

# Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds

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Fat reserves influence the orientation of migrating songbirds at ecological barriers, such as expansive water crossings. Upon encountering a body of water, fat migrants usually cross the barrier exhibiting ‘forward’ migration in a seasonally appropriate direction. In contrast, lean birds often exhibit temporary ‘reverse’ orientation away from the water, possibly to lead them to suitable habitats for refueling. Most examples of reverse orientation are restricted to autumn migration and, in North America, are largely limited to transcontinental migrants prior to crossing the Gulf of Mexico. Little is known about the orientation of lean birds after crossing an ecological barrier or on the way to their breeding grounds. We examined the effect of fat stores on migratory orientation of both long- and short-distance migrants before and after a water crossing near their breeding grounds; *Catharus* thrushes (Swainson’s and gray-cheeked thrushes, *C. ustulatus* and *C. minimus*) and white-throated sparrows *Zonotrichia albicollis* were tested for orientation at the south shore of Lake Ontario during spring and autumn. During both spring and autumn, fat birds oriented in a seasonally appropriate, forward direction. Lean thrushes showed a tendency for reverse orientation upon encountering water in the spring and axial, shoreline orientation after crossing water in the autumn. Lean sparrows were not consistently oriented in any direction during either season. The responses of lean birds may be attributable to their stopover ecology and seasonally-dependent habitat quality.

The amount of a migrant’s stored fat upon arrival at a stopover site can influence the bird’s length of stay, motivation to continue migration, habitat selection, foraging behavior and efficiency, and its orientation (e.g. Cherry 1982, Bairlein 1985, Biebach et al. 1986, Loria and Moore 1990, Yong and Moore 1997, Moore and Aborn 2000). Especially important stopover sites are located near a geographical feature, or ecological barrier, like a desert or a large body of water. Birds can add significant fat reserves at such stopover sites to prepare for or recover from crossing the barrier (Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Yong and Moore 1993, 1997).

Most research on the effect(s) of an ecological barrier and a bird’s fuel reserves on its migratory orientation has been carried out during autumn migration at stopover sites prior to water crossings (such as the Baltic Sea and the Gulf of Mexico). Upon encountering water, fat birds tend to orient forward along their seasonally appropriate migratory direction to cross the barrier (Lindström and Alerstam 1986, Sandberg et al. 1991, Åkesson et al. 1996, Sandberg and Moore 1996, Åkesson 1999, Sandberg et al. 2002).

Lean birds, on the other hand, tend to search for habitat with better foraging opportunities (Loria and Moore 1990, Moore and Aborn 2000), which can lead to temporary ‘reverse’ orientation away from the barrier (and opposite their seasonally appropriate migratory direction) towards foraging sites already passed along their migratory route (Alerstam 1978, Lindström and Alerstam 1986, Sandberg et al. 1988, 1991, 1998, 2002, Sandberg 1994, 2003, Åkesson et al. 1996, Sandberg and Moore 1996, Bäckman et al. 1997, Åkesson 1999).

Little research has been done to understand the role of fat stores on orientation in either ecological or physiological contexts (Sandberg 2003). Orientation choices by lean birds at ecological barriers may be influenced by other migratory factors (e.g. season, location along the migratory path, or stopover quality). Three largely unaddressed questions guided the design of our experiments: (1) Do fuel reserves influence a bird’s orientation during spring migration at an ecological barrier near its breeding grounds? (2) Do fuel reserves influence a bird’s orientation after it has crossed an ecological barrier? (3) Do species that differ in migratory ecology (e.g. migratory route or stopover ecology) differ in

their orientation responses at ecological barriers? To answer these questions, we examined the effect of fat stores on the orientation of three North American passerines, two transcontinental migrants (Swainson's thrush *Catharus ustulatus* and gray-cheeked thrush *Catharus minimus*) and one short-distance, temperate migrant (white-throated sparrow *Zonotrichia albicollis*), prior to crossing Lake Ontario in spring and after crossing the lake in autumn.

## Materials and methods

### Study site and dates

Experiments were conducted at the Braddock Bay Bird Observatory on the south shore of Lake Ontario, near Rochester, NY, USA (43°19'N, 77°43'W). Radar and telemetry studies have shown that passerines cross the Great Lakes during both spring and autumn (e.g. Cochran et al. 1967, Diehl et al. 2003; the distance across Lake Ontario at this longitude is ~75–80 km).

