

# Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues

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Night migratory songbirds can use stars, sun, geomagnetic field, and polarized light for orientation when tested in captivity. We studied the interaction of magnetic, stellar, and twilight orientation cues in free-flying songbirds. We exposed *Catharus* thrushes to eastward-turned magnetic fields during the twilight period before takeoff and then followed them for up to 1100 kilometers. Instead of heading north, experimental birds flew westward. On subsequent nights, the same individuals migrated northward again. We suggest that birds orient with a magnetic compass calibrated daily from twilight cues. This could explain how birds cross the magnetic equator and deal with declination.

Billions of songbirds migrate between continents twice each year, but their orientation capabilities are almost exclusively studied in the laboratory. We presented birds with experimentally altered orientation cues and followed their subsequent migratory flights in the wild. Avian navigation capabilities are very precise (1), with many individuals returning to the same breeding sites year after year (1–3) after a voyage of up to 25,000 km (4, 5). Migratory songbirds can orient on the basis of compass information from the sun and its associated polarized light patterns (6–9), the stars (10–12), the earth's magnetic field (13, 14), and the memorization of spatial cues en route (15, 16). However, the interactions and relative importance of these cues remain unclear and a source of much debate (7, 17–18). Our knowledge about the orientation mechanisms of songbirds relies almost exclusively on data from cue-manipulated captive migrants tested in various orientation cages, on vanishing bearings based on the first few hundred meters of flight (19, 20), and to a much lesser degree on field data (ringing and radar and visual observations) from unmanipulated natural migrants (7, 15, 21).

**Testing five hypotheses.** On clear evenings, we fitted *Catharus* thrushes with radio transmitters and placed them in outdoor cages in an artificial eastward-turned magnetic field from about sunset until the sun was 11° or more

below the horizon when they were set free (22). We then radio-tracked (22–28) them in flight to obtain heading data. Because *Catharus* thrushes do not compensate for wind drift but individuals maintain nearly constant preferred headings from night to night (26), we used measured headings for orientation analyses (22).

Our data on the birds' headings enabled us to distinguish between the five most likely migratory orientation hypotheses: *Catharus* thrushes use either (i) a magnetic compass or (ii) a star compass, which dominate over all other cues [e.g., (19, 20, 29, 30)]. Alternatively, (iii) *Catharus* thrushes may use twilight cues provided by the sunset direction and/or the associated polarization patterns (when available) for selecting a migratory direction and the stars (when available) for maintaining that direction during nocturnal flight (7), that is, a star compass calibrated daily from twilight cues. As another possibility, (iv) the birds could use twilight cues (when available) for selecting a migratory direction and a geomagnetic compass for maintaining that direction during nocturnal flight (23), that is, a magnetic compass calibrated daily from twilight cues. Finally, (v) *Catharus* thrushes could use magnetic cues for selecting a migratory direction during the twilight period and a star compass or dead-reckoning strategy for maintaining that direction during nocturnal flight (19, 31), in other words, a visual compass calibrated daily from magnetic cues. This hypothesis becomes particularly plausible if birds can only sense the geomagnetic field when sufficient amounts of light are available (32, 33). Figure 1, A to C, illustrates the predicted outcomes of our experiment based on each of the five hypotheses.

