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Orientation of Nocturnally Migrating Swainson's Thrush at Dawn and Dusk: Importance of Energetic Condition and Geomagnetic Cues

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ABSTRACT.—We studied the early morning cage orientation of nocturnally migrating Swainson's Thrushes (Catharus ustulatus) during three fall migration seasons. The results were compared with earlier free-flight release tests under starry skies and were found to be consistent with continuation of migratory flights in the expected seasonally appropriate direction. Energetic condition proved decisive: fat birds chose directions in accordance with migration across the Gulf of Mexico, whereas lean birds oriented away from the coast, possibly in search of habitats suitable for refuelling. Whereas the orientation of fat Swainson’s Thrushes was affected by experimental shifts of the magnetic field, the response during morning tests was larger than expected. A parallel series of orientation cage experiments performed during evening twilight showed a response to deflected magnetic fields that was close to the expected shift, which suggests a difference in integration of directional information between early morning and evening twilight activity. However, within-individual response to deflected magnetic fields was of the same magnitude during both morning and evening tests.

RESUMEN.—Estudiamos la orientación al amanecer de individuos de la especie migratoria nocturna Catharus ustulatus en jaulas durante tres estaciones migratorias de otoño. Los resultados fueron comparados con datos anteriores de ensayos de liberación de vuelo libre bajo cielos estrellados y resultaron consistentes con la continuación de los vuelos migratorios en la dirección esperada (adecuada para la estación). La condición energética resultó ser decisiva: las aves con más grasa corporal eligieron direcciones hacia el Golfo de México, mientras que las aves con poca grasa corporal se orientaron en dirección opuesta a la costa, posiblemente en busca de hábitats apropiados para reabastecerse. Aunque la orientación de los individuos de C. ustulatus con mayor contenido de grasa fue afectada por cambios experimentales en el campo magnético, la respuesta durante las pruebas realizadas en la mañana fue mayor que la esperada. Una serie paralela de experimentos de orientación en jaulas realizados durante el ocaso mostró un cambio cercano al esperado con los cambios del campo magnético. Esto sugiere que existe una diferencia entre el amanecer y el ocaso en la manera en que la información direccional es integrada. Sin embargo, la respuesta de un individuo en particular a los cambios en el campo magnético fue de la misma magnitud durante las pruebas realizadas en la mañana y en la tarde.

Most neotropical landbird migrants fly at night. Nocturnal migration typically commences during the first hour after sunset, peaks around 2200 h, and wanes at midnight or shortly thereafter (Kerlinger and Moore 1989). Although most nocturnally migrating songbirds end their migratory flight well before dawn, migrants have been observed to undertake "morning flights" (Rabol 1967, Alerstam 1978, Gauthreaux 1978, Bingman 1980, Hall and Bell 1981, Wiedner et al. 1992). The function of morning flight is open to speculation (Moore et al. 1995), but is likely to depend on the bird's physiological condition and the ecological context within which the migrant finds itself. When migrants end their flight at night, initial selection of habitat probably occurs early in the morning, and morning flights may reflect a period of exploration on the part of migrants seeking habitat in which to rest and forage (see Terrill and Ohmart 1984, Lindström and Alerstam 1986, Wiedner et al. 1992). Other observations suggest that birds may engage in morning flight to compensate for drift experienced during nocturnal migration (sensu Lack and Williamson 1959; see Gauthreaux 1978, Moore 1990). If nocturnal migrants select a direction at the time of takeoff and subsequently try to maintain that direction during a night's flight, then the next morning would be a convenient time to reorient if displacement has occurred (Vleugel 1954, Lowery and Newman 1955, Moore 1987). For other night migrants, movement in the morning hours may simply
The Swainson’s Thrush is a Nearctic species that migrates through various parts of the Americas, including Mexico during fall migration with Swainson’s Thrushes. Able (1977) tested several species of migrants on Block Island, off the northeastern coast of North America, in orientation cages, and interpreted the activity as a phototactic response to the rising sun. Somewhat similar results were obtained with four different European migrants, which showed a compromise orientation between the expected migratory direction and the sunrise azimuth (Åkesson and Sandberg 1994). In other early morning cage experiments, results indicate that nocturnal bird migrants may perform migration flights during early morning, and that both visual and magnetic cues may be involved in directional selections. Migrating European Robins (Erithacus rubecula) oriented in the expected migratory direction and responded to experimental shifts of the magnetic field under clear skies, but only when the birds showed migratory activity during the night preceding the tests (Wiltschko and Höck 1972).

