The Auk 127(1):108–118, 2010

PATTERNS OF FUEL USE AND STORAGE IN MIGRATING PASSERINES IN RELATION TO FRUIT RESOURCES AT AUTUMN STOPOVER SITES

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Abstract.—Fuel deposition rates of migrating birds may indicate the quality of habitat at stopover sites, yet little is known about how diet habits and food availability affect fat and protein metabolism in free-living songbirds at stopover sites. We compared plasma indicators of fat deposition (triglyceride), fat catabolism (B-hydroxybutyrate), and protein catabolism (uric acid) among passerine species that are frugivorous to a variable degree during autumn stopover on Block Island, Rhode Island. We also compared plasma lipid metabolites from 3 of these species that were captured at 2 stopover sites with different fruit abundance. The more frugivorous Hermit Thrushes (*Catharus guttatus*) had the highest plasma triglyceride, and uric acid was highest in the least frugivorous species sampled on Block Island, but other differences among species were not clearly related to diet. B-hydroxybutyrate was more variable among the species sampled on Block Island. Plasma triglyceride was significantly higher in Hermit Thrushes captured on Block Island, where fruit resources were abundant, than in Hermit Thrushes captured at a mainland site in southern Rhode Island, where less fruit was available. Our results suggest that diet habits may influence fat and protein metabolism in migrating passerines, but careful study design and statistical analyses are necessary to control for or minimize the effects of the many influential factors that affect plasma metabolites so they can be used to assess fuel deposition in free-living birds and to compare the quality of migration stopover sites. *Received 6 June 2008, accepted 27 May 2009.*

Key words: migration, plasma metabolites, seasonal frugivory, songbirds, stopover.

Patrones de Uso y Almacenamiento de Combustible en Paseriformes Migratorios con Relación a Recursos de Fruta en Sitios de Paradas Migratorias de Otoño

Resumen.—La tasa de acumulación de recursos energéticos por parte de las aves que se encuentran en migración puede indicar la calidad del hábitat en los sitios de paradas migratorias. Sin embargo, se sabe poco sobre acerca de cómo los hábitos de alimentación y la disponibilidad de alimentos afectan el metabolismo de las grasas y proteínas de aves silvestres en los sitios de parada. Comparamos indicadores plasmáticos de la acumulación de grasas (triglicéridos), del catabolismo de las grasas (B-hidroxibutirato) y del catabolismo de proteínas (ácido úrico) entre especies de aves paseriformes con dependencia variable de una dieta frugívora durante las paradas migratorias de otoño en Block Island, Rhode Island. También comparamos metabolitos lipídicos plasmáticos de otras tres especies que fueron capturadas en dos sitios de parada migratoria que diferían en la abundancia de frutos. La especie más frugívora, *Catharus guttatus*, tuvo la mayor cantidad de triglicéridos plasmáticos, y el ácido úrico fue más alto en la especie menos frugívora que fue muestreada en Block Island. Sin embargo, otras diferencias entre especies no se relacionaron claramente con la dieta. El B-hidroxibutirato fue el indicador plasmático más variable entre las aves muestreadas en Block Island. Los triglicéridos plasmáticos fueron significativamente más altos en individuos de *C. guttatus* capturados en Block Island, donde los frutos eran un recurso abundante, que en los individuos de la misma especie capturados en un sitio continental en el sur de Rhode Island, donde había menos frutos disponibles. Nuestros resultados sugieren que los hábitos alimenticios pueden influenciar el metabolismo de las grasas y proteínas en paseriformes migratorios. Sin embargo, es necesario delinear diseños experimentales cuidadosos y análisis de datos adecuados para controlar o minimizar los efectos de otros factores que también influencian los metabolitos plasmáticos, de modo de que éstos puedan ser usados para determinar la acumulación de energía en aves silvestres y para comparar la calidad de los diferentes sitios de paradas migratorias.

Annual migrations of birds between breeding and wintering grounds involve energetically demanding nocturnal flights fueled primarily by stored fat (Blem 1980). Small songbirds must regularly stop between flights to accumulate energy stores to continue migration. Food abundance is important for efficient refueling and can influence the time spent at stopover sites (Bibby and Green 1981; Schaub and Jenni 2000, 2001a). In addition, the quality of food resources can affect the rate at which energy stores

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The Auk, Vol. 127, Number 1, pages 108–118. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2009.09139

are replaced (Bairlein and Gwinner 1994, Bairlein 2002). Thus, migration success depends on the availability of high-quality habitats that provide adequate food resources, particularly in areas along migration corridors that support large numbers of birds during migrations.

Because many migrants use stopover sites to increase their energy stores, measuring fuel deposition rates of birds during stopovers can provide information about the quality and use of specific sites. Fuel deposition rates are typically assessed by measuring mass change of birds recaptured during stopovers or by comparing body mass of birds captured at different times of day to infer rate of mass gain as daily foraging progresses (Winker et al. 1992; Winker 1995; Dunn 2000, 2002). The first approach is limited by small sample sizes because few birds are recaptured during short stopovers, whereas the second approach assumes that arrival times and rates of mass gain are similar among all individuals (Dunn 2000, 2002), and the results of these two types of analyses are sometimes inconsistent (Winker et al. 1992, Bonter et al. 2007). Plasma metabolite profiling avoids these limitations and provides information about fuel use and deposition over the past several hours in individual birds captured once. For example, plasma concentrations of lipid metabolites increase during fat deposition (triglyceride) and catabolism (B-hydroxybutyrate, nonesterified fatty acids, glycerol), and plasma uric acid increases during protein catabolism (Stevens 1996). Accordingly, plasma triglycerides and B-hydroxybutyrate were directly related to mass changes of captive birds over a period of several hours (Jenni-Eiermann and Jenni 1994, Jenni and Schwilch 2001) to several days (Williams et al. 1999, Seaman et al. 2005). Plasma metabolite profiling has been used to detect differences in fuel deposition rates of migrating birds and habitat quality at stopover sites (Schaub and Jenni 2001b; Guglielmo et al. 2002, 2005; Ydenberg et al. 2002; Acevedo Seaman et al. 2006; Williams et al. 2007). Here, we use plasma metabolite profiling to compare fuel deposition rates among a variety of songbirds throughout autumn migration at a stopover site and among selected songbirds with different foraging strategies at 2 stopover sites with different fruit abundance.