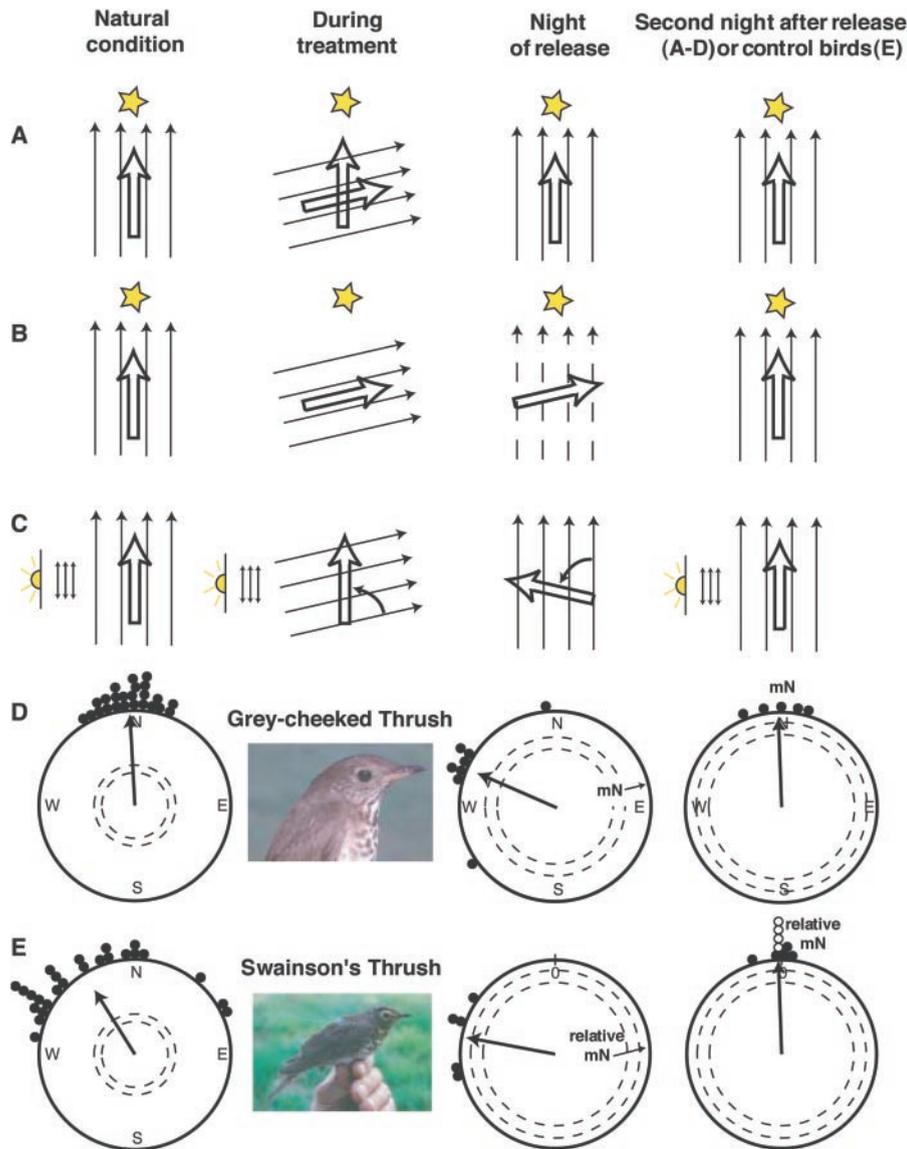
**Treatment shifts free-flight direction.** Natural migrating gray-cheeked thrushes, *C. minimus*, show very consistent northerly headings (mean = 357°,  $r = 0.973$ ,  $P < 0.001$ , and

95% and 99% confidence intervals for mean of 268° to 320° and 260° to 328°, respectively). Birds taking off after being exposed to clockwise changes in the magnetic field (70° to 90°, mean = 77°,  $r = 0.990$ , and  $n = 8$ ) headed in westerly directions (mean = 294°,  $r = 0.871$ ,  $n = 8$ ,  $P < 0.001$ ; 95% and 99% confidence interval for mean 268° to 320° and 260° to 328°, respectively). These headings are in very close agreement with the mirror-image directions (mean of 283°) predicted if the birds had calibrated a magnetic compass from sunset-related twilight cues (Fig. 1C). The difference in headings between the magnetically treated birds and the natural migrants is highly significant (compare columns 1 and 3 in Fig. 1D) {Watson-Williams test:  $F = 54.41$ ,  $F_{1,30[\alpha = 0.001(2)]} = 15.2$ ,  $P < 0.001$ }. Five gray-cheeked thrushes that were exposed to the changed magnetic field did not migrate the night they were treated, but flew to nearby woods, and, 1 to 6 nights later (controls, Figs. 1D, column 4, and 2A), headed in the normal northerly migratory direction (mean = 358°,  $r = 0.972$ ,  $n = 5$ ,  $P < 0.01$ , and 95% and 99% confidence intervals for mean of 341° to 16° and 336° to 21°, respectively). Their headings were significantly different from the birds that took off during the night of treatment (compare columns 3 and 4, Fig. 1D) { $F = 16.52$ ,  $F_{1,11[\alpha = 0.005(2)]} = 15.2$ ,  $P < 0.005$ ; 99% confidence intervals do not overlap} but not different from the headings of the natural migrants (compare columns 1 and 4, Fig. 1D) { $F = 0.07$ ,  $F_{1,27[\alpha = 0.50(2)]} = 1.38$ ,  $P = 0.79$ }. Because control birds were in the wild during the evening before their departure, they experienced the normal unchanged geomagnetic field during the last twilight period before departure. We therefore suggest that gray-cheeked thrushes recalibrate their magnetic compass from twilight cues on a daily basis.

