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A PHYSIOLOGICAL ASSESSMENT OF SEASONAL DIFFERENCES IN SPRING AND AUTUMN MIGRATION STOPOVER AT BRADDOCK BAY, LAKE ONTARIO

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Abstract. This study investigated seasonal differences in fat deposition and nutritional status of migrating passerine birds at an important stopover site on the south shore of Lake Ontario. Birds were captured during spring and autumn stopovers, and their plasma metabolites were measured as indicators of refueling rates (plasma triglyceride) and nutritional state (plasma uric acid). *Catharus* thrushes had higher plasma triglyceride and lower plasma uric acid in autumn than in spring, whereas Red-eyed Vireos had higher plasma triglyceride in spring than in autumn, but no seasonal differences in plasma uric acid. There were no seasonal differences in plasma triglyceride concentrations in White-throated Sparrows (*Zonotrichia albicollis*) and Blackpoll Warblers (*Setophaga striata*), although White-throated Sparrows had plasma uric acid higher in spring than in autumn, suggesting they were consuming more protein than were those captured during autumn migration. These data suggest that songbirds use this site for refueling during both spring and autumn, but substantial seasonal differences in fat and protein metabolism indicate seasonal shifts in habitat use by some species. Results of this study emphasize the importance of considering seasonal differences in food availability and interspecific differences in stopover site use when these sites are managed to provide high-quality habitat across seasons for a range of songbird species.

Key words: bird migration, plasma metabolites, refueling performance, habitat use, diet, stopover ecology.

Evaluación Fisiológica de las Diferencias Estacionales en las Paradas Migratorias de Primavera y Otoño en la Bahía Braddock, Lago Ontario

Resumen. En este estudio investigo las diferencias estacionales en el depósito de grasa y en el estatus nutricional de paserinos migrantes en un sitio de parada importante en la costa sur del Lago Ontario. Las aves fueron capturadas durante las paradas de primavera y otoño, y se midieron sus metabolitos plasmáticos como indicadores de las tasas de reaprovisionamiento (triglicéridos plasmáticos) y del estado nutricional (ácido úrico plasmático). Los zorzales del género *Catharus* tuvieron triglicéridos plasmáticos y ácido úrico plasmático más bajos en otoño que en primavera, mientras que los individuos de *Vireo olivaceus* tuvieron triglicéridos plasmáticos más elevados en primavera que en otoño pero no hubo diferencias estacionales en el ácido úrico plasmático. No hubo diferencias estacionales en las concentraciones de triglicéridos plasmáticos en *Zonotrichia albicollis* y *Setophaga striata*, aunque *Z. albicollis* tuvo ácido úrico plasmático más elevado en primavera que en verano, sugiriendo que estuvo consumiendo más proteína que aquellas capturadas durante la migración otoñal. Estos datos sugieren que las aves canoras usan este sitio para reaprovisionarse tanto en primavera como en verano, pero diferencias estacionales sustanciales en el metabolismo de las grasas y las proteínas indican desplazamientos estacionales en el uso del hábitat por parte de algunas especies. Los resultados de este estudio enfatizan la importancia de considerar las diferencias estacionales en la disponibilidad de alimentos y las diferencias entre especies en el uso de los sitios de parada cuando estos sitios son manejados para brindar hábitat de alta calidad para un grupo de especies de aves canoras a lo largo de todo el año.

INTRODUCTION

Annual migrations between breeding and wintering grounds are energetically extremely costly for small songbirds and require rapid storage and use of large lipid reserves (Blem 1980). Small songbirds are particularly vulnerable because they rely on stopover sites to rest and replenish body fat and protein (McWilliams et al. 2004) but must overcome the challenges of acquiring food in unfamiliar habitats over a matter of days before continuing migration.

