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EFFECTS OF FAT AND LEAN BODY MASS ON MIGRATORY LANDBIRD STOPOVER DURATION

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ABSTRACT.—We used quantitative magnetic resonance body composition analysis and radiotelemetry to examine whether fat and lean body mass affected stopover durations of 11 birds captured during autumn migration in New York City, USA. Two Swainson's Thrushes (*Catharus ustulatus*), two Hermit Thrushes (*C. guttatus*), and seven Ovenbirds (*Seiurus aurocapilla*) were used in the study. Ovenbird stopover duration was significantly and negatively related to fat mass but unrelated to lean body mass. The same relationships were found when data from all three species were combined to increase sample sizes. Birds that departed within 1 day had fat stores upon capture that represented at least 11% of their total body mass whereas those with fat content <6% of total body mass remained for no fewer than 4 days. Arrival fat mass clearly influenced time birds spent at the site but lean body mass did not. Conditions for increasing or maintaining fat stores provided by urban stopover sites may affect the migration timing of birds. *Received 26 May 2009. Accepted 16 September 2009.*

Migrating landbirds require several stopovers for rest and refueling, as most are incapable of completing their migration in a single flight. Time and energy spent during stopover periods greatly exceeds that spent aloft (Wikelski et al. 2003, Bowlin et al. 2005), and behavior of birds at stopover sites can greatly influence their overall migration success. Factors that govern a bird's decision to terminate a stopover and begin the next flight have received much attention, particularly through development of theoretical models of optimal migration strategies (Alerstam and Hedenström 1998, Houston 1998). There is evidence that fuel stores, refueling rate, distance from final destination, date, predation risk, and weather conditions can individually, or in some combination influence a bird's length of stay at a given stopover site (Wang and Moore 1997, Åkesson and Hedenström 2000, Danhardt and Lindström 2001, Dierschke and Delingat 2001, Schaub et al. 2008).

Field studies of the effects of intrinsic and extrinsic factors on stopover duration are hampered by the difficulty of knowing when birds arrive at, and depart from, the site of interest. Several studies have measured stopover duration using mark-recapture data, while assuming birds were marked upon arrival and final recapture occurred on their actual departure date (e.g., Cherry 1982, Wang and Moore 1997, Morris and Glasgow 2001). The latter assumption can be especially tenuous, as migrants may learn to avoid mist nets (MacArthur and MacArthur 1974) or move beyond the coverage area within the stopover site (Chernetsov and Mukhin 2006, Tsvey et al. 2007). This method also relies on condition and behavior of the small proportion of birds that are recaptured to represent the majority, when recaptures may be biased towards individuals in poor condition that remain at the site for a relatively long time (Guglielmo et al. 2005, Morris et al. 2005, Hays 2008). More recently, survival analyses and other probabilistic models have been used to relax these assumptions and improve accuracy of stopover duration estimates based on mark-recapture data (Schaub et al. 2001, 2008), although large sample sizes are generally needed (Schaub 2006). Radio tracking offers another approach for measuring stopover duration that does not rely on recaptures and allows knowing departure date with near certainty (Chernetsov and Mukhin 2006, Tsvey et al. 2007). Drawbacks of radiotelemetry include high equipment costs, possible effects of transmitters on bird behavior, and the assumption that birds are captured upon arrival.

Examining the effect of energetic condition on stopover duration is complicated by the need for accurate, non-lethal measurements of body composition. Commonly used condition indices (e.g., body mass, size-corrected body mass, visual fat scores) can potentially provide reliable estimates of fat content (Conway et al. 1994, Spengler et al. 1995, Seewagen 2008). However, their accuracy may be species-specific (Skagen et al. 1993, Spengler et al. 1995, Seewagen 2008) or weak-

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ened by inter-observer variation (Krementz and Pendleton 1990), and they do not provide separate, direct measures of fat and lean body mass. Quantitative magnetic resonance analysis (QMR; Taicher et al. 2003, Tinsley et al. 2004) in contrast provides accurate, objective, and direct measures of the fat and lean body mass of small birds (CGG, unpubl. data).

We attached radio transmitters on 11 migrant songbirds at our study site in New York City during autumn 2008 in a pilot study to test the feasibility of radio tracking birds in an urban setting. We used a QMR body composition analyzer on all captured migrants for a concurrent study of body composition dynamics during stopover refueling. The stopover duration and body composition data obtained by radiotelemetry and QMR, respectively, afforded an additional opportunity to examine relationships between these variables. We coupled telemetry and QMR data to examine if arrival fat and lean body mass affected the stopover durations of these 11 migrants.