The wide spread of headings (west through north to northeast, Fig. 1E, column 1) of naturally migrating Swainson's thrushes, *C. ustulatus*, meant that we had to use each individual bird as its own control. Therefore, in addition to headings obtained on the night of experimental release, we also measured headings for the same Swainson's thrushes on at least one subsequent night of migration. All of these second (control) flights occurred under clear skies that provided solar, twilight, as well as stellar cues. Headings of naturally migrating individual Swainson's thrushes followed during several consecutive migratory flights (26) (Figs. 1E, column 4, and 2B and fig. S2) were very consistent between nights (first night's heading relative to second night's heading: mean = 358°,  $r = 0.990$ ,  $n = 5$ ,  $P < 0.002$ , and 95% and 99% confidence intervals for mean of 348° to 8° and 345° to 12°, respectively). In contrast, headings of Swainson's thrushes followed on the night when they had been exposed to clock-

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**Fig. 1.** (A to C) Predicted orientation responses of birds with respect to potential orientation mechanisms and their interactions. (D and E) The actual orientation responses of free-flying gray-cheeked and Swainson's thrushes, respectively. (A) If the stars or the magnetic field show simple domination, or if the stars are calibrated from twilight cues, there should be no effect of the magnetic treatment after release (third and fourth column). (B) If birds use their magnetic compass to calibrate a celestial compass at sunset, they should head east on the first night after treatment and then in the normal northerly migratory direction. (C) If twilight cues are used to calibrate the magnetic compass on a daily basis, birds experiencing a magnetic field turned toward the east should orient toward the west during the same night after release. On subsequent nights they should return to their normal northerly migratory direction. (A to C) The four thin parallel arrows indicate the horizontal direction of the magnetic field lines experienced by the birds. The thick arrow indicates the expected orientation of the birds. The star indicates the unchanged directional information potentially available from celestial cues. (D) Each dot at the circle periphery indicates the measured true heading of one free-flying gray-cheeked thrush during natural migration (left column), after treatment (middle column), or after flying to nearby woods after treatment and migrating on a subsequent night (right column). The arrows indicate the length and direction of the group mean vectors. The inner and outer dashed circles indicate the radius of the group mean vector needed for significance ( $P < 0.05$  and  $P < 0.01$ , respectively) according to the Rayleigh test (42). mN, true magnetic north. (E) Each dot at the circle periphery indicates the heading of one free-flying Swainson's thrush during natural migration (left column) on the night of treatment, relative to its heading on its subsequent flight (standardized to  $0^\circ$ ) from an unmanipulated environment (middle column), or during natural migration, relative to its heading on its subsequent natural night's flight, standardized to  $0^\circ$  (right column). Open dots indicate four additional relative headings of one individual followed for 6 nights, but only the first data point for that individual was used for statistical analysis to avoid pseudoreplication. Relative mN is magnetic north on first night relative to magnetic north on second night. Note that the directional spread in natural headings in (D) is narrow (column 1), thus control birds (column 4) suffice to document an effect of magnetic treatment (column 3), whereas in (E), Swainson's thrushes show wide variation in natural migratory headings (column 1), forcing us to use each individual as its own control during its subsequent migratory flight initiated under natural conditions (column 3).