Morning orientation experiments with North American night-migrating warblers also revealed seasonally appropriate northerly orientation in spring and a clear response to artificial shifts of the skylight polarization pattern (Moore 1986). When juvenile and adult Sedge Warblers (Acrocephalus schoenobaenus) captured in northern Italy during fall migration were tested in orientation cages at dawn, adults were well oriented along the migratory direction, whereas juveniles showed more intense but less concentrated directional activity (Spina and Bezzi, 1990).

We conducted orientation cage and free-flight release experiments at the northern coast of the Gulf of Mexico during fall migration with Swainson’s Thrush (Catharus ustulatus) to investigate daytime orientation behavior of a typically night-migrating North American passerine. This species has been observed to make both predawn flights (D. A. Cimprich pers. comm.) and early morning (daylight) flights (Hall and Bell 1981) during the migratory season. Do Swainson’s Thrushes display activity in orientation cages during early morning hours, and if so, does that activity represent ongoing migration in the seasonally appropriate direction? How does morning activity compare to the migratory orientation behavior of Swainson’s Thrushes at their normal departure and arrival times? How does energetic condition influence orientation of migratory activity? If morning activity is an expression of continuing migration, then we would expect to find the same difference between fat and lean birds as we expected to find during evening experiment, namely that Swainson’s Thrushes should show seasonally appropriate southerly orientation if they had deposited adequate fat stores for long-distance migration (cf. Sandberg and Moore 1996). Lean birds, on the other hand, were expected to either suppress migratory activity (e.g. Moore and Kerlinger 1991, Sandberg et al. 1991, Yong and Moore 1993) or reorient in search for suitable stopover sites (e.g. Alerstam 1978; Lindström and Alerstam 1986; Sandberg et al. 1988, 1991, 1998; Sandberg 1994; Sandberg and Moore 1996; Bäckman et al. 1997).

Is orientation of morning activity influenced by geomagnetic cues? It is widely accepted that migratory birds integrate directional information from both celestial and geomagnetic cues for their orientation (see reviews in Berthold 1991, Papi 1992, Wehner et al. 1996). Although much is known about the capacity of migrants to use different kinds of directional information, the sensory basis of the morning orientation of typically night-migrating birds is virtually unknown. We exposed Swainson’s Thrushes to experimental manipulations of the local geomagnetic field during both the morning and evening twilight periods, that is, just before their impending long-distance flight across the Gulf of Mexico (cf. Sandberg and Moore 1996).

Methods.—The Swainson’s Thrush is a Nearctic nocturnal migrant whose breeding range covers the boreal forests in Alaska, Canada, and western and northeastern United States. Swainson’s Thrush is a long-distance migrant who spends the winter from Mexico in the north, to Peru and northwest Argentina in the south (Ridgely and Tudor 1989, Rappole et al. 1995). Populations of this species regularly migrate across the Gulf of Mexico during both fall and spring.

Experimental birds were mist-netted during fall migration just prior to the impending trans-Gulf crossing. After capture, the birds were weighed to the nearest 0.10 g using an Ohaus electronic balance, assigned to a visually estimated fat class according to a seven-class scale, where no fat is equal to 0 and maximum fat corresponds to 6 (see Pettersson and Hasselquist 1985), and measured for wing chord (method 3 in Svensson 1992). The birds were then driven by car to a nearby test site (~20 km east of the capture site) located on the Ft. Morgan peninsula (30°10’N, 88°00’W) within the Bon Secour National Wildlife Refuge, Alabama. At the test site, birds were held indoors in individual cages (30 × 38 × 38 cm) placed in a room that allowed exposure to the natural photoperiod, the local geomagnetic field and ambient temperature. Birds were fed ad libitum with a mixed diet consisting of mealworms (Tenebrio sp.), moistened Monkey Biscuits (Hill’s Products, Premium Nutritional Products, Mission, Kansas), wild berries, and fresh vitaminized water.

Orientation tests were performed in an open area adjacent to the beach. The local geomagnetic field has a total intensity of approximately 52,000 nT, an inclination of 62° and a declination of +2°.
Orientation experiments were carried out from the beginning of September until the end of October in 1992 (release experiments), and 1997–1999 (cage tests). Swainson’s Thrushes were subjected to the following test conditions:

(1) Orientation cage tests at dusk and dawn. All cage experiments were performed in modified Emlen funnels which allowed automatic registration of migratory restlessness in eight 45° sectors (cf. Sandberg et al. 1988). Each orientation cage was connected to a data logger from which data could be downloaded to a computer after the test was completed. The funnels were placed on top of plastic crates (experiments within magnetic coils; see below) about 0.3 m above ground level. That arrangement allowed birds to see ~160° of the sky overhead.

