Lipid Content of Nearctic-Neotropical Migratory Passerines Killed During Stopovers in a New York City Park

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Abstract - Urban parks often represent the only stopover habitats available to migrating birds encountering expansive metropolitan areas. Green spaces remaining within cities may therefore be valuable to migrants; yet studies of migrants in this context are few. I examined the lipid content of birds killed by window collisions in spring and autumn in a small recreational park in New York City to assess the energetic condition of migratory passerines utilizing an urban habitat as a stopover site. I compared chemically determined fat content (expressed as a lipid index: g fat / g lean dry mass) and visible subcutaneous fat scores between seasons, autumn age classes, and birds grouped by family and foraging guild. Average total body fat (as % of dry mass) was 29.4% in spring and 24.1% in autumn; few lean birds were found in either season. Birds in spring were significantly fatter than in autumn. In spring and autumn, no differences in fat content (i.e., fat scores and lipid indices) were observed between warblers and thrushes. In spring, there were no differences in fat content between warbler foraging guilds, whereas in autumn, ground/understory-foraging warbler species were fatter than warbler species associated with arboreal foraging. In autumn, the fat content of immature birds was comparable to that of adults. It could not be determined whether the high fat content of birds found here was acquired during stopovers in the study site or if birds arrived with substantial fat stores remaining from previous stopovers. The likelihood of each scenario and the value of urban parks to migratory birds are discussed.

Introduction

Migration places great energy demands on birds, and stopover habitats where depleted fat reserves can be quickly restored are critical to successful migrations (Moore et al. 1995). Recent broad-scale habitat loss along migration flyways has increased concern about the conservation of many migratory species that already face pressures from anthropogenic changes on their breeding and wintering grounds. In the northeastern United States, urban land covers approximately one third of the region, considerably limiting the amount of stopover habitat available to birds migrating through this area (Dettmers and Rosenberg 2000). Here, the habitats remaining within cities may be of particular importance to en route migrants (Dettmers and Rosenberg 2000, Mehlman et al. 2005). Yet the use of urban habitats by migrating birds remains poorly understood, and it is uncertain whether such areas can serve as adequate stopover sites. The high densities at which birds often occur in these small green spaces and the prevalence of exotic vegetation may prohibit migrants from adequately gaining body mass as a result of intense competition for limited resources. With increasing urbanization, municipal parks and similar fragments will account for a growing proportion

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of the stopover sites available to migrating birds. Investigating migrant utilization of existing urban habitats is an important step towards understanding the effect that further urban sprawl will have on bird migration.

The goal of this study was to examine the energetic condition of transient birds utilizing an urban habitat as a stopover site. I measured the lipid content of Nearctic-Neotropical migratory passerines killed by window collisions during spring and autumn stopovers in a small recreational park on the heavily urbanized island of Manhattan, New York City, NY. The birds' lipid content was considered indicative of their energetic condition (Morton et al. 1991).

Methods

Study site

Chelsea Park is a rectangular, 1.4-ha recreational park located between 27th and 28th Streets and 9th and 10th Avenues (40°45'N, 73°59'W) in the borough of Manhattan. An artificial turf sports field accounts for approximately 1/3 of the park's total area; the remaining area consists of asphalt basketball and handball courts, a children's playground, a two-story government office building, and a historical monument surrounded by park benches and annual flower beds. No natural or artificial water bodies are present. The park's perimeter is lined with 27 mature Platanus x acerifolia Aiton (London plane trees) that range in height from approximately 15-20 m. An additional 28 London plane trees of similar size are distributed throughout the park interior. The interior tree density creates a closed canopy that conceals most of the park's understory conditions when viewed from above. All but nine of the interior and perimeter trees stand in tree-pits, as the majority of the park's ground is impermeable surface. Aside from the tree-pits, the annual beds around the office building and monument represent the only permeable and vegetated areas in the park. The beds are planted with two non-native species, *Itea virginica* L. (Virginia sweetspire "Henry's garnet") and Liriope muscari Decne. (big blue lilyturf).

Study specimens

Throughout spring and autumn 2005 and 2006, dead birds were salvaged daily from beneath the large, highly reflective windows of a 6-story building (341 Ninth Avenue) that abuts the northern boundary of Chelsea Park (see Gelb and Delacretaz 2006 for details). The windows reflect the Park's greenery, giving a false appearance of additional habitat. As a result, many migrants are killed by daytime collisions with these windows during stop-overs in Chelsea Park.