wise changes in the magnetic field toward the east ( $70^\circ$  to  $90^\circ$ , mean =  $86^\circ$ ,  $r = 0.991$ , and  $n = 5$ ) were oriented in directions turned  $55^\circ$  to  $103^\circ$  counterclockwise toward the west relative to their heading during the following migratory flight (first night's heading relative to second night's heading standardized to  $0^\circ$ : mean =  $281^\circ$ ,  $r = 0.950$ ,  $n = 5$ ,  $P < 0.005$ , and 95% and 99% confidence intervals for mean of  $258^\circ$  to  $304^\circ$  and  $251^\circ$  to  $311^\circ$ , respectively) (Figs. 1E and 2B). The headings on the first night relative to the second night are significantly different between the treated and the nontreated birds [ $F = 57.49$ ,  $F_{1,8}[\alpha = 0.001(2)] = 31.6$ ,  $P < 0.001$ ; 99% confidence intervals do not overlap; compare columns 3 and 4 in Fig. 1E], and the headings of the treated birds are significantly different on the night of treatment than on following nights [ $P < 0.01$ , because 99% confidence interval ( $251^\circ$  to  $311^\circ$ ) for orientation on the first night relative to the second night does not include  $0^\circ$ ]. The results fit the predictions (Fig. 1C) only if Swainson's thrushes used a magnetic compass that was calibrated from sunset-related twilight cues.

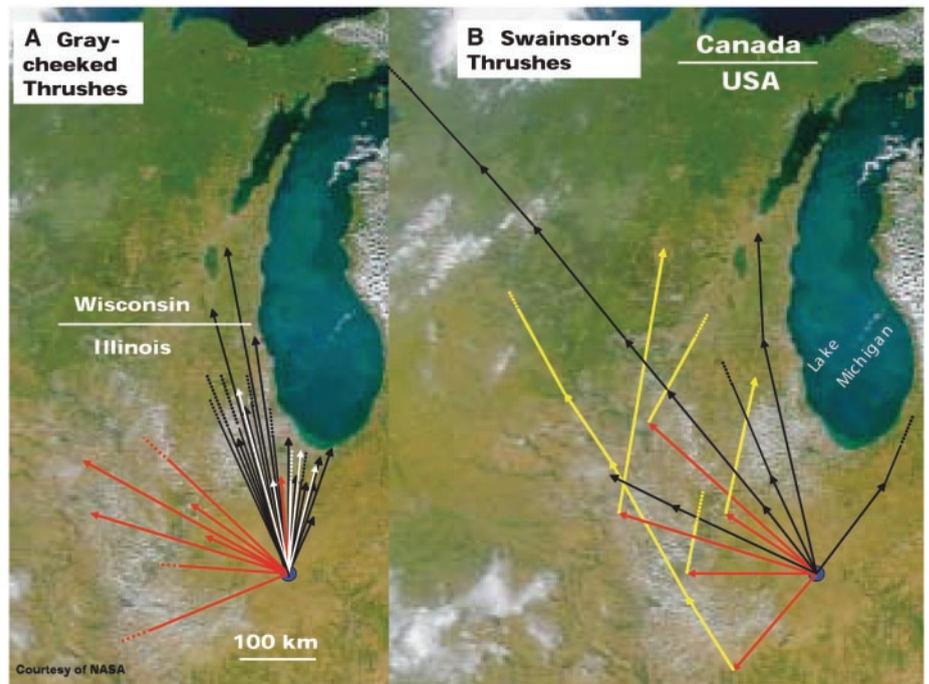
**Magnetic cue during flight.** The fact that the birds' headings in the treated groups were deflected implies that the magnetic field was sensed by the birds while stationary in a cage (for the calibration) and also in flight after departing from the coil system (for en route orientation). We therefore suggest that *Catharus* thrushes use their geomagnetic compass not only before takeoff (7) but also as the primary cue during nocturnal migratory flight after takeoff (23, 34). Our experimental *Catharus* thrushes continued flying in westerly (inappropriate) directions in spite of their opportunity to reorient on the clearly visible stars. Thus, our experimental birds seem to have either ignored the stars as an orientation cue altogether, or they may have calibrated them from the magnetic field after takeoff. Our data suggest that the time it takes *Catharus* thrushes to determine a magnetic compass direction while aloft must be relatively short, because we recorded several headings of treated birds within a few minutes after takeoff and all of these headings were already deflected. Furthermore, if magnetoreception in *Catharus* thrushes is light-dependent (32, 33), the amount of light needed for magnetic orientation was minimal: At our release site, light available at the time of release on starlit nights was measured to be 0.0003 to 0.002 lux. Considering the high homogeneity of our experimental magnetic fields (22) and the symmetrical nature of any minor artifacts, it is highly unlikely that our results could be caused by systematic magnetic map effects (22, 35).

