

PLASMA METABOLITES AND MASS CHANGES OF MIGRATORY LANDBIRDS INDICATE ADEQUATE STOPOVER REFUELING IN A HEAVILY URBANIZED LANDSCAPE

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Abstract. Large concentrations of migrating landbirds in cities have been well documented, but the refueling conditions urban stopover sites provide are almost entirely unknown. We compared plasma triglyceride (indicator of mass gain) and B-OH-butyrate (indicator of mass loss) concentrations in landbirds in three New York City forests to those of conspecifics in two less disturbed, non-urban forests outside the city to evaluate the quality of urban stopover habitats. We quantified diurnal mass gains with regressions of body mass and capture time and measured arthropod biomass in leaf litter to assess food abundance for ground-foraging insectivores. Metabolite concentrations in Ovenbirds (*Seiurus aurocapilla*) at urban and non-urban sites did not differ during spring or autumn. In autumn, triglyceride levels of Swainson's Thrushes (*Catharus ustulatus*) indicated significantly higher refueling rates at the urban sites. In the Yellow-rumped Warbler (*Dendroica coronata*), butyrate was lowest outside the city, suggesting better refueling conditions there, but differences in triglyceride did not suggest a consistent difference between the habitats in refueling rates. Autumn triglyceride and butyrate levels of three additional species did not indicate different rates of refueling within and outside the city. In the city, significant mass-gain rates ranged from 1.0 to 2.5% of total body mass hr⁻¹. At no point during either season was there a consistent difference between habitat types in arthropod biomass. Our results suggest that although the availability of stopover habitats may be low in cities, migrating birds using these sites may refuel at rates comparable to those stopping in less disturbed areas.

Key words: nearctic–neotropical migrant, New York City, refueling rate, stopover site quality, urban habitat.

Metabolitos Plasmáticos y Cambios de Peso de Aves Terrestres Migratorias Indican Reaprovisionamiento Adecuado en Sitios de Parada en Paisajes Altamente Urbanizados

Resumen. Las grandes concentraciones de aves terrestres migratorias en las ciudades han sido bien documentadas, pero las condiciones para el reaprovisionamiento que brindan los sitios de parada urbanos son casi enteramente desconocidas. Comparamos las concentraciones plasmáticas de triglicéridos (indicador de aumento de peso) y de B-OH-butiratos (indicador de pérdida de peso) en las aves terrestres provenientes de tres bosques de la ciudad de Nueva York con las concentraciones en aves coespecíficas provenientes de dos bosques no urbanos menos disturbados ubicados afuera de la ciudad, para evaluar la calidad de los ambientes de parada urbanos. Cuantificamos los aumentos de peso diurnos con regresiones del peso corporal y del momento de captura y medimos la biomasa de artrópodos en la hojarasca para establecer la abundancia de alimentos para las aves insectívoras que forrajeaban en el suelo. Las concentraciones de metabolitos en *Seiurus aurocapilla* en los sitios urbanos y no urbanos no difirieron durante la primavera o el verano. En otoño, los niveles de triglicéridos de *Catharus ustulatus* indicaron tasas de reaprovisionamiento significativamente más altas en los sitios urbanos. En *Dendroica coronata*, los butiratos fueron más bajos afuera de la ciudad, sugiriendo mejores condiciones de reaprovisionamiento allí, pero las diferencias en los triglicéridos no sugirieron una diferencia consistente en las tasas de reaprovisionamiento entre los ambientes. Los niveles de triglicéridos y butiratos en otoño de otras tres especies no indicaron diferencias entre las tasas de reaprovisionamiento dentro y fuera de la ciudad. En la ciudad, las tasas significativas de incremento de peso fueron entre 1.0 y 2.5% del total del peso corporal hr⁻¹. En ningún punto durante cualquiera de las estaciones hubo una diferencia consistente entre los tipos de ambiente en la biomasa de artrópodos. Nuestros resultados sugieren que aunque la disponibilidad de ambientes de parada en las ciudades puede ser baja, las aves migratorias que usan estos sitios pueden reabastecerse a tasas comparables con las de aquellas aves que paran en áreas menos disturbadas.

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INTRODUCTION

Nearctic–neotropical migrants commonly pass through the most densely populated, urbanized regions of North America. City parks and other urban forest fragments often represent the only stopover habitat available to landbirds crossing expansive metropolitan areas (Brawn and Stotz 2001, Mehlman et al. 2005, Seewagen 2008a). The resulting high concentrations of migrants in cities during spring and autumn has been well documented and has made many urban parks popular bird-watching destinations (Fowle and Kerlinger 2001, Milne 2007). Despite recognition of this phenomenon for at least a century (e.g., Chapman 1910), it remains largely unknown whether habitats remaining within cities provide migrating birds with the resources they need during stopovers. Urban habitats have the potential to serve as suitable stopover sites that facilitate bird migration, but they also have the potential to be energy sinks, luring birds into poor conditions for refueling. The high density at which migrants can occur, and often degraded habitat in urban parks, may elevate resource competition and constrain the ability of birds to recover energy and nutrient stores.

Most studies of migrant landbirds at urban stopover sites have examined habitat associations and patterns of abundance, richness, and diversity (Brawn and Stotz 2001, Hostettler et al. 2005, Rodewald and Matthews 2005, Pennington et al. 2008). Such measures could provide misleading information about habitat quality (Van Horne 1983, Johnson 2007, Cerasale and Guglielmo 2010), particularly in urban landscapes where migrants' stopover-site selection is restricted to the little habitat available. The presence of large numbers of migrants at an urban stopover site cannot be considered indicative of high-quality habitat, as it may simply reflect a lack of alternative refugia within the surrounding inhospitable matrix.

A more useful indicator of a stopover site's quality is the rate at which migrants are able to refuel (Dunn 2000, Guglielmo et al. 2005). We are aware of only two studies that have taken this approach toward evaluating the quality of urban stopover sites. Seewagen and Slayton (2008) recently provided the first evidence of high-quality habitat at an urban stopover site, showing several species of landbirds to have gained significant body mass in a New York City park. Similarly, Craves (2009) found *Catharus* thrushes were able to gain significant body mass during stopovers in an urban riparian habitat in the city of Dearborn, Michigan. These studies demonstrate that urban habitats have the potential to be suitable stopover sites for landbirds, but generalization of their findings elsewhere is limited by extreme variation within and between cities in habitat characteristics such as forest size, vegetation composition, predators, food availability, and levels of human disturbance that likely affect a site's quality for migrants. Studies in a diversity of habitats within multiple North American cities will be necessary for the refueling conditions available to

nearctic–neotropical migrants at urban stopover sites to be better understood.

To assess the quality of urban stopover habitat further, we examined opportunities for refueling provided by three New York City parks well known for their use as stopover sites by migratory songbirds. We employed both a conventional technique based on capture data and a physiological method for measuring the refueling rates of wild birds. The conventional technique examines the relationship between the body masses of single-capture birds and the time of day at which they were captured (e.g., Winker et al. 1992). A significant positive relationship between these variables indicates that birds captured early in the morning weigh less than those captured later in the day and that they gain mass at the site. The slope of the regression line provides a numerical estimate of the actual rate of mass change. Drawbacks of this method are the need for a large sample size and the assumption that all birds in a sample have been at the stopover site for the same amount of time (Dunn 2000, Jones et al. 2002, Guglielmo et al. 2005).

The physiological approach uses concentrations of triglyceride (TRIG) and B-OH-butyrate (BUTY) in blood plasma to assess the extent to which migrants are replenishing or metabolizing fat stores, respectively (Jenni-Eiermann and Jenni 1994). Circulating TRIG rises in concert with increasing nutrient intake, as newly consumed or synthesized lipids are transported to adipose tissue for storage. Conversely, BUTY concentration decreases in response to feeding and rises during fat oxidation and mass loss. Hence the refueling rate is positively associated with TRIG and negatively associated with BUTY, and both metabolites reflect changes in body mass (Jenni-Eiermann and Jenni 1994, Williams et al. 1999, Cerasale and Guglielmo 2006). In small songbirds these concentrations' rapid response to changes in feeding rate (<20 min) allows them to indicate migrants' refueling performance at the time and location of sampling (Zajac et al. 2006), making metabolite profiling well-suited for field studies of stopover ecology and stopover-habitat quality (Schaub and Jenni 2001, Cerasale and Guglielmo 2010, Smith and McWilliams 2010).

