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Quantitative magnetic resonance analysis and a morphometric predictive model reveal lean body mass changes in migrating Nearctic–Neotropical passerines

Chad L. Seewagen · Christopher G. Guglielmo

Abstract Most studies of lean mass dynamics in free-living passerine birds have focused on Old World species at geographical barriers where they are challenged to make the longest non-stop flight of their migration. We examined lean mass variation in New World passerines in an area where the distribution of stopover habitat does not require flights to exceed more than a few hours and most migrants stop flying well before fat stores near exhaustion. We used either quantitative magnetic resonance (QMR) analysis or a morphometric model to measure or estimate, respectively, the fat and lean body mass of migrants during stopovers in New York, USA. With these data, we examined (1) variance in total body mass explained by lean body mass, (2) hourly rates of fat and lean body mass change in single-capture birds, and (3) net changes in fat and lean mass in recaptured birds. Lean mass contributed to 50% of the variation in total body mass among white-throated sparrows *Zonotrichia albicollis* and hermit thrushes *Catharus guttatus*. Lean mass of refueling gray catbirds *Dumetella carolinensis* and white-throated sparrows, respectively, increased 1.123 and 0.320 g h^{-1}. Lean mass of ovenbirds *Seiurus aurocapillus* accounted for an estimated 33–40% of hourly gains in total body mass. On average 35% of the total mass gained among recaptured birds was lean mass. Substantial changes in passerine lean mass are not limited to times when birds are forced to make long, non-stop flights across barriers. Protein usage during migration is common across broad taxonomic groups, migration systems, and migration strategies.

Keywords Protein catabolism · Stopover refueling · Nearctic–neotropical migrant · Urban habitat · Body composition

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Introduction

Most bird species undergo considerable fluctuations in body mass during migration, as mass is repeatedly lost during energetically demanding flights and replenished during stopover refueling. The energy density of fat is several-fold higher than that of protein and carbohydrates, and birds are unique among vertebrates in their ability to sustain high-intensity aerobic exercise primarily with fatty acid oxidation (Guglielmo 2010). It was at one time believed that changes in body mass of migrant birds were due to changes in fat mass alone (Odum et al. 1964), but more recently it has become clear that lean tissues can also significantly contribute to total body mass dynamics (Piersma 1990; Lindström and Piersma 1993; Karasov and Pinshow 1998).

Much of the evidence for lean mass changes during migration comes from shorebirds that have been shown to lose substantial organ and muscle mass during flight, which is later restored on stopover (e.g., Piersma et al. 1999). Atrophy of organs that are not needed during flight, such as digestive tract components, may be an adaptation to lower power requirements and basal metabolic rate, and in turn, increase flight efficiency (Jenni and Jenni-Eiermann 1998;

Piersma and Gill 1998; Biebach and Bauchinger 2003; Landys-Ciannelli et al. 2003), or may simply be a beneficial consequence of the relatively high turnover rates of these organs (Bauchinger and McWilliams 2009). Losses in flight muscle mass that accompany decreasing power requirements throughout a flight as birds become lighter may act to further economize energy expenditure (Pennycuick 1998; Lindström et al. 2000; Biebach and Bauchinger 2003). The steady supply of citric acid cycle intermediates needed for fat oxidation also necessitates the catabolism of some protein during flight (Jenni and Jenni-Eiermann 1998). Another potential benefit of protein breakdown is an increased liberation of water under dehydrating flying conditions (Jenni and Jenni-Eiermann 1998).