One factor that can influence fattening rates and stopover-site use by songbirds is food availability and quality. Many species of North American songbirds switch their diet to include large amounts of fruit during autumn migrations (Parrish 1997, 2000), and certain fruits that are high in energy and fat content may be selectively eaten by songbirds (Smith et al. 2007a). Therefore, habitats that support abundant fruit resources are likely to represent high-quality stopover sites for refueling birds during autumn migration (Smith and McWilliams 2010). However, seasonal comparisons of refueling

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rates are necessary to determine whether these habitats also represent high-quality stopover sites during spring, when insects constitute the main food source for refueling migrants. The migration strategies of birds represent trade-offs between maximizing fuel-deposition rates and minimizing time spent on migration (stopover duration) and predation risk, and these strategies are presumably influenced by extrinsic factors such as weather (Weber et al. 1998). Migration strategies may also be influenced by seasonal differences in selective pressures such as early arrival at breeding grounds, and this may contribute to differences in stopover-site use between spring and autumn migration in terms of refueling rates and stopover length (Morris and Glasgow 2001, Bonter et al. 2007). Integrating information about diet and metabolic refueling can provide insight into how birds use food resources across seasons and the overall quality of a stopover site.

Measuring the physiological condition and energy storage of birds during stopovers can provide information about the quality and use of specific stopover sites. Plasma metabolite profiling offers a useful means of evaluating energy metabolism and physiological condition of migrating songbirds because certain metabolites indicate fat deposition and mass gain over the previous several hours (plasma triglyceride; Jenni-Eiermann and Jenni 1994, Jenni and Schwilch 2001) and intake of dietary protein (uric acid; Smith et al. 2007b). Triglyceride concentrations are particularly useful for comparing fat deposition rates of free-living birds at stopover sites (Guglielmo et al. 2005, Smith and McWilliams 2010, Seewagen et al. 2011). Integration of information about refueling performance and food resources can be used to infer how birds use habitat and food resources at migration stopover sites (Cerasale and Guglielmo 2010, Smith and McWilliams 2010, MacDade et al. 2011). Thus, measurement of these metabolites in migrating songbirds can provide valuable information about habitat quality at migration stopover sites.

In recent decades, many populations of migratory songbirds have been declining (Hagan et al. 1992, Rappole and MacDonald 1994, DeGraaf and Rappole 1995), and these populations may be affected by events during migration (Moore et al. 1995, Sillett and Holmes 2002). Understanding mechanisms that drive seasonal differences in habitat requirements has important implications for informing conservation and management priorities for migratory bird populations and may enlighten managers in regard to cross-season conservation strategies that may serve to prevent future declines.

The goal of my study was to investigate seasonal differences in refueling performance of migrating songbirds at an important inland stopover site along the south shore of Lake Ontario. I measured plasma metabolite concentrations in migrating birds to gather information about physiological condition and diet across multiple migration seasons and examine habitat use by songbirds during their spring and autumn migrations. I tested the hypothesis that plasma triglyceride and uric acid concentrations of birds stopping over at this site in spring and autumn migration should differ in congruence with seasonal changes in food availability at this site. I predicted that omnivorous species that consume large amounts of fruit in autumn should have higher plasma triglyceride levels and lower plasma uric acid levels during autumn than during spring. I also predicted that granivorous and insectivorous species should have higher uric acid levels in the spring when insects are the main food resource, but that triglyceride levels may be higher in autumn when overall food abundance is greater at this site.

METHODS

STUDY SITE

I conducted this study at the Braddock Bay Bird Observatory (43° 19′ N, 77° 43′ W). The study area is located on the west spit of Braddock Bay, Lake Ontario, near Rochester, New York, and is characterized by a mix of early-successional habitat types. The shrub and understory community is dominated by native dogwoods (C*ornus* spp.), wild grapes (*Vitis* spp.), viburnums (*Viburnum* spp.), and invasive bush honeysuckles (*Lonicera* spp.) that provide abundant fruit during autumn (see Bonter et al. 2007 for habitat description).

SAMPLE COLLECTION

Birds were captured during four seasons of sampling: spring migration of 2009 and 2010 and autumn migration of 2008 and 2009. I focused on species that are commonly captured at the banding station during both spring and autumn migration: Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*C. minimus*), Veery (*C. fuscescens*), Red-eyed Vireo (*Vireo olivaceus*), White-throated Sparrow (*Zonotrichia albicollis*), and Blackpoll Warbler (*Setophaga striata*). Birds were captured daily, weather permitting, between sunrise and 6 hr after sunrise in 30-mm mesh mist nets placed along established net lanes. Sampling of the focal species was delayed until 1 hr after sunrise to allow birds to initiate daily foraging and physiologically transition from overnight fasting to a feeding state. Nets were checked every 30 min and captured birds were removed from nets and brought back to a central location for bleeding and banding. "Bleed time" was defined as the time elapsed between a bird being extracted from a net and its blood sample being taken; only birds that could be bled within 30 min of a net check were sampled. Birds were bled by puncture of the brachial vein with a 28-gauge needle, and up to 150 μL of blood was collected into heparinized capillary tubes. Tubes were centrifuged within 5 hr to separate plasma from red blood cells, and plasma was stored in 1.2-mL cryogenic vials at –80° C until analysis.