An important difference between the body mass–time of day regression technique and plasma metabolite profiling is that the former provides a quantitative measure of the refueling rate whereas the latter provides only a qualitative, or relative, measure (Guglielmo et al. 2005). Concentrations of metabolites in migrants using urban stopover sites are uninformative without reference to birds refueling under different conditions. We therefore examined migrants' levels of plasma metabolites in two nearby but less disturbed non-urban habitats north of New York City for direct comparison to conspecific migrants stopping over within the city. Similar metabolite profiles would indicate that the urban and non-urban habitats provide equivalent opportunities for refueling. In addition to measuring refueling performance, we measured the biomass of arthropods in leaf litter at all sites to assess the abundance

of food for ground-foraging insectivores such as the Ovenbird (*Seiurus aurocapilla*), which we expected to be one of the most common species captured in this study.

METHODS

STUDY SITES

New York City (NYC) is the most populous metropolitan area in the United States (U.S. Census Bureau 2000) and is crossed by four major bird migration routes (Rappole et al. 2000). Large concentrations of migrants regularly occur each spring and autumn in many of the city’s parks (Fowle and Kerlinger 2001, Mittelbach and Crewdson 1998). We studied migrants during stopovers in Prospect Park, Inwood Park, and Bronx

Park (Fig. 1). With city park officials, we selected these sites on the bases of feasibility, personal safety, potential for theft and vandalism of equipment, potential interference from park visitors and dogs, and habitat similarity (mature eastern deciduous forest >50 years old). Each park is an isolated habitat island within heavily urbanized surroundings (Fig. 1).

Prospect Park is a 213-ha public recreational space in the borough of Brooklyn (Kings County) that is visited by more than 6 million people per year (Wells 1998). The park contains mowed lawns and other grassy, open areas, woodland, artificial water bodies, an ice rink, a small zoo on its eastern edge, and a network of asphalt walking paths and roads for official use. Mature deciduous forest represents approximately half of the park’s total area (Wells 1998). We captured birds in the

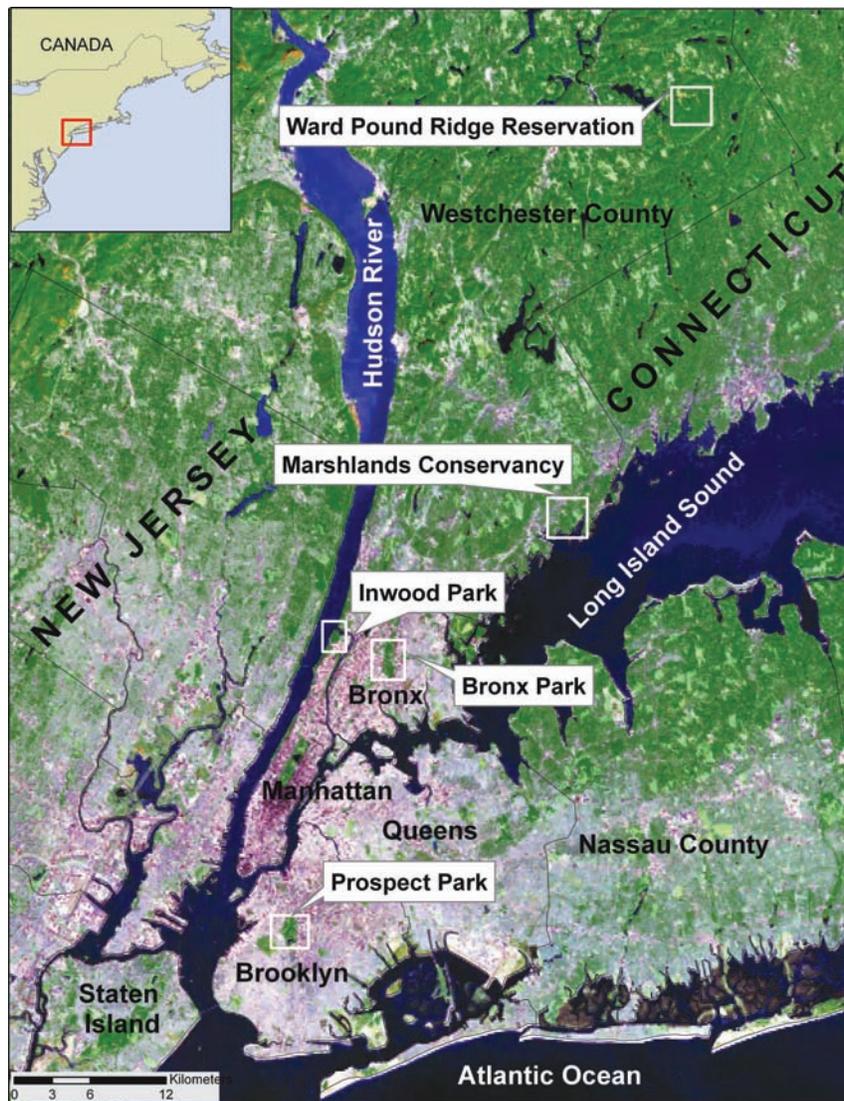


FIGURE 1. Canopy cover and study sites in New York City and Westchester County, New York.

area known as “the Ravine” (40° 39′ 49″ N, 73° 58′ 12″ W) within the 100-ha forest in the center of the park (Mittelbach and Crewdson 1998). The Ravine contains an artificial stream, a mature tree community composed primarily of black cherry (*Prunus serotina*), red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), and willows (*Salix* spp.) and a woody understory of mostly arrowwood viburnum (*Viburnum dentatum*) and shadbush (*Amelanchier humilis*).

Inwood Park is 80 ha in area and located on the northwestern corner of Manhattan (New York County). The western edge of the park is atop the Hudson River ridge; to the east, the park sharply transitions down into a valley containing an old-growth tulip poplar stand (Mittelbach and Crewdson 1998, Horenstein 2007). Nonforested recreational facilities are limited to the northeastern corner and encompass approximately ¼ of the park’s total area; the majority of the remaining area is wooded. We captured birds in mature deciduous woods along the ridge, east of Overlook Meadow and west of West Ridge Road (40° 52′ 22″ N, 73° 55′ 33″ W). Here, the most common trees are black cherry, chestnut oak (*Quercus prinus*), and white ash (*Fraxinus americana*), and the understory is composed mostly of black cherry seedlings and saplings, blackberry (*Rubus* spp.), and arrowwood viburnum (see also Fitzgerald and Loeb 2008).

The grounds of the Bronx Zoo and New York Botanical Garden constitute what is known as Bronx Park, located in Bronx County. Bronx Park is a 229-ha mosaic of natural and partially artificial outdoor animal exhibits, manicured gardens, displays of exotic flora, and remaining native forest. The Bronx River bisects the park as it descends south from the Kensico Reservoir in Westchester County toward the East River. We captured birds in a 4.9-ha section of native forest along the Bronx River on the eastern side of the Bronx Zoo (40° 51′ 6″ N, 73° 52′ 28″ W). This area does not contain any animal exhibits or holding facilities and is not accessible to zoo visitors (see Seewagen and Slayton 2008 for more details).