A bird's rate of protein loss during flight is thought to be a function of the size of its remaining fat stores, with greatest rates occurring when fat stores drop below 5–10% of total body mass (Jenni et al. 2000; Schwilch et al. 2002). In absolute terms, the amount of protein catabolized is parallel to the amount of fat catabolized (Bauchinger and Biebach 1998). Perhaps for these reasons, extreme fluctuations in lean body mass are best known in shorebirds which make exceptionally long non-stop flights and come close to exhausting fat stores relative to other groups of migratory birds. Most passerines, in contrast, migrate in shorter bouts and likely reach critically low fat stores only when crossing large expanses of inhospitable habitat such as oceans and deserts. It is these geographical barriers that push passerine migrants toward maximum utilization of endogenous energy sources, and therefore, it is at these crossings, we would expect to observe the most substantial changes in passerine lean mass. Indeed, most of the literature on lean mass dynamics in free-living passerines concerns Palearctic migrants before or after crossing the Sahara Desert and Mediterranean Sea (e.g., Karasov and Pinshow 1998; Deerenberg et al. 2002; Schwilch et al. 2002; Biebach and Bauchinger 2003; Bauchinger et al. 2005). These studies provide strong evidence that passerine migrants incur significant protein loss during passage over large geographical barriers, and subsequent stopover refueling includes the deposition of both fat and lean mass.

Under less demanding situations when stopover habitat is more contiguous, however, it is less certain how much lean tissue passerines catabolize in flight and rebuild during stopovers (Åkesson et al. 1992; Bauchinger and Biebach 2005). Between the Great Lakes and Gulf of Mexico, for example, there are no significant barriers impeding refueling by forest dwelling, Nearctic–Neotropical migratory passerines in eastern North America (Tankersley and Orvis 2003). Metropolitan and agricultural areas may be viewed as man-made barriers (Moore et al. 1995; Mehlman et al. 2005), but even the largest urban and agricultural landscapes are incomparable in size to natural barriers like the Sahara Desert and the Gulf of Mexico, and usually have several habitat fragments within that can be used as stopover sites when needed (Swanson et al. 2003; Mehlman et al. 2005; Seewagen and Slayton 2008).

In this study, we examined lean mass variation in migratory passerines during stopovers in New York City (NYC), USA, where no major barriers exist immediately to the north or south, and most migrants arrive with ample fat stores (Seewagen 2008a; Seewagen and Slayton 2008). Lean mass dynamics have seldom been studied in New World passerine species or in passerines at a stopover site that is not in close proximity to a large geographical barrier. As it has only recently been demonstrated that migrants can successfully refuel during stopovers in heavily developed, urbanized landscapes (Seewagen and Slayton 2008; Craves 2009; Seewagen et al., unpublished data), an additional goal of this study was to learn whether lean mass contributed to total body mass changes previously observed in birds at our urban study sites. Determining the extent to which lean tissues are replenished during stopover refueling is important for understanding the most important nutrient sources that stopover habitats must provide (Karasov and Pinshow 1998).

We used two sources of body composition data to explore lean mass variation in Nearctic–Neotropical migrants. The first was obtained by quantitative magnetic resonance (QMR) analysis of birds captured during autumn 2008 in Bronx Park, NYC. QMR analysis is a fast, accurate, non-invasive technique for directly measuring the fat and wet lean body mass of small vertebrates (Taicher et al. 2003; Jones et al. 2009; Nixon et al. 2010; McGuire and Guglielmo, in press), including passerine birds (Guglielmo et al., unpublished data). The second data set was obtained by using an existing predictive model (Seewagen 2008b) to estimate, based on total body mass and visible subcutaneous fat score, the fat mass of birds captured during spring 2007–2008 in Bronx Park and Prospect Park, NYC when the QMR unit was unavailable. With these datasets, we examined (1) the proportion of variance in total body mass explained by differences in lean body mass, after controlling for body size, (2) hourly rates of fat and lean body mass change during stopover refueling, and (3) fat and lean mass changes in recaptured birds.

Methods

Study sites

We used data collected in Bronx and Prospect Parks, NYC as part of an ongoing research program investigating landbird migrant stopover biology in urban habitats. NYC is crossed by the Atlantic migration routes of many

Nearctic–Neotropical passerine species and its parks are well-known for receiving large concentrations of passage migrants (Mittelbach and Crewdson 1998; Fowle and Kerlinger 2001). Bronx and Prospect Parks are primarily composed of mature, eastern deciduous forest and provide suitable stopover habitat for migrating passerines (Seewagen and Slayton 2008; Seewagen et al. 2010; Seewagen et al., unpublished data). Stopovers at these sites often span multiple days (Seewagen and Guglielmo 2010; Seewagen et al. 2010).