METHODS

Study Site and Animal Capture.—We captured birds during autumn 2008 on the grounds of the Bronx Zoo as part of an ongoing study of urban stopover ecology of migrant songbirds. The Bronx Zoo is a 107-ha park in Bronx County, New York, USA. Our study site was a 4.9-ha fragment of riparian forest on the eastern edge of the zoo that does not contain exhibits and is not open to visitors (40° 85′ N, 73° 87′ W). Red oak (*Quercus rubra*), sweet gum (*Liquidambar styraciflua*), swamp dogwood (*Cornus foemina*), and willows (*Salix* spp.) are the dominant tree species in the area. Previous research has suggested this site offers suitable refueling conditions for landbird migrants (Seewagen and Slayton 2008; CLS and CGG, unpubl. data).

Birds were captured in mist nets from sunrise until ~1200 hrs during 4 September to 22 October. Captured birds were marked with a U.S. Geological Survey aluminum leg band, measured (unflattened wing length to 1 mm), and weighed on a digital balance to 0.1 g. Approximately 75 µl of blood was collected by brachial veinipuncture for a separate study.

Magnetic Resonance Analysis.—Conscious birds were scanned within 45 min of capture and banding in a QMR body composition analyzer (Echo-MRI, Echo Medical Systems, Houston, TX, USA) housed in a customized mobile laboratory (Glendale Recreational Vehicles, Strathroy, ON, Canada) at the study site. Birds were scanned in duplicate on the ''small bird'' and ''two-accumulation'' settings of the Echo-MRI software, yielding measures of fat mass and wet lean body mass to 0.001 g. Total scanning time was ~4 min/individual and the average coefficient of variation for individual birds was 1.7% for fat and 0.4% for wet lean mass. Raw QMR scan data were transformed using calibration equations for small birds developed with House Sparrows (*Passer domesticus*) and Zebra Finches (*Taeniopygia guttata*) in a laboratory validation study (CGG, unpubl. data). Validation indicated the relative error for predictions of fat and wet lean mass were ± 11% and ± 1.5%, respectively.

Radiotelemetry.—We radiomarked each Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*C. guttatus*), and Ovenbird (*Seiurus aurocapilla*) captured beginning 3 October until all 11 transmitters we had were deployed. These species were used because they are relatively common migrants in the area, body masses are amenable to radiotelemetry, and they are the focus of concurrent studies in progress at the site. The 0.5-g transmitters (A2415, Advanced Telemetry Systems, Isanti, MN, USA) were affixed after QMR scanning with eyelash adhesive directly to a cleared area of skin in the interscapular region (adapted from Raim 1978). Birds were held in bags for ~15 min to allow the adhesive to dry and released within 50 m of where originally captured.

We could not be certain birds were captured and marked upon arrival. Eight of 11 birds were marked on days when migrant capture rates were high (~double) relative to the 2 previous days at this site and at two affiliated banding stations elsewhere in New York City. This increased our confidence these individuals were new arrivals and marked during their first day at the stopover site (*sensu* Tsvey et al. 2007). However, we use the term ''minimum stopover duration'' hereafter because of this uncertainty.

We checked for presence/absence daily at sunrise, noon, and sunset using a handheld Yagi antenna and receiver (R4500S, Advanced Telemetry Systems, Isanti, MN, USA) from within the study site. We searched for birds from other points throughout the zoo including roofs of two three-story buildings if we initially failed to detect a signal from within the study site. We assumed

TABLE 1. Means ± SD and ranges of total body mass, fat mass, lean body mass, and minimum stopover durations of three species of migratory landbirds radiotracked during autumn stopovers in New York City, USA.

Species	*n*	Total body mass (g)	Fat mass (g)	Lean body mass (g)	Stopover duration (days)
Swainson's Thrush	2	27.3, 30.1	1.700, 2.410	22.760, 26.119	4, 5
Hermit Thrush	2	30.2, 34.6	1.570, 4.000	27.103, 29.089	2, 7
Ovenbird	7	20.0 ± 1.3	2.461 ± 1.069	17.009 ± 0.795	4.3 ± 5.0
		18.3–21.7	1.068–3.911	15.713–18.145	1–14

birds had left the area permanently and resumed migration if they were undetected for at least 4 consecutive days. We considered a stopover of 1 day as the initial capture of a bird at the site in the morning and departure any time that night.

