The energetics and stopover ecology of Neotropical migrant passerines in an urban park

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ABSTRACT

Due to the overlap of the Atlantic Flyway with some of the most urbanized regions of North America, the habitats remaining within cities may play an important role in bird migration. Yet, the use of urban parks by migrating birds is currently poorly understood. To determine if an urban habitat is serving as a suitable stopover site, I investigated the energetics of 8 species of migratory songbirds in Bronx Park (Bronx, NY) during two consecutive spring and fall migrations. Fat score, body mass, and rate of mass gain of birds of different ages and sexes were compared within and between migration seasons. For comparison to other studies, I calculated possible flight ranges. Fat score and condition index was significantly higher in spring for most species. There were few significant sexual differences in fat score or condition index in spring and few significant age-related differences in fall. Rate of mass change was positive in 12 of 17 possible combinations of species and season. Rates of mass gain were greater in spring than fall for most species. Flight ranges were comparable to those calculated in studies in rural areas and suggest most migrants in Bronx Park store enough energy to fly longer distances than are possible in the course of one night at the assumed average flight speed of small passerines. High fat scores, condition indices, and flight ranges, and positive rates of mass gain demonstrate the study site is a place where migrants can sufficiently restore depleted energy reserves. These findings highlight the importance of conserving and properly managing the remaining green spaces in urban areas situated along migratory bird flyways.

The conservation of Neotropical migratory birds is greatly complicated by their life history characteristics and the spatial scales at which they move (Moore et al. 1995, Yong et al. 1998). To date, most conservation strategy has focused on breeding and wintering habitats while the habitats in between that are necessary for migration to be possible have been largely undervalued (McCann et al. 1993). The work of Frank Moore and his colleagues has been instrumental in heightening awareness of the importance of stopover habitat in the life cycle of Neotropical migrants (e.g. Moore and Kerlinger 1987, Moore et al. 1995, Woodrey and Moore 1997, Yong et al. 1998, see Hutto 1998). Yet as recently as 1995, the study of stopover ecology was still considered to be in its infancy (Rappole 1995, Moore et al. 1995).

Given that migration places great energy demands on birds (Blem 1980), habitats where depleted energy reserves can be quickly restored become critical to successful migration. Reductions in the amount of suitable stopover habitat results in increased bird densities and competition, which may in turn lower fat deposition rates and hinder migration. Fewer stopover sites may also force birds (especially hatching-year individuals) to settle in poorer quality habitat (Moore and Simmons 1992, Moore et al. 1995). Collectively, habitat loss, degradation, and fragmentation are making the most taxing phase of a migratory bird's life even more problematic. Unless habitat requirements for migration are met, conservation efforts focused on breeding and wintering grounds may be compromised (Moore and Simmons 1992, Moore et al. 1995).

Considering the overlap of the Atlantic Flyway with some of the most urbanized regions of North America, the habitats remaining within cities may play an important role in bird migration (see Mehlman et al. 2005). The New York City to Boston corridor in particular has experienced the greatest urbanization in the Northeast (Dettmers and Rosenberg 2000) and New York City's parks have become refuges for migrants in an area where stopover sites are few and far between. Each spring and fall the city's green spaces are bustling with birds, a phenomenon that has gained places such as Central Park international recognition as premiere birding locations. Although there is little doubt the parks are great for birding, nothing is known of the energetics and stopover ecology of the birds using them. Most urban parks, besides being small, have historically been managed for aesthetics and recreational purposes and are dominated by exotic ornamental plant species, leaving their food supply and adequacy with regard to migratory bird stopover habitat in question. The parks have the potential to serve as valuable stopover sites that facilitate bird migration but they also have the potential to be detrimental energy sinks. It is currently unknown in which way these areas are affecting migrants. In this study I applied traditional stopover ecology research methods in a New York City park to measure the quality of an urban habitat as a migratory bird stopover site.

METHODS

Site description

Bronx County, New York has a human population of approximately 1.4 m and a total land area of 42 sq mi. The population density is 31,709 people/sq mi (US Census Bureau 2004). Bronx Park is a 565 acre city park at the center of the county. It is composed almost entirely of the campuses of the Bronx Zoo and the New York Botanical Garden. The Bronx River, beginning at the Kensico Reservoir in Westchester County to the north, bisects Bronx Park before joining the East River to the south. My study area was a 12 acre section of riparian and upland forest habitat on the grounds of the Bronx Zoo. The site does not contain any animal exhibits and is not open to zoo visitors. The west edge of this area is a dry upland deciduous forest dominated by Black oak (*Quarcus velutina)* and Sweet gum (*Liquidambar styraciflua)* with a scattering of White ash (*Fraxinus Americana)*, Mockernut (*Carya tomentosa)*, Black cherry (*Prunus serotina)* and American elm (*Ulmus Americana)*. The upland forest transitions rapidly down a steep gradient to the east into a riparian zone with wet or seasonally wet soils. The most prevalent riparian species are willows (*Salix spp.)* and Swamp dogwood (*Cornus foemina*) (Slayton, unpubl. data). Two notable invasive species, Japanese knotweed (*Polygonum cuspidatum*) and Oriental bittersweet (*Celastrus orbiculatus*), are also present. The eastern edge of the study area ends at the west shore of the Bronx River.

It should be noted that Bronx Park is extremely heterogeneous, with a mosaic of remaining natural habitats, landscaped and partially artificial habitats created for zoo exhibits, and various exotic plantings in the botanical gardens. Data collection for this study was limited to a small section of the park that offered appropriate mist-netting conditions. Therefore, the birds captured here may not be representative of all of the birds using Bronx Park in its entirety as a stopover habitat.