Many passerine species in eastern North America switch from a primarily insectivorous diet on their breeding grounds to a primarily frugivorous diet during autumn migration (Parrish 1997). This dietary plasticity allows birds to utilize fruit resources that are often superabundant during autumn and that are presumably less energetically expensive to find and eat than insect prey (Parrish 2000). In addition, many temperate fruits are high in fat or sugar (Thompson and Willson 1979, White 1989, Smith et al. 2007a), which may facilitate migratory fattening (Bairlein and Simons 1995, Stevens 1996). We hypothesized that higher fruit consumption can enhance fuel deposition rates of birds during migratory stopovers. We tested this hypothesis in two ways: (1) we compared plasma metabolites from a variety of songbirds that differed in degree of frugivory while they inhabited a stopover site with abundant fruit, and (2) we compared fuel deposition rates of 3 songbird species with different foraging strategies while they inhabited 2 stopover sites that differed in fruit abundance. Because we are involved in long-term (>40 years) bird-banding programs at both the southern New England stopover sites used in the present study, our objectives also included determining the relative importance of environmental and methodological variables that may influence plasma lipid and protein metabolite concentrations and their interpretation as indicators of physiological and nutritional state of migrating songbirds.

Methods

Study areas.—We conducted our study at 2 locations in southern Rhode Island. Block Island, which is located ~19 km off the southern coast of Rhode Island (41°12′N, 71°35′W), is ideally located to receive large numbers of migrating birds that frequently drift offshore when they encounter the strong northwesterly winds typical during autumn in southern New England's coastal areas. These migrants reorient themselves and concentrate at the north end of the island before flying back to the mainland to continue migration (Able 1977). The Clay Head Preserve comprises a large area of maritime shrubland habitat at the north end of the island (~77 ha) that serves as a stopover site for many of these passerine species during autumn migrations (Baird and Nisbet 1960, Reinert et al. 2002). This area is characterized during autumn by superabundant wild fruits that provide a food resource for passerine migrants during autumn stopover (Parrish 1997, Smith et al. 2007a). The shrubland community is dominated by woody fruit-bearing shrubs, such as Arrowwood Viburnum (*Viburnum dentatum*), Northern Bayberry (*Myrica pensylvanica*), Black Chokeberry (*Aronia melanocarpa*), and Common Winterberry (*Ilex verticillata*). The dense understory also contains fruiting plant species such as American Pokeweed (*Phytolacca americana*), Virginia Creeper (*Parthenocissus quinquefolia*), and Northern Dewberry (*Rubus flagellaris*). Highly invasive species, namely Oriental Bittersweet (*Celastrus orbiculatus*), Multiflora Rose (*Rosa multiflora*), and Autumn Olive (*Elaeagnus umbellata*) are also present within Clay Head Preserve.

The Kingston Wildlife Research Station (KWRS) is located in southern Rhode Island in South Kingstown (41°27′N, 71°31′W). The landscape of this area is primarily deciduous forest patches fragmented by developed land and agricultural fields. Banding of songbirds has occurred each fall since 1956 along a set of established net lanes within deciduous woodland and early-successional habitats in the canopy openings. The forest canopy is dominated by White Ash (*Fraxinus americana*), Red Maple (*Acer rubrum*), and oaks (*Quercus* spp.). Dominant fruiting species in the understory and canopy openings include Common Greenbrier (*Smilax rotundifolia*), Oriental Bittersweet, European Privet (*Ligustrum vulgare*), and Fox Grape (*Vitis labrusca*). Arrowwood Viburnum, American Pokeweed, Virginia Creeper, and Common Winterberry are rare and occur in isolated patches in the understory and canopy openings.

Within-site comparisons.—We sampled blood from 8 species of migratory passerines that commonly occur on Block Island. These species were selected because they were captured in sufficient numbers ($n \geq 10$) and differ in level of frugivory while on Block Island during autumn migration. Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Dendroica coronata*), Gray Catbird (*Dumetella carolinensis*), and Red-eyed Vireo (*Vireo olivaceus*) are highly frugivorous during autumn migration on Block Island (≥74% fruit in fecal samples; Parrish 1997). White-throated Sparrow (*Zonotrichia albicollis*), Dark-eyed Junco (*Junco hyemalis*), and Blue-headed Vireo (*V. solitarius*) consume considerably

less fruit and more insects than these other species during autumn migration (≤62% fruit in fecal samples; Parrish 1997). Blood samples from 2 White-crowned Sparrows (*Z. leucophrys*) were combined with those from the congeneric White-throated Sparrow (hereafter "*Zonotrichia*") for the analyses.

We designed our blood-sampling protocol so that it could fit within the typical daily schedule at bird-banding stations. We captured birds using 30-mm nylon mist nets situated along established trails within the shrubland habitat in Clay Head Preserve during autumn 2005. Nets were opened at sunrise on each morning of operation, and birds were included in subsequent analyses if they were captured 1–6 h after sunrise. This ensured that birds had begun foraging in the morning before they were captured. Birds were extracted from nets at intervals of 20–30 min and then brought to a central location where they were held in cloth holding-bags until morphological measurements and blood samples were obtained. We drew ~50 μL of blood from the brachial vein after puncture with a 27-gauge needle and collected it in heparinized capillary tubes. After blood was drawn, we measured wing chord and body mass and then released the birds. We recorded the time of day as net check time when birds were extracted from nets and then converted the time of day to number of full hours plus fractions of hours after sunrise (hereafter "hours after sunrise"). This controlled for changes in time of sunrise as the season progressed. Bleed time was recorded as the time elapsed between the net check and blood sampling. Only birds for which bleed time was ≤30 min were included in subsequent analyses. Blood samples were centrifuged at 8,000 rpm for 10 min to separate plasma from red blood cells, and plasma was then stored at −80°C until analysis.

Between-site comparisons.—We captured and bled Hermit Thrushes, Yellow-rumped Warblers, and White-throated Sparrows at KWRS and on Block Island. We selected these species because they are commonly captured at both sites and are seasonally frugivorous during autumn migration (Parrish 1997). We conducted blood sampling, processed blood, and measured birds using the same procedures described above. Birds were then banded with serially numbered federal aluminum leg bands and released. Nets were operated at both sites on 4 days in 2004 (21, 23, 26, and 28 October) and 4 days in 2005 (16, 18, 20, and 27 October). The simultaneous capture of birds at both sites minimizes differences in weather or migration patterns among sampling days at the 2 sites. We also minimized temporal variation in daily foraging by including only birds captured within the same 2.5-h period in the morning at each site on each sampling day.

We assessed frequency of occurrence of 10 plant species that produce fruits and the presence of ripe fruit at each site in 2005 to compare the availability of fruit resources between sites for the following species: Arrowwood Viburnum, Northern Bayberry, American Pokeweed, Virginia Creeper, Black Chokeberry, *Rosa* spp., Oriental Bittersweet, Common Winterberry, Common Greenbrier, and European Privet. Sampling was conducted within twenty-four 4-m^2 plots located 1 m into the vegetation along the established net lanes or trails. We recorded the presence of plant species that produce fruits and the presence of ripe fruit on these plants in each plot on Block Island and at KWRS on 6 and 7 October 2005, respectively. We recognize that there may be annual variation in fruit production and that fruit availability may have been different in 2004 and 2005. However, such variation is likely to affect these 2 sites similarly each year given their relative proximity.