Data collection

Data were collected from spring and autumn migrants mist-netted from sunrise until approximately 1100 EST, 1–31 May and 8 September–20 October, 2007–2008. All birds were weighed on a digital balance to the nearest 0.1 g and fat-scored on a 6-point scale (Seewagen 2008b). Unflattened wing length was measured to 1 mm and birds were banded with aluminum USGS leg bands.

The body composition of birds captured in Bronx Park during autumn 2008 was determined by QMR analysis within 45 min following capture and banding. The QMR unit (Echo-MRI-B, Echo Medical Systems, Houston, TX, USA) was customized by the manufacturer for analyses of small birds and bats, with a 7 cm diameter antenna and a magnetic field strength of approximately 0.05 T. The instrument was housed in a climate-controlled, mobile laboratory (Glendale Recreational Vehicles, Strathroy, ON, Canada) parked at our study site and powered by either the onboard generator or a direct connection to a nearby street-lamp post. We calibrated the unit daily by running the Echo-MRI software's "system test" on a 94 g canola oil standard provided by the manufacturer. Scans of 5 g canola oil standards were also conducted periodically throughout the day to ensure the unit was functioning properly.

Awake birds were placed in plastic holding tubes, inserted into the QMR analyzer, and scanned in duplicate using the "small bird" (<50 g) and "two accumulation" (four replicate scans for a total scan duration of 110 s) settings of the Echo-MRI software. The instrument reported fat and lean body mass measurements to 0.001 g. Fat mass measurements were later slightly adjusted to improve accuracy using a calibration equation (calibrated fat mass = raw QMR fat mass × 0.94) developed from house sparrows *Passer domesticus* and zebra finches *Taeniopygia guttata* in a laboratory validation (Guglielmo et al., unpublished data). Mean relative errors for predictions of chemically extracted fat and lean mass in our validation study were ±11% and ±1.5%, respectively. Our QMR unit measured the body composition of small bats with similar accuracy (McGuire and Guglielmo, in press). Detailed descriptions of QMR physics and additional validations of

Echo-MRI body composition analyzers are provided by Taicher et al. (2003), Tinsley et al. (2004), Jones et al. (2009), and Nixon et al. (2010).

It should be noted that in QMR analysis, wet lean body mass does not include non-fat components such as skeleton or feathers and in this way differs from fat-free body mass provided by chemical extraction; although, the two are highly correlated. It is uncertain to what extent gut contents are detected during QMR scanning and reflected in body composition measurements. We assume fat and protein content of undigested food items register as fat and lean body mass, respectively. Because the diets of our study species consist of foods (insects, fruits, and/or seeds) that are highly digestible (50–90%; reviewed by Karasov 1990), the majority of the material in the gut can be considered, in effect, part of the bird. Retention times for small passerines that consume insects, fruits, or seeds are relatively short (<45 min; Karasov 1990; Levey and Karasov 1994), however, and it is likely most birds had emptied their guts during the time elapsed between capture and QMR scanning. Birds commonly defecated during extraction from mist nets and banding, or in holding bags while waiting to be scanned, and we assume contributions of gut contents to body composition measurements were negligible.

Study species

We analyzed QMR data from the gray catbird *Dumetella carolinensis*, hermit thrush *Catharus guttatus*, and white-throated sparrow *Zonotrichia albicollis* because these were the migratory passerines that provided the largest sample sizes (*n* > 20). Sample sizes of all other species were <10 birds which we considered inadequate for statistical analyses.