Data collection

In the spring and fall of 2004 and 2005, birds were captured and recaptured in 10 to 12 mist nets, operated from sunrise to approximately 12 PM, 5 days per week. Fall mist-netting took place between the first week of September and the second week of October; spring mist-netting took place between the last week of April and first week of June. The nets were set in 10 locations throughout the study site. Six locations were within close proximity to the river's edge (<10m), while the remaining four locations were 20-30m further away in the upland deciduous forest.

Nets were checked approximately every 30 minutes. Captured birds were placed in individual cloth bags and walked back to a processing station. Birds were aged and sexed (Pyle 1997), measured (unflattened wing-chord and tail length in mm), weighed to the nearest 0.1g (Ohaus 400g digital balance), examined for signs of wing and body molt, and banded with federal serial numbered metal bands. Visible subcutaneous fat in the furcular hollow was rated on a 6-point scale similar to that described by Helms and Drury (1960): (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, (5) filled to bulging and at least partially covering keel. Fat classes were assigned by the same observer throughout the study, with the exception of 5 days in fall of 2004 and 2 days in fall of 2005, to minimize inter-observer variation (Krementz and Pendleton 1990). As part of a separate study, breath (i.e. exhaled CO_2) was collected from certain species for stable isotope analysis (see Hatch et al. 2002, Podlesak et al. 2005), as was fecal matter when available. The analyses of these samples are not complete and no results are presented here.

Data Analysis

Species were selected for which there were sample sizes greater than 12 for each season, and that are classified as Neotropical migrants by Rappole (1995:173-182). The focal species are: Black-throated blue warbler (*Dendroica caerulescens*), Common yellowthroat (*Geothlypis trichas*), Magnolia warbler (*Dendroica magnolia*), Myrtle warbler (*Dendroica coronata*), Northern waterthrush (*Seiurus noveboracensis*), Ovenbird (*Seiurus aurocapillus*), Swainson's thrush (*Catharus ustulatus*), Veery (*Catharus fuscescens*), and Wood thrush (*Hylocichla mustelina*). For certain analyses, some species could not be included because of the nature of the analysis. For example, Wood thrush was not included in tests for sexual differences in fat score and condition index due to the low number of females captured. Probability values <0.05 are considered significant for all of the statistical tests performed.

Data collected in 2004 and 2005 were tested for annual variation. Magnolia warbler and Myrtle warbler fat scores were significantly higher in fall of 2004 than fall of 2005, and fall condition index was higher in 2004 than 2005 for Myrtle warbler and Northern waterthrush. No other data differed significantly between years for any species and were therefore combined.

Since fat score data are ordinal, I used Mann-Whitney *U* tests to examine differences in fat scores (Benson and Winker 2005) between spring and fall, between adults and immatures in fall, and between males and females in spring.

Fat content is often responsible for most of the variation in body mass among migratory passerines, and when standardized for body size, an individual's mass is reasonably indicative of its fat content (Connell et al. 1960, Rogers and Odum 1964, Rogers and Odum 1966, Winker et al. 1992, Woodrey and Moore 1997, McNair et al. 2002). To compare body masses of birds of different ages and sexes and between seasons while controlling for differences in body size, I calculated a condition index by dividing mass (g) by wing-chord (mm) (Benson and Winker 2005) and tested for significant differences using analysis of variance (ANOVA). Since differences in total body mass may not always be entirely attributable to differences in fat content (Piersma 1990, Scott et al. 1994, Karasov and Pinshow 1998), I tested the relationship between condition index and fat score in spring and fall with Pearson product-moment correlations. A strong positive correlation was found in 16 of 17 possible combinations of species and season (Table 1), supporting the ability of the condition index to reflect differences in lipid stores.

An alternative method of comparing body masses between seasons while controlling for differences in body size is analysis of covariance (ANCOVA), with body mass as the dependent variable, season as the independent variable, and wing-chord as a covariate (Woodrey and Moore 1997). For comparison, I applied this method in addition to the ANOVA of condition index.

TABLE 1. Seasonal differences in fat score (Mann-Whitney U) and condition index (ANOVA)(values presented are mean ± SD) in passerine migrants in Bronx Park, Bronx, New York (2004-2005).

SPECIES	SEASON	n	FAT SCORE	P	CONDITION	F	P	r^a	P^a
Black-throated blue warbler	Spring	18	2.94 ± 1.31	0.012	0.172 ± 0.010	13.47	0.001*	0.579	0.009
	Fall	26	1.81 ± 1.55		0.156 ± 0.017			0.753	<0.001
Common yellowthroat	Spring	82	2.83 ± 1.53	0.000	0.199 ± 0.015	9.11	0.003*	0.628	<0.001
	Fall	58	1.85 ± 1.51		0.191 ± 0.016			0.516	<0.001
Magnolia warbler	Spring	14	3.50 ± 0.760	0.000	0.164 ± 0.012	44.47	0.000*	0.575	0.031
	Fall	48	1.56 ± 1.13		0.142 ± 0.010			0.312	0.073
Myrtle warbler	Spring	98	2.88 ± 1.07	0.000	0.187 ± 0.014	116.78	0.000*	0.657	<0.001
	Fall	102	1.47 ± 1.15		0.167 ± 0.012			0.719	<0.001
Northern waterthrush	Spring	68	2.70 ± 1.44	0.005	0.241 ± 0.024	12.68	0.001*	0.776	<0.001
	Fall	40	1.90 ± 1.34		0.225 ± 0.020			0.534	<0.001
Swainson's thrush	Spring	36	2.71 ± 1.25	0.011	0.343 ± 0.033	0.03	0.870*	0.774	0.000
	Fall	15	1.60 ± 1.72		0.341 ± 0.049			0.835	<0.001
Ovenbird	Spring	67	2.12 ± 1.24	0.118	0.272 ± 0.020	1.20	0.277*	0.643	<0.001
	Fall	20	1.63 ± 1.26		0.266 ± 0.018			0.611	0.005
Wood thrush	Spring	20	1.25 ± 0.910	0.035	0.481 ± 0.029	19.80	0.000*	0.642	0.002
	Fall	14	2.64 ± 1.91		0.549 ± 0.059			0.840	<0.001
Veery	Spring	24	1.92 ± 1.06	-	0.328 ± 0.025	-	-	0.606	0.002
	Fall	-	-	-	-	-	-	-	-

[a] Comparison of fat score and condition index using Pearson's product-moment correlation.
*Significance agrees with ANCOVA of body mass and season. See methods.

