mean orientation for juvenile white-crowned sparrows recorded at the western sites (sites 2–4). Expected courses are presented at sites east (clear skies, overcast, null magnetic field) of the magnetic North Pole for different orientation mechanisms.

(A) Constant geographic course at all sites.

(B) Constant magnetic course at all sites.

(C) Magnetic compass courses recalibrated on the basis of solar information, demonstrated under overcast skies, and resulting in a magnetic course shifted toward south (to the right) after recalibration.

(D) Celestial compass courses recalibrated on the basis of magnetic information and shown in a null magnetic field where magnetic compass information is absent.

(E) Expected courses from each experimental site (number refers to sites in Table 1) to center of expected wintering area as calculated for an initial great-circle route (i.e., shortest route between two points). Ranges of directions along rhumbline routes (i.e., constant compass course) for the same sites are 148°–178° from sites west of the magnetic North Pole (sites 2–4) and 190°–216° for sites east (sites 6–9).

(F) Expected courses from each experimental site (indicated by numbers) to site of capture as initial great-circle routes (ranges of directions for rhumbline routes from the same sites are from west sites, 119°–230°, and east sites, 240°–280°).

tion), which was caused by the displacement (−95° shift of mN between sites 4 and 6, Table 1), perhaps in combination with the gradual shift in photoperiod—by showing a similar shift in orientation after the same displacement history as the adults. The juveniles and the adults did not select a constant geographic or geomagnetic course or recalibrate their innate magnetic compass, which would have resulted in an expected clockwise course shift relative to magnetic north under simulated overcast skies (Figure 2C). They also did not recalibrate their innate celestial compass, which would have lead to an expected counterclockwise shift under clear skies (Figure 2D). As a response to the displacement, a counterclockwise shift relative to the initial mean orientation was observed. The displaced juvenile white-crowned sparrows did not respond to the change in declination in the same way as a group of juveniles exposed to the same type of cue conflict at the control site in Inuvik (−90° shift produced by magnetic coils) [21]. The Inuvik birds exposed to the cue-conflict for only 1–2 hr simply followed the shift in magnetic direction and either recalibrated or ignored their celestial compass (or compasses).

Because the control birds tested in the breeding area did not shift their orientation over the season, the shifted mean orientation cannot be explained by white-crowned sparrows' use of an inherited migration program set by an internal clock that triggers course shifts during migration [2]. Furthermore, both displaced juveniles and adults responded in a similar way but shifted their courses to slightly different degrees, probably responding to the same external information available during transport and at the experimental sites. A candidate parameter that expresses the most dramatic shift during the displacement and that coincided with the recorded shift in orientation is geomagnetic declination. Declination, defined by both geographic and magnetic north, varies mainly with longitude in this area [9] (Table 1, Figure 1A), and it could in theory be used to define longitude [e.g., 22–26]. In contrast to determining latitude via a number of convenient cues [e.g., 10–12, 27, 28], defining one's longitude is problematic in large parts of the Earth. It took mariners in the 18th century several decades to solve this problem by using very precise chronometers and measuring sun elevation [12]. A similar mechanism has been proposed for birds, but a biological clock with the precision needed for this conceptually demanding task has not yet been described for any animal [13]. Across the North American continent, declination provides such information, varying with longitude (Figure 1B [9, 14, 23]; see also [29]). At the end of the experimental period (from site 7 and onward, except at site 8, where it was entirely overcast during the test), our white-crowned sparrows were able to use stars to define geographic north (i.e., rotation center of sky), presumably by facilitating the use of declination for navigation. Defining the exact angle of declination at high latitudes is still likely to be difficult because of the steep geomagnetic field lines (cf. [30]) and the low variation of the sun elevation during the day in the polar summer. Our displaced white-crowned sparrows experienced a daily variation in sun elevation between 22° in the north (site 5) and 43° (site 1) or more (>45°, site 9) in the south (Table 1), on which basis the birds were to define the rotation center of the sky. Stars are available only during a limited period in autumn before migration is initiated in the breeding area, starting