Gray catbird is a widespread migrant that breeds across most of the U.S. and winters from the coastal mid-Atlantic U.S. to the Neotropics (Cimprich and Moore 1995). The white-throated sparrow's breeding range spans the U.S.–Canada border east of the Rocky Mountains and its wintering range extends from New England to Florida and Texas (Falls and Kopachena 2010). Eastern populations of the hermit thrush breed throughout the northeastern U.S. and the majority of Canada south of the tree-line, and primarily over-winter from New Jersey and the mid-Atlantic states to southern Florida (Jones and Donovan 1996). Although gray catbirds nest and white-throated sparrows over-winter in NYC (CLS, personal observation), we assumed the majority of the individuals in our samples were on autumn migration. No gray catbirds or white-throated sparrows in the study were recaptured within the field season (unlike year-round resident species), which increased our confidence that these birds did not remain at

the site and were migrants en route to other locations. We further believe the gray catbirds in our sample were not local breeders or young of the year from the study area because they were not in molt, which suggests they nested or hatched north of our site and were in the process of autumn migration when and where we captured them.

We used the predictive model to study body composition changes in ovenbirds *Seiurus aurocapillus*. The ovenbird is a long-distance Neotropical migrant that breeds across much of Canada and the eastern U.S., and over-winters throughout Central America and the Caribbean islands. Ovenbirds do not nest or over-winter in NYC (Van Horn and Donovan 1994; DeCandido and Allen 2005). We used this species because it had the most sufficient sample sizes of the species with an available model for estimating the fat mass of living birds (Seewagen 2008b).

Data analyses

We used SPSS 17.0 (SPSS Inc., Chicago, IL, USA) for all analyses and accepted significance at $P \leq 0.05$. All data met normality assumptions.

Fat, lean, and total body mass data that were significantly correlated with wing length were size-adjusted using a scaled mass index (Eq. 2, Peig and Green 2009). The scaled mass index, unlike multiple regression with a size measurement included as an additional independent variable, allowed us to control for the effects of body size on both the independent and dependent variables. Another attractive characteristic of the scaled mass index is that unlike mass-length residuals (Green 2001), it retains original units of measurement.

QMR measurements

After controlling for structural size, we regressed fat and lean body mass against total body mass to determine the proportion of the variation in total body mass explained by these two components (Piersma and Jukema 1990; Piersma and Van Brederode 1990; Wirestam et al. 2008). We used major axis (MA) type II regression to find the line of best fit through the data because our independent variable likely contained error, variables were measured in the same units, and the slope of the line was of foremost interest (Sokal and Rohlf 1981; Warton et al. 2006). This and similar regression approaches to body composition data have received criticism for overestimating the influence of lean mass on total body mass variation (Lindström and Piersma 1993; van der Meer and Piersma 1994) and are also unable to determine whether lean body mass differences among birds at a stopover site are due to preexisting differences upon arrival, or increases in lean mass during the stopover period. We therefore conducted two additional analyses to

determine whether migrants gained lean mass during stopover refueling at our study sites.

First, we used linear regression to relate fat and lean body mass to time of capture (expressed as hours since sunrise). A significant, positive relationship between lean body mass and capture time would indicate that birds captured early in the morning have lower lean body mass than those captured later in the day, and diurnal lean mass gain occurs at the site. This is analogous to the widely used technique of measuring total body mass changes in passerines during stopover, whereby a regression of total body mass and time of capture is used to estimate an hourly mass gain rate (e.g., Dunn 2000, 2001; Carlisle et al. 2005; Bonter et al. 2007; Seewagen and Slayton 2008). Second, we calculated net changes in the fat and lean body mass of birds that were recaptured 1 day or more after their initial capture and that had gained at least 1 g of total body mass between captures.

Predictive model

We used a predictive model based on total body mass and visible subcutaneous fat score to estimate the fat mass of ovenbirds (Seewagen 2008b) captured during spring research seasons at Bronx and Prospect Parks when the QMR unit was unavailable. Simple linear regressions of estimated fat mass and total body mass against time of capture were then used to quantify hourly rates of fat and total body mass gain; the difference between the slopes was taken to represent the contribution of lean mass to gains in total body mass.

Results

We captured and analyzed with QMR 31 gray catbirds, 21 hermit thrushes, and 40 white-throated sparrows (total body mass of one sparrow was not recorded due to scribe error) during autumn in Bronx Park. With the predictive model we estimated the fat mass of 43 and 102 ovenbirds captured during spring in Bronx and Prospect Parks, respectively. Fat mass as a percentage of total body mass upon capture was on average 13% in gray catbirds, 9% in hermit thrushes, and 11% in white-throated sparrows during autumn in Bronx Park, and 15% in ovenbirds in both Bronx and Prospect Parks during spring (Table 1).