I estimated rate of mass change using linear regressions of condition index and time of day (Winker et al. 1992, Morris et al. 1996, Woodrey and Moore 1997, Dunn 2000, Jones et al. 2002, Carlisle et al. 2005). I chose this method instead of the more traditional

approach of using recapture data to calculate rate of mass change because few individuals were recaptured during the study. Additionally, since recaptured birds always represent a minority of a study's total captured birds, such individuals may not be representative of the much larger number of migrants using a stopover site (Winker et al. 1992, Dunn 2000, Jones et al. 2002, Carlisle et al. 2005). Recaptures have been shown to be leaner at first capture than birds captured only once (Moore and Kerlinger 1987, Winker et al. 1992) and often lose mass following their first capture before eventually gaining mass (Mueller and Berger 1966, Loria and Moore 1990, Schwilcht and Jenni 2001). Moreover, by only examining recaptured birds, the majority of body mass data goes unused.

TABLE 2. Spring sexual differences in fat score (Mann-Whitney U) and condition index (ANOVA)(values presented are mean ± SD) in passerine migrants in Bronx Park, Bronx, New York (2004-2005).

SPECIES	SEX	n	FAT SCORE	P	CONDITION	F	P
Black-throated blue warbler	Male	10	2.70 ± 1.34	0.336	0.171 ± 0.009	0.32	0.581
	Female	8	3.25 ± 1.28		0.166 ± 0.014		
Common yellowthroat	Male	59	2.63 ± 1.59	0.059	0.198 ± 0.020	0.32	0.573
	Female	23	3.35 ± 1.27		0.200 ± 0.016		
Myrtle warbler	Male	63	2.76 ± 0.962	0.154	0.185 ± 0.013	4.43	0.038
	Female	34	3.12 ± 1.23		0.191 ± 0.015		
Swainson's thrush	Male	17	3.06 ± 1.18	0.158	0.343 ± 0.027	0.02	0.879
	Female	16	2.44 ± 1.32		0.345 ± 0.038		
Ovenbird	Male	35	1.89 ± 1.08	0.271	0.271 ± 0.019	0.79	0.380
	Female	11	2.36 ± 1.43		0.278 ± 0.030		

TABLE 3. Autumn age-related differences in fat score (Mann-Whitney U) and condition index (ANOVA) (values presented are mean ± SD) in passerine migrants in Bronx Park, Bronx, New York (2004-2005).

SPECIES	AGE	n	FAT SCORE	P	CONDITION	F	P
Black-throated blue warbler	HY	14	1.79 ± 1.53	0.937	0.158 ± 0.018	0.28	0.602
	AHY	12	1.83 ± 1.64		0.155 ± 0.015		
Common yellowthroat	HY	33	1.46 ± 1.39	0.010	0.190 ± 0.018	0.03	0.862
	AHY	25	2.40 ± 1.53		0.191 ± 0.012		
Magnolia warbler	HY	18	1.41 ± 1.18	0.419	0.142 ± 0.012	0.00	0.987
	AHY	17	1.71 ± 1.11		0.142 ± 0.006		
Myrtle warbler	HY	51	1.49 ± 1.10	0.847	0.167 ± 0.010	0.16	0.689
	AHY	51	1.45 ± 1.21		0.168 ± 0.014		
Northern waterthrush	HY	18	1.72 ± 1.18	0.594	0.223 ± 0.015	0.50	0.480
	AHY	22	2.05 ± 1.46		0.227 ± 0.023		
Swainson's thrush	HY	6	1.83 ± 1.60	0.325	0.350 ± 0.069	0.36	0.560
	AHY	9	1.44 ± 1.88		0.335 ± 0.033		
Ovenbird	HY	10	1.56 ± 1.33	0.798	0.260 ± 0.018	2.54	0.128
	AHY	10	1.70 ± 1.19		0.273 ± 0.017		

Flight range calculations are common in stopover ecology literature (e.g. Winker et al. 1992, Woodrey and Moore 1997, McNair et al. 2002). Although the precision of such estimates are subject to question, here I present flight ranges to allow for comparisons to other studies. I estimated lipid mass by subtracting lean body masses (in Connell et al. 1960 and Dunning 1993) from the body masses of living birds captured during the study.

To make the flight range estimates slightly more conservative I assumed only 95% of a bird's fat is metabolically available and the remaining 5% of energy demand is contributed by protein (Battley et al. 2001, McWilliams et al. 2004, Battley and Piersma 2005). Using an energy value of fat of 39.5 kJ/g (Castro and Myers 1988, McNair et al. 2002), I determined the energy available for flight in the form of fat by multiplying 39.5 kJ/g by 95% of the estimated lipid mass. Flight metabolism was calculated using model b of Castro and Myers (1988):

$$M = 3.167 \times W^{1.464} \times L^{-1.614}$$

where **M** is flight metabolism (kJ/h), **W** is body mass (g), and **L** is wing length (cm). The energy value (kJ) of each bird's stored fat was divided by its flight metabolism (kJ/h) to determine the number of hours of possible fight. I converted hours to distance assuming an average flight speed of 38.5 km/h for small passerines (Pennycuick 1997, McNair et al. 2002). All calculations were made for each individual bird and mean and standard deviation are presented (Table 5).