**Preflight solar calibration.** Our results indicate that free-flying, naturally migrating Swainson's and gray-cheeked thrushes use a magnetic compass as primary orientation

mechanism in flight (28). This magnetic compass, however, does not seem to be based on a fixed magnetic heading relative to magnetic north. Instead, the magnetic heading used during migration seems to be calibrated relative to the solar azimuth during the sunset and/or twilight period. A calibration could be accurate within a degree or so for several days because solar twilight azimuths change slowly with time. Thus, well-oriented flights initiated after overcast days (23, 26) could be guided by a previously calibrated magnetic compass. The calibrating twilight cue could be the setting sun itself and/or the polarized light patterns in the overhead sky. Overhead polarized skylight is the most likely cue because it seems to be sufficient and preferred over the sun itself in several orientation cage experiments (7, 9, 36–38).

**Discussion.** Birds calibrating their magnetic compass from a solar azimuth reference would be unsusceptible to changes in declination, which can be as much as  $-20^\circ$  to  $+30^\circ$  within the North American continent. Similarly, breeding in a magnetic anomaly would be unproblematic for the birds' orientation. A twilight-calibrated magnetic compass could also explain one of the enigmas of bird migration, namely how migratory songbirds, known to have a magnetic inclination compass (13, 14), can cross the magnetic equator without becoming disoriented (34, 39). Birds using a sunset-calibrated magnetic compass are predicted to follow curved tracks because the sunset direction varies up to  $\pm 25^\circ$  with latitude and time of year. Such a feature may prove problematic to some species and advantageous to others. The clockwise changes implicit with the twilight-calibrated magnetic compass in spring will in general produce a crescent route through Central America or over the Caribbean Sea and Gulf of Mexico, avoiding the more direct but long over-water trans-Atlantic route. It is unclear whether a twilight-calibrated magnetic compass would possess similar adaptive advantages for migration from Africa to Europe or elsewhere.

Differences in orientation mechanisms of birds between continents could be one reason why our findings are inconsistent with the results of many orientation funnel experiments, which suggest that migrants rely on a dominating uncalibrated magnetic compass or on a magnetically calibrated stellar (or other visual) compass for orientation [e.g., (19, 29, 31, 40, 41)]. It is also conceivable that birds use different cue calibrations under different ecological scenarios. For example, a pure reliance on the geomagnetic field without reference to the sun when facing a major ecological barrier could explain dissimilar results for Swainson's thrushes that were tested in orientation cages (Gulf of Mexico) (29). Alternatively, our data allow the possibility that not all hypotheses about orientation mechanisms deduced in orientation cages can be generalized to free-flying birds migrating under natural conditions, where all



**Fig. 2.** Tracks of free-flying (A) gray-cheeked thrushes and (B) Swainson's thrushes. Arrows indicate the direction and ground track of flights if the flights were conducted under no-wind conditions (22). Data are depicted differently in (A) and (B) because for gray-cheeked thrushes experimental and control birds are different individuals, whereas in Swainson's thrushes the same experimental individuals were followed for at least two successive nocturnal migrations (because of the large spread in natural headings) (Fig. 1). Connected arrows show flights of the same individual during successive nights. Arrows depict natural migratory flights in black; experimental birds for which the magnetic field was turned east before takeoff, red; subsequent night flights of experimental birds, yellow; and experimental birds that did not migrate on the night of magnetic treatment but did so 1 to 6 days later, white. Broken lines indicate that birds were lost during tracking at the site where the broken lines start.