Fat and lean mass contributions to total mass variation

Fat and lean body mass were significantly related to total body mass in the gray catbird (Table 2). Regression coefficients were weak, however, leading to poor slope estimates for fat and lean components that illogically sum to

Table 1 Total body mass (TBM), lean body mass (LBM), and fat mass (FM) of migratory landbirds during stopovers in Bronx Park (BP) and Prospect Park (PP), New York City, USA, spring and autumn 2008

	Season	Site	n	TBM (g)	LBM (g)	FM (g)
Gray catbird	Autumn	BP	31	40.5 ± 2.8	30.802 ± 2.597	5.435 ± 2.397
Hermit thrush	Autumn	BP	21	31.2 ± 2.0	24.450 ± 1.514	2.763 ± 1.078
Ovenbird	Spring	BP	43	21.0 ± 1.2		3.2 ± 0.7
	Spring	PP	102	20.6 ± 1.7		3.0 ± 1.0
White-throated sparrow	Autumn	BP	39	25.9 ± 2.2	19.719 ± 1.344	2.887 ± 1.260

TBM measured by digital balance. FM of ovenbirds estimated with a predictive model (see "Methods"); FM and LBM of other species measured with quantitative magnetic resonance analysis. Values are means $\pm$ SE

Table 2 Relationships of fat and lean body mass with total body mass in migratory landbirds during autumn 2008 stopovers in Bronx Park, New York City, USA

	Tissue	r^2	F	df	P	b
Gray catbird	Fat	0.21	7.8	1, 29	0.009	0.8
	Lean	0.18	6.7	1, 29	0.017	1.0
Hermit thrush	Fat	0.63	32.2	1, 19	<0.001	0.5
	Lean	0.27	7.0	1, 19	0.016	0.5
White-throated sparrow	Fat	0.43	27.4	1, 37	<0.001	0.4
	Lean	0.53	42.2	1, 37	<0.001	0.5

Slopes (b) obtained by major axis type II regression represent the changes in fat and lean body mass (g) per 1 g of total body mass, after controlling for body size

far greater than 1. Stronger relationships between fat and lean body mass and total body mass were found in the hermit thrush and white-throated sparrow (Table 2). Fat mass and lean body mass each increased 0.5 g per 1 g of total body mass in the hermit thrush. Regression slopes indicated that white-throated sparrows increased 0.4 g in fat mass and 0.5 g in lean body mass per 1 g increase in total body mass (Table 2). Fat and lean slopes in this species also do not sum to exactly 1 which we assume is due to error surrounding QMR measurements and/or size-adjustment procedures.

Hourly mass changes

The relationship between lean body mass and capture time was significant in the gray catbird ($r^2 = 0.21$, df = 1, 29, $P = 0.010$) and marginally significant in the white-throated sparrow ($r^2 = 0.09$, df = 1, 38, $P = 0.058$), and indicated rates of lean body mass gain of 1.123 and 0.320 g h^{-1}, respectively. Lean body mass was unrelated to capture time in the hermit thrush ($r^2 = 0.02$, df = 1, 19, $P = 0.49$). Fat mass was not related to capture time in any species (gray catbird: $r^2 = 0.08$, df = 1, 29, $P = 0.13$; white-throated sparrow: $r^2 = 0.01$, df = 1, 38, $P = 0.59$; hermit thrush: $r^2 = 0.08$, df = 1, 19, $P = 0.22$).