RESULTS

Age and sex ratios
Chi square tests found a significant bias towards males in spring for Common yellowthroat, Magnolia warbler, Myrtle warbler, and Ovenbird (all P<0.05). A significant male bias was also found in Wood thrush and Northern waterthrush, although my confidence in reliably sexing individuals of these species is lower than the others. No bias was found in Swainson's thrush or Black-throated blue warbler, a species reliably sexed in spring due to dramatic sexual plumage dimorphism. In fall, Wood thrush was the only species that showed a significant age bias (86% HY, *n*=14).

Fat score and condition index
Few lean birds were captured during this study. Mean fat scores were modest regardless of species, age, sex, or season (Tables 1-3). Fat score and condition index were significantly higher in spring than fall in Black-throated blue warbler, Common yellowthroat, and Magnolia warbler (all P<0.02)(Table 1). Swainson's thrush fat scores were significantly greater in spring than fall (P=0.01) but the condition index difference was not significant (P=0.87). Ovenbird fat scores and condition index values were higher in spring than fall, but not significantly. Although fat score and condition index data for Myrtle warbler and Northern waterthrush differed significantly between fall of 2004 and 2005, each fall season on its own was significantly lower than the spring, and therefore the data were combined for the tests of seasonal differences presented in Table 1 and age-related differences presented in Table 3. Wood thrush was the only species with fat scores and condition index values significantly higher in fall than spring (P=0.035 and 0.000 respectively). The ANCOVA of body mass and season agreed with the ANOVA of condition index and season in all species except Swainson's thrush (Table 1).

In spring, female fat scores averaged higher than male scores in 4 of the 5 species examined, although differences were not statistically significant. Similarly, the condition index was greater for females than males in 4 species, but the difference was significant only in Myrtle warbler (Table 2).

Autumn fat scores differed significantly between the age groups in Common yellowthroat only (HY mean=1.46, AHY mean=2.40, P=0.01). Autumn condition index did not differ significantly between age groups in any of the 7 species tested (Table 3).
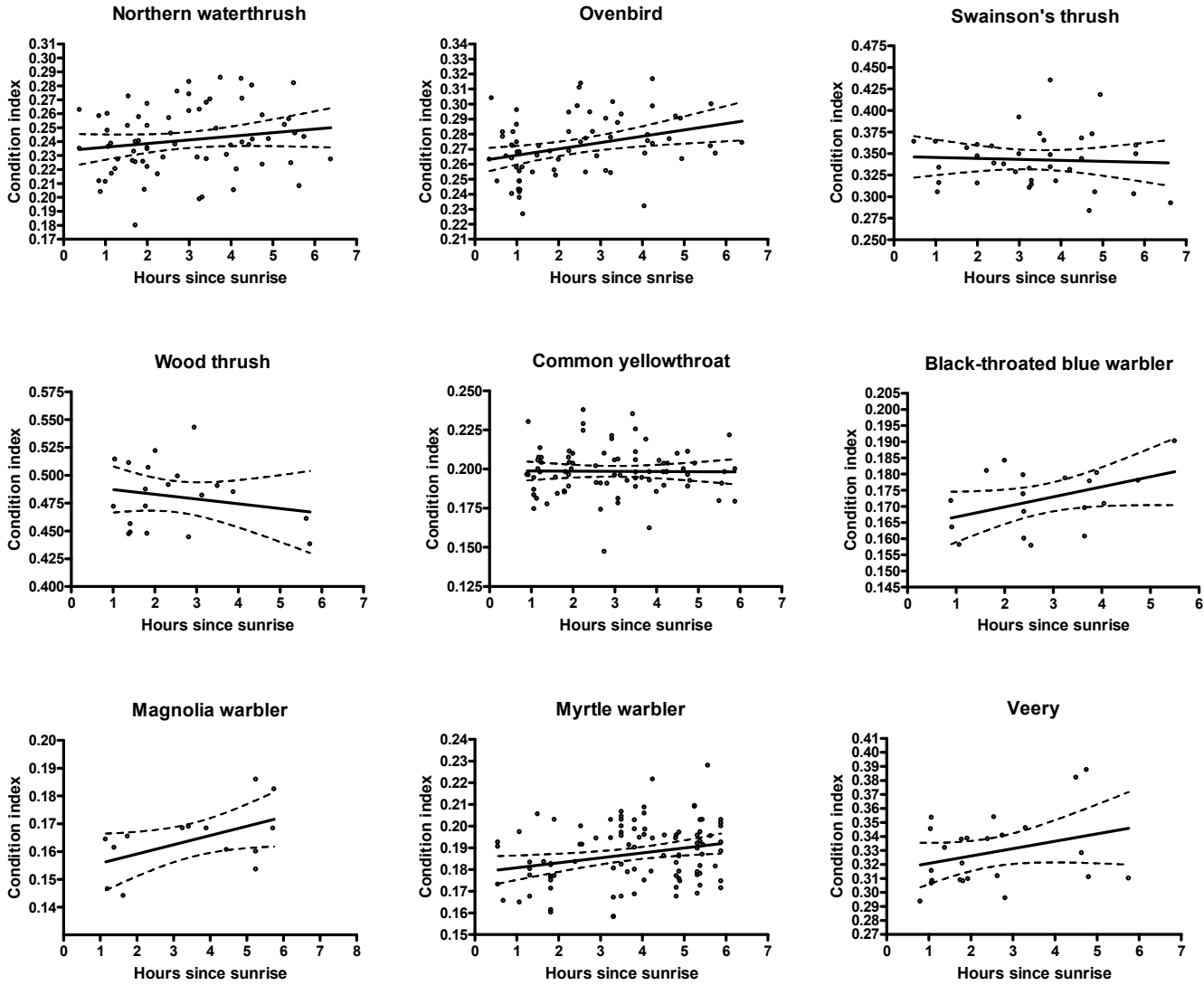

FIGURE 1. Spring estimates of rate of mass change using linear regressions of condition index (mass/wing-chord) and hours since sunrise at time of capture. See Table 4 for regression statistics.