Following blood sampling, birds were banded with a U.S. Geological Survey aluminum leg band. Birds were aged and sexed when possible according to criteria in Pyle (1997). Their unflattened wing length (mm) and body mass (± 0.1g) were

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measured, and their subcutaneous fat load was scored on the 6-point scale of Helms and Drury (1960). Capture time was recorded as the hour after sunrise of the net check in which birds were captured. All birds were then released at the site of capture.

PLASMA METABOLITE ANALYSES

Plasma was diluted two- to three-fold with 0.9% NaCl prior to all metabolite assays. Plasma triglyceride was measured by sequential colorimetric endpoint assay by methods described in Guglielmo et al. 2005 (Sigma, St. Louis, MO: 5 µL plasma, 240 µL glycerol reagent, 60 µL triglyceride reagent). Uric acid was measured by colorimetric endpoint assay (TECO Diagnostics, Anaheim, CA: 5 µL sample, 300 µL reagent). All measurements were repeated until the coefficient of variation between replicate wells was <10%.

STATISTICAL ANALYSES

For all analyses I used SAS version 9.2 (SAS Institute, Cary, NC). I used one-way ANOVA to compare differences in average body mass of birds captured in spring and autumn. Plasma uric acid concentrations were $\log_{10}(x + 1)$ transformed to normalize the data. I corrected body mass for individual variation in body size by calculating a condition index defined by [body mass (g)/wing length (mm)] × 100 (Winker 1995, Bonter et al. 2007). All species of the genus *Catharus* were pooled for analyses because samples of the Gray-cheeked Thrush (n = 5 autumn; n = 9 spring) and Veery (n = 4 autumn; n = 7 spring) were small. To investigate the relative importance of covariates that may influence plasma metabolite concentrations, I analyzed metabolite datasets for each species separately (see Smith and McWilliams 2010). I evaluated a set of candidate models containing all combinations of the following variables: year (autumn 2008, spring 2009, autumn 2009, spring 2010), Julian date of capture, capture time, bleed time, and condition. I calculated second-order Akaike's information criterion corrected for small sample sizes (AIC_c) and used differences in AIC_c ($\Delta AIC_c = AIC_{c\,i} - AIC_{c\,\min}$) to rank candidate models and considered models with $\Delta AIC_c < 2$ to have substantial support (Burnham and Anderson 2002). I then calculated the relative importance [$w + (j)$] of each variable by summing w_i across all candidate models in which a given variable (j) occurred (Burnham and Anderson 2002).

I used ANCOVA to test for explicit differences in metabolite concentrations between spring and autumn for each species. Relative importance values generated from AIC_c results guided selection of covariates for inclusion in ANCOVA models, and I retained variables with relative importance values >0.8 in ANCOVA models for a given species. To test for seasonal differences in metabolite concentrations when no covariates were retained I used ANOVA. Values are reported as mean ± standard error and significance was set at $P < 0.05$.

RESULTS

A total of 40 Blackpoll Warblers, 49 Red-eyed Vireos, 48 White-throated Sparrows, and 75 *Catharus* thrushes were sampled during the migration periods of autumn 2008 through spring 2010 (Tables 1 and 2). Birds were captured between 5 May and 29 May during spring migration and between 6 September and 13 October during autumn migration. The average body mass of Blackpoll Warblers captured in spring (13.2 ± 0.2 g) was significantly higher than in autumn (11.9 ± 0.4 g; $F_{1,39} = 7.6$, $P < 0.01$). In contrast, the average body mass of Red-eyed Vireos was significantly lower in spring (17.7 ± 0.7 g) than in autumn (18.9 ± 0.4 g; $F_{1,48} = 1.2$, $P = 0.03$). There was no difference in the average body mass of White-throated Sparrows captured in spring (25.5 ± 0.5 g) and autumn (25.3 ± 0.3 g; $F_{1,47} = 0.1$, $P = 0.77$) or in that of thrushes captured in spring (32.1 ± 0.1 g) and autumn (31.7 ± 0.6 g; $F_{1,74} = 7.5$, $P = 0.63$).