This site has been examined in earlier studies of stopover ecology (Seewagen and Slayton 2008, Seewagen and Guglielmo 2010, 2011). Seewagen and Slayton (2008) used the body mass–time of day regression technique to measure refueling rates of migrants captured here 2004–2006 and concluded the area represented high-quality stopover habitat. We chose to include this site in the present study, despite this previous finding, because metabolite concentrations in migrants and measures of invertebrate biomass from an urban site thought to be high-quality stopover habitat would, in addition to data collected from the non-urban sites, provide useful context in which to view metabolite concentrations and invertebrate biomass at Inwood and Prospect parks.

Non-urban habitats studied for comparison to the NYC sites were the Marshlands Conservancy and Ward Pound Ridge Reservation in Westchester County, New York (hereafter “Westchester”) (Fig 1.). Westchester has a total land area

of 1122 km², beginning at the northern border of NYC and extending north to Putnam County, east to Connecticut and the Long Island Sound, and west to the Hudson River. Despite the areas’ proximity, the human population density and land cover of Westchester and NYC differ strikingly. Westchester’s population density (850 people km⁻²) is only one twelfth of that of NYC (10 464 people km⁻²; U.S. Census Bureau 2000), and >70% of Westchester’s total land area is forest cover, whereas <20% of NYC’s land area is forest cover (Medley et al. 1995, Cadenasso et al. 2007, Nowak et al. 2007). Forest composition, however, is generally similar (Cadenasso et al. 2007). Our five study sites do not significantly differ in tree diameter (site means range 28–35 cm diameter at breast height) or basal area (site means range 9–16 m² ha⁻¹) (CLS, unpubl. data).

The Marshlands Conservancy is a 57-ha wildlife preserve along an inlet of the Long Island Sound 12 km northeast of the NYC border. As the area is a designated sanctuary, recreational activities are limited to trail walking, and dogs are not permitted. The sanctuary contains a mix of salt marsh, shrub/scrub, open field, and mature deciduous forest (Wells 1998). We captured birds in the forested area behind the welcome center and east of the large field (40° 57′ 14″ N, 73° 42′ 8″ W). Mature American beech (*Fagus grandifolia*) and American sweetgum (*Liquidambar styraciflua*) trees create a tall, closed canopy and a shaded, open understory. A stream passes through the area and feeds a nearby pond.

The Ward Pound Ridge Reservation (hereafter “Pound Ridge”) covers 1746 ha and is the county’s largest park (Wells 1998). It is 41 km north of the NYC border and spans the towns of Lewisboro and Pound Ridge. Much of the park is former farmland that began to succeed into hardwood forest in the 1920s. Wetlands, marshes, evergreen stands, and meadows and old fields are also represented. The topography is varied by hills, ridges, stream valleys, and Cross River Mountain. Recreational facilities are limited to camping shelters, picnic areas, and 50 km of hiking and horseback riding trails (Wells 1998). We captured birds in deciduous woods between Old Schoolhouse and Michigan roads and west of the Michigan Road camping shelters (41° 15′ 1″ N, 73° 36′ 5″ W). The area contains a slow ephemeral stream and moist areas covered in mosses and eastern skunk cabbage (*Symplocarpus foetidus*). Highbush blueberry (*Vaccinium corymbosum*) is prevalent in the understory, and red maple (*Acer rubrum*), American hornbeam (*Carpinus caroliniana*), and black gum (*Nyssa sylvatica*) are the dominant species of mature trees.

STUDY SPECIES

We recorded data from several forest-dwelling, nocturnally migrating passerines commonly found in NYC during spring and autumn. Ten species provided sample sizes large enough for body mass–time of day regressions and/or comparisons of plasma metabolites: the Veery (*Catharus fuscescens*), Swainson’s Thrush (*C. ustulatus*), Hermit Thrush (*C. guttatus*),

Wood Thrush (*Hylocichla mustelina*), Black-throated Blue Warbler (*Dendroica caerulescens*), Yellow-rumped Warbler (*D. coronata*), Black-and-white Warbler (*Mniotilta varia*), Ovenbird, Northern Waterthrush (*Parkesia noveboracensis*), Common Yellowthroat (*Geothlypis trichas*), and White-throated Sparrow (*Zonotrichia albicollis*).

We place emphasis on the Ovenbird because our sample of this species across study sites in both seasons was largest, allowing for the most robust analyses. The Ovenbird is a long-distance migrant that breeds across much of Canada and the eastern United States and winters throughout Central America and the Caribbean islands (Van Horn and Donovan 1994). The Ovenbird inhabits forests during all periods of its life cycle and is most commonly observed on the ground, where it forages for leaf-litter arthropods (Stenger 1958, Van Horn and Donovan 1994, Burke and Nol 1998).

The Ovenbird nests in Westchester in very low abundance relative to other parts of its range (NYSBBA 2007, Sauer et al. 2008), yet it is among the most commonly observed species in Westchester during migration, and we assumed all individuals in our samples were en route to other locations. We recaptured no Ovenbirds in a successive year or season, increasing our confidence that they did not remain in the study sites to breed. Ovenbirds do not nest in NYC (NYSBBA 2007, DeCandido and Allen 2005).

BIRD CAPTURE AND BLOOD SAMPLING

We captured spring and autumn migrants passively at each study site in 6–10 mist nets from 1 to 31 May and from 8 September to 20 October in 2007 and 2008. Nets were operated from approximately sunrise to 11:00 EST for 3 or 4 days per week in NYC and 5 days per week in Westchester. Each site in Westchester had its own field crew of two individuals, whereas two other field crews of two or three individuals each shared coverage of the three NYC study sites. Effort was greater in Westchester because of the greater difficulty there in obtaining samples.

We checked nets approximately every 8 min so blood could be collected before plasma metabolite concentrations responded significantly to a change in feeding state (Guglielmo et al. 2005, Zajac et al. 2006). We assumed captured birds to have been in the net the entire time since the net was last checked (i.e., ~8 min) and so measured “bleed time” conservatively as the time elapsed between the previous net check and blood-sample collection. Blood was not collected if bleed time would have exceeded 20 min.

We took up to 10% of calculated total blood volume (Fair et al. 2010) by brachial veinipuncture with a 26-gauge needle collected it into one-step, heparinized capillary/centrifuge tubes (Sarstedt microvette CB300). Samples were stored in coolers until nets were closed for the day, then centrifuged for 5 min. Plasma was transferred to 0.6-mL cryogenic tubes and stored at -80°C for up to 3 months until analysis.

After taking blood, we banded each bird with a U.S. Geological Survey aluminum leg band, identified it to age and sex when possible (Pyle 1997), measured its wing (unflattened, to 1 mm), scored fat on a 6-point scale (Seewagen 2008b), weighed it to 0.1 g on a digital balance, and released it.

ANALYSES OF PLASMA METABOLITES

We diluted plasma samples threefold with 0.9% NaCl to increase their volume. We measured metabolites on a microplate spectrophotometer (Biotec Powerwave X340) by methods described by Guglielmo et al. (2002, 2005). Briefly, TRIG was determined from the difference of concentrations of free and triacylglycerol-bound glycerol during endpoint assay (Sigma, Trinder reagent A and B) and BUTY was measured directly by kinetic endpoint assay (kit E0907979, R-Biopharm). We analyzed TRIG first, then BUTY if sufficient sample remained. Samples were analyzed in duplicate and values were averaged (all CV < 15 %).

FOOD ABUNDANCE

Ovenbirds forage almost exclusively on the forest floor (Holmes and Robinson 1988), and biomass of leaf-litter arthropods is considered a measure of the availability of Ovenbird food (Burke and Nol 1998, Strong and Sherry 2000). Other migrants we studied, such as the thrush species, also often feed on leaf-litter invertebrates (Holmes and Robinson 1988). We collected 0.4-m² of leaf litter from the surface to the ground within twelve 1-m² plots at each site. Plots were spaced every 10 m along two 60-m transects. Transects were parallel and ~30 m apart. We sampled between 08:00 and 13:00 EST at the beginning, middle, and end of a field season. Arthropods were sampled during spring in 2007 and 2008 and during autumn in 2008 only.