Measurement of plasma metabolites.—We measured concentrations of triglyceride (TRIG), B-hydroxybutyrate (BUTY), and uric acid in plasma collected for within-site comparisons among species captured on Block Island, and we measured TRIG and BUTY in plasma collected for between-site comparisons (Block Island vs. KWRS). We measured TRIG by sequential endpoint assay (Sigma, St. Louis, Missouri; 5 μL plasma, 240 μL reagent A, 60 μL reagent B) by first measuring free glycerol and then subtracting free glycerol concentration from measured total triglyceride concentration. We measured BUTY by kinetic assay (R-Biopharm, Marshall, Michigan; 5 μL sample, 150 μL working solution, 3 μL BUTY dehydrogenase, read kinetically for 30 min) using a method similar to that of Guglielmo et al. (2005). We measured uric acid by endpoint assay (TECO Diagnostics, Anaheim, California; 5 μL sample, 300 μL reagent). Samples with small plasma volumes were diluted 2-fold to 3-fold with 0.9% NaCl before all assays, and we repeated measurements until the coefficient of variation between replicates was <10%.

Statistical analyses.—The bird species that we used vary considerably in overall body size, and these structural differences in body size will influence body mass (Connell et al. 1960). Thus, we adjusted body mass for a measure of body size by using the residuals from linear regression of body mass and wing length in all subsequent analyses. We used an information-theoretic approach to investigate the importance of 5 variables for explaining variation in TRIG, BUTY, and uric acid concentrations of birds during autumn stopover on Block Island. We evaluated a model set containing all possible combinations of species, hours after sunrise, date, size-corrected body mass, and bleed time. We calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) and used differences in AIC_c ($\Delta_i = AIC_{ci} - AIC_{cmin}$) to rank candidate models (Burnham and Anderson 2002). We considered candidate models with $\Delta_i < 2$ substantially supported (Burnham and Anderson 2002). We used Akaike weights (w_i) to calculate evidence ratios (w_1/w_j; Burnham and Anderson 2002) to determine the relative likelihood of each candidate model (w_j) compared with the highest-ranked model (w_1). We then calculated the relative importance ($w+(j)$) of each explanatory variable by summing the w_i across all candidate models in which that variable occurred (Burnham and Anderson 2002). We used Pearson's correlation coefficients to clarify the direction of the relationship between the highest-ranked continuous variables and metabolite concentrations. We then used analysis of covariance (ANCOVA) with post hoc Tukey's HSD tests to test for explicit differences in metabolite concentrations among the species captured on Block Island in autumn 2005. We used relative importance values as a guide to determine which variables (hours after sunrise, date, bleed time, and body mass adjusted for body size) to include as covariates in ANCOVA. We then eliminated covariates that did not contribute significantly to the model.

We conducted preliminary analyses to determine whether metabolite concentrations differed between years in all birds except Hermit Thrush because of small sample sizes in 2004. Two-factor analysis of variance (ANOVA) with year and species as fixed variables revealed no differences between years; therefore, we combined years for all subsequent analyses. Bleed time was not recorded for all birds in 2004 at KWRS; therefore, we determined

whether bleed time could be excluded as an explanatory variable by calculating Pearson's correlation coefficients between bleed time and metabolite concentrations and comparing bleed time among sites and species with two-way ANOVA for all other samples for which bleed time was recorded. Bleed time was not significantly correlated with TRIG ($P = 0.81$) or BUTY ($P = 0.10$) concentrations, and average bleed time was similar between sites ($F = 2.1$, df = 1 and 58, $P = 0.15$) and among species ($F = 0.1$, df = 2 and 58, $P = 0.91$), presumably because we limited our site-comparison data set by species, time of day, and date. Our study design for the between-site comparison effectively controlled for date by limiting sampling to 4 days each year. Thus, we eliminated bleed time and date as potential covariates. We used an information-theoretic approach (as described above for within-site comparisons) to evaluate the importance of site, species, hours after sunrise, and size-corrected body mass for explaining variation in TRIG and BUTY concentrations in birds captured at the 2 stopover sites. We then used two-way ANOVA with site and species as fixed factors to test for explicit differences in TRIG concentrations between sites. Heterogeneity of variance of BUTY concentrations between sites for Hermit Thrush and between species at KWRS precluded the use of two-way ANOVA to test for specific site differences. Thus, we used one-way ANOVA to compare BUTY concentrations among species on BI and the Kruskal-Wallis test to compare BUTY concentrations among species at KWRS. We then used two-sample *t*-tests using the Satterthwaite approximation for degrees of freedom when there was unequal variance between species or sites. Species-specific differences in BUTY concentrations between sites were considered significant at $P = 0.017$, taking into account Bonferroni correction for comparing 3 species.

We calculated percent presence (number of plots present / total plots × 100) of each fruiting plant species and presence of ripe fruit separately for each site and year for tabular representation of plant presence data. We used chi-square tests (2 × 2 contingency tables) to compare the frequency of occurrence for each fruiting plant species or ripe fruit between sites.

The TRIG, BUTY, and uric acid concentrations of birds captured on Block Island during autumn 2005 deviated from normality. Therefore, we log $(X + 1)$ transformed TRIG and BUTY, and we transformed uric acid using the fourth root power transformation, $X^{(0.25)}$, which normalized the data. These transformed metabolite concentrations were used for all within-site analyses on Block Island. The BUTY concentrations of birds captured at KWRS and on Block Island were log $(X + 1)$ transformed and, consequently, the data were normally distributed for between-site comparisons. All statistical tests were calculated using SAS, version 9.1 (SAS Institute, Cary, North Carolina), with the significance level set at $P < 0.05$.

RESULTS

Variation in plasma metabolites of birds captured on Block Island.—Species, hours after sunrise, and size-corrected body mass were included in the highest-ranked model explaining variation in plasma TRIG (see Table 1 for raw metabolite concentrations used for within-site analyses); however, 2 other models also had substantial support, with $\Delta_i < 2$ (Table 2). Relative importance values suggested that species and hours after sunrise were more important than date, bleed time, and size-corrected body mass for explaining variation in TRIG (Table 3). Hours after sunrise was consistently positively correlated with TRIG across species (overall: $r = 0.36$, $P < 0.001$; Hermit Thrush: $r = 0.47$, $P = 0.001$; Yellow-rumped Warbler: $r = 0.43$, $P = 0.01$; Gray Catbird: $r = 0.39$, $P = 0.05$; Red-eyed Vireo: $r = 0.21$, $P = 0.51$; *Zonotrichia*: $r = 0.60$, $P = 0.01$; Dark-eyed Junco: $r = 0.38$, $P = 0.15$; Blue-headed Vireo: $r = 0.47$, $P = 0.12$).