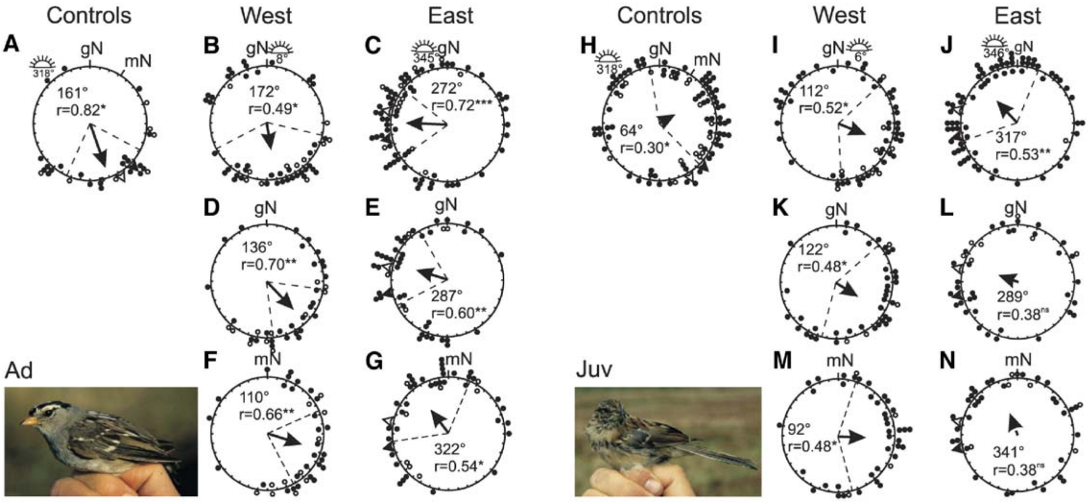

Figure 3. Orientation of Displaced White-Crowned Sparrows in High-Arctic North America

Orientations of individual birds were recorded in cages under clear skies (adults: [A–C], juveniles: [H–J]) and simulated overcast (adults: [D–G], juveniles: [K–N]) in autumn at nine tundra sites (eight presented in the graph), in the breeding area (site 1), and after longitudinal displacement in western (sites 2–4) and eastern (sites 6–9) high-arctic North America. Data from the magnetic North Pole (site 5) are not included but are presented in Table 1. The symbols (filled, unimodal; open, axial) inside the circles indicate the grand mean orientation of the experimental birds as calculated for a number of tests at several sites, and mean orientation for single tests at different sites are given outside the circles. The calculated migratory directions along an initial great-circle route (i.e., shortest route between two sites, GC; open arrowhead) and rhumbline route (i.e., constant compass course, RL; filled arrowhead) from the breeding site to the wintering area are indicated in (A) and (H), and the mean directions (GC, open arrowheads; RL, filled arrowheads) from eastern sites (sites 6–9) toward the site of capture are indicated in (C), (E), (G), (J), (L), and (N). The length of the arrow (r) is a measure of the scatter of the circular distribution, ranging from 0 to 1 and being inversely related to scatter [17]. Mean angle of orientation (given in degrees), vector length (r), and significance levels (indicated as ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$) according to the Rayleigh test [17] are given for the distributions inside the circles. Distributions for experiments under simulated overcast skies at sites west and east of the magnetic North Pole are plotted both relative to geographic north (west, ad in [D] and juv in [K]; east, ad in [E] and juv in [L]), and magnetic north (west, ad in [F] and juv in [M]; east, ad in [G] and juv in [N]). Ninety-five percent confidence limits are given as hatched lines. Vectors for distributions not significantly different from random are indicated by a broken line. Mean direction toward the sun in the middle of the test period is given for experiments under clear-sky conditions.

in mid August. Accuracy in determining the exact declination is made more difficult by the fact that two measurements are necessary (direction of magnetic and geographic north). However, one can assume that defining a positive versus a negative declination is easier. Thus, the area close to the zero declination can, at least in theory, be used as a regional signpost defining longitude, or as the geomagnetic pole itself, possibly triggering a course shift in a way similar to that which has been observed for a horizontal magnetic field [20].