Ovenbird total body mass was significantly related to time of capture at Bronx Park ($r^2 = 0.20$, df = 1, 41, $P = 0.003$) and increased 0.5 g h^{-1}. Fat mass was also significantly related to capture time ($r^2 = 0.17$, df = 1, 41, $P = 0.006$), increasing 0.3 g h^{-1} and accounting for 60% of the increase in total body mass. At Prospect Park, ovenbird total body mass and fat mass were significantly, yet weakly, related to time of capture (total body mass: $r^2 = 0.05$, df = 1, 100, $P = 0.029$; fat: $r^2 = 0.06$, df = 1, 100, $P = 0.018$). Total body mass increased 0.3 g h^{-1}, of which an estimated 0.2 g h^{-1} (67%) was fat.

Recaptured birds

Eight migrants were recaptured and reanalyzed with QMR. Four of these birds (three hermit thrushes and one ovenbird) refueled and gained at least 1 g of total body mass between captures. One hermit thrush gained almost only fat, whereas the other two had increases in lean mass that accounted for 28 and 65% of their total body mass increase (Table 3). The ovenbird gained 1.831 g of lean body mass between captures which represented 44% of its total body mass increase.

Discussion

Studies of lean mass changes in free-living migrants have been primarily limited to long-distance migrant shorebirds and Palearctic passerines at the Sahara Desert where they are challenged to make the longest non-stop flight of their migration. Much less is known about lean tissue changes in Nearctic–Neotropical passerine species, or in passerines when stopover habitat is more continuously available and shorter flights are possible (Åkesson et al. 1992; Bauchinger and Biebach 2005). In this study, we observed lean mass changes in Nearctic–Neotropical migratory passerines that had likely flown only a few hours prior to arrival. Each of our four approaches to the

Table 3 Changes in total body mass (TBM; measured by digital balance), fat mass (FM) and lean body mass (LBM; measured with quantitative magnetic resonance) of four passerines recaptured during stopovers in Bronx Park, New York City, USA, autumn 2008

Species	First capture			Days	Recapture			Change			% as LBM
	TBM	FM	LBM		TBM	FM	LBM	ΔTBM	ΔFM	ΔLBM	
Hermit thrush	29.5	1.981	23.798	3	31.1	2.766	24.834	1.6	0.785	1.036	65
Hermit thrush	31.9	1.850	25.278	4	33.8	3.705	25.318	1.9	1.856	0.040	2
Hermit thrush	28.4	2.058	21.669	5	31.2	3.904	22.446	2.8	1.846	0.777	28
Ovenbird	18.3	1.068	15.149	8	22.5	3.835	16.982	4.2	2.767	1.833	44

All mass data expressed in grams

data suggested lean mass was considerably variable and migrants were building lean tissue during stopovers.

The relationships of fat and lean body mass with total body mass were weak in the gray catbird and did not yield informative estimates of the contributions of each tissue to variation in total body mass. However, regression analyses indicated that in hermit thrushes and white-throated sparrows, lean mass accounted for 48–53% of the differences among individuals in size-corrected total body mass. Lean body mass was positively related to time of day in the gray catbird and white-throated sparrow, indicating accumulation of lean mass during stopover refueling at Bronx Park. Marsh (1983) similarly noted that gray catbird lean mass was greater in the evening than in the morning at a stopover site. Total body mass of ovenbirds in Bronx and Prospect Parks increased at a greater rate than fat mass, suggesting that lean mass accounted for 36–48% of the increase in total body mass. Despite a small sample size, the recaptured birds provide direct evidence of the extent to which migrants deposited lean mass during stopovers, with lean mass accounting for 28–65% of the total body mass gained in three of the four individuals. The hermit thrush that gained almost only fat had the highest lean body mass of thrushes at first capture, suggesting that lean mass upon arrival may be a primary determinant of how much lean versus fat mass a bird gains during stopover.

The contributions of lean tissue to total body mass variation that we found are comparable to similar field studies of both passerines and shorebirds. For instance, lean tissue accounted for 37% of changes in total body mass in blackcaps refueling after crossing the Sahara Desert (Karasov and Pinshow 1998). Garden warblers lost (and presumably later recovered) up to 50% of their organ and muscle mass during flights across the Sahara (Bauchinger et al. 2005). Piersma and Van Brederode (1990) estimated that shorebird species preparing to depart African wintering grounds gained 25–45% of their total body mass in the form of lean mass. Lean mass accounted for half of the total body mass increases of bar-tailed godwits *Limosa lapponica* staging in the Wadden Sea (Piersma and Jukema 1990). Red knots *Calidris canutus islandica* gained 22% of their total body mass as lean mass during stopovers in Iceland (Piersma et al. 1999).