The model explaining plasma BUTY concentrations was more complex because species, hours after sunrise, date, and bleed time were included in the highest-ranked model (Table 2). In addition, there were 3 other models with $\Delta_i < 2$, which were only 1.6–1.9 times less likely to explain more variation than the highest-ranked model (Table 2). Relative importance values suggest that species, date, and bleed time were more important than hours after sunrise and size-corrected body mass (Table 3). Date was negatively correlated with BUTY, and correlation coefficients were variable among species (overall: $r = -0.17$, $P = 0.04$; Hermit Thrush: $r = -0.06$, $P = 0.69$; Yellow-rumped Warbler: $r = -0.59$, $P < 0.001$; Gray Catbird: $r = -0.14$, $P = 0.50$; Red-eyed Vireo: $r = -0.88$, $P < 0.001$; *Zonotrichia*: $r = 0.03$, $P = 0.90$; Dark-eyed Junco: $r = 0.43$, $P = 0.10$; Blue-headed Vireo: $r = 0.18$, $P = 0.58$). Bleed time was positively correlated with BUTY, although the strength of this correlation varied considerably among species (overall: $r = 0.15$,

TABLE 1. Capture data and metabolite concentrations for migratory birds sampled on Block Island, Rhode Island, during autumn 2005. Mean (± SE) concentrations of plasma triglyceride (TRIG), B-hydroxybutyrate (BUTY), and uric acid (UA) are provided although transformed values were used in all statistical analyses.

Species[a]	*n*	Date[b]	HAS[c]	Bleed time[d]	Mass[e]	TRIG (mM)	BUTY (mM)	UA (mM)
Hermit Thrush	43	289–307	3.02 ± 0.19	16 ± 1	31.4 ± 0.3	2.44 ± 0.12	0.95 ± 0.08	0.36 ± 0.03
Gray Catbird	25	277–301	3.28 ± 0.27	15 ± 1	42.7 ± 0.8	1.53 ± 0.13	1.39 ± 0.13	0.37 ± 0.04
Yellow-rumped Warbler	34	277–307	3.33 ± 0.23	15 ± 1	13.8 ± 0.3	1.75 ± 0.11	2.53 ± 0.18	0.36 ± 0.04
Red-eyed Vireo	12	277–294	2.99 ± 0.28	15 ± 1	18.6 ± 0.5	1.69 ± 0.15	1.56 ± 0.24	0.50 ± 0.06
Zonotrichia	16	289–300	3.01 ± 0.31	16 ± 1	25.8 ± 0.7	1.72 ± 0.22	2.37 ± 0.34	0.79 ± 0.05
Dark-eyed Junco	16	290–307	2.96 ± 0.32	18 ± 1	19.9 ± 0.7	1.80 ± 0.17	1.60 ± 0.28	0.71 ± 0.09
Blue-headed Vireo	12	289–307	4.26 ± 0.33	13 ± 1	15.7 ± 0.5	2.01 ± 0.28	1.44 ± 0.12	1.00 ± 0.09

[a] *Zonotrichia* includes White-throated Sparrow and White-crowned Sparrow.
[b] Range of all capture dates for a given species. Date = Julian date of capture, where 277 = 4 October 2005.
[c] Mean (± SE) hours after sunrise at capture.
[d] Mean (± SE) minutes between net extraction and blood sampling.
[e] Mean (± SE) body mass (g) at blood sampling.

TABLE 2. Model selection results for the 5 highest-ranked candidate models that explain variation in plasma metabolite concentrations of birds sampled on Block Island, Rhode Island, during autumn 2005. Models are ranked on the basis of Akaike weights (w_i).

Metabolite and model[a]	n	K[b]	Maximized $\log_e(L)$[c]	AIC_c	Δ_i	w_i	w_1/w_j[d]
Triglyceride							
Y = species + HAS + mass	158	10	379.1	−736.65	0.00	0.340	
Y = species + HAS	158	9	377.4	−735.50	1.16	0.190	1.8
Y = species + HAS + mass + date	158	11	379.4	−734.93	1.72	0.144	2.4
Y = species + HAS + mass + bt	158	11	379.1	−734.47	2.19	0.114	3.0
Y = species + HAS + date	158	10	377.6	−733.66	3.00	0.076	4.5
B-hydroxybutyrate							
Y = species + HAS + bt + date	156	11	328.1	−632.40	0.00	0.337	
Y = species + HAS + mass + bt + date	156	12	328.8	−631.51	0.89	0.216	1.6
Y = species + bt + date	156	10	326.4	−631.34	1.06	0.198	1.7
Y = species + mass + bt + date	156	11	327.5	−631.08	1.32	0.174	1.9
Y = species + HAS + date	156	10	324.1	−626.63	5.77	0.019	17.9
Uric acid							
Y = species + date	136	9	341.2	−662.90	0.00	0.310	
Y = species + bt + date	136	10	341.9	−661.99	0.91	0.197	1.6
Y = species + mass + date	136	10	341.4	−661.11	1.78	0.127	2.4
Y = species + HAS + date	136	10	341.2	−660.67	2.23	0.102	3.0
Y = species + mass + bt + date	136	11	342.2	−660.23	2.67	0.082	3.8

[a] Parameters: Y = transformed metabolite concentrations (see text), HAS = hours after sunrise at capture, date = Julian date of capture, mass = residuals from linear regression of body mass and wing length, and bt = time (min) between net extraction and blood sampling.
[b] Number of estimable regression parameters in model including the intercept and variance.
[c] Calculated as: $[-0.5n*\log_e(RSS/n)]$, where RSS is the residual sum of squares.
[d] Evidence ratio where w_1 = the highest-ranked model.

$P = 0.06$: Hermit Thrush: $r = 0.29$, $P = 0.06$; Yellow-rumped Warbler: $r = -0.03$, $P = 0.87$; Gray Catbird: $r = 0.40$, $P = 0.05$; Red-eyed Vireo: $r = 0.01$, $P = 0.97$; *Zonotrichia*: $r = 0.55$, $P = 0.03$; Dark-eyed Junco: $r = 0.12$, $P = 0.67$; Blue-headed Vireo: $r = 0.35$, $P = 0.27$).