MODEL SELECTION

Plasma triglyceride concentrations showed considerable model selection variation for all species except the Blackpoll Warbler, for which the model with capture time and condition had substantial support (Table 3). Relative importance values clarified that capture time was most important in explaining variation in triglyceride concentrations of Blackpoll Warblers (Table 4). Capture time and season best described variation in plasma

TABLE 1. Metabolite concentrations in migrating birds captured in spring at the Braddock Bay Bird Observatory.

Species	n[a]	Triglyceride (mM)	Uric acid (mM)
Blackpoll Warbler	32, 29	1.76 ± 0.11	0.94 ± 0.07
Red-eyed Vireo	31, 30	2.13 ± 0.09	0.88 ± 0.07
White-throated Sparrow	13, 13	2.02 ± 0.21	1.01 ± 0.09
Catharus thrushes	54, 53	1.99 ± 0.07	0.72 ± 0.04

[a]Sample sizes for plasma triglyceride and plasma uric acid, respectively, for a given species.

TABLE 2. Metabolite concentrations in migrating birds captured in autumn at the Braddock Bay Bird Observatory.

Species	n[a]	Triglyceride (mM)	Uric acid (mM)
Blackpoll Warbler	8, 8	1.53 ± 0.23	0.74 ± 0.14
Red-eyed Vireo	18, 18	1.49 ± 0.15	0.73 ± 0.75
White-throated Sparrow	35, 34	1.54 ± 0.09	0.65 ± 0.04
Catharus thrushes	21, 20	2.28 ± 0.15	0.38 ± 0.05

[a]Sample sizes for plasma triglyceride and plasma uric acid, respectively, for a given species.

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triglyceride for Red-eyed Vireos, and condition was the most important variable for describing plasma triglyceride concentrations in White-throated Sparrows and *Catharus* thrushes (Table 4).

Model selection results for plasma uric acid provided support for multiple plausible models for the Blackpoll Warbler, Red-eyed Vireo, and *Catharus* thrushes (Table 3). Model selection results for the White-throated Sparrow were unambiguous, with the model containing year ranked highest in the candidate set (Table 3). Relative importance values indicated that year was the most important variable for explaining variation in plasma uric acid concentrations of White-throated Sparrows, and bleed time was important in explaining variation in plasma uric acid concentrations of Red-eyed Vireos and *Catharus* thrushes (Table 4).

TABLE 3. Results of AIC_c model selection for explanatory variables that describe variation in concentrations of plasma triglyceride and plasma uric acid in birds sampled at Braddock Bay Bird Observatory. Models are ranked by Akaike weights (w_i) and only models with $\Delta AIC_c < 2$ are shown.

Model[a]	*K*	ΔAIC_c[b]	w_i
Plasma triglyceride			
Blackpoll Warbler			
Capture time, condition	4	0 (–46.85)	0.40
Red-eyed Vireo			
Year, date, capture time, bleed time	8	0 (–62.93)	0.31
Year, capture time, bleed time	7	0.91	0.20
White-throated Sparrow			
Date, condition	4	0 (–47.79)	0.18
Date, capture time, condition	5	0.61	0.13
Condition	3	0.73	0.12
Year, condition	6	1.41	0.09
Catharus			
Date, condition	4	0 (–90.37)	0.20
Date, bleed time, condition	5	1.16	0.11
Year, condition	6	1.58	0.09
Date, capture time, condition	5	1.64	0.09
Plasma uric acid			
Blackpoll Warbler			
Condition	3	0 (–180.26)	0.24
Date	3	0.85	0.15
Date, condition	4	1.81	0.10
Red-eyed Vireo			
Date, bleed time	4	0 (–243.17)	0.20
Bleed time	3	0.89	0.13
Year, bleed time	6	1.40	0.10
White-throated Sparrow			
Year	5	0 (–248.93)	0.34
Catharus			
Date, bleed time	4	0 (–389.96)	0.25
Year, bleed time	6	0.48	0.20
Date, bleed time, condition	5	1.78	0.10
Year, date, bleed time	7	1.91	0.10

[a]Year = sampling season and year combination when captured (autumn 2008–spring 2010), date = Julian date of capture, capture time = hour after sunrise at capture; bleed time = time in minutes between bird being extracted from the net and bled, condition = body mass (g) corrected for wing length (mm, see Methods).
[b]Minimum AIC_c in parentheses.
[c]$Log_{10}(x + 1)$ transformed concentrations were used in analyses.