Rate of mass change

The relationship between condition and time of capture was significant or marginally significant in only 5 out of 17 possible combinations of species and season. In all 5 instances of significant or marginally significant relationships, slopes were positive. Overall, slopes were positive in 12 of the 17 possible combinations of species and season and negative in 5. No negative slopes were significant. Black-throated blue warbler, Magnolia warbler, Myrtle warbler, Northern waterthrush, and Ovenbird exhibited greater rates of mass gain in spring than fall. Swainson's thrush showed a negative change in

condition in both seasons, with a steeper negative slope in fall. Wood thrush and Common yellowthroat experienced a loss in condition in spring and a gain in fall (Figures 1-2 and Table 4).
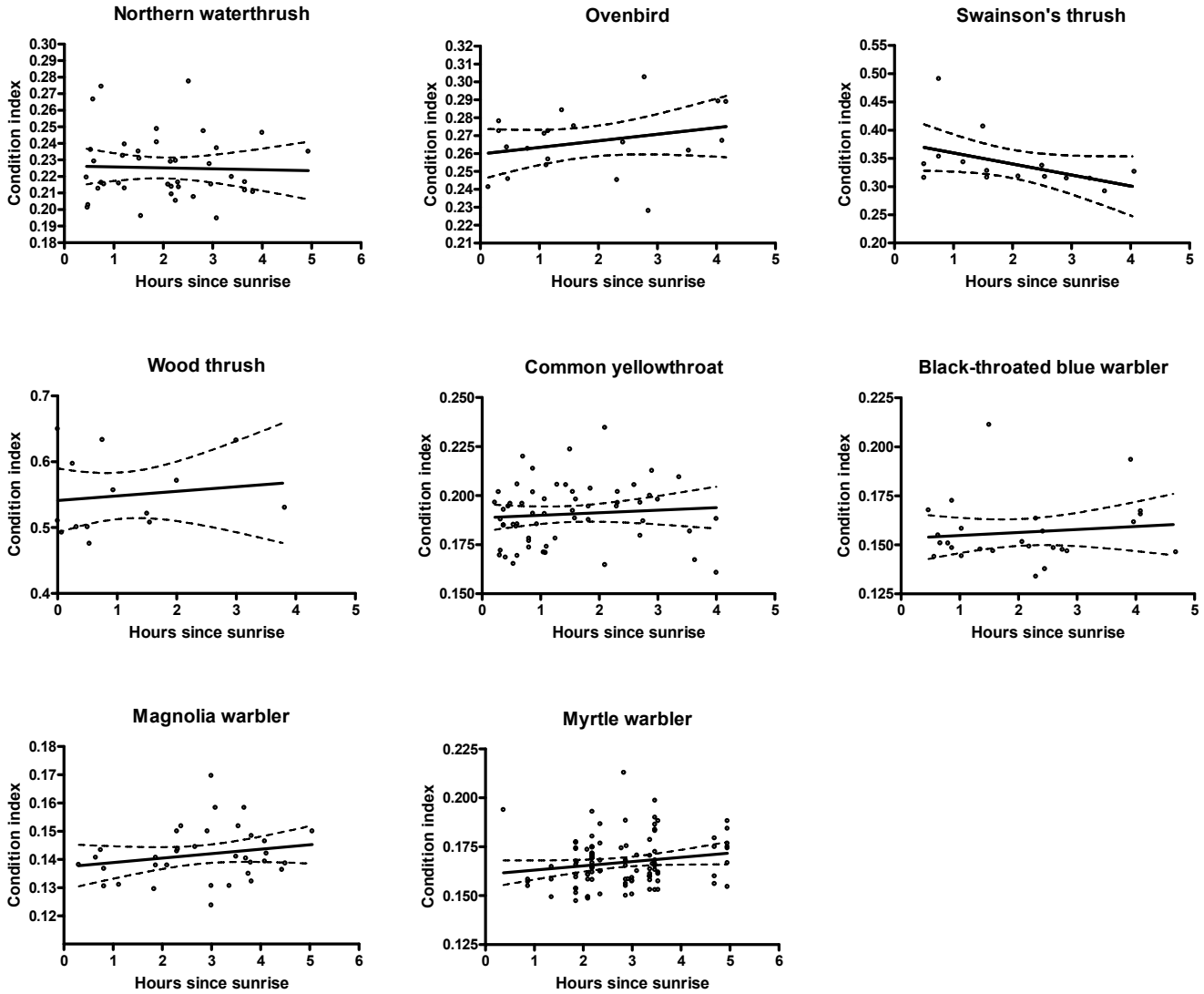

FIGURE 2. Autumn estimates of rate of mass change using linear regressions of condition index (mass/wing-chord) and hours since sunrise at time of capture. See Table 4 for regression statistics.

Flight ranges
Flight ranges were greater in spring than fall for all species except Ovenbird, a result caused by the heavier body masses of the birds captured in spring. Spring distances ranged from 472.68 km for Common yellowthroat to 947.66 km for Swainson's thrush and fall distances ranged from 406.10 km for Common yellowthroat to 785.20 km for Swainson's thrush (Table 5).