Statistical Analyses.—We used standardized residuals from linear regressions of lean body mass and wing length to correct lean body mass for body size variation. We could not adjust fat mass in the same manner because fat mass was not significantly related to wing length. We instead divided fat mass by total body mass and arcsine-root transformed the proportions (Zar 1999, Gotelli and Ellison 2004).

We used backwards selection multiple regression with adjusted fat and lean body mass as predictor variables, and number of days of stopover as the response variable to examine the effect of body composition on stopover duration. Collinearity did not occur, as fat and lean body mass were not significantly correlated. We performed the analyses on Ovenbird data alone and on data from all three species combined.

Age and gender were not considered because sample sizes were small and not all birds could be confidently assigned to age or gender classes. All variables met normality assumptions. We conducted tests with SPSS 16.0 and interpreted results as significant when $P < 0.05$. Mean (± SD) values are reported.

RESULTS

We radiomarked two Swainson's Thrushes, two Hermit Thrushes, and seven Ovenbirds. Swainson's Thrushes were marked on 2 and 6 October, and Hermit Thrushes were marked on 10 and 11 October. Four Ovenbirds were marked on 3 October and three were marked on 6 October.

Minimum stopover durations ranged from 1 to 14 days (Table 1). Three individuals departed within 1 day and the remainder stayed for at least 2 days. Initial fat content ranged from 6 to 8% of total body mass in Swainson's Thrushes, from 5 to 12% in Hermit Thrushes, and from 6 to 18% in Ovenbirds. An Ovenbird was recaptured on the eighth day of its 14 day stopover; total body mass (measured by digital balance) increased 4.2 g (23% of original), and fat and lean body mass (measured by QMR) increased 2.767 g (259% of original) and 1.884 g (11% of original), respectively.

The initial fat loads of birds that stayed at the site for only 1–2 days ($n = 5$) averaged 14 ± 3% of total body mass, whereas the initial fat loads of birds that stayed for the longest periods (7, 8, and 14 days; $n = 3$) averaged 6 ± 0.5% of total body mass. Ovenbird stopover duration was unrelated to lean body mass ($r^2 = 0.02$, $F_{2,4} = 0.36$, $P = 0.58$), and significantly and negatively related to fat mass ($r^2 = 0.74$, $F_{1,5} = 13.95$, $P = 0.013$). The same relationships were found when data from all three species were combined to increase sample sizes (lean: $r^2 = 0.03$, $F_{2,8} = 0.00$, $P = 0.98$; fat: $r^2 = 0.56$, $F_{1,9} = 11.31$, $P = 0.008$; Fig. 1). The relationship between fat and stopover duration appeared non-linear, and we explored the fit of an exponential model to the data *a posteriori*. The exponential model was also highly significant ($r^2 = 0.71$, $F_{1,9} = 22.08$, $P = 0.001$; Fig. 1).

DISCUSSION

This is the first combination of magnetic resonance technology and radiotelemetry to examine the influence of fat and lean body mass on stopover duration to our knowledge. We believe this is also the first description of autumn stopover durations of migrants within a major urban center.

Fat mass upon presumed arrival date appeared to strongly influence how long birds remained at the stopover site. This is consistent with other findings that lean birds stop over longer than fatter birds (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008; but see Safriel and Lavee 1988, Salewski and Schaub 2007). The

