



# Avian orientation: effects of cue-conflict experiments with young migratory songbirds in the high Arctic

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The migratory orientation of juvenile white-crowned sparrows, *Zonotrichia leucophrys gambelli*, was investigated by orientation cage experiments in manipulated magnetic fields performed during the evening twilight period in northwestern Canada in autumn. We did the experiments under natural clear skies in three magnetic treatments: (1) in the local geomagnetic field; (2) in a deflected magnetic field (mN shifted  $-90^\circ$ ); and (3) after exposure to a deflected magnetic field (mN  $-90^\circ$ ) for 1 h before the cage experiment performed in the local geomagnetic field at dusk. Subjects showed a mean orientation towards geographical east in the local geomagnetic field, north of the expected migratory direction towards southeast. The sparrows responded consistently to the shifted magnetic field, demonstrating the use of a magnetic compass during their first autumn migration. Birds exposed to a cue conflict for 1 h on the same day before the experiment, and tested in the local geomagnetic field at sunset, showed the same northerly orientation as birds exposed to a shifted magnetic field during the experiment. This result indicates that information transfer occurred between magnetic and celestial cues. Thus, the birds' orientation shifted relative to available sunset and geomagnetic cues during the experimental hour. The mean orientation of birds exposed to deflected magnetic fields prior to and during testing was recorded up to two more times in the local geomagnetic field under natural clear and overcast skies before release, resulting in scattered mean orientations.

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Migratory songbirds use information from the sun, the pattern of polarized skylight, stars and the geomagnetic field for orientation (reviewed in Emlen 1975; Able 1980; Baker 1984; Moore 1987; Wiltschko & Wiltschko 1995). Experiments in which birds have been exposed to cue-conflict situations have resulted in more or less clear shifts relative to the manipulated external information (reviewed in Able 1993; Åkesson 1994; Wiltschko et al. 1998; Åkesson & Bäckman 1999; Wiltschko & Wiltschko 1999). Different species of passerines give different responses to similar experimental conditions at widely separated geographical sites. These results have led to discussions as to whether different bird species use the available compasses in a different hierarchical order or depending on the ecological situation experienced before testing (Able 1993; Åkesson 1994). More recent analyses of cue-conflict experiments suggest that birds do not respond immediately to, for example, magnetic field shifts, but do so only after a number of repeated exposures. Therefore, the variability in test procedures

used by different researchers to investigate effects of magnetic field shifts have been criticized (Wiltschko et al. 1998; Wiltschko & Wiltschko 1999).

Migratory songbirds at high geographical and geomagnetic latitudes meet potential problems when using information from both stars and the geomagnetic field for orientation (Alerstam et al. 1990; Alerstam & Gudmundsson 1999). For much of the polar summer, stars are not available for orientation at high geographical latitudes, resulting in limited possibilities for migratory birds to use a star compass before they begin autumn migration. In areas close to the geomagnetic poles, the geomagnetic field lines are steep (Skiles 1985), and an inclination compass is expected to be unreliable for orientation (Wiltschko & Wiltschko 1972; for responses to artificial vertical magnetic fields see Åkesson 1994; see, however, Åkesson et al. 2001). It is largely unknown whether species differences exist in the use of celestial and magnetic compasses and, in particular, whether the functional characteristics of the orientation system of migrating birds breeding at high geomagnetic latitudes differ from those of other bird species (Sandberg et al. 1991, 1998; Åkesson 1994; Åkesson et al. 1995; Alerstam 1996; Weindler et al. 1998).

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We performed orientation cage experiments to investigate whether juvenile white-crowned sparrows, *Zonotrichia leucophrys gambellii*, breeding at high geomagnetic latitudes in northern Canada, use the magnetic field for orientation during migration, and whether information transfer occurs between magnetic and celestial compass systems, as has been shown for migratory birds at lower latitudes (e.g. Sandberg et al. 2000). Therefore, we repeatedly recorded the birds' migratory orientation in circular cages shortly after local sunset under natural clear to partly covered sky conditions, and in different magnetic fields, during the autumn migration period. The migratory orientation of individual birds was recorded in (1) the local geomagnetic field (inclination +82°), (2) a shifted magnetic field (mN -90°, inclination +82°) during the cage experiment, and (3) after clear sky exposure for 60 min at 2–4 h prior to sunset to the same magnetic field shift (mN -90°, inclination +82°), but with orientation recorded in the local geomagnetic field (inclination +82°). To identify any aftereffects of the cue conflict (e.g. Wiltschko et al. 1998), we recorded the birds' migratory orientation at sunset one or two additional times in the local geomagnetic field under clear and natural overcast skies.