DISCUSSION

Age and sex ratios
Birds of different ages are believed to follow different autumn migration routes (Rappole 1995:87). Banding sites on the Atlantic coast have frequently observed age ratios skewed towards hatching-year birds during fall migrations (Robbins et al. 1959, Murray 1966, Ralph 1981, Morris et al. 1996), a phenomenon referred to as the "coastal effect" (Ralph 1981). In Bronx Park, Wood thrush was the only species of 8 examined to show a significant bias towards hatching-year individuals. This suggests either the site is far enough inland to receive an equal distribution of birds of both age groups, or the adherence of age groups to their suspected routes is not as strict as implied by the results of other coastal banding studies. At a far inland site in Vermont, Rimmer and McFarland (2000) found hatching-year individuals accounted for 94% of the transients captured, demonstrating the possibility of age groups to deviate from their expected routes. A third possible explanation for the unexpectedly high proportion of adult birds captured in Bronx Park is competitive exclusion of hatching-year birds from the study site by adult birds. Recall, the study site is only a 12 acre section of a 565 acre park and is not necessarily representative of all of the different habitats found within. The study site was selected because it offered the most appropriate mist-netting conditions and capturing birds was less feasible in other areas of the park. However, it is likely the study site also represents the most desirable habitat in the park for most migrant species. Considering adults may exclude immature birds from higher-quality food sources (Terrill 1987, Moore et al. 1995, Yong et al. 1998) and adults are believed to be superior to hatching-year birds in their ability to find high quality stopover habitats (Moore and Simmons 1992), the high proportion of adult birds captured in the site may be a result of the site being the highest quality patch of habitat within the park.

The cause of the spring sex bias found in this study is unclear. Habitat use, foraging behavior, stopover length, fat storage, and other aspects of stopover ecology can all vary between the sexes during spring migration (Hutto 1998). Pressure for males to migrate faster and arrive on breeding grounds before females (Yong et al. 1998) may drive greater competition from males for resources during stopovers. Similar to the age ratio in fall, the male bias found in spring for many of the focal species may also be a result of the study site being the highest quality habitat within the greater parkland, as males out-compete and exclude females from the area. Further study is needed to determine if the sex bias is present throughout the entire park or unique to the study site.

Fat score and condition index
The "spring fatter" hypothesis (Sandberg and Moore 1996, Benson and Winker 2005) suggests that migrants should carry more fat in spring since resources on breeding grounds are temporally limited and unpredictable, and arriving with stored fat provides insurance in the event that resources are initially scarce. Arriving with large fat stores may also allow females to produce larger and earlier clutches and allow males to devote more time to territory defense or mate solicitation (Sandberg and Moore 1996). The higher spring fat scores and condition index values found in this study support the "spring fatter" hypothesis and are consistent with the seasonal differences in energetic condition found by Winker et al. (1992).

During spring stopovers, intersexual competition may affect the energetic condition of birds (Lindstrom et al. 1990). Yong et al. (1998) found migrating male Wilson's warblers to be significantly fatter than females and show greater rates of mass gain, although it is uncertain if this was the result of males out-competing females for resources or simply a reflection of differences in the energy demands of the sexes during spring migration. Carlisle et al. (2005) found no evidence of intersexual competition during spring stopovers in Idaho. Similarly, in this study fat score and condition index data provided no evidence of intersexual competition affecting the energetic condition of migrants in the study site. However, this ignores the possibility that males are excluding females from this habitat. I expect the more dominant females that would be able to resist exclusion and remain in the area to also be able obtain the resources they need with the same efficiency as males and therefore show similar fat scores and condition indices. From this study, it cannot be determined whether competitive exclusion in fact occurred.

TABLE 4. Summary of linear regressions of condition (mass/wing-chord) and hours since sunrise at time of capture. Equations are $Y = mX + b$, where b is the Y-intercept, m is the slope (change in condition per hour), and X is time. Correlation coefficient, r, is the measure of the strength of the relationship between time and condition. F values indicate how well the regressions fit the data and P values indicate the level of significance (P<0.05 considered significant).

SPECIES	SEASON	n	b	m	r	F	P	ΔCond./day[a]	Δg./day[b]
Black-throated blue warbler	Spring	18	0.164	0.003117	0.427	3.56	0.077	0.0374	2.31
	Fall	26	0.153	0.001528	0.117	0.33	0.571	0.0183	1.15
Common yellowthroat	Spring	82	0.199	-0.000104	0.009	0.01	0.933	-0.0012	-0.07
	Fall	58	0.189	0.001294	0.088	0.44	0.509	0.0155	0.83
Magnolia warbler	Spring	14	0.152	0.003338	0.518	4.40	0.058	0.0400	2.33
	Fall	35	0.137	0.001563	0.206	1.46	0.236	0.0188	1.10
Myrtle warbler	Spring	98	0.179	0.002281	0.254	6.60	0.012	0.0274	1.94
	Fall	102	0.161	0.002176	0.178	3.26	0.074	0.0261	1.83
Northern waterthrush	Spring	68	0.234	0.002577	0.169	1.94	0.169	0.0309	2.30
	Fall	40	0.226	-0.000549	0.032	0.04	0.842	-0.0066	-0.50
Swainson's thrush	Spring	36	0.347	-0.001152	0.054	0.99	0.755	-0.0138	-1.35
	Fall	15	0.379	-0.019460	0.460	3.50	0.084	-0.2335	-22.53
Ovenbird	Spring	67	0.262	0.004215	0.329	7.91	0.007	0.0506	3.70
	Fall	20	0.260	0.003685	0.278	1.50	0.236	0.0442	3.30
Wood thrush	Spring	20	0.492	-0.004285	0.198	0.74	0.403	-0.0514	-5.43
	Fall	14	0.541	0.007035	0.141	0.24	0.632	0.0844	8.89
Veery	Spring	24	0.315	0.005292	0.306	2.28	0.146	0.0635	6.03
	Fall	-	-	-	-	-	-	-	-

[a] Projected diurnal change in condition calculated by multiplying change in condition per hour (m) by 12 hours.
[b] Projected diurnal change in mass calculated by multiplying the diurnal change in condition by the average wing-chord for each species. See Table 5 for wing-chord averages.