We shifted the direction of magnetic north by using pairs of magnetic coils with a quadratic cross-section (1 × 1 m clearance between coils in a pair). Coil frames were made of aluminium and wound with 20 turns of 12 gauge insulated copper wire composed of 19 strands (diameter = 2.2 mm). A regulated power supply was used to produce homogeneous magnetic fields. By orienting such a pair of coils along the geomagnetic southeast–northwest axis, we were able to shift position of magnetic north 90° clockwise without altering the total field intensity and inclination.

The Swainson’s Thrushes were tested for their directional preferences under two different magnetic conditions, both of which were performed under clear skies at sunrise as well as at sunset (maximum 30% cloud cover with the position of the sun clearly visible): (1) control, when the birds had access to the unmanipulated local geomagnetic field; and (2) deflected, when magnetic north was shifted 90° clockwise, that is, towards approximately geographic east. During experiments performed at dusk, birds were placed inside the orientation cages ~20 min before local sunset. Registration of migratory activity started at sunset and lasted for 1 h. Experiments at dawn started at local sunrise and lasted for 2 h.

(2) Free-flight release experiments under starry skies. To study orientation behavior of Swainson’s Thrush under as natural conditions as possible, we used the release technique described by Sandberg et al. (1991). A small chemiluminescent plastic container (Cyolume Lightstick, green 95281-17, American Cyanamid Company, Parsippany, New Jersey) was attached to the two outermost tailfeathers with transparent adhesive tape. Before attachment, the stick was flexed, which broke a small enclosed glass container allowing two chemical components to mix. The following chemical reaction produces a clear green light which, under weather circumstances with good visibility, can be seen at distances of 700–1,000 m. The light capsule is designed to fall off as soon as the tape gets wet.

The test birds were lightly tossed straight up into the air and then followed using 10 × 40 binoculars until they vanished from view. Flight behavior of each singly released individual was registered and vanishing times were recorded using a stop-watch. Vanishing bearings were measured to the nearest 1° with a compass. We considered a release to be successful only if the bird gained considerable height (>30 m above ground) and vanished from sight without descending or landing. Free-flight releases were carried out under clear starry skies (<30% cloud cover) with light or no winds (at ground level). Releases commenced ~1.5 h after sunset when all traces of horizon glow had disappeared.

Prior to all tests described above, birds were weighed and assigned as being either lean (fat score ≤3; see above) or fat (fat score ≥4). Visual classification of subcutaneous fat is independent of body size and it also avoids problems with mass-related variation caused by differences in gut, water, and protein contents (Blem 1990, Rogers 1991, Kaiser 1993).

Individual Swainson’s Thrushes were tested only once under each specific experimental condition as described above. Each bird’s migratory activity was quantified (50 registrations minimum) and a mean heading was calculated by vector addition, following standard procedures (Batschelet 1981). When the mean vector length resulting from doubling the angles ($r_2$) was larger and thus provided a better description of the circular distribution than the unimodal vector length ($r$), we used a mean axis of orientation as the basis of the analysis. Mean angles were pooled for each separate test condition, resulting in sample mean vectors. Vanishing bearings of released Swainson’s Thrushes were treated in the same way and a mean direction was calculated for each independent sample.

The Rayleigh test was applied to test for significant directional preferences (see Batschelet 1981). Differences in mean angles between experimental categories were examined by using the ‘one-way classification test’ ($F$-test, df = 1; Mardia 1972). The scatter of headings around the mean angle, as given by the mean vector lengths, was compared by applying the ‘test for the homogeneity of concentration parameters’ ($t$, Mardia 1972). Confidence intervals (95%) are according to Batschelet (1981).