Spring data for thrushes were collected during May in 2004–2006, and for sparrows during April and May in 2006–2007. Autumn orientation for all birds was assessed from mid-September to mid-October in 2005. Data from both species of thrushes were pooled for analyses (mean orientation did not differ significantly between these two species).

### Experimental procedure

Birds were captured with mist-nets three to seven hours before testing, and their subcutaneous fat was assessed using a six-point scale; 0 indicating no visible fat and 5 indicating the fattest birds (Helms and Drury 1960). Between capture and testing, the birds were held indoors and given access to food (mealworms for thrushes and a seed mixture for sparrows) and water *ad libitum*. Just after sunset (when the sun was no longer visible on the horizon) and prior to testing, the birds were placed for one hour in small, non-magnetic cages in an open field to give them access to natural magnetic and celestial cues, including the horizon and zenith, for compass calibration (e.g., Cochran et al. 2004, Muheim et al. 2006).

Orientation experiments were carried out in a shed (geomagnetic field properties ranging from 49,600 to 54,300 nT in intensity and 69.6°–70.2° in inclination measured with a 3-axis magnetometer, model #539, Applied Physics Systems; declination = –12°). The orientation of the birds was tested for approximately one hour in funnel-shaped aluminum cages (Emlen and Emlen 1966), lined with typewriter correction paper (Tipp-Ex, BIC Germany). To eliminate access to visual cues, each funnel was covered with a translucent “white”, opaque Plexiglas top. Two to three incandescent light bulbs in parabolic reflectors pointed upwards towards the ceiling provided diffuse illumination (verified with a spectrophotometer; Ocean Optics USB 2000). Thus, birds had access to directional information from the geomagnetic field only.

### Statistical analysis

To determine the orientation of each bird, the number of scratch marks on the Tipp-Ex paper was counted for each of twelve 30° sectors (Emlen and Emlen 1966). The total number of scratches was used as an estimate of migratory activity (birds that left fewer than 35 scratches were classified as ‘inactive’, arbitrarily). For ‘active’ birds, nightly orientation was determined using vector addition and tested for bimodality (Batschelet 1981). For birds that exhibited stronger axial orientation (as determined by which analysis, unimodal or bimodal, resulted in the longest vector length), the end of the axis with the most scratches was used as the bird's preferred direction (as e.g. in Muheim and Åkesson 2002).

For each species and season, the birds were grouped according to fat score. Pooled bearings from adjacent fat scores with similar mean directions (or responses) were grouped into one of two classes, ‘fat’ or ‘lean’. This allowed us to determine the minimum fat score for each species and each season that resulted in forward orientation. Group mean vectors (mean angular direction,  $\alpha$ , and mean vector length,  $r$ ) were calculated from the bearings of all birds within a group, and analyzed for significant orientation using Rayleigh's test for uniformity. A Watson  $U^2$  test was used to determine whether distributions of independent groups differed significantly in direction or scatter (Batschelet 1981). All circular statistics were calculated using Oriana software (Kovach Computing).

## Results

### Orientation of Swainson's and gray-cheeked thrushes

Fat thrushes with a fat score of  $\geq 2$  exhibited seasonally appropriate orientation: southwards towards their wintering grounds during autumn (Fig. 1A), and to the north towards their breeding grounds during spring (Fig. 1B). In both seasons, the orientation of lean thrushes (fat scores of 0 and 1) was significantly different from that of fat birds (spring: Watson  $U^2 = 0.311$ ,  $P < 0.005$ ,  $df = 11$ ; autumn:  $U^2 = 0.346$ ,  $P < 0.002$ ,  $df = 15$ ). During spring migration, eight of eleven lean thrushes exhibited reverse orientation towards the south, with a group mean vector, although statistically insignificant, opposite to that of fat birds (Fig. 1D). During autumn migration, lean thrushes oriented axially along an ESE-WNW axis (Fig. 1C), a direction parallel to the shoreline of Lake Ontario.