Species and date were included in the highest-ranked model explaining plasma uric acid concentrations (Table 2). Models that included bleed time or size-corrected body mass also had substantial support. Relative importance values clarified that species and date were the most important variables explaining uric acid concentrations (Table 3). However, we did not detect a significant correlation between date and uric acid (overall: $r = -0.09$, $P = 0.27$; Hermit Thrush: $r = -0.25$, $P = 0.12$; Yellow-rumped Warbler: $r = -0.35$, $P = 0.10$; Gray Catbird: $r = -0.13$, $P = 0.59$; Red-eyed Vireo: $r = -0.52$, $P = 0.08$; *Zonotrichia*: $r = 0.21$, $P = 0.43$; Dark-eyed Junco: $r = -0.11$, $P = 0.67$; Blue-headed Vireo: $r = -0.40$, $P = 0.22$).

TABLE 3. Relative importance ($w + (j)$) of predictor variables that explain variation in plasma metabolite concentrations of migratory birds on Block Island, Rhode Island, during autumn 2005.

Model set[a]	Species	HAS[b]	Date[c]	Mass[d]	Bleed time[e]
Triglyceride	1.000	1.000	0.293	0.646	0.250
B-hydroxybutyrate	1.000	0.605	0.963	0.417	0.959
Uric acid	1.000	0.176	0.859	0.342	0.430

[a] Transformed metabolite concentrations were used for analyses (see text).
[b] Hours after sunrise at capture.
[c] Julian date of capture.
[d] Residuals from linear regression of body mass and wing length.
[e] Time (minutes) between net extraction and blood sampling.

Hermit Thrush had higher TRIG concentrations than all other species after accounting for hours after sunrise (species: $F = 8.2$, df = 6 and 157, $P < 0.001$; HAS: $F = 35.8$, df = 1 and 157, $P < 0.001$; Fig. 1). We detected a significant species*date interaction for BUTY. If we restricted our data set to October samples only when we captured 90% of individuals, this interaction was no longer significant. We found significant differences in BUTY concentrations among species captured during October while controlling for both date and bleed time (species: $F = 17.2$, df = 6 and 140, $P < 0.001$; date: $F = 14.0$, df = 1 and 140, $P < 0.001$; bleed time: $F = 15.6$, df = 1 and 140, $P < 0.001$). Yellow-rumped Warbler had higher BUTY concentrations than all other species except *Zonotrichia* spp. (Fig. 1), and *Zonotrichia* had higher BUTY concentrations than Hermit Thrush and Gray Catbird (Fig. 1). *Zonotrichia*, Dark-eyed Junco, and Blue-headed Vireo had higher concentrations of uric acid than the other 4 species after correcting for date (species: $F = 25.0$, df = 6 and 135, $P < 0.001$; date: $F = 7.9$, df = 1 and 135, $P = 0.001$; Fig. 1).

Site differences in plasma metabolites.—Site and species were included in the highest-ranked model explaining variation in plasma TRIG concentrations (see Table 4 for raw lipid metabolite concentrations used for between-site analyses); however, the model that included site, species, and hours after sunrise also had substantial support (Table 5). Species and site differences were the most important variables, and hours after sunrise and body mass were less important for explaining variation in TRIG concentrations of birds captured at the 2 sites (Table 6). Concentrations of TRIG were higher in birds captured on Block Island than in those from KWRS, and this difference can primarily be attributed to higher TRIG concentrations in Hermit Thrushes from Block

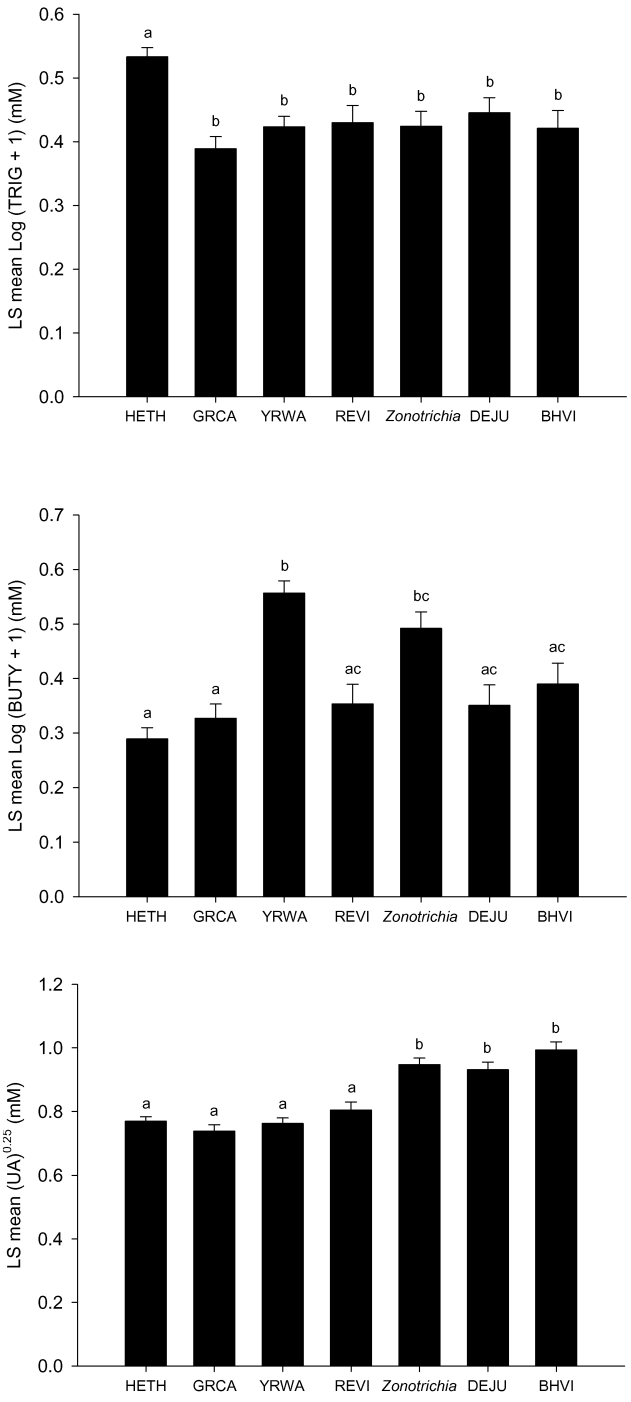

FIG. 1. Least-squares (LS) means (± SE) of plasma triglyceride (log [TRIG + 1]), B-hydroxybutyrate (log [BUTY + 1]), and uric acid ($UA^{0.25}$) concentrations after correcting for significant covariates (see text) for migratory passerine species captured on Block Island, Rhode Island, in autumn 2005. Abbreviations: HETH = Hermit Thrush, GRCA = Gray Catbird, YRWA = Yellow-rumped Warbler, REVI = Red-eyed Vireo, DEJU = Dark-eyed Junco, and BHVI = Blue-headed Vireo. *Zonotrichia* includes White-throated and White-crowned sparrows. Bars with different letters within each graph are significantly different.