cues are continuously available in their natural form. The fact that birds orient in their appropriate migratory direction in orientation cages even after months in captivity [e.g., (32)] suggests that orientation cage results are valuable for elucidating the basic orientation capabilities of migratory birds. Cue-conflict experiments in cages [e.g., (7, 17–19, 31, 40)] show that birds can, in principle, transfer information between specific orientation cues. Nevertheless, migratory restlessness in a cage is not identical to natural mid-air flight, and orientation cages provide birds with simplified cue environments. Particularly in complex cue-conflict experiments, previous experience of the birds, non-present but normally relevant cues, time spent in captivity, and small variations in the experimental setup could alter delicate interactions between the cues. We therefore support Moore's (7) assertion that "it is essential that results of orientation cage studies be interpreted in the light of field observations of migratory behavior and experiments with free-flying migrants." We suggest that the simple yet reliable twilight-calibrated magnetic compass may be used by many other species of night migratory birds in the wild.

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## Supporting Online Material

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Materials and Methods

Figs. S1 and S2

Tables S1 and S2

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# Southern Ocean Iron Enrichment Experiment: Carbon Cycling in High- and Low-Si Waters

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The availability of iron is known to exert a controlling influence on biological productivity in surface waters over large areas of the ocean and may have been an important factor in the variation of the concentration of atmospheric carbon dioxide over glacial cycles. The effect of iron in the Southern Ocean is particularly important because of its large area and abundant nitrate, yet iron-enhanced growth of phytoplankton may be differentially expressed between waters with high silicic acid in the south and low silicic acid in the north, where diatom growth may be limited by both silicic acid and iron. Two mesoscale experiments, designed to investigate the effects of iron enrichment in regions with high and low concentrations of silicic acid, were performed in the Southern Ocean. These experiments demonstrate iron's pivotal role in controlling carbon uptake and regulating atmospheric partial pressure of carbon dioxide.

The Southern Ocean exerts a major control on the partial pressure of carbon dioxide ( $p\text{CO}_2$ ) in the atmosphere. Because rates of photosynthesis and biological carbon export are low in Antarctic waters, macronutrients are largely unused, and upwelled  $\text{CO}_2$  entering the atmosphere (1, 2) sustains the relatively high interglacial atmospheric  $\text{CO}_2$  of the present day (3).

Southern Ocean surface waters contain extremely low iron concentrations (4, 5), and the low rates of primary production have been attributed to iron deficiency. Recent open-ocean iron enrichment experiments demonstrate the

validity of this hypothesis in the Southern Ocean (6, 7). Martin (8) proposed that natural variations in the atmospheric iron flux ultimately regulate primary production in the Southern Ocean and influence the  $p\text{CO}_2$  of the atmosphere, thereby potentially affecting the radiative balance of the planet. Syntheses of models, field observations, and paleoceanographic data (3, 9, 10, 11, 12) support a role for iron-regulated changes in Southern Ocean macronutrient use. Indeed there is a strong inverse correlation between iron-rich dust, marine production, and atmospheric  $p\text{CO}_2$  over the past four glacial cy-

cles as recorded in Antarctic ice cores (13). These observations support the "iron hypothesis" as proposed by Martin (8), yet the magnitude of the iron enrichment effect on marine production and atmospheric  $p\text{CO}_2$  remains uncertain.

Although all Southern Ocean surface waters have high concentrations of nitrate and phosphate, silicic acid concentrations differ markedly from north to south. Subantarctic waters north of the Antarctic Polar Front Zone (APFZ) have low Si concentrations (1 to 5  $\mu\text{M}$ ), whereas high Si (>60  $\mu\text{M}$ ) is found to the south (fig. S1). Diatoms, which require Si for growth, are believed responsible for much of the carbon export from the surface to the deep sea (14). In

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