## METHODS

### Subjects

We captured 36 juvenile white-crowned sparrows in Inuvik (68°22'N, 133°43'W), Northwest Territories, Canada, with mist nets at the end of the breeding period (15 July to 10 August 1999). The age of the birds was identified by plumage characteristics (Pyle et al. 1987). The birds were kept indoors in cages at the Aurora Research Institute in Inuvik during the following autumn migration period, during which time we recorded the birds' migratory orientation in circular cages (15 August to 7 September 1999). White-crowned sparrows breed in the northern part of Canada and winter in the southern U.S.A. (Chilton et al. 1995). The population of white-crowned sparrows breeding in the area of Inuvik spends the winter in southwestern U.S.A. (Mewaldt 1964; Chilton et al. 1995). Thus, their expected autumn migration course towards geographical southeast follows an initial great circle route of ca. 135° and a rhumb line route of ca. 151° (Imboden & Imboden 1972), as calculated from the breeding area in Inuvik to an approximate central position in the wintering range in westernmost Texas. To reach the wintering areas, white-crowned sparrows migrate solitarily at night and depart from breeding areas in north Canada in mid-August to early September (Chilton et al. 1995; personal observations).

Subjects were kept in separate cages (200 × 200 mm and 400 mm high) in a room with windows facing geographical north, allowing the birds to experience the natural light regime but not to see outdoor celestial cues. The cages were constructed of nonmagnetic materials, i.e. wood with plastic nets. The birds were kept indoors in cages between 15 and 30 days after capture, until we began the orientation cage experiments. We fed the birds

with a mixture of mealworms, seeds, fruits and a food mixture for insectivorous birds and water with vitamins. Subjects stored large amounts of visible subcutaneous fat (for a scale for visual fat classification, see Pettersson & Hasselquist 1985), preparing for migration while they were kept in cages (for mass increase and fat levels during the experimental period, see Åkesson et al. 2001). After conducting the experiments, we released the birds near the sites of capture, on 7 September at the latest. We did not expect the cue conflict to have a lasting effect on the birds' orientation, because calibration of compasses has been shown to occur within short periods, and after magnetic field shifts of different directions (Sandberg et al. 2000). Permission to perform the project was given by the Canadian Wildlife Service, and the local Hunters and Trappers and Animal Care Committees.

### Experimental Set-up and Procedure

We used modified Emlen funnels (Emlen & Emlen 1966), with a top diameter of 300 mm and an inner height of 150 mm, lined with Tipp-Ex paper to record the birds' migratory activity (Rabøl 1979). A 25-mm-high plastic shielding was attached to the edge of the plastic tops, which allowed the birds to see ca. 140° of the sky above at zenith. The orientation cages were constructed of nonmagnetic materials, and the tops of the cages were covered with fine-mesh plastic net, allowing the birds to see the natural sky. We used four experimental set-ups with electromagnetic coils (modified Helmholtz coils 800 × 800 mm, powered by 12-V car batteries), each consisting of two coils arranged in pairs around the orientation funnel to shift the horizontal component of the geomagnetic field (for technical specifications, see Sandberg et al. 1988).

We performed cage experiments outdoors in the open backyard of the Aurora Research Institute in Inuvik. The group of birds exposed to a shifted magnetic field for 1 h under clear skies at daytime were kept in cages where they were allowed to see both landmarks nearby and the sky above at zenith. Experiments under clear sky conditions allowed the birds to see the natural sky through the top netting of the funnels. We performed experiments under natural skies with cloud cover varying from 0/8 (cloudless skies) to 8/8 (completely overcast skies). Experiments began at or shortly after local sunset and continued for 60 min. In the first part of the experimental period, which had a relatively extended sunset period, we performed two experiments during the same night. Birds were exposed to natural sunset skies, during periods with a sun elevation at its lowest position, -9° below the horizon in the middle of the experimental hour (range: -1° - -9°), allowing the birds to see stars during at least part of the experimental period (i.e. at sun elevations below -4°; Åkesson et al. 1996).