Island than in those from KWRS (site: $F = 6.7$, df = 1 and 71, $P = 0.01$; species: $F = 3.3$, df = 2 and 71, $P = 0.04$; site*species: $F = 3.1$, df = 2 and 71, $P = 0.05$; Fig. 2).

Species and hours after sunrise were included in the highest-ranked model explaining variation in plasma BUTY concentrations, but 2 other models had substantial support (Table 5). Interspecific differences and hours after sunrise had the highest relative importance values, whereas site and body mass were less important for explaining variation in plasma BUTY concentrations of birds at the 2 stopover sites (Table 6). Overall, BUTY concentrations were similar between sites ($t = 1.0$, df = 70, $P = 0.33$; Fig. 2). Hermit Thrushes had the lowest BUTY concentrations of the 3 species on Block Island ($F = 13.6$, df = 2 and 39, $P < 0.001$), but there were no interspecific differences in BUTY concentrations at KWRS ($\chi^2 = 0.4$, df = 2, $P = 0.84$; Fig. 2).

Site differences in fruit availability.—In 2005, the following plant species that produce fruits were more common on Block Island than at KWRS: Arrowwood Viburnum, Northern Bayberry, Virginia Creeper, Black Chokeberry, and *Rosa* spp. (Table 7). By contrast, Common Greenbrier and European Privet were less common on Block Island than at KWRS (Table 7). The following plant species more commonly had ripe fruit on Block Island than at KWRS: Arrowwood Viburnum, Virginia Creeper, Black Chokeberry, and *Rosa* spp. (Table 7). There were significantly more fruits present on Common Greenbrier and European Privet at KWRS than on Block Island (Table 7).

DISCUSSION

Our results demonstrate that plasma lipid and protein metabolites differ among species of migrating songbirds during autumn migration, which may be attributable, in part, to interspecific differences in diet habits and fruit availability at stopover sites. In addition, factors such as time of capture, time taken to bleed the bird, and date may affect individual plasma lipid and protein metabolite concentrations in different ways. However, standardized protocols that limit blood sampling to a portion of the day or that restrict sampling to certain species or periods of the migration season will further minimize the influence of these potentially confounding variables on plasma metabolite concentrations in free-living birds.

Plasma triglyceride as an indicator of fattening.—Our results suggest that plasma TRIG is likely the single most useful lipid metabolite for assessing fattening and fuel deposition in free-living migratory birds. Plasma TRIG was relatively unaffected by most potentially confounding factors common in field studies, such as time lag between net extraction and blood sampling or date of capture. Plasma TRIG values consistently increased with hours after sunrise when birds were captured, and this positive relationship between time of day and TRIG has been shown in many species of free-living passerines (Jenni and Jenni-Eiermann 1996, Jenni-Eiermann and Jenni 1997, Guglielmo et al. 2005). Concentrations of TRIG increase rapidly in response to the onset of feeding after sunrise and may eventually plateau (Jenni-Eiermann and Jenni 1996, 1997). We did not detect such a plateau, although we only sampled birds ≤6 h after sunrise.

Plasma TRIG concentrations in our study indicated that fattening rates of migrating songbirds differ among species and

TABLE 4. Capture data and plasma metabolite concentrations for 3 migratory species captured on Block Island (BI) and at Kingston Wildlife Research Station (KWRS), Rhode Island, during autumn 2004 and 2005.

Species	Site	*n*	HAS[a]	Mass[b]	TRIG[c]	BUTY[d]
Hermit Thrush	KWRS	8	2.06 ± 0.22	29.8 ± 0.5	1.29 ± 0.19	2.18 ± 0.59
	BI	15	2.34 ± 0.22	31.9 ± 0.5	2.04 ± 0.08	1.16 ± 0.14
Yellow-rumped Warbler	KWRS	11	2.14 ± 0.17	14.0 ± 0.5	1.22 ± 0.19	2.42 ± 0.29
	BI	19	2.50 ± 0.14	13.6 ± 0.4	1.47 ± 0.09	2.47 ± 0.21
White-throated Sparrow	KWRS	11	2.27 ± 0.25	25.1 ± 0.6	1.31 ± 0.20	2.25 ± 0.30
	BI	9	2.44 ± 0.17	25.4 ± 0.6	1.32 ± 0.17	2.53 ± 0.38

[a] Mean (± SE) hours after sunrise at capture.
[b] Mean (± SE) body mass (grams) at blood sampling.
[c] Mean (± SE) concentrations (mM) of plasma triglyceride.
[d] Mean (± SE) concentrations (mM) of plasma B-hydroxybutyrate. Transformed values were used in all analyses (see text).

TABLE 5. Model selection results for the 5 highest-ranked candidate models that explain variation in plasma metabolite concentrations of birds sampled on Block Island and at Kingston Wildlife Research Station, Rhode Island, during autumn 2004 and 2005. Models are ranked on the basis of Akaike weights (w_i).

Metabolite and model[a]	*n*	*K*[b]	Maximized $\log_e$(L)[c]	AIC_c	Δ_i	w_i	w_1/w_j[d]
Triglyceride							
Y = site + species	73	5	50.8	−90.64	0.00	0.423	
Y = site + species + HAS	73	6	51.2	−89.12	1.53	0.197	2.1
Y = site + species + mass	73	6	50.8	−88.31	2.33	0.132	3.2
Y = site + species + HAS + mass	73	7	51.3	−86.83	3.81	0.063	6.7
Y = site	73	3	46.2	−86.11	4.53	0.044	9.7
B-hydroxybutyrate							
Y = species + HAS	73	5	144.4	–277.81	0.00	0.300	
Y = species	73	4	142.8	–276.99	0.83	0.199	1.5
Y = site + species + HAS	73	6	145.0	–276.66	1.15	0.168	1.8
Y = species + HAS + mass	73	6	144.4	–275.57	2.24	0.098	3.1
Y = site + species	73	5	143.0	–275.19	2.63	0.081	3.7

[a] Parameters: Y = metabolite concentration (log [*X* + 1] transformed values were used for B-hydroxybutyrate analyses), HAS = hours after sunrise at capture, and mass = residuals from linear regression of body mass and wing length.
[b] Number of estimatable regression parameters in model including the intercept and variance.
[c] Calculated as $[-0.5n^*\log_e(RSS/n)]$, where RSS is the residual sum of squares.
[d] Evidence ratio where w_1 = the highest-ranked model.

stopover sites, and these differences may be related to diet and quality of food resources at stopover sites in addition to other species-specific traits. For example, Hermit Thrush had the highest plasma TRIG concentrations, and it is also one the most frugivorous of the species that we studied. However, Hermit Thrush is also one of the heaviest species sampled, and some previous studies of songbirds have demonstrated a positive relationship between plasma TRIG and body mass (Guglielmo et al. 2005, Cerasale and Guglielmo 2006) or fat mass (Smith and McWilliams 2009). We found that body mass was only moderately related to plasma TRIG across species even after correcting for overall body size, and visual estimates of subcutaneous fat revealed that Hermit Thrush had average fat scores compared with other species. Therefore, the higher TRIG concentrations of Hermit Thrush in the present study are not likely attributable simply to the larger overall body size of this species compared with other, smaller-bodied species.