Results.—Of the 21 Swainson’s Thrushes that were released under clear skies in fall 1992, 16 (76%) were classified as successful. As shown in Figure 1A, the thrushes showed a nonsignificant mean departure direction towards geographic east. Average duration of tracking intervals was $63 \pm 27$ s (SD). Given an approximate airspeed of $10$ m s$^{-1}$ (Pennycuick 1975), the mean tracking distance was 600–700 m. When total sample was subdivided into lean and fat birds, the result revealed a distinct and significant difference, that is, a majority of the lean birds chose north-
Fig. 1. Release experiments under clear starry skies with Swainson’s Thrush during fall migration 1992. (A) Summary result of releases in the local geomagnetic field; (B) and (C) are mean orientation of lean and fat birds, respectively. The direction towards magnetic north (mN) is shown in relation to geographic north (gN). Each circle on the periphery of the diagrams represents the vanishing bearing of one individual. The mean vector ($\alpha$) of each sample is illustrated by an arrow whose length is proportional to the mean vector length ($r$) and drawn relative to the radius of the circle (radius = 1). Mean vectors are surrounded by the 95% confidence interval (shaded) for samples that are significantly different from random. Significance levels ($P$) are according to Batschelet (1981).

Swainson’s Thrushes were tested in cages under clear morning skies and in the local geomagnetic field during the fall migration season in 1997, and showed a nonsignificant axial mean orientation (unimodal $r = 0.06$; see Fig. 2). However, when that data set was subdivided into lean and fat birds, respectively, a clear and significant difference in orientation behavior emerged. Whereas lean birds selected a northerly mean direction (Fig. 2B), fat birds chose a mean course between south–southeast and south ($F = 36.9, df = 1$ and 10, $P < 0.001$; Fig. 2). There were no statistical differences between orientation results obtained in free-flight release experiments under starry skies and in cage tests during early morning hours (cf. Figs. 1 and 2).

During fall migration in 1998, we restricted the early morning cage tests to include only fat birds and performed a preliminary test series wherein we shifted the direction of geomagnetic north 90° clockwise. As shown in Figure 3, fat controls continued to show a southeasterly mean orientation that was statistically inseparable from the corresponding result obtained in 1997 ($F = 0.03, df = 1$ and 20, ns). When the magnetic field was deflected 90° clockwise, the birds responded with an unexpectedly large 190° clockwise shift ($F = 36.6, df = 1$ and 13, $P < 0.001$, Fig. 3). In view of that unexpected result, we repeated the experiment during the fall migration period in 1999. As in previous seasons, fat controls continued to show a southeasterly mean direction (Fig. 4). There were no statistical differences in mean direction between fat controls in any of the fall seasons 1997–1999 ($F \leq 0.07, df = 1$ and 20–23, ns). The deflection experiment in 1999 yielded a slightly less pronounced shift of 150° clockwise, significantly different from the control direction ($F = 41.9, df = 1$ and 31, $P < 0.001$). Although the difference in relation to controls decreased, there was no statistical difference between the deflected groups in 1998 and 1999, respectively ($F = 1.2, df = 1$ and 25). Summary results of the early morning orientation are presented in Figure 5.

During fall migration in 1999, we conducted a parallel series of cage experiments during evening twilight to investigate whether the observed unexpectedly large shift in response to deflected magnetic fields during early morning tests (see above) would also be manifested at the time of sunset. Again, only fat birds were used as test subjects. The results of evening tests are shown in Figure 6. Controls selected a mean direction towards south, which corresponded well with early morning tests in 1999 ($F = 3.1, df = 1$ and 24, ns). When Swainson’s Thrushes were exposed to a 90° clockwise shifted magnetic field at sunset they responded with a 108° clockwise...
FIG. 2. Orientation cage experiments with Swainson’s Thrush during early morning hours in fall 1997. The mean position of the sun one hour after sunrise (i.e. in the middle of the test period) is indicated outside each circular diagram. See Figure 1 for further details.

FIG. 3. Mean orientation of fat Swainson’s Thrushes during early morning in fall 1998. (A) Orientation cage performance in the local unmanipulated geomagnetic field (control); and (B) directional behavior of thrushes tested in a magnetic field where magnetic north was experimentally shifted 90° clockwise (deflected). Other details as in Figures 1 and 2.

Because a subsample of Swainson’s Thrushes was tested under both control and deflected conditions, it was possible to investigate effect of the experimental treatment at the individual level. There were sufficient data for 1999 only and those results are shown in Table 1. The means of differences ($\alpha_{aD-C}$; see Table 1) do not reveal any difference between morning ($\alpha_{aCC} = 94°$) and evening ($\alpha_{aCC} = 91°$) tests, but instead show an effect of the deflection of the magnetic field that is close to the expected 90° clockwise shift in both cases. Furthermore, it was also possible to compare directional selections in morning and evening experiments within control and deflected tests, respectively. By subtracting morning control and deflected direction from the corresponding evening control and deflected direction for each individual ($\alpha_{aCC}/\alpha_{aDD}$; see Table 1) and subsequently calculating means of differences, we obtain a measure of consistency with which thrushes oriented at dawn and dusk. If the birds would have made exactly the same
Cage experiments: Morning tests 1999

FIG. 4. Orientation cage behavior of fat Swainson’s Thrush during early morning in fall 1999. For further details, see Figures 1–3.