The birds' migratory orientation was recorded in the following experimental conditions, in sequence.

(1) Control: natural clear sky conditions in the local geomagnetic field (inclination +82°).

(2) Deflected: natural clear sky conditions in a shifted magnetic field (magnetic north, mN, shifted  $-90^\circ$ , inclination  $+82^\circ$ ).

(3) Pre-exposed: birds were exposed to a shifted magnetic field during the afternoon (mN  $-90^\circ$ , inclination  $+82^\circ$ ) for 60 min 2–4 h before local sunset, when given access to natural clear sky conditions, but birds' orientation was recorded under natural sky conditions at sunset (clear to partly covered skies, cloud cover 0–6/8) in the local geomagnetic field (inclination  $+82^\circ$ ).

(4) Clear sky after, Overcast after final one to two experiments under natural sky conditions (clear and overcast skies) in the local geomagnetic field (inclination  $+82^\circ$ ), with birds that had been previously exposed to a shifted magnetic field during the time of experiment at sunset or during pre-exposure in the afternoon during the previous day(s).

### Possible Outcomes

If the white-crowned sparrows used a magnetic compass, we expected a shift of mean orientation with the magnetic shift (experimental condition 2 above). If the birds instead mainly relied on celestial cues at dusk, they were expected not to follow the magnetic shift (2 above), but to keep the orientation similar to the control group tested in the local geomagnetic field (1 above). Birds exposed to a cue conflict (i.e. shifted magnetic field under natural clear skies; 3 above) before the experiment at sunset were expected to respond differently to the pre-exposure, depending on which cues were most important to them at sunset. At least three responses to the cue-conflict exposure during daytime are likely. (1) If compass course transfer occurred from the birds' magnetic compass to visual cues, and visual cues were used at sunset, then they would shift their preferred course according to the magnetic field deflection (i.e. similar orientation as Deflected group (2) towards geographical north). (2) If information was instead transferred from visual cues to the magnetic field, and the magnetic field was used at dusk, then we expected a course shift in mean orientation to the right relative to the control direction proportional to the magnetic shift that was experienced shifted to the left in the daytime (i.e. orientation towards geographical southwest at dusk). (3) If the birds calibrated their compasses at sunset or later at night, they would ignore the magnetic field shift experienced earlier the same day, and select the migratory course based on the cues available at dusk as in the Control condition.

### Data Reduction and Statistics

The activity of the birds was recorded as claw marks in the pigmented papers (Tipp-Ex). We used papers showing birds' responses with at least 40 registrations crossing a horizontal line in the cage and recorded during 1 h in further analyses. We calculated the mean orientation of individual birds during each test by using vector addition. An arrow indicates the mean angle of orientation ( $\alpha$ ), and the length of the arrow is a measure of the scatter of the