If the degree of seasonal frugivory is positively related to plasma TRIG, Hermit Thrush should have the highest TRIG, along with other primarily frugivorous species (Yellow-rumped Warbler, Red-eyed Vireo, and Gray Catbird). However, these other species did not have TRIG levels as high as those in Hermit Thrush, which suggests that interspecific differences within a site cannot be fully explained by diet habits. Further support for the importance of diet habits on plasma TRIG concentrations is provided by our finding that plasma TRIG was higher in Hermit

TABLE 6. Relative importance ($w + (j)$) of predictor variables that explain variation in plasma metabolite concentrations of migratory passerines captured on Block Island and at Kingston Wildlife Research Station, Rhode Island, in autumn 2004 and 2005.

Model set	Site	Species	HAS[a]	Mass[b]
Triglyceride	0.895	0.916	0.332	0.249
B-hydroxybutyrate[c]	0.327	0.997	0.618	0.250

[a] Hours after sunrise at capture.
[b] Residuals from linear regression of body mass and wing length.
[c] Log (*X* + 1) concentrations were used in analyses.

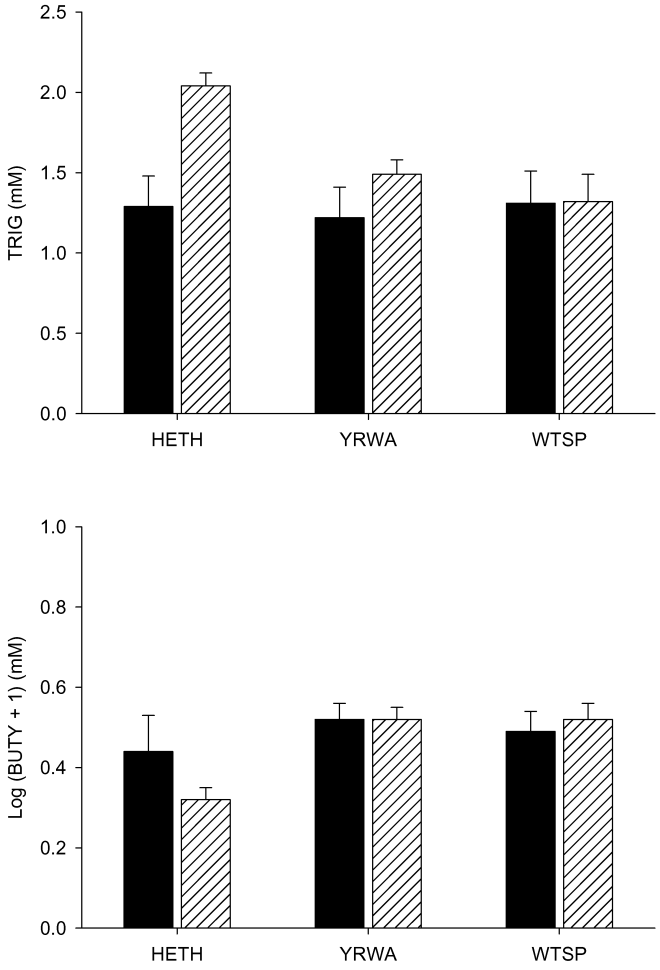

FIG. 2. Mean (± SE) plasma triglyceride (TRIG) and B-hydroxybutyrate (log [BUTY + 1]) concentrations in Hermit Thrushes (HETH), Yellow-rumped Warblers (YRWA), and White-throated Sparrows (WTSP) captured at Kingston Wildlife Research Station (solid bars) or on Block Island (hatched bars), Rhode Island, during autumn migration, 2004 and 2005.

TABLE 7. Presence of 10 plant species (percent occurrence in twenty-four 4-m^2 plots) on Block Island (BI) and at Kingston Wildlife Research Station (KWRS), Rhode Island, and presence of ripe fruits (percent occurrence in the same plots) of each plant species during 2005.

	Plant presence (%)			Fruit presence (%)		
Species	BI	KWRS	χ^2 [a]	BI	KWRS	χ^2 [a]
Arrowwood Viburnum	83	38	10.5**	50	8	10.1**
Northern Bayberry	29	0	8.4**	13	0	3.2
Virginia Creeper	38	0	11.1**	29	0	4.4**
American Pokeweed	4	0	1.0	4	0	1.0
Black Chokeberry	17	0	4.4*	17	0	4.4*
Common Winterberry	8	8	0.0	4	4	0.0
Oriental Bittersweet	42	54	0.8	29	38	0.4
Common Greenbrier	4	75	25.2***	0	21	5.6*
Rosa spp.	71	13	16.8***	58	8	13.5***
European Privet	0	71	26.3***	0	46	14.3***

[a] $*P < 0.05$, $**P < 0.01$, $***P < 0.001$; df = 0.05 and 1.

Thrushes captured on Block Island, where high-quality native fruits are abundant, than in Hermit Thrushes captured at KWRS, where fruit availability and quality were much lower. In addition, Hermit Thrushes captured on Block Island had higher plasma TRIG than Yellow-rumped Warblers and White-throated Sparrows, and these interspecific differences were absent in birds captured at KWRS, where fruit was less abundant.

We recognize that there are many other differences between species and our study sites, in addition to fruit resources, that may contribute to variation in plasma TRIG concentrations. For example, Hermit Thrushes, White-throated Sparrows, Dark-eyed Juncos, and Yellow-rumped Warblers all winter on Block Island to some extent (S. Comings pers. comm.); however, species that are strictly migrants during autumn on Block Island (Blue-headed Vireo and Red-eyed Vireo) showed no extraordinary pattern of fat deposition. Gray Catbird is the only species sampled in our study that is known to breed on Block Island (S. Comings pers. comm.), and plasma TRIG was lowest in this species, perhaps because some birds were not yet in migratory state. It is also possible that the fuel deposition rate was influenced by age or sex (Woodrey and Moore 1997, Yong et al. 1998, Jones et al. 2002, Heise and Moore 2003). Age is not likely an important factor explaining interspecific variation in fuel deposition rates on Block Island, because nearly all birds captured were hatch-year. In general, more older birds are captured at KWRS than on Block Island, but this is not likely a significant factor for Hermit Thrushes, most of which captured at KWRS were hatch-year. Further, Dark-eyed Junco was the only species in which more males than females were captured (among individuals that could be reliably sexed). Molt is probably irrelevant to the interspecific differences in plasma metabolites reported here, because most of the birds sampled were just completing their prebasic molt and so were at relatively similar molt stages. In addition, plasma lipid metabolites do not correlate strongly with intensity of molt throughout the prebasic molting period in migratory songbirds (Jenni-Eiermann and Jenni 1996). Given that diet and other interspecific differences may contribute to variation in plasma metabolite concentration, such interspecific comparisons should be undertaken with caution or limited to species with very similar life histories, diet habits, and migration strategies.