Geomagnetic signposts that are based on angle of inclination and/or field intensity and result in shifts in orientation have been shown to be used by both birds and sea turtles migrating long distances [10, 31] but have never been shown to be used for declination (e.g., [14, 15, 23, 26]). Simulated displacements with exposure to regional values of geomagnetic parameters have also been shown to trigger extensive refuelling before barrier crossing (i.e., Saharan desert) in juvenile songbirds [32], demonstrating inherited reactions to external cues met en route during migration. Navigation via gradient combinations of inclination and total field intensity [10, 33, 34] in high-arctic North America is complicated because the same combinations of gradient values occur at two or more locations in western and eastern Canada (Figure 1B) [9, 29]. This was true near sites 2 and 9, where we tested the birds' orientation (Table 1 and Figure 1B) and found very different geographic courses selected by the white-crowned sparrows at the western compared to the eastern site. A geomagnetic bicoordinate gradient map learned in a restricted region of the arctic [33, 34] would result in approximately the same expected courses toward southeast (toward both breeding and wintering areas) from site 2 and site 9 (Table 1). Both adult and juvenile white-crowned sparrows in our experiments obviously responded by abruptly shifting their orientation, selecting westerly courses in the east at site 9, courses directed toward the site of capture. Thus, lack of gradual course corrections suggests that a local gradient map was not used but that cues available at more-distant sites that vary across longitudes were used. It is not clear from these experiments whether the white-crowned sparrows used true navigation via some sort of a map, at least in part based on geomagnetic information, or whether they recorded their route of transport during displacement in relation to some external information (e.g., light intensity) [33, 35]. However, before we captured them, the juvenile white-crowned sparrows had a very short time window at their disposal (1–3 weeks after fledging), presumably with very restricted movements (<1–2 km) [36], during which they could establish any sort of local map but when they established a migratory course.

Table 1. Orientation in White-Crowned Sparrows in High-Arctic North America

													Dir. to Capture Site	
Site	Location	Date	Tot. Int. (nT)	Incl.	Decl.	Exp. Cond.	Sun Azim.	Sun Elev.	N	α/α_2	r/r_2	95% CI	GC	RL
1. Inuvik[a]	68.4°N, 133.7°W	Aug. 9, 1999–Aug. 30, 1999	58477	81.8°	32.8°E	Clear skies	309°/331°	−1°/−9°	24 (ad)	130°	0.50**	±48°	—	—
									151 (juv)	17°	0.13	—	—	—
2. Ivvavik	69.5°N, 139.6°W	Aug. 4, 1999	57989	81.5°	32.1°E	Clear skies	335°	0°	10 (ad)	138°/318°	0.48	—	116°	119°
									14 (juv)	144°/324°	0.36	—	116°	119°
3. Banks Isl.	73.7°N, 115.6°W	Aug. 11, 1999	58387	87.1°	39.5°E	Clear skies	20°	0°	15 (ad)	171°	0.26	—	237°	228°
									15 (juv)	83°	0.47*	±75°	237° (*)	228° (*)
3. Banks Isl.	"	Aug. 12, 1999	"	"	"	Overcast	4°	0°	12 (ad)	154°	0.68**	±47°	237° (*)	228° (*)
									14 (juv)	106°	0.40	—	237°	228°
4. Melville Isl.	75.1°N, 107.7°W	Aug. 13, 1999	58099	88.6°	28.8°E	Clear skies	1°	0°	14 (ad)	152°/332°	0.47**	—	243°	230°
									14 (juv)	154°	0.32	—	243°	230°
4. Melville Isl.	"	Aug. 14, 1999	"	"	"	Overcast	22°	1°	13 (ad)	116°	0.20	—	243°	230°
									13 (juv)	128°	0.54*	±65°	243° (*)	230° (*)
5. Ellef Ringnes Isl.[b]	79.0°N, 105.1°W	Aug. 18, 1999	57266	89.7°	0°	Clear skies	3°	2°	14 (ad)	175°	0.41	—	231°	216°
									14 (juv)	122°	0.58**	±55°	231° (*)	216° (*)
5. Ellef Ringnes Isl.	"	Aug. 19, 1999	"	"	"	Overcast	4°	2°	13 (ad)	68°	0.29	—	231°	216°
									13 (juv)	250°	0.26	—	231°	216°
6. Ellesmere Isl.	76.4°N, 87.1°W	Aug. 22, 1999	57290	87.9°	66.3°W	Overcast	17°	4°	15 (ad)	302°	0.59**	±51°	264° (ns)	240° (*)
									13 (juv)	246°	0.22	—	264°	240°
6. Ellesmere Isl.	"	Aug. 23, 1999	"	"	"	Clear skies	308°	0°	14 (ad)	83°/263°	0.16	—	264°	240°
									14 (juv)	285°	0.16	—	264°	240°
7. Devon Isl.	74.5°N, 82.4°W	Aug. 24, 1999	57420	87.1°	59.8°W	Clear skies	347°	−3°	14 (ad)	279°	0.48**	±86°	275° (ns)	249° (ns)
									13 (juv)	315°	0.62**	±52°	275° (ns)	249° (*)
7. Devon Isl.	"	Aug. 25, 1999	"	"	"	Clear skies	350°	−4°	14 (ad)	271°	0.51**	±68°	275° (ns)	249° (ns)
									14 (juv)	58°/238°	0.33	—	275° (-)	249°
8. Baffin Isl.	68.5°N, 66.8°W	Aug. 30, 1999	57381	83.2°	44.4°W	Overcast	316°	−5°	14 (ad)	245°	0.46	—	301°	270°
									13 (juv)	327°	0.28	—	301°	270°
9. Iqaluit	63.6°N, 68.2°W	Sept. 2, 1999	57826	81.5°	35.6°W	Clear skies	307°	−6°	15 (ad)	294°	0.59**	±50°	309° (ns)	280° (ns)
									13 (juv)	319°	0.47	—	309°	280°