COMPARISON OF SPRING AND AUTUMN MIGRATION

Triglyceride concentrations of Blackpoll Warblers were not significantly different in birds captured during spring and autumn after the effects of capture time were accounted for (season: $F_{1,37} = 1.7$, $P = 0.20$; capture time: $F_{1,37} = 12.6$, $P < 0.01$, Fig. 1). Red-eyed Vireos had significantly higher triglyceride concentrations in the spring after accounting for capture time and year (season: $F_{1,44} = 9.4$, $P < 0.01$; capture time: $F_{1,44} = 13.9$, $P < 0.001$; year: $F_{2,44} = 1.34$, $P = 0.34$; Fig. 1). In the White-throated Sparrow, after accounting for condition, there was a trend toward higher triglyceride concentrations in spring than in autumn, though this relationship was not significant (season: $F_{1,45} = 3.7$, $P = 0.06$; condition: $F_{1,45} = 8.8$, $P < 0.01$; Fig. 1). *Catharus* thrushes captured in autumn had triglyceride concentrations significantly higher than did those captured in spring (season: $F_{1,72} = 5.9$, $P = 0.02$; condition: $F_{1,72} = 5.8$, $P = 0.02$; Fig. 1).

Plasma uric acid concentrations did not vary seasonally in Blackpoll Warblers (season: $F_{1,35} = 2.2$, $P = 0.15$; Fig. 2) or in Red-eyed Vireos after the influence of bleed time was accounted for (season: $F_{1,45} = 3.5$, $P = 0.02$; bleed time: $F_{1,45} = 6.2$, $P = 0.2$; Fig. 2). However, White-throated Sparrows had significantly higher plasma uric acid concentrations in spring than in autumn after correction for year (season: $F_{1,44} = 17.0$, $P < 0.001$; year: $F_{1,44} = 2.2$, $P = 0.15$; Fig. 2). In contrast, *Catharus* thrushes had significantly higher plasma uric acid concentrations in autumn than in spring after the effects of bleed time were accounted for (season: $F_{1,70} = 31.3$, $P < 0.0001$; bleed time: $F_{1,70} = 14.7$, $P < 0.001$; Fig. 2).

DISCUSSION

The south shore of Lake Ontario is a geographically important inland stopover area for migrating passerines. Here, birds are either approaching a substantial water crossing to continue their spring migration or have just completed an overnight lake crossing upon arriving at the site in autumn. These two scenarios may necessitate different strategies for birds stopping over in this region, and such differences in migration strategies may result in individual, species, or seasonal variation in stopover habitat use and refueling performance. Bonter et al. (2007) demonstrated that large numbers of migrants use stopover habitat along the immediate shoreline at Braddock Bay Bird Observatory to refuel and are able to acquire adequate food resources, as shown by average daily mass gains. Furthermore,

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TABLE 4. Relative importance values generated from AIC_c modeling of explanatory variables that may influence within-season plasma concentrations of triglyceride and uric acid. The value is the sum of w_i from all models in which a given variable occurs.

Model set	Year[a]	Date[b]	Capture time[c]	Bleed time[d]	Condition[e]
Triglyceride					
Blackpoll Warbler	0.03	0.27	0.99	0.23	0.67
Red-eyed Vireo	0.81	0.65	0.99	0.66	0.18
White-throated Sparrow	0.32	0.46	0.36	0.24	0.90
Catharus	0.38	0.60	0.34	0.35	0.82
Uric acid[f]					
Blackpoll Warbler	0.04	0.42	0.29	0.26	0.58
Red-eyed Vireo	0.33	0.44	0.25	0.89	0.27
White-throated Sparrow	0.87	0.30	0.19	0.22	0.20
Catharus	0.52	0.61	0.23	0.99	0.26

[a]Year = sampling season when captured (autumn 2008–spring 2010).
[b]Date = Julian date of capture.
[c]Capture time = hour after sunrise at capture.
[d]Bleed time = time in minutes between bird being extracted from the net and bled.
[e]Condition = body mass (g) corrected for wing length (mm; see Methods).
[f]$Log_{10}(x + 1)$-transformed concentrations were used in analyses.