We extracted arthropods from litter samples in Berlese funnels, identified them to order, oven-dried them at 60 °C for 12 hr, and weighed them to 0.0001 g. We considered those difficult to see without magnification (<1 mm) negligible and did not process them. Ovenbirds forage unselectively, and we assumed all taxonomic orders of arthropods to be potential prey (Stenger 1958, Burke and Nol 1998).

STATISTICAL ANALYSES

We considered the number of nearctic–neotropical migratory birds captured at each study site to be a general measure of migrants’ density and compared captures by site with a chi-squared goodness-of-fit test. We first adjusted the number of birds captured at each site for differences among sites in capture effort (i.e., number of mist nets and hours operated) by averaging the total number of net-hours (number of nets × total number of hours operated) at all five sites and then dividing the actual effort at each site by this average to calculate a correction factor. We divided the total number of migrants captured at each site by the correction factor to correct the absolute

numbers for equal effort, then used the chi-squared test on the corrected values (Swanson et al. 2003).

We adjusted migrants' body mass to body size (wing length) in each species with a scaled-mass model (Peig and Green 2009) unless an initial simple linear regression of body mass and body size was nonsignificant ($P > 0.05$). We used simple linear regression to examine the relationship between body mass or size-adjusted body mass and capture time (expressed as hours since sunrise) (Winker et al. 1992, Carlisle et al. 2005, Seewagen and Slayton 2008) and obtained the hourly rate of mass change from the β coefficient. Often this technique is applied only to species with samples sizes of more than 50 (Jones et al. 2002) or 100 (Dunn 2002, Bonter et al. 2007) birds, but in our study we had few species with such large sample sizes and we chose a lower criterion of $n \geq 30$ to allow more species to be included in the analyses.

We used general linear models with a backward selection ($\alpha = 0.1$) procedure to identify variables that contributed to differences among sites in plasma TRIG and BUTY concentrations. Variables examined were capture time, body mass or size-adjusted body mass, Julian date, year, and bleed time. We compared metabolite concentrations by site with analysis of covariance (ANCOVA), with variables retained by the general linear model entered as covariates (Guglielmo et al. 2005). All covariates met assumptions of equal variance and homogeneous slopes. We tested differences among sites in metabolites with analysis of variance (ANOVA) when no covariates were identified.

Combining TRIG and BUTY into a refueling index with principal components analysis (e.g., Schaub and Jenni 2001, Guglielmo et al. 2005) did not change the results qualitatively, so we report only the results of the aforementioned analyses of TRIG and BUTY individually. We could not consider possible effects of age and sex because sample sizes at some sites were small, most of the species examined cannot be reliably sexed in the field, and the skills of the field crews at aging and sexing varied by study site.

We tested for differences among sites in invertebrate biomass with repeated-measures ANOVA to account for multiple sampling sessions throughout a season, with site, period (early, middle, late), and their interaction entered as fixed factors. We compared differences among the sites in biomass during each spring period individually with ANOVA because of a significant interaction between site and period in the repeated-measures analysis.

We ran statistical analyses with R version 2.1.0 (R Development Core Team 2009) and SPSS version 17.0 (SPSS 2001) and interpreted results as significant when $P \leq 0.05$, except in the backward selection procedures, where we retained variables at $P < 0.1$. We used Tukey HSD tests for all post-hoc, pairwise comparisons and $\log_{10} + 1$ transformed non-normal data to meet assumptions of parametric tests. Values are reported as means \pm SE.

TABLE 1. Total captures of nearctic–neotropical migratory landbirds during spring and autumn 2007 and 2008 in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York. Totals captured at the two sites differed significantly after correction for unequal effort (see Methods).

| Season and study site | Net-hr | Absolute captures | Corrected captures | χ^2_4 | P |
|-----------------------|--------|-------------------|--------------------|------------|--------|
| Spring | | | | 1604 | <0.001 |
| Bronx | 739 | 413 | 521 | | |
| Inwood | 798 | 557 | 650 | | |
| Prospect | 531 | 654 | 1148 | | |
| Marshlands | 1428 | 206 | 135 | | |
| Pound Ridge | 1165 | 37 | 30 | | |
| Autumn | | | | 1131 | <0.001 |
| Bronx | 1204 | 534 | 723 | | |
| Inwood | 1235 | 640 | 845 | | |
| Prospect | 738 | 437 | 966 | | |
| Marshlands | 2219 | 267 | 196 | | |
| Pound Ridge | 2759 | 135 | 80 | | |

RESULTS

RELATIVE ABUNDANCE OF MIGRANTS

After correction for unequal effort, total captures of migrants during both spring and autumn differed significantly by site (Table 1); more migrants were captured in Prospect Park than at any other site. On average, spring and autumn migrants were captured in NYC at more than triple the rate they were captured in Westchester (Fig. 2).

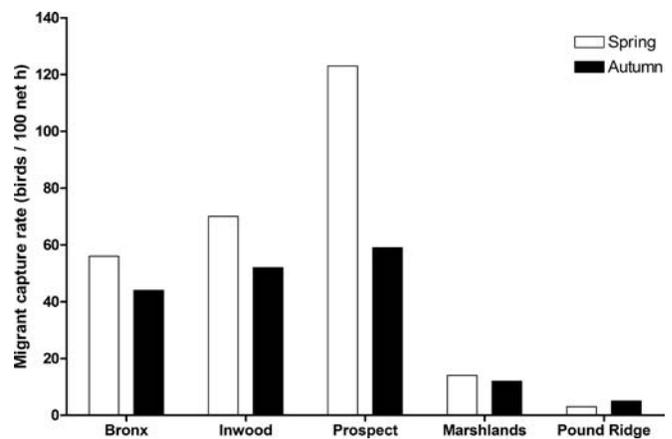


FIGURE 2. Rates of capture of nearctic–neotropical migratory landbirds at stopover sites in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York, 2007–2008. Capture rate expressed as number of migratory birds captured per 100 net-hours and calculated as (total migrants captured/total net-hours) \times 100. One net-hour is equivalent to one mist net operated for 1 hr.

TABLE 2. Mean (\pm SE) body mass and diurnal mass changes of migratory landbirds during stopovers in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands), New York, 2007–2008. Hourly mass change rates determined from β coefficients of linear regressions of body mass and capture time when $P \leq 0.1$. Mass change only examined when $n \geq 30$.

| Species | Site | Season | n | Body mass (g) | r^2 | P | g hr ⁻¹ | % mean mass hr ⁻¹ |
|-----------------------------|------------|--------|-----|----------------|-------|-------|--------------------|------------------------------|
| Veery | Prospect | Autumn | 46 | 33.6 \pm 0.5 | 0.05 | 0.15 | | |
| Swainson's Thrush | Prospect | Autumn | 37 | 31.8 \pm 0.5 | 0.00 | 0.97 | | |
| Black-throated Blue Warbler | Inwood | Autumn | 40 | 9.4 \pm 0.1 | 0.05 | 0.16 | | |
| Yellow-rumped Warbler | Prospect | Spring | 39 | 10.2 \pm 0.1 | 0.13 | 0.03 | 0.18 \pm 0.08 | 1.8 |
| | Inwood | Spring | 32 | 13.5 \pm 0.2 | 0.00 | 0.91 | | |
| Black-and-white Warbler | Inwood | Autumn | 58 | 11.9 \pm 0.1 | 0.01 | 0.61 | | |
| | | Spring | 44 | 11.0 \pm 0.1 | 0.05 | 0.14 | | |
| | Marshlands | Autumn | 48 | 11.8 \pm 0.1 | 0.08 | 0.07 | 0.30 \pm 0.16 | 2.5 |
| Ovenbird | Bronx | Spring | 44 | 21.0 \pm 0.2 | 0.20 | 0.003 | 0.45 \pm 0.14 | 1.0 |
| Northern Waterthrush | Prospect | Spring | 41 | 20.0 \pm 0.2 | 0.02 | 0.29 | | |
| | | Autumn | 102 | 20.6 \pm 0.2 | 0.05 | 0.03 | 0.33 \pm 0.15 | 1.6 |
| | Bronx | Spring | 33 | 18.1 \pm 0.3 | 0.04 | 0.29 | | |
| Common Yellowthroat | Prospect | Autumn | 35 | 18.6 \pm 0.4 | 0.00 | 0.80 | | |
| | | Spring | 98 | 18.1 \pm 0.2 | 0.00 | 0.79 | | |
| | Bronx | Spring | 41 | 11.0 \pm 0.1 | 0.14 | 0.02 | 0.24 \pm 0.10 | 2.2 |
| | | Autumn | 57 | 10.2 \pm 0.1 | 0.00 | 0.83 | | |
| | | Spring | 38 | 11.1 \pm 0.1 | 0.02 | 0.48 | | |
| White-throated Sparrow | Prospect | Spring | 80 | 10.6 \pm 0.1 | 0.01 | 0.47 | | |
| | | Autumn | 32 | 10.2 \pm 0.2 | 0.02 | 0.43 | | |
| | Marshlands | Autumn | 37 | 10.0 \pm 0.1 | 0.01 | 0.60 | | |
| | | Autumn | 106 | 26.1 \pm 0.2 | 0.01 | 0.43 | | |
| | Inwood | Autumn | 41 | 26.0 \pm 0.8 | 0.01 | 0.65 | | |
| | Prospect | Autumn | 43 | 24.9 \pm 0.3 | 0.08 | 0.06 | 0.41 \pm 0.21 | 1.6 |