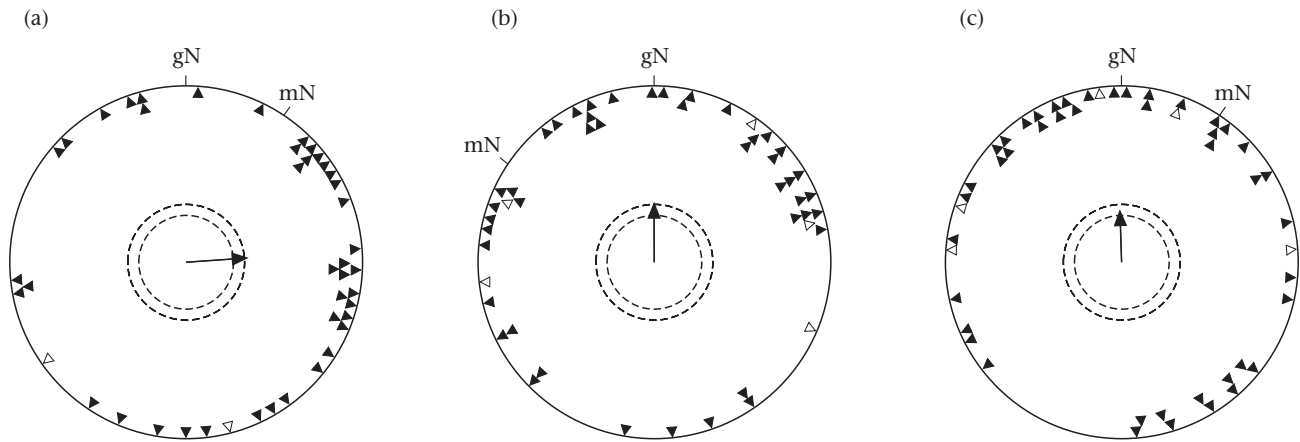
circular distribution (inversely related to the angular scatter,  $r$ , range 0–1;  $r_2$  given for axial distributions; Batschelet 1981). Mean orientation for axial distributions ( $\alpha_2$ ) was calculated by doubling the angles (Batschelet 1981). We used the Rayleigh test to determine whether the circular distribution differed significantly from random (Batschelet 1981). We excluded from further analysis experiments in which individual birds failed to show a reasonably well-defined orientation (the limit was arbitrarily set to  $P > 0.05$  according to the Rayleigh test; cf. Batschelet 1981; for selection criteria, see Sandberg et al. 1988; Åkesson 1994). Based on these criteria, we excluded only 5.2 ( $N=11$ ) and 2.9% ( $N=6$ ) of the tests because of low activity or disorientation, respectively. For individual birds showing significant unimodal orientation, the measure of scatter of the distributions varied between 0.05 and 0.75 (median=0.27). The median bird activity recorded as scratches across a horizontal line in the cages was 869 (range for all birds 26 (subject excluded due to low activity, see above)–2535 registrations). Axial distributions were reported if  $r_2 > r$  by at least 0.02 for individual tests. For individuals with a significant axial mean orientation (15 out of 191 experiments), we used only the side of the axis with the majority of the registrations for statistics (Figs 1, 2; open symbols). Mean orientations for individual birds were used to calculate sample mean vectors and axes of orientation (Batschelet 1981). We analysed differences in scatter of distributions between groups by a 'test for the homogeneity of concentration parameters'; given no difference in scatter, we compared the mean orientation between groups with Mardia's (1972) one-way classification test (denoted by  $F_{1, ap}$ ). We used the 95% confidence interval (CI) to analyse whether the mean orientation differed from the direction of the sun's position in the middle of the test hour and from the expected migratory courses (Batschelet 1981).

We calculated the angles of inclination ( $81.8^\circ$ ) and declination ( $32.8^\circ$ ), as well as the total field strength (58 477 nT) for Inuvik based on the Canadian Geomagnetic Reference Field model CGRF 2000 (Geological Survey of Canada). The accuracy of the magnetic field parameters calculated based on this model can be approximated to 200 nT for the horizontal component and 280 nT for the vertical component. Error in inclination, as calculated for average field values at the Resolute Bay Observatory, is  $0.2^\circ$ .

## RESULTS

### Control Direction of Migration

The juvenile white-crowned sparrows showed an easterly mean orientation when recorded during the natural autumn migration period under clear and partly covered skies in the local geomagnetic field of Inuvik (Fig. 1a, Table 1). The mean angle of orientation for the control group was significantly different from the expected migratory direction towards southeast along an initial great circle (ca.  $135^\circ$ ) and a rhumb line route (ca.  $151^\circ$ ) as calculated for a central position of the expected wintering area in westernmost Texas ( $P < 0.05$ ; Mewaldt 1964;