Most of the birds used in this study were collected (and presumed to have died) during daylight hours (Gelb and Delacretaz 2006). The exact time between death and collection was unknown, but was estimated to be no longer than six hours (Y. Gelb, New York City Audubon Society, New York, NY, pers. comm.). Collected birds were bagged and frozen until the time of processing. The specimens used here represented 29 Nearctic-Neotropical migratory species (Appendix A).

Lab procedures

Specimens were thawed at room temperature until flexible enough to manipulate. Visible subcutaneous fat in the furcular hollow was scored on a 6point scale (Moore and Kerlinger 1987): (0) no visible fat; (1) trace of fat, but not completely lined; (2) completely lined with thin fat layer; (3) filled with fat but still concave; (4) filled with fat even with pectoralis or slightly bulging; and (5) filled to bulging and at least partially covering keel. Fat was scored by the same individual throughout the study to avoid inter-observer variation (Krementz and Pendleton 1990). Specimens were then weighed to the nearest 0.001 g (Denver 410-g digital balance). Fall birds were aged as hatching-year (HY) or after-hatching-year (AHY) by plumage characteristics and extent of skull ossification (Pyle 1997). A ventral midline incision was made from the furcula to the cloaca to expose the thoracic and abdominal cavities, and carcasses were oven-dried to a constant mass at 75 °C. Dry carcasses were re-weighed and homogenized (including feathers) with an electric blender. Duplicate 1-g (± 0.100 g) samples of the homogenate of each bird were placed in cellulose thimbles, and soluble fat was extracted with petroleum ether in a Soxtec apparatus (FOSS Inc., Laurel, MD). Following extraction, samples were oven-dried overnight and weighed the following day. The percentages of mass lost from both samples were averaged to yield total body fat %.

Statistical analyses

Because birds were collected only when fatal window collisions occurred, the total sample of study specimens was composed of a wide array of species with most species represented by no more than a few individuals. These small samples prohibited analysis at the species level. Instead, birds were grouped by family into *Parulidae* (wood warblers), *Turdidae* (thrushes), and *Vireonidae* (vireos). Wood warblers were further separated by foraging guild because of the considerable difference in canopy and understory habitat availability in Chelsea Park. Species that primarily forage among the foliage of trees and tall shrubs were placed in the group "arboreal warblers" and species that are more restricted to foraging on or near the ground were placed in the group "ground/ understory warblers" (Appendix A).

I used a lipid index (g fat / g lean dry mass, where fat mass equals total body fat percentage multiplied by total dry body mass, and lean dry mass equals total dry body mass minus fat mass) to control for body-size variation when comparing chemically-derived fat content (Johnson et al. 1985, Rogers 1991), because multiple species were grouped together.

I used Mann-Whitney U-tests to investigate differences in fat scores (Benson and Winker 2005, Hailman 1965) among seasons, families, foraging guilds, and autumn age classes. Unpaired, two-tailed t-tests were used to examine differences in lipid indices within these groups, with lipid index as the dependent variable and season, family, foraging guild, or age as the independent variable. In some cases, one of the two lipid-index groups being compared was not normally distributed. T-tests were still used in these situations because the tests remain robust if assumptions are not met, especially when sample sizes do not differ markedly and two-tailed tests are performed (Zar 1999).

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Data from both years were pooled in each of the above analyses after no significant annual differences in lipid indices (Spring: t=0.76, df=49, P=0.45; Autumn: t=0.17, df=76, P=0.87) or fat scores (Spring: Z=1.84, P=0.07; Autumn: Z=1.11, P=0.27) were found among all birds. Statistical tests were performed with SYSTAT, version 10.0. Results were considered significant when $P \le 0.05$. When tests of lipid indices yielded insignificant results retrospective power analyses (GPOWER; Faul and Erdfelder 1992) were conducted to determine if Type II errors may have occurred ($\alpha = 0.05$, effect size = 0.5).

Results

Average total body fat percentage was 29.4% in spring and 24.1% in autumn. In spring, 80.4% of all birds were >20% fat and only 2.0% were <10% fat. In autumn, birds >20% fat accounted for 58.8% of all birds, while 3.8% of birds were <10% fat. Lipid indices and fat scores were significantly higher in spring than autumn when all birds were grouped together (Table 1). Comparisons of individual groups among seasons showed that warblers (both guilds combined) were significantly fatter in spring than autumn (Table 1). Thrushes and ground/ understory warblers showed no significant seasonal differences in lipid indices

Table 1. Seasonal differences in body fat percentage, lipid index (t-test), and fat scores (Mann-Whitney *U* - test) of migratory passerines killed during stopovers in Chelsea Park, New York City. Values presented are mean \pm SD. Body fat percentage calculated as subsample lipid mass/ dry mass and lipid index calculated as total lipid mass/total lean dry mass; see Methods. * = P < 0.1, ** = P < 0.05, *** = P < 0.005.