Plasma B-hydroxybutyrate as an indicator of fat catabolism.— The most variable of the 3 metabolites measured in this study was BUTY, and the most plausible explanatory AIC_c models included covariates such as bleed time. The positive relationship between bleed time and plasma BUTY concentrations in birds captured in our study has previously been described in free-living birds, though not consistently across all studies or species (Jenni-Eiermann and Jenni 1996; Guglielmo et al. 2002, 2005; Acevedo Seaman et al. 2006). Given that BUTY increases rapidly during transitions between physiological states and short-term fasts during the day (Jenni-Eiermann and Jenni 1991, 1997; Jenni and Jenni-Eiermann 1992), bleed time is an important covariate to measure in studies of free-living birds so that its influence on metabolite concentrations can be addressed. Plasma BUTY was also negatively related to date of capture, although this relationship appeared to be important in only a few species, like the Yellow-rumped

Warbler and the Red-eyed Vireo. The effect of date on BUTY concentrations in our study is difficult to interpret because sampling of a given bird species varied through time. Our results suggest that date will likely always be an important confounding factor in such analyses, because many different species migrate at different times within a given season.

Plasma BUTY was different among bird species captured on Block Island, even after controlling for date and bleed time, which suggests that additional factors influence BUTY concentrations. Hermit Thrush and Gray Catbird are highly frugivorous, and they had the lowest BUTY concentrations during autumn migration on Block Island, where fruit was abundant. However, other differences between species were not clearly related to diet. If BUTY is negatively affected by fruit availability, we would expect plasma concentrations to be higher at KWRS, where availability of high-energy fruits, such as Arrowwood Viburnum, is lower than on Block Island. However, site was of relatively low importance for explaining BUTY concentrations, and the interspecific differences in BUTY among birds captured on Block Island were not apparent at KWRS. We conclude that BUTY is a less consistent indicator of fuel deposition rates than TRIG in migratory passerines because of the many additional potential sources of variation.

Plasma uric acid as an indicator of protein catabolism.—Plasma uric acid concentrations differed substantially between bird species captured on Block Island. In general, less frugivorous species had higher concentrations than more frugivorous species. Given that plasma uric acid was positively related to protein intake in previous studies of captive birds (Goldstein et al. 2001, Smith et al. 2007b), the lower concentrations in free-living frugivorous birds may occur because most fruits have less protein than other available foods (Smith et al. 2007a).

Plasma uric acid was also influenced, to a lesser degree, by date of capture, although the fact that there was not a significant correlation between uric acid and date of capture for any of the species suggests that the relationship between these 2 variables may be nonlinear. If plasma uric acid is related to consumption of high-protein insect resources, this could explain the decline in plasma uric acid as autumn progressed and insect resources declined. The effect of date is not straightforward, because most of our birds were captured later in the season, primarily because of adverse weather that precluded mist netting on earlier dates. Uric acid may be useful for studies of free-living birds, because it seems to reliably indicate dietary protein intake in captive studies and because it was less sensitive to other factors like bleed time, time of day, and body mass.

Implications for habitat quality and migration monitoring at stopover sites.—Fruit availability can influence the abundance of frugivorous landbird species and their use of specific habitats during autumn migration (Blake and Hoppes 1986, Martin and Karr 1986, Parrish 2000, Suthers et al. 2000, Rodewald and Brittingham 2004). Our data suggest that highly frugivorous migratory species can refuel at a faster rate when fruit diversity, quality, and availability are high, as demonstrated by higher plasma TRIG in birds captured on Block Island. The fruit resources present at KWRS are dominated by a few species that have low energy density (e.g., Oriental Bittersweet) or that are avoided by migrating birds and persist into the winter (e.g., European Privet) more than the common high-energy fruits (e.g., Arrowwood Viburnum) found in the maritime shrubland habitat on Block Island. Therefore, these high-quality fruit resources may be a useful indicator of habitat quality at stopover sites. However, stopover habitats must provide sufficient amounts of other foods, such as insects, that can be utilized by less frugivorous species that are unable to rely primarily on fruits during autumn stopover.

Plasma metabolites can provide useful information about fuel deposition and resource use of birds at migration stopover sites, provided that several important variables are considered. Although plasma TRIG and BUTY can accurately indicate differences in mass change between sites in field-captured birds (Guglielmo et al. 2005), we suggest that plasma TRIG and uric acid, but not BUTY, are the best candidates for use at banding and monitoring stations. Within a given stopover site, plasma TRIG can provide information about short-term fuel deposition in individuals, and uric acid may provide information about relative amounts of dietary protein in birds captured once. Further, we found that plasma TRIG and uric acid were less sensitive to variation in bleed time than BUTY. This is particularly important when it is unfeasible to continuously monitor nets to record the exact time of capture. However, we stress that minimizing the time between net capture and bleed time is critical to ensuring that plasma TRIG represents the feeding state of individual birds.

Plasma lipid metabolites may reliably indicate fattening rates of birds, although comparisons among species should be limited to species with similar diet habits and to seasons when birds eat similar foods, because large differences in dietary macronutrient composition, particularly sugar and protein content, may influence lipid metabolite concentrations (Smith et al. 2007b, Smith and McWilliams 2009). Given these potential diet effects, plasma lipid metabolites are likely to be most useful for providing qualitative estimates of the trajectory of fat deposition in individual free-living birds. Using such metabolites to quantitatively estimate amount of fat deposition in free-living birds will require additional studies that directly measure both metabolite concentrations and actual fat deposition rates in conjunction with measurements of dietary macronutrient intake.

Acknowledgments

We thank S. Comings and the Nature Conservancy for field support on Block Island. We are grateful to P. Paton, L. Duda, D. Cooper, M. McEnroe, and A. Albrecht for cooperation and assistance with blood sampling and banding at Kingston Wildlife Research Station. Use of wild birds was approved under University of Rhode Island Institutional Animal Care and Use Committee protocol no. AN05-04-020. Funding was provided by the Rhode Island Agricultural Experiment Station, Sigma-Xi Grants-in-Aid of Research to S.B.S., and a National Science Foundation grant (IBN-9984920) to S.R.M. This is contribution 5213 of the University of Rhode Island Agricultural Experiment Station.

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Associate Editor: K. Winker