**Figure 1.** Results of orientation experiments with juvenile white-crowned sparrows under natural clear skies in Inuvik, northwestern Canada in autumn. Experiments were performed in the local geomagnetic field (a, Control: inclination +82°), in a deflected magnetic field (b, Deflected: mN deflected 90° to the west, mN –90°, inclination +82°), and in the local geomagnetic field (c, Pre-exposed: birds exposed to a deflected magnetic field in the afternoon, mN –90°, and orientation recorded in the local geomagnetic field). ▲, △: Mean orientation of a single bird during one experimental hour; △: birds with a preferred bimodal orientation. Arrows indicate mean angles of orientation of the groups: length of arrow is a measure of the scatter of the circular distribution (range 0–1; the radius of a circle was inversely related to the angular scatter). For each condition, the directions towards magnetic north (mN) and geographical north (gN) are indicated. Inner circles indicate the 5% and 1% significance levels according to the Rayleigh test, respectively (Batschelet 1981) (see Table 1).

**Table 1.** Results of orientation cage experiments performed with juvenile white-crowned sparrows in northwestern Canada in autumn

Group	$\alpha/\alpha_2$	$N$	$r/r_2$	$P$	95% CI $P$ GC, $P$ RL	Sun azimuth $P$
Control before	86°	44	0.34	0.005	±34°*,*	308°*
Deflected, all	360°	49	0.31	0.009	±36°*,*	313°*
Deflected, experiments 1,2	322°	34	0.32	0.028	±41°*,*	314°
Deflected, experiments 3,4	46°	15	0.62	0.002	±30°*,*	310°*
Pre-exposed	359°	49	0.27	0.027	±41°*,*	309°*
Clear sky after	180°–0°	33	0.21	0.24	—	303°
	329°	33	0.05	0.93	—	303°
Overcast after	41°–221°	16	0.25	0.37	—	326°
	313°	16	0.10	0.85	—	326°
Clear sky and overcast after	194°–14°	49	0.17	0.23	—	309°
	321°	49	0.06	0.82	—	309°

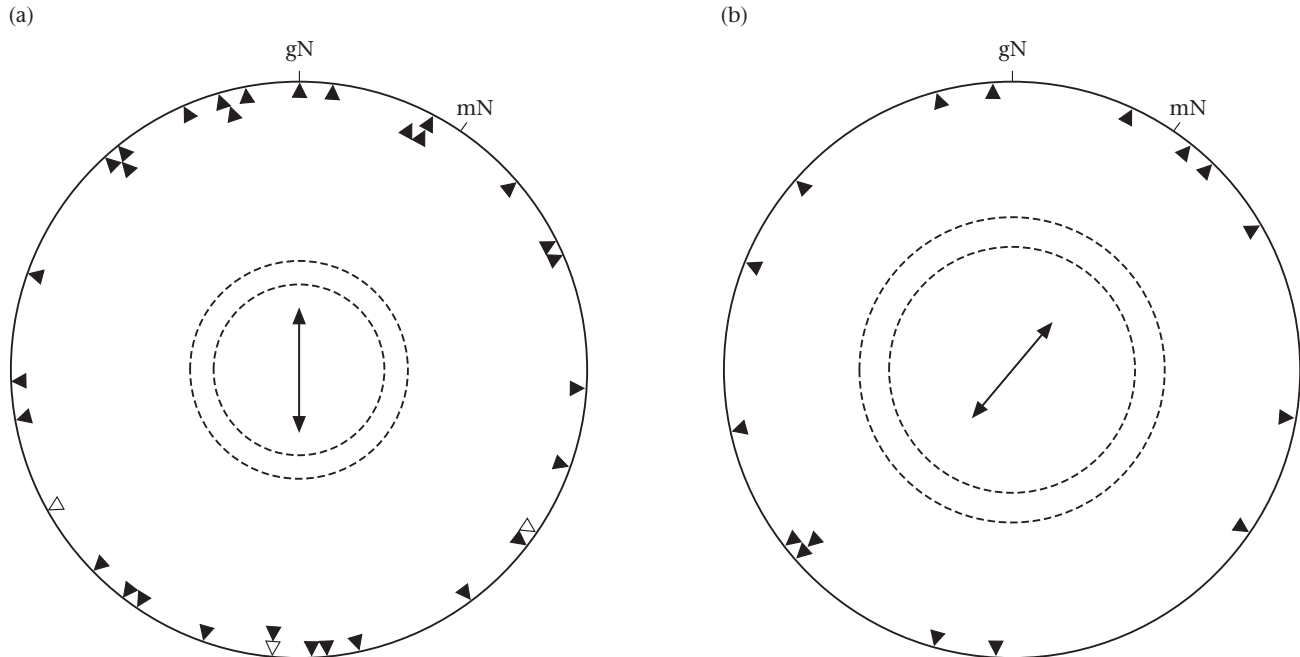
Mean angle of orientation ( $\alpha$ ,  $\alpha_2$ ) relative to geographical north, vector lengths ( $r$ ,  $r_2$ ) and number of tests ( $N$ ) under natural clear and partly overcast skies are given. Significance levels are given according to the Rayleigh test (Batschelet 1981). The mean directions towards the position of the sun (Sun azimuth) in the middle of the experimental hour are given. The 95% confidence intervals (95% CI) are also given. Asterisks denote significant ( $P < 0.05$ ) deviations from the expected migratory directions (GC: great circle route 135°; RL: rhumb line route 151°) and from the mean sun azimuth. For groups with  $r_2 > r$ , the statistics for the unimodal distribution are included below the statistics for the axial distribution.