### Orientation of white-throated sparrows

White-throated sparrows with a fat score of  $\geq 3$  oriented in a seasonally appropriate migratory direction: southwards towards their wintering grounds during autumn (Fig. 2A), and towards the more northern regions of their breeding range during spring (Fig. 2B). Lean sparrows (fat scores 0–2) were not significantly oriented in either autumn (Fig. 2C) or spring (Fig. 2D), i.e., the distributions of bearings were indistinguishable from random. In autumn, the distribution of bearings of lean sparrows was significantly

## Swainson's and gray-cheeked thrushes

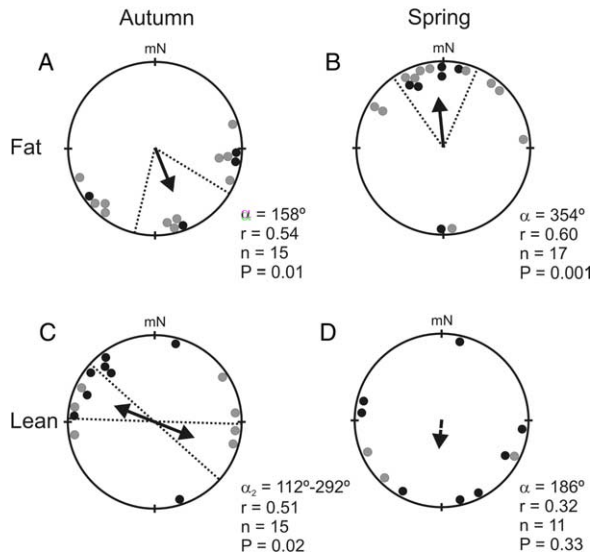


Figure 1. Magnetic orientation of fat and lean thrushes during autumn and spring migration at the Braddock Bay Bird Observatory. Each dot represents the bearing of one bird (black dots: Swainson's thrushes, gray dots: gray-cheeked thrushes). The arrows represent the group mean vector for either unimodal ( $\alpha$ ) or axial ( $\alpha_2$ ) distributions. The length of each vector is drawn relative to the mean vector length  $r$ , with the radius of the circle being  $r = 1$  (solid lines: significantly oriented groups according to the Rayleigh test, dashed lines: not statistically significant). The dotted lines around the mean vectors show the 95% confidence intervals of significantly oriented distributions.

different from that of fat sparrows (Watson  $U^2 = 0.398$ ,  $P < 0.001$ ,  $df = 10$ ), but not in spring (Watson  $U^2 = 0.046$ ,  $P > 0.5$ ,  $df = 13$ ).

## White-throated sparrows

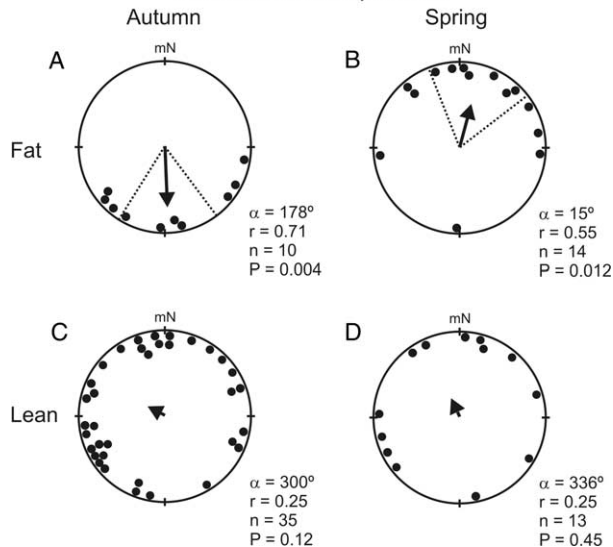


Figure 2. Magnetic orientation of fat and lean white-throated sparrows during autumn and spring migration at the Braddock Bay Bird Observatory. Each dot represents the bearing of one sparrow. Vectors, confidence intervals and statistical values are plotted as in Fig. 1.

## Nocturnal activity of birds

Activity, or migratory restlessness, was analyzed by examining: (1) the frequencies of 'active' and 'inactive' birds, and (2) the number of scratches made by active birds. No association was found between fat class (fat or lean) and the number of 'active' and 'inactive' sparrows or thrushes tested during autumn or spring ( $2 \times 2$  contingency tables, all  $\chi^2$  tests had  $P > 0.7$ ). For 'active' birds (shown in Fig. 1 and 2), we examined whether the number of hops ( $\log_{10}$ -transformed to be suitable for parametric analysis) was influenced by fat class and/or season; a  $2 \times 2$  ANOVA was performed for both thrushes and sparrows. Activity levels of 'active' thrushes and sparrows did not differ between lean and fat birds ( $F = 0.187$  and  $0.817$ ,  $P = 0.67$  and  $0.37$  for thrushes and sparrows, respectively). However, thrushes exhibited significantly more activity during autumn than during spring ( $F = 4.944$ ,  $P = 0.03$ ). In sparrows, median values of activity were higher in autumn than in spring, but the difference was not significant ( $F = 2.494$ ,  $P = 0.12$ ).