Group	Season	n	%	fat	%	range
All wood warblers (Paruli	dae) Spring	37	28.92	± 10.04 7.89-46.		39-46.00
	Fall	53	22.74	± 11.96	6.6	60-54.87
Arboreal	Spring	15	26.88	3 ± 10.69	13.0	04-46.00
	Fall	39	19.85	5 ± 10.92	6.6	50-48.13
Ground/understory	Spring	18	31.98	3 ± 8.40	18.4	48-45.66
	Fall	14	28.55	5 ± 12.33	13.9	91-54.87
Thrushes (Turdidae)	Spring	12	32.31	± 7.29	20.0	9-43.26
	Fall	12	26.68	3 ± 10.64	12.8	37-50.83
Vireos (Vireonidae)	Spring	2	21.33	3 ± 6.29	16.8	38-25.78
	Fall	8	22.97	7 ± 7.51	12.8	32-37.54
All birds	Spring	51	29.42	2 ± 9.48	7.8	39-46.00
	Fall	80	24.13	3 ± 11.26	6.6	50-54.87
Group	Lipid index	t	df	Fat sc	ore	Ζ
All wood warblers	0.435 ± 0.209	2.11**	88	$2.56 \pm$	1.30	0.24***
	0.322 ± 0.245	-	-	$1.46 \pm$	1.48	-
Arboreal	0.404 ± 0.238	1.71*	52	$2.33 \pm$	1.35	3.00***
	0.290 ± 0.214	-	-	$1.08 \pm$	1.22	-
Ground/understory	0.492 ± 0.185	0.54	30	$2.94 \pm$	1.21	0.23
2	0.446 ± 0.295	-	-	$2.62 \pm$	1.61	-
Thrushes (Turdidae)	0.493 ± 0.158	0.63	20	$3.00 \pm$	1.41	1.50
	0.439 ± 0.244			$2.08 \pm$	1.38	
Vireos (Vireonidae)	0.275 ± 0.102	-	-	3.50 ± 0	0.71	-
	0.310 ± 0.138	-	-	1.63 ± 0	0.92	-
All birds	0.443 ± 0.198	2.20**	127	$2.67 \pm$	1.32	4.04***
	0.356 ± 0.233	-	-	$1.58 \pm$	1.34	-

(power = 0.22 and 0.27, respectively) or fat scores, whereas arboreal warblers had significantly higher fat scores and marginally higher lipid indices in spring than fall (Table 1). Among groups in spring, there were no significant differences in lipid indices or fat scores (all P > 0.1), but statistical power of the lipid index t-tests was low (all warblers v. thrushes: power = 0.31; ground/understory v. arboreal warblers: power = 0.28). In autumn, ground/understory warblers had significantly higher lipid indices (t = 2.12, df = 51, P = 0.04) and fat scores (Z = 3.23, P < 0.01) than arboreal warblers, while no significant differences were observed between thrushes and all warblers (t-test: t = 1.28, df = 61, P = 0.21, power = 0.34; Mann-Whitney: Z = 1.38, P = 0.17). Differences in lipid indices and fat scores between all HY (n = 21) and AHY (n = 29) warblers in autumn were not statistically significant (t-test: t = 1.62, df = 48, P = 0.11, power = 0.40; Mann-Whitney: Z = 1.58, P = 0.11).

Discussion

Season, age, and family differences

The seasonal differences in lipid indices and fat scores found here do not necessarily reflect a greater availability of food in Chelsea Park in spring, as the fattening strategies of migrants may vary between spring and autumn. The "spring fatter hypothesis" (Sandberg and Moore 1996) suggests that migrants should carry more fat in spring than in fall as insurance against potentially unfavorable environmental conditions encountered upon arrival on breeding grounds. Other hypothesized benefits of arriving on breeding grounds with ample fat stores include greater reproductive output by females and the allowance of males to devote less time to foraging, and more time to mate solicitation and territory defense (Sandberg and Moore 1996, Smith and Moore 2003). In a study of high-latitude migrants in Alaska, Benson and Winker (2005) did not find evidence to support the spring fatter hypothesis. Conversely, a recent study in Bronx Park, New York City found migrants were heavier and fatter in spring than fall (Seewagen 2005; C.L. Seewagen and E.J. Slayton, Wildlife Conservation Society, Bronx, NY, unpubl. data). The significantly higher spring fat loads of birds in Chelsea Park are consistent with these other findings in New York City and the spring fatter hypothesis.