Chilton et al. 1995). The mean orientation of the control group differed significantly from the position of the sun in the middle of the test hour ( $P < 0.05$  in all cases; Table 1), which suggests that the birds' mean orientation was not a result of a phototactic response.

### Effects of Magnetic Field Deflections

Birds exposed to a magnetic field deflection (mN shifted –90°) responded to the deflection by shifting their mean angle of orientation towards north (–86°) corresponding well to the degree of the magnetic shift (Fig. 1b, Table 1). The mean orientation of the Deflected

group differed significantly from the orientation of the Control group ( $F_{1,91} = 11.8$ ,  $P < 0.001$ ; Mardia 1972). The mean orientation of the Deflected birds differed significantly from the direction towards the position of the sun in the middle of the experimental hour ( $P < 0.05$ ; Table 1). The orientation of the Deflected birds (condition 2) was repeatedly recorded in a shifted magnetic field at least two and up to four times. When the Deflected group was divided in half on the basis of the number of experiments experienced (test number 1 and 2 compared with test 3 and 4), we found a pattern where the white-crowned sparrows during their first two tests closely followed the magnetic shift (tests 1 and 2) and birds in the latter group



**Figure 2.** Orientation cage experiments with juvenile white-crowned sparrows performed twice on different nights after magnetic field deflections in the local geomagnetic field under natural clear skies (a, cloud cover 0–7/8) and under natural overcast skies (b, 7–8/8; see Fig. 1, Table 1).

(tests 3 and 4), responded to the deflection by shifting their orientation to a smaller degree (Table 1).

### Effects of Cue-conflict Exposures Before Experiment

Pre-exposed birds, which had been temporarily exposed to a shifted magnetic field (mN shifted  $-90^\circ$ ) under natural clear skies in the afternoon, showed a northerly mean orientation when recorded in the local geomagnetic field under natural clear sky conditions shortly after sunset (Fig. 1c, Table 1), significantly different from the mean orientation of the control group ( $F_{1,91}=10.9$ ,  $P<0.005$ ). The mean orientation of the Pre-exposed group was not significantly different from the mean orientation of birds exposed to a deflected magnetic field during testing ( $F_{1,96}=0.0015$ , NS). The mean orientation of the pre-exposed birds differed significantly from both the sun azimuth as well as from the expected migratory direction towards the southeast ( $P<0.05$  in both cases; Table 1).

Experiments under natural clear and overcast skies performed in the local geomagnetic field with all birds at least one day after the Deflected or Pre-exposed conditions resulted in scattered mean orientations (Fig. 2a, b, Table 1). In both cases, the mean orientation was not significantly different from random ( $P>0.05$ ; Table 1).