HOURLY MASS CHANGE

For eight species of migrants our sample from at least one study site was sufficient ($n \geq 30$) during spring or autumn for us to investigate the relationship between body mass and capture time. Sample sizes and regression statistics are presented in Table 2.

Spring.—In Prospect Park, the Ovenbird and Black-throated Blue Warbler showed hourly body mass gains, whereas body masses of the Common Yellowthroat, Northern Waterthrush, and Black-and-white Warbler did not significantly change over time (Table 2). The body masses of the Ovenbird, Yellow-rumped Warbler, and Common Yellowthroat did not change over time in Inwood Park. The Ovenbird and Common Yellowthroat gained body mass in Bronx Park; the Northern Waterthrush did not (Table 2).

Autumn.—In Prospect Park, the relationship between body mass and capture time was not significant for the Veery, Swainson's Thrush, and Common Yellowthroat; it approached significance for the White-throated Sparrow (Table 2). The White-throated Sparrow's body mass was unrelated to capture time in Inwood and Bronx parks. The body mass of the Black-throated Blue Warbler did not change at Inwood Park, and that of the Northern Waterthrush and Common Yellowthroat did not change at Bronx Park (Table 2). Mass

gain in the Yellow-rumped Warbler was not significant at Inwood Park and approached significance at Marshlands Conservancy. The Common Yellowthroat did not gain significant body mass at Marshlands Conservancy (Table 2). For no other species was the sample size from Westchester adequate for examination of mass change.

PLASMA METABOLITES

We obtained a number of blood samples sufficient for comparisons by site from six species: Swainson's Thrush, Hermit Thrush, Wood Thrush, Yellow-rumped Warbler, Ovenbird, and Common Yellowthroat. Mean metabolite values and sample sizes for all species sampled are shown in Table 3. Variables identified as significant covariates and controlled for in site comparisons differed by species (Table 4). TRIG was positively associated, and BUTY was negatively associated, with time of capture in most species, reflecting the transition from overnight fasting or flight to morning feeding.

In the Ovenbird, TRIG and BUTY concentrations did not differ by site during spring (TRIG: $F_{4,128} = 0.5$, $P = 0.73$; BUTY: $F_{4,113} = 1.2$, $P = 0.32$; Fig. 3). No other spring migrants provided a sufficient sample size ($n \geq 5$) from at least one non-urban site to allow meaningful statistical comparisons to the urban sites. TRIG concentration in Ovenbirds did

TABLE 3. Mean \pm SE plasma triglyceride (TRIG) and B-OH-butyrate (BUTY) concentrations (mmol L⁻¹) of migratory landbirds during stopovers in New York City and Westchester County, New York, 2007–2008. Sample sizes in parentheses.

| Species | Season | New York City | | | | | | Westchester County | | | | | | | |
|------------------------|--------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|------------------------|----------------------|------------------------------|----------------------|---|---|---|---|
| | | Bronx Park | | Inwood Park | | Prospect Park | | Marshlands Conservancy | | Ward Pound Ridge Reservation | | | | | |
| | | TRIG | BUTY | TRIG | BUTY | TRIG | BUTY | TRIG | BUTY | TRIG | BUTY | | | | |
| Veery | Spring | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | Autumn | 2.41 (1) | 0.21 (1) | — | — | 1.83 \pm 0.39 (9) | 0.85 \pm 0.15 (9) | 2.16 (1) | 0.66 (1) | 1.41 \pm 0.22 (4) | 0.92 \pm 0.16 (4) | | | | |
| Swainson's Thrush | Spring | 2.07 \pm 0.14 (27) | 0.69 \pm 0.06 (25) | 3.01 \pm 0.52 (18) | 0.74 \pm 0.06 (18) | 2.21 \pm 0.32 (16) | 0.66 \pm 0.07 (16) | 2.32 \pm 0.30 (3) | 0.86, 0.93 (2) | 2.05, 3.00 (2) | 0.92, 0.33 (2) | | | | |
| | Autumn | 2.52 \pm 0.62 (10) | 0.66 \pm 0.11 (10) | 2.03 \pm 0.24 (8) | 0.63 \pm 0.14 (8) | 2.01 \pm 0.13 (35) | 0.52 \pm 0.06 (35) | 2.61 \pm 0.65 (7) | 0.54 \pm 0.06 (7) | 1.24 \pm 0.18 (6) | 0.69 \pm 0.22 (6) | | | | |
| Hermit Thrush | Spring | — | — | — | — | — | — | — | — | — | — | — | — | — | |
| | Autumn | 2.53 \pm 0.29 (16) | 0.37 \pm 0.07 (13) | 3.16 \pm 0.53 (8) | 0.45 \pm 0.12 (7) | 2.12 \pm 0.48 (5) | 0.50 \pm 0.07 (5) | 1.64 \pm 0.17 (5) | 0.71 \pm 0.20 (5) | 2.17 \pm 0.34 (8) | 0.37 \pm 0.07 (8) | | | | |
| Wood Thrush | Spring | 2.43 \pm 0.38 (7) | 0.53 \pm 0.07 (7) | 1.69 \pm 0.15 (13) | 0.70 \pm 0.10 (11) | 1.65 \pm 0.26 (4) | 0.71 \pm 0.15 (4) | 1.68 \pm 0.43 (4) | 0.68 \pm 0.10 (4) | 3.42 \pm 1.73 (3) | 0.92, 0.64 (2) | | | | |
| | Autumn | 1.30 \pm 0.33 (5) | 0.88 \pm 0.34 (5) | 1.28 \pm 0.14 (14) | 0.68 \pm 0.06 (14) | 1.12 \pm 0.14 (9) | 0.67 \pm 0.10 (9) | 1.35 \pm 0.28 (14) | 0.55 \pm 0.06 (14) | 1.06 \pm 0.24 (3) | 0.77 \pm 0.16 (3) | | | | |
| Yellow-rumped Warbler | Spring | 1.86 \pm 0.23 (11) | 1.07 \pm 0.22 (8) | 3.04 \pm 0.25 (27) | 1.01 \pm 0.12 (20) | 2.05 \pm 0.29 (9) | 1.07 \pm 0.18 (6) | 2.16 \pm 0.39 (4) | 0.81 (1) | — | — | | | | |
| | Autumn | 0.85 \pm 0.13 (12) | 1.54 \pm 0.20 (12) | 1.53 \pm 0.11 (31) | 1.79 \pm 0.17 (31) | 0.42 (1) | 1.59 (1) | 1.75 \pm 0.12 (36) | 1.20 \pm 0.07 (33) | 1.75 \pm 0.17 (12) | 0.81 \pm 0.06 (11) | | | | |
| Ovenbird | Spring | 1.65 \pm 0.11 (35) | 1.03 \pm 0.11 (33) | 1.52 \pm 0.09 (34) | 0.96 \pm 0.09 (29) | 1.67 \pm 0.11 (40) | 1.02 \pm 0.11 (37) | 1.48 \pm 0.22 (15) | 0.85 \pm 0.16 (10) | 2.05 \pm 0.78 (7) | 0.60 \pm 0.23 (7) | | | | |
| | Autumn | 1.14 \pm 0.10 (14) | 1.07 \pm 0.19 (12) | 1.33 \pm 0.54 (11) | 1.40 \pm 0.29 (11) | 1.50 \pm 0.37 (21) | 1.28 \pm 0.17 (21) | 1.46 \pm 0.17 (28) | 0.94 \pm 0.09 (28) | 0.75 \pm 0.04 (4) | 1.46 \pm 0.29 (4) | | | | |
| Northern Waterthrush | Spring | 1.95 \pm 0.18 (33) | 1.03 \pm 0.11 (29) | 3.76 \pm 2.34 (7) | 1.01 \pm 0.27 (6) | 1.63 \pm 0.09 (57) | 1.16 \pm 0.09 (52) | 1.83 \pm 0.43 (4) | 1.12 \pm 0.21 (4) | — | — | | | | |
| | Autumn | 1.47 \pm 0.14 (31) | 1.08 \pm 0.12 (31) | 1.28 \pm 0.22 (3) | 1.05 \pm 0.17 (3) | 1.42 \pm 0.18 (20) | 1.21 \pm 0.13 (20) | 1.65 \pm 0.49 (4) | 1.19 \pm 0.31 (4) | — | — | | | | |
| Common Yellowthroat | Spring | 2.39 \pm 0.59 (26) | 0.98 \pm 0.13 (21) | 2.56 \pm 0.40 (25) | 1.03 \pm 0.15 (17) | 1.66 \pm 0.14 (28) | 1.46 \pm 0.21 (20) | 1.42 \pm 0.26 (4) | 1.12 \pm 0.16 (3) | — | — | | | | |
| | Autumn | 1.43 \pm 0.12 (38) | 1.08 \pm 0.08 (38) | 1.48 \pm 0.40 (18) | 1.18 \pm 0.14 (16) | 1.26 \pm 0.12 (21) | 1.47 \pm 0.12 (19) | 1.10 \pm 0.08 (22) | 1.63 \pm 0.20 (21) | 0.55 (1) | 0.97 (1) | | | | |
| White-throated Sparrow | Spring | 2.30 \pm 0.43 (13) | 0.97 \pm 0.11 (13) | 1.94 (1) | 2.17 (1) | 1.48 \pm 0.23 (4) | 2.35 \pm 0.65 (3) | 1.62 (1) | 1.08 (1) | — | — | | | | |
| | Autumn | 1.44 \pm 0.10 (69) | 1.24 \pm 0.09 (67) | 1.75 \pm 0.21 (39) | 1.66 \pm 0.24 (38) | 1.70 \pm 0.14 (36) | 1.50 \pm 0.16 (33) | 1.76 \pm 0.21 (4) | 1.39 \pm 0.20 (4) | 1.31 \pm 0.32 (4) | 1.90 \pm 0.37 (4) | | | | |