Many studies of age-related differences in stopover ecology have found adults to be in greater energetic condition than immature migrants during autumn stopovers (e.g., Morris et al. 1996, Wang et al. 1998, Woodrey and Moore 1997, but see Jones et al. 2002). Banding data collected in New York City, however, did not fit this trend, with HY and AHY birds found to be in comparable energetic condition (Seewagen 2005; C.L. Seewagen and E.J. Slayton, unpubl. data). The autumn fat loads of adult and immature birds in this study also did not differ significantly, although statistical power was low.

Ground/understory warblers had higher lipid indices and fat scores than arboreal warblers in autumn despite a very limited amount of herbaceous plants and woody shrubs, and consequent lack of a true understory in which to forage. If migrants are attempting to deposit fat during stopovers in Chelsea Park, the relatively abundant canopy habitat does not appear to favor those species that are primarily arboreal foragers.

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Twelve of the 14 individuals in the autumn ground/understory warbler sample were represented by only two species: *Geothlypis trichas* L. (Common Yellowthroat) and *Seiurus aurocapillus* L. (Ovenbird). If migrants typically arrive in Chelsea Park with fat stores remaining from previous stopovers, the higher fat content of the ground/understory warbler group may then simply reflect a tendency for these two species to carry greater fat loads than those species in the arboreal warbler group.

Stopover site quality

The refueling rate of birds is the standard indicator of stopover habitat quality (Dunn 2000, 2001). Estimating refueling rate, however, requires data acquired by capturing live birds. Inappropriate habitat conditions (e.g., lack of a sufficient understory for mist-netting) and the presence of park-users make live capture in Chelsea Park unfeasible. Examining the lipid stores of window casualties was the only practical means of obtaining energetic-condition data.

A limitation of considering fat content indicative of stopover site quality is the necessary assumption that birds did not arrive with equal or greater fat stores deposited at previous stopovers. Without accompanying mass-change data, it cannot be certain whether the fat loads of birds used in this study were deposited during stopovers in Chelsea Park or were deposited elsewhere prior to arrival. As such, I offer two interpretations of the results reported here.

The first interpretation assumes that the majority of fat was acquired by the birds during stopovers in Chelsea Park. Under this scenario, the data suggest the park is indeed a stopover site in which migrants can adequately replenish energy stores, as the fat content found in this study is similar to that typically observed in migrating songbirds (e.g., Caldwell et al. 1963; Child 1969; Rogers and Odum 1964, 1966). Seewagen and Slayton (In press) concluded that an urban park in another section of New York City is also a high-quality stopover site; although, the characteristics of that site (e.g., larger size, primarily native tree and understory plant communities, permanent natural water source) are drastically different than those of Chelsea Park. If the fat content of birds examined in this study was in fact deposited in Chelsea Park, it then suggests that the behavioral plasticity of birds during migration (see Petit 2000) allows them to exploit even the most atypical and unfamiliar habitats to replenish energy stores.

The second interpretation assumes that the birds arrived in Chelsea Park already possessing considerable quantities of stored fat. The low proportion of lean birds (<10% fat) suggests this interpretation (assuming there are no hidden biases in the tendencies of fat and lean birds to collide with windows). But barring an unfavorable change in weather or the encounter of a significant ecological barrier, why would birds terminate a night flight when they still have plenty of energy to continue? Perhaps large metropolitan areas act as artificial geographical barriers (Moore et al. 1993), and birds encountering cities behave in the same way as they often do when approaching natural obstacles—land and further increase existing energy stores before attempting to overcome the barrier. Perhaps birds land with fat stores remaining as a margin of safety against potentially poor feeding conditions (Woodrey and Moore 1997) in an unknown

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city environment. Possibly, urban light pollution causes navigational disorientation and birds seek places to land until they can re-orient and continue. Direct observations of nocturnal migrants from the top of New York City's Empire State Building (<1 km NE of Chelsea Park), however, recently provided little evidence to suggest that this illuminated skyscraper (and presumably other similar buildings) disorients migrants and that migrants cannot adequately negotiate the City's matrix (DeCandido 2007; DeCandido and Allen 2006; R. DeCandido, Hawk Mountain Sanctuary, Orwigsburg, PA, pers. comm.).