Locations of sites, dates and experimental conditions for orientation cage experiments performed under natural clear and simulated overcast skies. The calculations of total field intensity (Tot. Int.), angles of inclination (Incl.), and declination (Decl.) of the geomagnetic field are based on the Canadian Geomagnetic Reference Field model CGRF 2000 by Geological Survey of Canada. Sun azimuths (Sun Azim.) and elevations (Sun Elev.) in degrees are given for the middle of the experimental hours. Mean angle of orientation (α, unimodal and α_2, bimodal), vector length (r, unimodal and r_2, bimodal) and number of birds are given for adult (ad) and juvenile (juv) white-crowned sparrows in each cage experiment at the experimental sites. Data for bimodal distributions are given for distributions where $r_2 > r$. Significance levels without brackets are given for the Rayleigh test (*, $p < 0.05$ and **, $p < 0.01$) [17]. Calculated directions from the test site to the capture site (site 1) are given as initial great circle (GC, i.e., shortest distance) and rhumbline (RL, i.e., constant compass course) routes. Significance levels (95% CI, given within brackets under GC and RL; ns, $p > 0.05$; *, $p < 0.05$) [7], denote whether a distribution is significantly different from the calculated courses leading from the test site and to the capture site.

[a] Geomagnetic field information according to CGRF 2000 given for the middle of the experimental period (August 18, 1999).

[b] Experiments performed at the magnetic North Pole in 1999. On the basis of measurements collected during spring of 1999, the position of the magnetic North Pole was calculated as 79.7°N, 106.5°W.

The displaced white-crowned sparrows most likely used information available at the experimental site to select their courses, possibly in combination with the natural photoperiod shift caused by the longitudinal crossings. During transport, they were exposed to passive displacement onboard an icebreaker following circuitous routes at irregular speeds when breaking ice and were kept in a distorted magnetic field onboard. No solar or stellar cues were available during transport, but the birds had access to daily changes of light intensity, and they had restricted access to odors from outdoors. Each of these features represents information potentially contributing to a map sense [8, 13, 14, 26, 32–34]. At the tundra sites, the white-crowned sparrows could obtain natural geomagnetic and celestial information, as well as other map information, for 1–2 days. Still, our birds did not react by shifting their courses until they had passed east of the magnetic North Pole and the zero-declination line.

Our experiments show that both adult and juvenile white-crowned sparrows, common long-distance migrants, shifted their orientation in response to long-distance displacement. The results suggest that the white-crowned sparrows possess a navigation system based on a combination of celestial and geomagnetic information, possibly declination [e.g., 26–29], to correct for longitudinal displacements. The experiments also showed that experimental birds were able to select those courses on the basis of geomagnetic information alone, despite the steep magnetic field lines experienced in high-arctic North America.

Experimental Procedures

We captured adult and juvenile white-crowned sparrows at Inuvik (site 1), northwestern Canada, at the end of the breeding period (July–August) and divided them into two groups. One group was kept in the breeding area, and the other group was transported onboard an icebreaker to unfamiliar sites along a northeasterly route to the magnetic North Pole, located on Ellef Ringnes Island (site 5), and thereafter farther toward the southeast (Figure 1A; see also [30]). By performing repeated cage experiments, we recorded the birds' orientation in the breeding area (controls, site 1) and at eight experimental sites, three (2–4) west of, four (6–9) east of, and one (5) at the magnetic North Pole (Figure 1A). Data for each site and test, divided for age groups, are given in Table 1. Further information on experimental procedures and expected courses are given in Figure 1 and in the Supplemental Data.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two tables and are available with this article online at http://www.current-biology.com/cgi/content/full/15/17/1591/DC1/.

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