Several studies have found adult migrants to be in superior energetic condition to hatching-year migrants at stopover sites in autumn and suggested immature birds are poorer foragers than adults (Burger 1988, Yong et al. 1998, Jones et al. 2002, but see Heise and Moore 2003), subject to exclusion from high quality habitats by adults (Terrill 1987, Moore et al. 1995, Yong et al. 1998), and less efficient than adults at extracting nutrients from food (Yong et al. 1998). The majority of species in my study, however,

showed no significant differences between the age groups in fat score or condition index. The ability of inferior hatching-year birds to attain a level of energetic condition equal to that of adults may indicate the site is rich in resources (Jones et al. 2002). If the site is indeed the highest quality habitat within the park, it is also possible the hatching-year birds captured in the site were the only ones for which there was room after all of the adults had settled in the area. Other hatching-year birds may have been excluded to areas outside the study site and been in poorer condition than those within as a result. As in spring, however, it is unknown if any exclusion occurred.

TABLE 5. Estimates of lipid mass, metabolic rate, hours of possible flight, and flight ranges for transient passerines in Bronx Park, Bronx, New York (values presented are mean ± SD).

SPECIES	SEASON	WING (mm)	MASS (g)	FAT[a]	kJ[b]	FLIGHT COST (kJ/h)[c]	HOURS[d]	DISTANCE (km)[e]
Black-throated blue warbler	Spring	61.70	10.6 ± 0.67	2.84 ± 0.64	113.18 ± 25.31	5.36 ± 0.44	20.94 ± 3.37	806.18 ± 129.75
	Fall	62.58	9.78 ± 1.01	2.03 ± 0.96	80.94 ± 38.16	4.65 ± 0.76	16.80 ± 4.95	646.65 ± 190.71
Common yellowthroat	Spring	53.43	10.6 ± 0.81	2.13 ± 0.77	84.69 ± 30.77	6.74 ± 0.77	12.28 ± 3.66	472.68 ± 141.04
	Fall	53.54	10.21 ± 0.99	1.76 ± 0.94	69.96 ± 37.26	6.35 ± 0.76	10.57 ± 4.95	406.10 ± 190.55
Magnolia warbler	Spring	58.14	9.54 ± 0.68	2.49 ± 0.65	99.17 ± 25.72	5.04 ± 0.53	19.45 ± 3.57	748.72 ± 137.42
	Fall	58.80	8.33 ± 0.59	1.34 ± 0.56	53.26 ± 22.46	4.05 ± 0.41	12.88 ± 4.57	495.72 ± 175.89
Myrtle warbler	Spring	71.03	13.29 ± 1.01	3.00 ± 0.96	119.43 ± 38.26	5.92 ± 0.66	19.81 ± 4.81	762.50 ± 185.13
	Fall	70.10	11.71 ± 0.94	1.50 ± 0.89	59.55 ± 35.34	5.02 ± 0.56	11.37 ± 5.81	437.92 ± 223.72
Northern waterthrush	Spring	74.22	17.88 ± 1.78	3.99 ± 1.70	158.67 ± 67.46	8.53 ± 1.23	17.91 ± 5.97	689.47 ± 229.91
	Fall	75.45	16.98 ± 1.53	3.13 ± 1.45	124.68 ± 57.87	7.70 ± 1.00	15.70 ± 5.58	604.41 ± 214.97
Swainson's thrush	Spring	97.31	33.39 ± 3.72	8.75 ± 3.54	348.29 ± 140.76	13.71 ± 1.91	24.61 ± 7.14	947.66 ± 274.77
	Fall	96.47	32.89 ± 4.97	8.27 ± 4.72	329.20 ± 187.90	13.66 ± 3.03	20.40 ± 7.41	785.20 ± 285.28
Ovenbird	Spring	73.15	19.88 ± 1.58	4.14 ± 1.50	164.93 ± 59.63	10.18 ± 1.10	15.82 ± 4.57	608.92 ± 175.77
	Fall	74.55	19.85 ± 1.40	4.11 ± 1.33	163.53 ± 52.74	9.85 ± 0.99	16.33 ± 4.04	628.67 ± 155.62

[a] Quantity of metabolically available fat calculated as 95% of the difference of body mass and fat-free body mass (see text).
[b] Energy available for flight in the form of fat, calculated as fat mass multiplied by 38kJ/g.
[c] Flight metabolism calculated using model b of Castro and Myers (1988)(see text).
d Hours of possible flight calculated as kJ divided by flight cost.
e Flight range calculated as hours multiplied by the assumed flight speed of 38 km/h.