TABLE 4. Variables retained by general linear models with backward selection and included as covariates in comparisons of metabolites by study site. TRIG = triglyceride, BUTY = B-OH-butyrate, B = bleed time, D = Julian date, M = body mass, T = time since sunrise, Y = year. Positive or negative symbols indicate direction of effect. The Ovenbird was the only species for which the sample size was sufficient for evaluation in spring. All species listed were examined during autumn; dashes indicate that no variables explained significant variation in plasma metabolite concentration.

| Species | Spring | | Autumn | |
|-----------------------|----------------|--------|------------|--------|
| | TRIG | BUTY | TRIG | BUTY |
| Swainson's Thrush | | | +T | -T, +Y |
| Hermit Thrush | | | +T, -B | — |
| Wood Thrush | | | — | — |
| Yellow-rumped Warbler | | | +T, +D | +M |
| Ovenbird | +T, -Y, +D, -B | -T, +B | +T, +Y, +M | -T, +D |
| Common Yellowthroat | | | +T, -Y | -T |

not differ by site during autumn either ($F_{3,68} = 0.5, P = 0.68$). Ovenbird BUTY differed by site ($F_{3,67} = 3.0, P = 0.04$), with birds at Marshlands Conservancy having generally lower levels than birds in NYC, but no pairwise comparisons were significant (all $P > 0.07$; Fig. 4). There were significant differences among sites in the Swainson's Thrush TRIG concentrations during autumn ($F_{4,64} = 2.7, P = 0.04$); in post-hoc tests, TRIG concentrations of birds at the NYC sites and the Marshlands Conservancy were higher than those of birds at Pound Ridge (all $P < 0.04$) but were not different from each other (all $P > 0.08$; Fig. 4). In autumn, BUTY levels of Swainson's Thrush did not differ by site ($F_{4,63} = 0.7, P = 0.60$; Fig. 4). TRIG concentrations in Yellow-rumped Warblers differed by site during autumn ($F_{3,84} = 4.2, P = 0.01$), with concentrations at Inwood Park and the two Westchester sites higher

than at Bronx Park (all $P < 0.05$) but not different from each other (all $P > 0.1$; Fig. 4). Yellow-rumped Warbler BUTY also differed by site ($F_{3,80} = 11.7, P < 0.001$), with highest levels at Inwood Park and lowest levels at Pound Ridge (Fig. 4). In the Common Yellowthroat, TRIG did not differ by site during autumn ($F_{3,96} = 0.3, P = 0.84$) but BUTY did ($F_{3,92} = 3.0, P = 0.04$), being generally lower in NYC than in Westchester (Fig. 4). In autumn, TRIG and BUTY concentrations did not differ by site in the Hermit Thrush (TRIG: $F_{4,39} = 1.0, P = 0.45$; BUTY: $F_{4,37} = 1.4, P = 0.26$) or Wood Thrush (TRIG: $F_{3,41} = 0.1, P = 0.97$; BUTY: $F_{3,41} = 0.7, P = 0.59$; Fig. 4).

FOOD ABUNDANCE

During spring, total arthropod biomass was represented primarily by 11 taxonomic categories: Diplopoda (26%), Isopoda (14%), Coleoptera (13%), adult Lepidoptera (11%), Chilopoda (10%), Formicidae (5%), other Hymenoptera (4%), Hemiptera (4%), Araneae (3%), larval Lepidoptera (3%), and Diptera (2%). During autumn, total arthropod biomass was represented primarily by 10 categories: Diplopoda (19%), Isopoda (17%), Coleoptera (16%), Hemiptera (12%), Lepidoptera (9%), Orthoptera (8%), Araneae (7%), Collembola (5%), Diptera (2%), and Opiliones (2%). The proportion of most categories at the various sites was similar (data not shown).

Trends in arthropod biomass through the spring varied greatly by site (site \times time period interaction: $F_{8,345} = 2.8, P = 0.005$); at some sites biomass increased, whereas at others it decreased or remained similar (Fig. 5). There were significant differences among sites in arthropod biomass early ($F_{4,115} = 2.6, P = 0.04$) and late ($F_{4,115} = 3.4, P = 0.01$) in the spring but not during the middle of the season ($F_{4,115} = 0.8, P = 0.56$). During early spring, biomass in Bronx Park was marginally higher than in Inwood Park ($P = 0.06$), but no pairwise comparisons were significant. Late in the spring, biomass was significantly greater in Inwood Park than in Bronx ($P = 0.03$) and Prospect parks ($P = 0.05$).