### DISCUSSION

The results of tests performed in a deflected magnetic field demonstrate that juvenile migrating white-crowned

sparrows, tested during autumn in the breeding area in northwestern high-arctic North America, possess a magnetic compass. Cage experiments performed with white-crowned sparrows from the same population and displaced to the area at and close to the magnetic North Pole showed that the birds were able to select meaningful migratory courses towards southeast on the basis of the geomagnetic field alone, also in steep magnetic fields without prior experience (Åkesson et al. 2001). This result is intriguing because of the potential difficulty of using a magnetic compass based on the angle of inclination at high geomagnetic latitudes (Wiltschko & Wiltschko 1972), and indicates that these birds' magnetic sense is very sensitive (Åkesson et al. 2001). Although the white-crowned sparrow has an extensive breeding distribution across northern Canada and migrates to wintering sites in the south U.S.A., there are different subspecies (Chilton et al. 1995) which will experience different angles of declination (e.g. Skiles 1985). Varying angles of declination are likely to cause orientation problems for birds using a magnetic compass migrating across longitudes at high geomagnetic and geographical latitudes (e.g. Alerstam et al. 1990, 2001; Alerstam & Gudmundsson 1999), and compass calibration on migration has been suggested to explain how birds might cope with this problem (Able & Able 1993, 1995, 1999). A related species, the Savannah sparrow, *Passerculus sandwichensis*, recalibrates its magnetic compass course relative to celestial cues during ontogeny as well as during migration (Able & Able 1990a, b, c, 1993, 1995, 1999). Experiments with European and Australian passerine migrants, however, indicate that the information transfer occurs from

magnetic to celestial cues, and that reactions to magnetic field shifts by shifting the birds' orientation under clear skies might take several days (Wiltschko & Wiltschko 1975a, b; Wiltschko et al. 1998; see also Åkesson 1994).

The white-crowned sparrows in our study showed immediate responses to the magnetic field shift, with the most obvious effect in the first two experiments under magnetic field deflections, and a smaller shift after two further repeated deflected magnetic field exposures. These results indicate that the birds initially follow the magnetic field shift by changing their courses, but later might recalibrate this course relative to visual cues at dusk. The results from the Pre-exposed group indicate that information transfer occurs from the magnetic field to celestial cues at daytime, and that this new magnetic course is kept when tested at dusk. This observation further supports the finding that compass calibration can occur after only a short exposure time (Sandberg et al. 2000), but also that magnetic-celestial compass calibration can occur in the daytime, presumably involving daytime celestial cues also at high geomagnetic latitudes (Able & Able 1993).

After-effects of cue-conflict experiments, demonstrating course shifts for several days, have been reported for nocturnal passerine migrants (Wiltschko et al. 1998). In our experiments, however, we were not able to record such persistent after-effects, because the mean orientations expressed by birds tested for a second and third time under natural clear and overcast skies in the local geomagnetic field were not different from random. If the deflected magnetic field exposure resulted in a recalibrated magnetic course (e.g. Able & Able 1995), we would expect birds to keep this new magnetic course under overcast skies without directional information available from the celestial cues. However, the scattered mean orientations did not support any such persistent magnetic compass orientation, and might be an effect of some birds still selecting the new deflected magnetic course while other individuals presumably were again heading in the expected migratory direction, perhaps once more recalibrating their compasses. It is unclear why the birds were able to respond immediately to a shifted magnetic field during the experiment as well as when tested in the local magnetic field after a short exposure to a deflected magnetic field the same day, but that the new course was no longer present when the birds' orientations were recorded for a second or third time under natural sky conditions. To explain these results, further experiments dissecting the functional characteristics of birds' compass calibration mechanism will be needed.

Our experiments show that young white-crowned sparrows born at high geomagnetic latitudes use a magnetic compass during autumn migration. Furthermore, the results suggest that the inherited magnetic course can be changed as a result of cue-conflict exposure. Birds transported between west and east North America experience a shift in declination of the same magnitude, that is in magnetic north relative to geographical north (Skiles 1985), as our birds did in our experimental manipulations. A calibration mechanism, enabling birds to transfer compass information between different systems of

orientation (Able & Able 1993, 1995, 1999) is likely to be of great importance to enable birds to orientate in these areas with complicated patterns of magnetic field changes.

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