FIG. 5. Summary results of the orientation behavior of Swainson’s Thrush tested in orientation cages during the early morning hours during fall migration in 1997–1999: (A) control tests in the local geomagnetic field, this data set was subdivided into lean (B) and fat (C) birds, respectively. Finally, (D) shows directional response when Swainson’s Thrush was exposed to a magnetic field that was deflected 90° clockwise from normal. Other details are given in Figures 1–3.

Discussion. — The function(s) and the sensory basis of activity displayed by nocturnal migrants during early morning hours have received scant experimental attention. Swainson’s Thrush, a typical long-distance, nocturnal migrant whose wintering grounds cover wide areas of South America, displayed well-directed cage activity towards southeast during morning experiments in the fall under local geomagnetic field conditions (controls). In addition, orientation of activity varied with energetic condition, such that birds that had deposited more than 6 g of fat (visual fat score ≥4; cf. Dunning 1992) headed in a south–southeasterly mean direction that would take them out across the Gulf of Mexico, whereas lean birds chose northerly directions (see Woodrey and Moore 1997). That result is consistent with other studies showing that the amount of stored fat is an important predictor for directional selections of migratory birds, especially when migrants are confronted with an ecological barrier such as the open sea (e.g. Sandberg et al. 1988, 1991, 1998; Sandberg 1994; Sandberg and Moore 1996; Bäckman et al. 1997). Fat birds about to cross a barrier orient in the expected migratory direction, whereas lean birds either become inactive or reorient in search of suitable stopover sites where they can accumulate necessary fuel stores for resuming onward migration (cf. Alerstam 1978).

The close similarity between results of morning experiments and the free-flight release tests made under starry skies suggest that morning activity displayed by fat Swainson’s Thrushes represents ongoing migration (see Bingman 1980, Moore 1986). In addition, the mean direction selected by fat birds during morning experiments is in excellent agreement with an initiation of a long-distance flight across the Gulf of Mexico heading towards the principal wintering areas of Swainson’s Thrush (Fig. 7). Other studies investigating orientation behavior of nocturnal migrants during early morning hours have revealed either phototactic responses towards...
Cage experiments: Evening tests 1999

**FIG. 6.** Migratory orientation of fat Swainson’s Thrush tested during clear evening twilight skies during fall migration 1999. For further details, see Figures 1–3.

Our experiments were not designed in a way that would allow us to evaluate the effect of preceding exposure to different winds along the migratory route. However, on the basis of our results we can rule out any phototactic attraction towards the sun azimuth during both early morning and evening twilight tests of Swainson’s Thrush because both lean and fat birds displayed mean directions that were significantly different from the position of the sun during the test period (mean sun position outside the 95% CI).

Our results show that geomagnetic cues are involved in the early morning orientation of nocturnally migrating birds (see also Wiltschko and Höck 1972). When Swainson’s Thrushes were exposed to a 90° clockwise deflection of magnetic north under clear morning skies, they responded with a shift in mean direction almost twice as large as was expected from the treatment. That unexpected result prompted us to run a parallel series of identical experiments at evening twilight to examine whether that reaction was peculiar to morning orientation behavior or not. The results from evening experiments turned out to be much closer to expectations (observed shift = 108° clockwise) and initially indicated a puzzling difference in use of directional cues between morning and evening tests. However, the experimental series that was performed during fall migration in 1999 enabled us to compare the response to deflected magnetic fields at the level of the individual during both morning and evening. Those comparisons clearly show that individual thrushes responded similarly to the experimentally shifted magnetic field during both time periods. We conclude that the unexpectedly large shift in mean direction observed during early morning deflected tests must originate from inter-individual differences in directional preferences.

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Table 1. Effects of experimental magnetic deflections on the orientation of individual Swainson’s Thrushes during fall migration in 1999. For morning and evening tests, $\alpha_c$ and $\alpha_d$ denote individual mean headings under control and deflected magnetic conditions, respectively; $\alpha_{c-d}$ gives difference between deflected and control direction; $\alpha_{cc}$ and $\alpha_{cd}$ give difference between evening and morning control and deflected directions, respectively. See text for further details.

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Notes


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