It is unclear whether birds are stopping over in Chelsea Park and other New York City parks as a reaction to an unfamiliar and inhospitable landscape, to replenish energy stores, or a certain degree of both. A study of live migrants in Bronx Park, New York City found few birds were lean (i.e., fat scores ≤ 1) upon initial capture, but nonetheless continued to gain substantial mass during stopover (Seewagen 2005; Seewagen and Slayton, in press), providing support for each scenario. Under either scenario, urban parks should represent a valuable resource to songbirds that need to cross metropolitan areas during migration. If migrants land in urban parks because their energy stores are depleted, then the value of urban parks is the provision of a place in which migrants can potentially refuel and continue further than may be possible if such stopover sites were completely absent. If the light pollution and composition of urban areas cause birds with ample fat stores remaining to stop over, the value of urban habitats is their provision of a place in which migrants can maintain their energy balance while reorienting. The potential importance of urban habitats to migrants warrants insurance of their conservation and proper management. This conclusion is particularly pertinent in the Northeast where Atlantic migration routes cross the most urbanized region of the United States.

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Appendix A. Number of individuals by species and foraging guild salvaged during spring and autumn 2005 and 2006 near Chelsea Park, New York City. Arboreal warbler species are indicated by "A" and ground/understory warbler species are indicated by "G/U."

	Foraging	# salvaged birds	
Species	guild*	Spring	Autumn
Setophaga ruticilla L. (American Redstart)	A ^{1,2}	1	1
Mniotilta varia L. (Black-and-White Warbler)	A^3	3	6
Dendroica striata Forster (Blackpoll Warbler)	$A^{1,4}$	1	2
Dendroica caerulescens Gmelin (Black-throated Blue Warbler)	A ^{3,5,6}	1	4
Dendroica virens Gmelin (Black-throated Green Warbler)	A ^{1,3}	0	1
Vireo solitarius Wilson (Blue-headed Vireo)	-	1	2
Vermivora pinus L. (Blue-winged Warbler)	$A^{3,7}$	1	0
Wilsonia canadensis L. (Canada Warbler)	-	4	0
Dendroica pensylvanica L. (Chestnut-sided Warbler)	A ^{1,8}	0	3
Geothlypis trichas L. (Common Yellowthroat)	G/U^1	3	6
Catharus minimus Lafresnaye (Gray-cheeked Thrush)	-	0	4
Dendroica magnolia Wilson (Magnolia Warbler)	A ^{1,9}	0	5
Oporornis philadelphia Wilson (Mourning Warbler)	$G/U^{10,7}$	¹¹ 0	1
Vermivora ruficapilla Wilson (Nashville Warbler)	A ^{1,3}	0	2
Parula americana L. (Northern Parula)	A ^{1,3}	6	10
Seiurus noveboracensis Gmelin (Northern Waterthrush)	G/U^1	4	1
Seiurus aurocapillus L. (Ovenbird)	G/U^1	10	6
Dendroica pinus Wilson (Pine Warbler)	A^1	0	2
Vireo olivaceus L. (Red-eyed Vireo)	-	1	6
Pheucticus ludovicianus L. (Rose-breasted Grossbeak)	-	0	4
Piranga olivacea Gmelin (Scarlet Tanager)	-	0	3
Catharus ustulatus Nuttall (Swainson's Thrush)	-	5	3
Vermivora peregrina Wilson (Tennessee Warbler)	A ^{1,3}	0	1
Catharus fuscescens Ridgway (Veery)	-	2	2
Wilsonia pusilla Wilson (Wilson's Warbler)	A ^{1,12}	1	1
Hylocichla mustelina Gmelin (Wood Thrush)	-	5	3
Helmitheros vermivorus Gmelin (Worm-eating Warbler)	$G/U^{1,3}$	1	0
Dendroica petechia L. (Yellow Warbler)	A^1	1	0
Dendroica coronata L. (Yellow-rumped Warbler)	A ^{1,3}	0	1

*Foraging guild was only determined for species of wood warbler (*Parulidae*). Foraging guild was determined from these authorities: ¹Todd (1940), ²Sherry and Holmes (1997), ³Bent (1963), ⁴Hunt and Eliason (1999), ⁵Holmes (1994), ⁶Holmes (1986), ⁷Gill et al. (2001), ⁸Richardson and Brauning (1995), ⁹Hall (1994), ¹⁰Pitoc-chelli (1993), ¹¹Cox (1960), and ¹²Ammon and Gilbert (1999). Canada Warbler was not included because it forages in trees, the understory, and on the ground (Conway 1999, Forbush and May 1955, Todd 1940).