Rate of mass change
The ability to replenish depleted fat stores may be the greatest constraint birds face during migration (Moore et al. 1995) and the rate at which migrants gain mass during stopovers is considered an indication of habitat quality (Dunn 2000). Here, I applied linear regressions of condition on time since sunrise to estimate rate of mass change as opposed to using recapture data. The former method first presented by Winker et al. (1992) avoids many of the caveats associated with recapture data and was most appropriate for this study due to the low number of recaptured birds. The method, however, is not without its own faults. For example, it assumes that all individuals of a given species captured throughout a day arrived at the stopover site that dawn (Dunn 2000, Jones et al. 2002). This assumption will seldom be met since stopovers often span multiple days (Mueller and Berger 1966, Moore and Kerlinger 1987, Morris et al. 1996, Woodrey and Moore 1997, Carlisle et al. 2005). This is problematic because rate of mass

change can be inconsistent over the course of a stopover (Mueller and Berger 1966, Loria and Moore 1990) and birds assumed to have arrived at the same time may in fact be in very different stages of their stopover. Additionally, unless there is enough data to inspect each age and sex class individually while maintaining adequate sample sizes, it is also assumed conspecifics of different ages and sexes are equal in their foraging and fat deposition abilities. I suspect it is these assumptions that often prevent linear regressions from detecting many significant relationships between energetic condition and time of day in most of the studies that have applied the method (e.g. Morris et al. 1996, Woodrey and Moore 1997, Carlisle et al. 2005, this study).

Although most interactions between condition and time of day were not significant here, those that were significant or marginally significant were positive, indicating the study site is a stopover habitat in which migrants can gain body mass. Furthermore, negative relationships were the minority (5 of 17) and none were significant. The extreme rate of mass loss predicted by the linear regression for Swainson's thrush in fall is likely a consequence of the small sample size. Swainson's thrushes with a high fat score and high body mass were captured shortly after sunrise on two occasions, strongly influencing the regression line towards a negative slope (see Figure 2). These data points may appear to be outliers, but were left in the regression because the birds had high corresponding fat scores. It is unlikely these individuals had just arrived in the study area as the linear regression method assumes. Rather they had most likely been in the area for one day or longer and this illustrates the effect that assuming all birds arrive at dawn can have on estimating mass change with this method.

Flight ranges
Precise flight range calculations are largely dependent on reliable estimates of lipid mass. A common non-destructive method of estimating lipid mass is to subtract chemically-derived fat-free body masses from the body masses of living birds (e.g. Winker et al. 1992, Morris et al. 1996, Woodrey and Moore 1997, McNair et al. 2002). Fat-free body mass, however, is a function of body size (Connell et al. 1960, Rogers and Odum 1964), differs between spring and fall (Connell et al. 1960, Child 1969), and varies with latitude (i.e. lean body tissues also change in mass throughout migration)(Child 1969, Piersma 1990). The birds from which published fat-free body masses were generated must therefore be similar in these respects to the living birds to which they are being applied for estimates of lipid mass to be reasonable. Infrequent reporting of such information along with lean body masses usually prevents ensuring this. It is therefore uncertain that published lean body masses are in fact representative of the true lean body masses of living birds captured during stopover ecology studies. Despite my concerns over their precision, flight range calculations are presented to allow for comparison to other studies that have taken this approach.

Woodrey and Moore (1997, Table 2) estimated Swainson's thrushes captured at their Gulf Coast study site in autumn were capable of flights of up to 740 km for hatching-year individuals and 1,290 km for adults. In this study, flight ranges were not calculated for separate age groups in the interest of maintaining larger sample sizes, but the overall estimate of 785 km is comparable to both distances calculated by Woodrey and Moore. It is not surprising this study's estimate is slightly lower than those of Woodrey and Moore because birds preparing for a non-stop flight across the Gulf of Mexico are expected to

deposit far greater amounts of fat than birds that are not approaching a major ecological barrier. Woodrey and Moore also predicted the possible flight ranges of Magnolia warblers: 1,290 km for hatching-year birds and 1,150 km for adults. These distances are far greater than my estimate of 496 km for both ages combined and again likely reflects the difference between birds preparing to cross a major geographical boundary versus birds not faced with such a situation.

On Appledore Island, Maine, Morris et al. (1996, Figure 1) estimated migrating Ovenbirds in fall to be capable of flights of approximately 900 km. This is greater than my estimate of 629 km for the species in the Bronx. However, at the assumed flight speed of 38.5 km/h for small passerines used in the flight range calculations, it would not be possible for Ovenbirds to travel such distances in the course of one night. Likewise, it would not be possible for Magnolia warblers or Swainson's thrushes to travel the estimated 496 or 785 km, respectively, in one night. Migrants leaving Bronx Park should therefore be expected to land next due to daybreak or an unfavorable change in weather, rather than a shortage of energy.

Flight range calculations suggest the study site in Bronx Park is a stopover habitat where birds possess amounts of energy sufficient to fuel upcoming migratory flights. Comparisons to other studies demonstrate that migrants in this urban habitat prepared for future flights to a similar extent as birds studied in more pristine habitats. While I do not consider flight ranges on their own to be reliable indicators of stopover habitat quality or the energetic condition of birds found at a stopover site, they can provide additional support to other indicators. Here, flight range estimates agree with rates of mass change and fat score and condition index data in that they suggest the study area is a habitat where migrants can deposit fat and attain a level of energetic condition suitable for continued migration.

CONCLUSION

As continent-wide urbanization proceeds, the fragments of habitat remaining within cities will account for an increasing proportion of the stopover sites available to migrating birds. It is therefore imperative to begin documenting whether such areas are providing migrants with the resources they need. This study demonstrates the ability of an urban habitat to serve as a suitable stopover site. It should also highlight the importance of conserving and properly managing the green spaces remaining within cities situated along the major flyways.

The findings of this study certainly should not be generalized across all urban habitats, as these areas are sure to vary dramatically with regard to size, vegetation communities, degree of human use/recreation, historical and current management practices, abundance of birds using them as stopover sites, and other factors that may influence the quality of the site as migratory bird stopover habitat. In order to more comprehensively understand the energetics and stopover ecology of migratory birds in urban parks, further research will be needed in a diversity of areas.

Acknowledgements

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