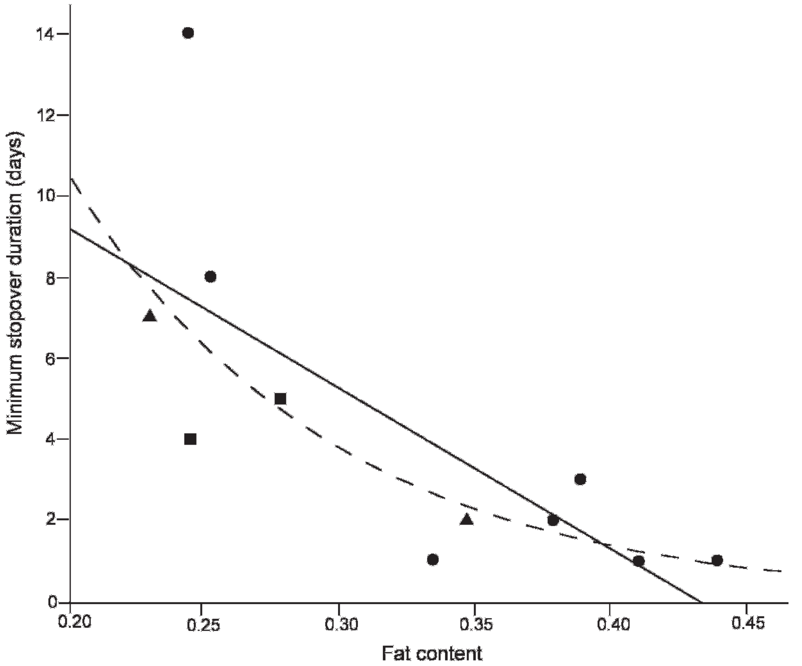

FIG. 1. Relationship between arrival fat content (arcsine-root transformed g fat/g total body mass) and minimum stopover duration of Swainson's Thrushes (squares), Hermit Thrushes (triangles), and Ovenbirds (circles) captured during autumn migration in New York City, USA. Solid and dashed lines represent linear ($r^2 = 0.56$, $F_{1,9} = 11.31$, $P = 0.008$) and exponential ($r^2 = 0.71$, $F_{1,\ 9} = 22.08$, $P = 0.001$) models, respectively.

arrival fat content of individuals that stayed for only 1 day was at least 11% of total body mass, whereas all individuals with fat content <6% of total body mass remained for no fewer than 4 days, suggesting a possible threshold fat level for departure. However, how much additional fat birds acquired between capture and departure is unknown.

We did not find any relationship between lean body mass and minimum stopover duration. Lean tissues (e.g., flight muscles, digestive organs) may contribute significantly to total body mass dynamics during migration. This is particularly apparent in shorebirds that routinely make exceptionally long non-stop flights and in passerines when they must cross ecological barriers (Biebach 1998, Karasov and Pinshow 1998, Battley et al. 2000, Guglielmo and Williams 2003). No formidable ecological barriers exist immediately north of New York City, and it is possible most arriving autumn passerine migrants have not recently metabolized substantial non-fat tissue, and rebuilding of lean mass is not a significant component of stopover refueling. This is not supported by the lean mass gained by the recaptured Ovenbird which accounted for ~40% of its total body mass increase. Four of eight other (non-radio-marked) birds that we recaptured during the season also had gains in lean mass (CLS and CGG, unpubl. data). It is unknown from our small sample sizes of recaptured and radio-marked birds whether migrants commonly deposit lean tissue at this site and if lean body mass affects departure timing. Fusani et al. (2009) did not find lean mass (muscle scores) to influence migratory restlessness in two of three species examined. This also suggests lean mass does not influence departure decisions. Further study on the relationship between lean body mass and stopover duration is needed.

Fuel load is not the only variable that can influence stopover duration; weather, predation risk, and date are also factors that possibly govern a bird's decision to depart a stopover site. Our small sample size of 11 birds prohibited including additional predictor variables in the analyses and we cannot assess any effect they may have had on stopover duration. However, the birds were marked on 5 days over a span of only 9 days; thus, they probably experienced similar predation risk and temporal pressure, and were exposed to comparable weather conditions. Arrival body composition likely differed among the individuals we studied more so than any of these potential extrinsic influences.

The recaptured Ovenbird may illustrate how multiple variables can affect stopover duration. This bird appeared to have stored sufficient fat to resume migration by its eighth stopover day, yet it remained at the site for 6 additional days. Overnight wind direction following recapture was primarily from the south until the night the bird departed when winds came from the north, the preferred direction of southbound passerines (Gauthreaux 1991). It is possible this bird was energetically prepared for departure by the eighth day but waited 6 additional days for more favorable overnight flying conditions. Six of the other birds similarly departed on nights with northern winds; the remaining four departed during eastern winds.

Our sample size was small, but arrival fat mass had a clear and strong effect on time birds remained at the stopover site. Similar relationships between stopover duration and some measure of energetic condition have been documented previously (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008), but the contributions of fat and lean mass were not addressed individually. Quantitative magnetic resonance scanning allowed us to separately examine how each tissue affected stopover duration. Arrival fat mass at our study site affected migrants' decisions to leave whereas lean body mass did not. Thus, the conditions for increasing or maintaining fat stores provided by this site and possibly other similar urban habitats can affect the migration timing of birds using them. Our results demonstrate quantitative magnetic resonance analysis can be useful under field conditions, and that combining it with telemetry and other approaches will improve our ability to understand the stopover biology of birds.

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