Laboratory studies of exercised or fasted at-rest birds have found that lean mass accounts for similar proportions of total body mass changes as those observed in wild birds. For example, captive garden warblers lost and regained 27% of their body mass as lean mass during fasting and a subsequent recovery period (Klaassen and Biebach 1994). Klaassen et al. (2000) showed that an average of 17% of the mass recovered by a thrush nightingale *Luscinia luscinia* following flights in a wind tunnel consisted of protein. Wirestam et al. (2008) found that increases in total body mass exceeded increases in fat mass in a laboratory study of four Palearctic passerine species, and attributed the remaining 36–67% of total body mass accumulation to lean tissues.

Interestingly, the lean body mass of gray catbirds and white-throated sparrows in our study was related to time of day, but fat mass was not. We speculate that this could reflect a necessary recovery of digestive tract mass lost en route to the stopover site before efficient nutrient assimilation and fat deposition could occur (Klaassen and Biebach 1994; Hume and Biebach 1996; Lindström et al. 1999; Piersma et al. 1999). Among the recaptured hermit thrushes, the bird recaptured after only 3 days had a higher relative contribution of lean mass to total mass gain than the birds recaptured after 4–5 days, which could also indicate some degree of biphasic mass gain (sensu Carpenter et al. 1993). Digestive organs often undergo the most substantial fluctuations in mass throughout migration (Piersma and Gill 1998; Biebach and Bauchinger 2003), as they are of little functional value during in-flight fasting, but are of utmost importance during stopover refueling. Digestive organs are also likely to decrease in mass early into a flight because of their relatively short carbon retention times and high turnover rates (Bauchinger and McWilliams 2009). Hence, digestive organs may represent the most variable lean tissues in short-distance passerine migrants such as hermit thrushes and white-throated

sparrows. Further study of this phenomenon will require the combination of QMR with imaging methods such as ultrasonography or magnetic resonance imaging.

Conclusion

Although our study sites are not near a geographical barrier, most migrants arrive in NYC with large fat stores, and we examined mostly temperate, short-distance migrant species, each of our approaches suggested lean mass changed considerably en route to or at our study sites. It is unlikely that large changes in lean mass of passerines are limited to times when birds are forced to make relatively long non-stop flights, when fat stores near depletion, or when energy contributions from other sources are necessary. The use of amino acids for Krebs cycle intermediates and gluconeogensis causes some protein breakdown regardless of flight duration or size of the fat stores (Jenni and Jenni-Eiermann 1998), and may account for the lean mass variation we observed. Further, protein catabolism may actually occur at greater rates during short-distance than long-distance flights (Jenni-Eiermann and Jenni 1991; Jenni and Jenni-Eiermann 1992) because costs of upregulating the mechanisms needed to fuel high intensity aerobic exercise with fat may not be economical for only short time periods (Jenni and Jenni-Eiermann 1998) and there is less urgency to conserve lean tissues (Bauchinger and Biebach 1998). Fast natural turnover rates of gastrointestinal organs (Bauchinger and McWilliams 2009) should also cause birds to lose lean mass even during short periods of active fasting.

Studies of protein usage in bird migration have been limited by the impossibility of killing a bird twice. QMR analysis represents a fast and accurate means of obtaining repeated body composition measurements of individuals and holds great promise for improving our understanding of lean mass fluctuations in both captive and free-living migratory birds. Despite a small sample size, the recaptured birds in this study provided us with perhaps the most clear quantitative information on lean body mass changes, and we encourage application of QMR technology in field studies with the potential to recapture large numbers of passage migrants. Repeated QMR measures offer the possibilities to study inter- and intraspecific variation in body composition change during stopover, as well as factors, such as age, sex, diet, and site that affect it.

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