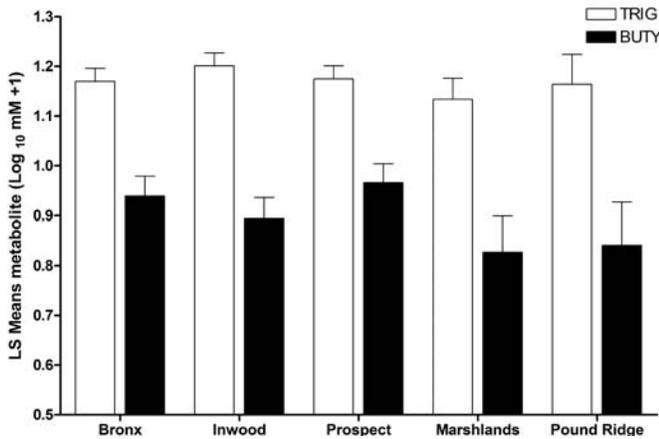


FIGURE 3. Concentrations of plasma triglyceride (TRIG) and B-OH-butyrate (BUTY) in Ovenbirds captured at stopover sites in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York, during spring 2007–2008. Metabolite values expressed as least-squares means + SE, covariates controlled for (Table 4). Sample sizes reported in Table 2.

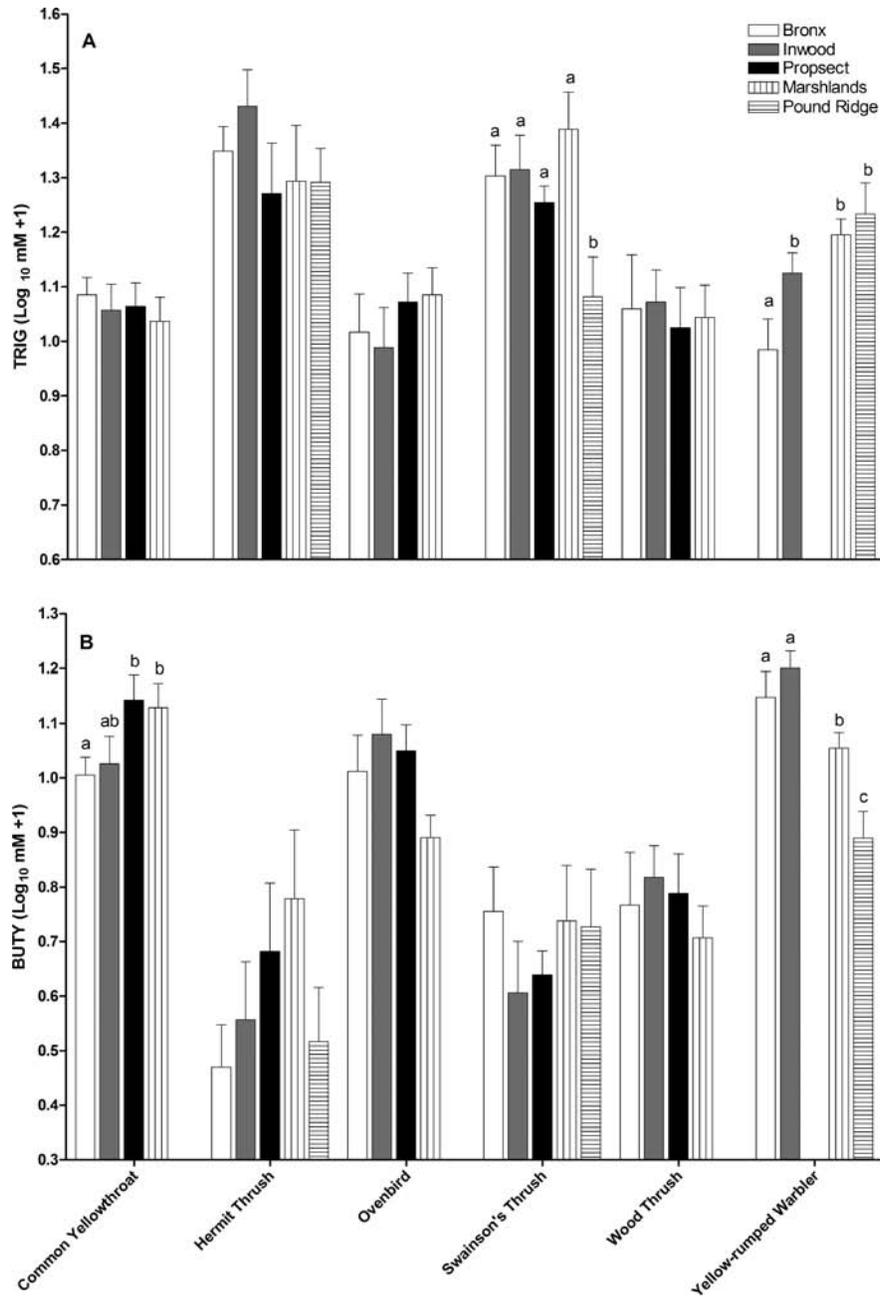


FIGURE 4. Concentrations of plasma triglyceride (TRIG [A]) and B-OH-butyrate (BUTY [B]) in migrant landbirds captured at stopover sites in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York, during autumn 2007–2008. Metabolite values are least-squares means + SE when covariates were controlled for and means + SE when no covariates were identified (Table 4). Letters indicate significant differences among sites within a species. Sample sizes reported in Table 2.

During autumn, the effects of the site × period interaction and period were not significant (interaction: $F_{8,165} = 1.6, P = 0.12$; period: $F_{2,173} = 0.8, P = 0.47$), and we dropped them from the model sequentially. Arthropod biomass averaged across all periods differed significantly by site ($F_{4,175} = 2.9, P = 0.02$), being significantly lower at Pound Ridge than at Marshlands Conservancy ($P = 0.03$) and Inwood Park ($P = 0.05$; Fig. 6).

DISCUSSION

Many city parks are famous for receiving exceptional concentrations of migrating birds (Fowle and Kerlinger 2001, Mehlman et al. 2005, Milne 2007), yet the resources provided by such habitats, and hence their true value as stopover sites, have been questionable. We found that refueling conditions

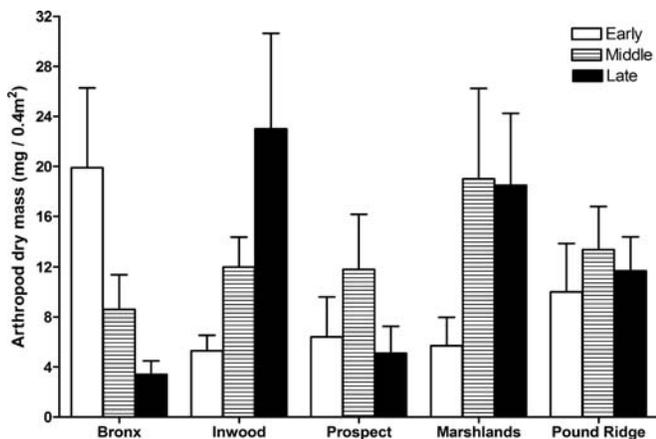


FIGURE 5. Mean + SE dry mass of arthropods in 0.4-m² leaf-litter samples collected from stopover sites for migratory birds in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York, over three periods during spring 2007–2008. Arthropod mass was significantly greater at Inwood Park than at Bronx and Prospect parks late in the spring; results of no other pairwise comparisons of sites within a period were significant.

were no poorer in NYC than in the less disturbed habitats examined outside of the city. Values of plasma metabolite for multiple species indicated that refueling performance in NYC and Westchester was comparable, and measures of arthropod biomass suggested similar abundance of food for ground-foraging insectivores in the two areas during both seasons. Our findings are consistent with earlier studies that have shown