## Discussion

In all three species, fat reserves affected orientation but not migratory activity during both spring and autumn migration on the south shore of Lake Ontario. Birds with ample fuel reserves exhibited seasonally appropriate orientation towards their migratory goal. Lean birds continued to be active, but ceased forward orientation. Our results show that: (1) fat reserves affect the orientation of migrants before crossing an ecological barrier close to their breeding grounds during the spring, (2) lean migrants cease forward migration after crossing an ecological barrier in autumn, and (3) there are differences between species in their responses to ecological barriers.

The primary question raised by our findings is what factor(s) can explain the seasonal differences within a species as well as differences between species in the orientation of lean birds. White-throated sparrows are short-distance, temperate migrants and both thrush species are long-distance, neotropical migrants. A wide variety of species that differ in migration distance and routes have been shown to exhibit reverse migration at ecological barriers (Sandberg et al. 1991, 1998, 2002, Åkesson et al. 1996, Sandberg and Moore 1996, Åkesson 1997, 1999). Thus, the distance of migration seems an unlikely candidate to explain the different behavior of lean thrushes and sparrows. Temporary reverse orientation of migrants at ecological barriers has been hypothesized to be an adaptive behavior that would lead lean birds away from inhospitable coastal or shoreline habitats to more suitable foraging sites, with more food, less competition, and/or fewer predators (Alerstam 1978, Lindström and Alerstam 1986, Lindström 1990, Åkesson et al. 1996, Åkesson 1997, 1999). If this hypothesis is correct, reverse orientation would be expected mainly at low quality stopover sites; where birds can not efficiently replenish fuel reserves, they should either orient towards more suitable sites already passed or exhibit exploratory movements to search for a more suitable habitat (e.g., Lindström and Alerstam 1986, Moore and Aborn 2000). However, in high quality stopover sites, where birds can

replenish fuel and gain mass efficiently, lean birds should be less likely to leave such habitats.

In the near-shore habitat around Braddock Bay, many migrants, including *Catharus* thrushes, gain mass at higher rates during autumn than during spring stopover, likely due to the effects of water temperature and near-shore air temperature on seasonal variation in available resources (Bonter et al. 2007). Braddock Bay is a low quality stopover site for thrushes during the spring; Swainson's thrushes do not gain appreciable mass during spring stopover (Bonter et al. 2007; no data are available for gray-cheeked thrushes in spring). Therefore, during spring, lean thrushes should orient to the south of Lake Ontario, as was their tendency in our experiments, where more suitable habitat for refueling may be found. In contrast, during autumn Swainson's and gray-cheeked thrushes both show significant hourly gains in mass at Braddock Bay (Bonter et al. 2007), indicating that the shoreline of Lake Ontario is a good stopover site at this time of year. Accordingly, during autumn migration, lean thrushes oriented bimodally along an ESE-WNW axis (Fig. 1B), which coincides with the shoreline of Lake Ontario roughly 20 km to either side of Braddock Bay.

Movement away from the lake shore to replenish fuel reserves does not seem to be necessary during either season for lean white-throated sparrows, which gain mass at comparable levels irrespective of season at Braddock Bay and at higher rates than thrushes (Bonter et al. 2007). Lack of consistent orientation among lean sparrows, as we found, could be the result of dispersal or habitat exploration near the lake shore (Loria and Moore 1990, Moore and Aborn 2000). Although both the shoreline orientation in lean thrushes and lack of orientation in lean sparrows during autumn may be, at least partially, attributed to the quality of foraging along the lake shore, the discrepancy in the orientation of lean sparrows and thrushes suggests that other factors need to be considered. Foraging strategies and habitat preferences have been linked with species-specific distance and orientation of movements during stopover (Moore and Aborn 2000, Chernetsov 2005, 2006). Furthermore, because lean white-throated sparrows did not orient in a consistent direction relative to the lake, we can not definitively conclude that this behavior is a response to encountering water. The lack of orientation in lean sparrows may simply be indicative of a decreased urge to migrate (Able 1977), which could occur even at sites far from an ecological barrier. Further orientation experiments with both thrushes and sparrows at locations both near and away from ecological barriers, and in habitats of known foraging quality for both species, would be helpful in examining some of these possible explanations.

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