more species gained mass at a greater rate in autumn than in spring (Bonter et al. 2007). I found that seasonal patterns in instantaneous refueling rates at this site, as measured by plasma triglyceride, varied by species with only the thrushes having significantly higher plasma triglyceride in autumn than in spring. This agrees with the hypothesis that an elevated plasma triglyceride level, and hence refueling performance, in autumn likely reflects the abundance of fruit resources at this site for which seasonally frugivorous species, like the *Catharus* thrushes, are most likely to benefit in terms of refueling performance. At this site, native fruit-bearing shrub species, namely, Silky Dogwood (*Cornus amomum*), Gray Dogwood (*Cornus racemosa*), and Red Osier Dogwood (*Cornus sericea*), dominate the open understory and are common throughout the early-successional habitat (Smith and Miller, unpubl. data). The fruits of these shrubs are high in energy and fat and are consumed at relatively high rates by songbirds during autumn (Smith et al. 2013), which could contribute to

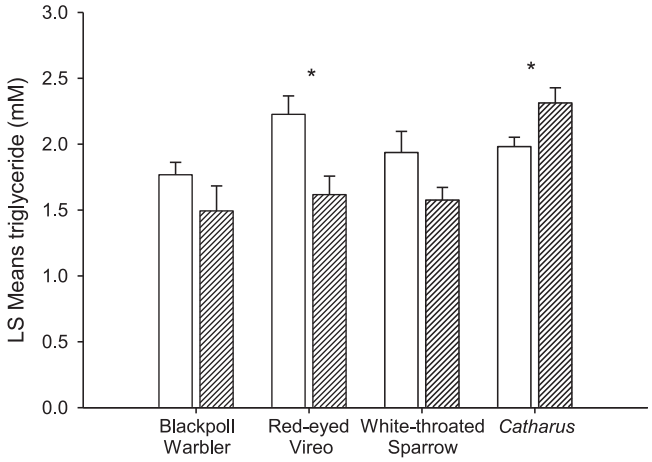


FIGURE 1. Least-squares mean ± SE concentration (mM) of plasma triglyceride of Blackpoll Warblers, Red-eyed Vireos, White-throated Sparrows, and *Catharus* thrushes captured at Braddock Bay Bird Observatory during spring (white bars) and autumn (shaded bars) migration. Least-squares means were generated from ANCOVA with correction of variables selected according to relative importance value generated from AIC_c model selection (see Results). Species with significant differences between spring and autumn plasma concentrations are designated with an asterisk.

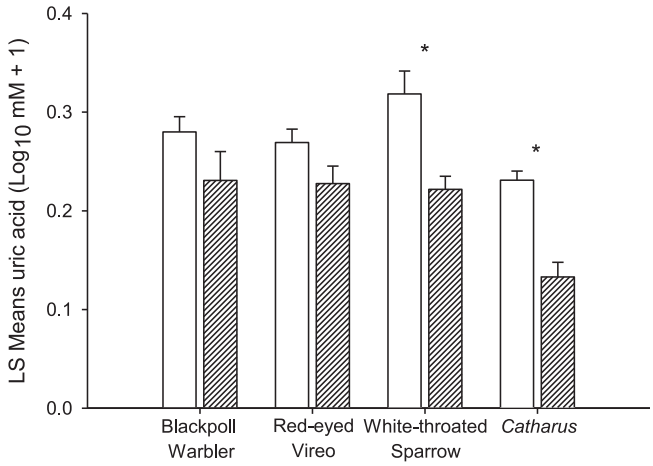


FIGURE 2. Least-squares mean ± SE plasma uric acid ($log_{10}[x + 1]$) concentration (mM) of Blackpoll Warblers, Red-eyed Vireos, White-throated Sparrows, and *Catharus* thrushes captured at Braddock Bay Bird Observatory during spring (white bars) and autumn (shaded bars) migration. Least-squares means were generated from ANCOVA with correction of variables selected according to relative importance value generated from AIC_c model selection (see Results). Species with significant differences between spring and autumn plasma concentrations are designated with an asterisk.

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Catharus thrushes increasing fat deposition in the autumn. Superior autumn refueling in thrushes is also consistent with previous studies documenting that highly frugivorous species tend to be in better body condition and have higher fat deposition rates than less omnivorous species, particularly at stopover sites with abundant high-quality fruit resources (Parrish 1997, 2000, Smith and McWilliams 2010).