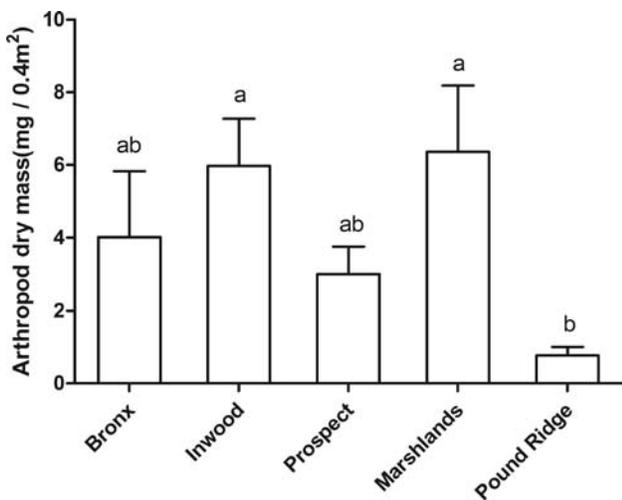


FIGURE 6. Mean + SE dry mass of arthropod in 0.4-m² leaf-litter samples collected from stopover sites for migratory birds in New York City (Bronx, Inwood, and Prospect parks) and Westchester County (Marshlands, Pound Ridge), New York, during autumn 2008. In contrast to spring (Fig. 5), data from three sampling periods were pooled because of the lack of a significant interaction of site × period. Letters indicate significant differences among sites.

migrants can successfully increase their body mass during stopovers in urban habitats (Seewagen and Slayton 2008, Craves 2009, Seewagen and Guglielmo 2011).

Urban ecosystems often support higher biomass of terrestrial invertebrates than non-urban habitats because of warmer microclimates caused by the heat-island effect (Raupp et al. 2010 and references within), which in turn could benefit insectivorous migratory birds refueling at urban stopover sites. In our study, differences among sites during spring were dependent on the time of season, but at no point was there a consistent trend for higher biomass of leaf litter arthropods in the urban habitats than in the non-urban habitats. There was also no indication that biomass was greater in the urban sites during autumn, although the site farthest outside NYC, Pound Ridge, had the lowest biomass. The abundance of food for the Ovenbird and similar ground-foraging insectivores in NYC and Westchester does not appear to differ overall.

Capture rates indicated a dramatic difference in the density of migrant landbirds in NYC and Westchester during both spring and autumn. A high density of migrants in urban habitats is a common phenomenon in cities along major migration routes and likely results from the limited habitat availability in urban landscapes. Indeed, the percentage of forest cover in NYC is less than one third that of Westchester, and migrants become concentrated in its small forest patches. In addition, earlier spring greening and delayed autumn dormancy of vegetation by as much as 2 weeks in urban forests, because of the heat-island effect (Roetzer et al. 2000, White et al. 2002, Zhang et al. 2004a, b), and the differing phenology of exotic plants that are common to disturbed habitats (Shustack et al. 2009) may actually attract migrants to urban stopover sites. Vegetation phenology appears to be an important cue migrants use to select a stopover site, as it can provide information about food availability (McGrath et al. 2009, Strode 2009). During our study, spring greening was noticeably later and autumn leaf fall was noticeably earlier in Westchester than in NYC (pers. obs.), possibly contributing to the observed disparity in densities of migrants.

Resource competition and territory defense by migrant passerines have been observed during stopover (Rappole and Warner 1976, Bibby and Green 1980, Dierschke et al. 2005, Buler 2006; but see Fasola and Fraticelli 1990), and mass gain can be density-dependent (Moore and Yong 1991, Kelly et al. 2002, Cerasale and Guglielmo 2010). For example, in the western U.S. Cerasale and Guglielmo (2010) found that food abundance at stopover sites with native vegetation and at those dominated by exotic salt cedar (*Tamarix* spp.) was similar, but Wilson’s Warblers (*Wilsonia pusilla*) were in fact able to refuel at higher rates in the salt cedar possibly because of a lower density of competitors. In our study, the Ovenbird’s TRIG concentrations in NYC and Westchester did not differ during spring or autumn, suggesting equal refueling rates despite the extreme difference in migrants’ density and similarity in food abundance across sites. Other species also indicated comparable refueling in NYC and

Westchester even though competition was likely greater at the urban sites. We do not know, however, how food abundance varied by site for some of these species that forage in strata other than the forest floor (e.g., Yellow-rumped Warbler).

Plasma metabolites of migrants in NYC can be further interpreted through comparisons to other studies in non-urban areas. TRIG levels in Ovenbirds migrating through NYC during spring and autumn were higher than the average in Ovenbirds wintering in Jamaica (Brown 2006); presumably, the nutrient intake of wintering Ovenbirds is only what is needed to maintain energy balance, and the species' higher TRIG levels during migratory stopover in NYC indicate energy accumulation above the minimum metabolic requirement. We are unaware of any reports of TRIG concentrations in migrating Ovenbirds. Average TRIG levels of spring migrant Swainson's Thrushes at Inwood and Prospect parks were higher than at a stopover site considered to be of high quality in Ontario, Canada (Guglielmo et al. 2005). Average TRIG levels of spring migrant Yellow-rumped Warblers were two to three times higher in NYC than at a national wildlife refuge in northwestern Ohio (MacDade 2009). During autumn, TRIG levels in Yellow-rumped Warblers at Bronx and Inwood parks were comparable to those during stopovers in Rhode Island, and Hermit Thrushes had higher average TRIG levels in NYC than in Rhode Island (Smith and McWilliams 2010). The average autumn TRIG concentration of Swainson's Thrushes at each NYC site was higher than or similar to the TRIG concentrations of migrating Swainson's Thrushes in northern California (Leist 2007). The similarity of TRIG levels in NYC and these non-urban areas further indicates that the NYC sites offer adequate, and possibly high-quality, refueling conditions for migrant landbirds.

In several cases we found no relationship between migrants' body mass and time of day, possibly because of inadequate sample sizes. The body mass–time of day regression technique requires large sample sizes to detect mass-change trends because of the great variation in body mass among individuals at a given time of day (Winker et al. 1992, Dunn 2000), and some investigators (Dunn 2002, Bonter et al. 2007) have therefore chosen to evaluate only species with samples of more than 100 birds. In our study, most samples were of less than 50 birds per species. Capturing birds during only the morning hours may also explain why we did not always detect changes in body mass over time. The regression technique is more often applied to birds captured over longer periods of the day (e.g., Dunn 2001, Jones et al. 2002, Morris et al. 2003, Bonter et al. 2007). Mass gain during our short sampling period may have been too subtle to result in significant relationships between body mass and time of capture, particularly during autumn when our sampling period was shorter than in spring because of later sunrise. Species for which the relationship between body mass and time of day was significant at the NYC sites gained mass at rates comparable to, and in most cases higher than, those of conspecifics in non-urban

areas (Winker et al. 1992, Dunn 2001, Bonter et al. 2007). These mass-gain rates were also similar to those measured in Bronx Park in an earlier study (Seewagen and Slayton 2008).

Our results add to a growing body of evidence that small and highly disturbed habitats that may otherwise be of little significance to wildlife have the potential to be valuable stopover sites for migrating birds (Seewagen and Slayton 2008, Craves 2009, Matthews and Rodewald 2010, Seewagen et al. 2010, Seewagen and Guglielmo 2011). However, these findings can be extended elsewhere only with much caution because of the wide variation within and among cities in intrinsic and extrinsic habitat characteristics that likely influence a site's quality. We hope that our studies in NYC will encourage investigations of stopover biology and stopover-habitat quality in other metropolitan areas of North America and around the world, and ultimately promote more science-based decision-making in cities with regard to migrating birds. It is important to recognize that our conclusions are not intended to advocate urbanization or other forms of habitat loss without concern for migratory birds. Instead, our results should highlight the importance of conserving and effectively managing natural areas even within human-dominated landscapes such as cities.

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