Red-eyed Vireos had higher plasma triglyceride concentrations in spring than in autumn. However, it is unclear whether seasonal changes in stopover habitat use, as indicated by concentrations of plasma metabolites, reflects a dietary switch among available food resources because concentrations of plasma uric acid did not vary with season. Furthermore, the average body mass of Red-eyed Vireos was lower in the spring than in autumn, which underscores the importance of using indices of instantaneous metabolic refueling in assessment of fat deposition of birds at stopover sites. White-throated Sparrows had higher levels of plasma uric acid in the spring than in autumn, which suggests they were consuming more protein-rich foods, like insects, during spring stopovers. This apparent shift in diet was not accompanied by significant seasonal differences in plasma triglyceride concentrations, though there was a trend toward higher triglyceride in White-throated Sparrows captured in spring. Food resources in the form of fruits, namely, native dogwoods and Arrowwood Viburnum (*V. dentatum*), which have high energy density and fat content (Smith et al. 2007a, 2013) are typically abundant at this site throughout the duration of autumn migration (Smith and Miller, unpubl. data). Nevertheless, plasma triglyceride concentrations in Blackpoll Warblers and White-throated Sparrows were not higher in autumn. The average body mass of Blackpoll Warblers was greater in the spring than in autumn, but plasma triglyceride concentrations did not indicate strong instantaneous differences in seasonal fat deposition rates.

Studies in urban areas (Seewagen and Slayton 2008), islands off the coast of the northeastern U.S. (Morris and Glasgow 2001), and other inland areas in the Great Lakes region (Winker et al. 1992) have documented seasonal differences in the stopover ecology of migrating passerines with trends toward better body condition and higher daily rates of mass gain during spring stopover. Several other studies have documented deviations from this pattern, with many species gaining mass at higher rates during autumn stopovers than in spring (Dunn 2002, Morris et al. 1994, Benson and Winker 2005, Bonter et al. 2007). Explanations for variation in seasonal patterns of stopover-site use often focus on site-specific attributes, such as fluctuations in daily weather patterns, low food abundance or quality, and proximity to ecological barriers to migration or breeding areas of certain species. Variation in seasonal habitat use and stopover behavior at Braddock Bay could also relate to migration strategy and proximity to breeding grounds. When arriving at this site in spring, White-throated Sparrows and Swainson's Thrushes are relatively close to their breeding grounds, and hence their need to accumulate large fat stores may be diminished. Other species, such as the Blackpoll Warbler, may be under different time or physiological constraints because they must travel farther to reach their breeding grounds in spring or may not be in the earliest stages of their migration upon reaching this site in autumn.

Seasonal differences in songbirds' stopover ecology may be related to intraspecific variation in stopover habitat use and behavior of individual birds related to sex or age within populations of a given species (Yong et al. 1998). However, differences in body mass, body fat loads, or timing of migration among age or sex classes are not always accompanied by age- or sex-related differences in rates of mass gain (Morris and Glasgow 2001, Jones et al. 2002, Benson and Winker 2005). My samples for birds that could be reliably sexed in both seasons were small, which precluded statistical analysis of the effects of sex on plasma metabolite concentrations. In addition, the majority of birds sampled in autumn were younger birds, which suggests that age effects on refueling rates are unlikely to have contributed substantially to the variation in refueling rates I observed.

Results of this study highlight the importance of considering seasonal differences in habitat use when stopover habitat is managed, particularly for species that may switch their diet between spring and autumn stopovers at the same sites. It also reinforces the benefits of using indices of metabolic refueling via plasma metabolite profiling for assessment of instantaneous rates of fat deposition and to help discern physiological differences in habitat use among species. Food availability is an important consideration in management of stopover habitat for small songbirds because length of time a bird must stay at a given site is often intricately related to food quality and abundance, particularly for energy-depleted migrants (Schaub and Jenni 2000, 2001). However, it is important to recognize that the habitat requirements of taxa with different dietary habits may not be congruent with those of seasonally frugivorous species in autumn. Studies aimed at identifying critical stopover sites or food resources for migrating birds should incorporate both spring and autumn seasons into their assessments, represent a range of taxa, and consider multiple years to capture the range of variation in stopover site use during annual migrations.

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