



CONTRIBUTION OF EMERGENT AQUATIC INSECTS TO REFUELING IN SPRING MIGRANT SONGBIRDS

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ABSTRACT.—Refueling by spring migrant landbirds is an important determinant of arrival timing and, thus, should also affect acquisition of high-quality territories and mates. Spring migrants can encounter adverse weather and low prey availability, but emergent aquatic insects (e.g., chironomid midges) may provide an important food resource in wetland areas. We used stable-carbon-isotope ($\delta^{13}\text{C}$) analysis of exhaled CO_2 as an indication of recent dietary intake (contributions from aquatic or terrestrial food webs), plasma lipid metabolite profiling to assess refueling performance, and arthropod sampling to investigate whether diet and refueling differed between Lake Erie shoreline and inland forest sites and how diet, condition, and midge availability (biomass) were associated with refueling along the lakeshore in northwestern Ohio in spring 2007 and 2008. Midge availability was not associated with refueling performance for Yellow-rumped Warblers (*Dendroica coronata*), Magnolia Warblers (*D. magnolia*), or White-throated Sparrows (*Zonotrichia albicollis*), but Magnolia Warblers had greater refueling performance as the day progressed. We detected no relationship between diet and refueling for any species; however, Yellow-rumped Warblers had a stronger aquatic $\delta^{13}\text{C}$ value at two shoreline sites than at other sites. In shoreline and inland sites, migrants used a combination of aquatic and terrestrial arthropods and received energetic benefits from their use, even within small shoreline sites (1.18–2.86 ha), which often had high densities of stopover migrants. We suggest that conservation and restoration of shoreline and inland forest patches within landscapes that contain wetlands can promote refueling by migrant landbirds. *Received 7 August 2009, accepted 26 August 2010.*

Key words: Chironomidae, diet, emergent aquatic insects, midges, migration, plasma lipid metabolites, refueling, songbirds, stable carbon isotopes, stopover ecology.

Contribución de los Insectos Acuáticos Emergentes al Reaprovisionamiento de las Aves Canoras Migratorias de Primavera

RESUMEN.—El reaprovisionamiento de las aves terrestres migratorias en la primavera es un determinante importante de la fecha de arribo y, por ende, debería también afectar la adquisición de territorios de alta calidad y de parejas. Los migrantes de primavera pueden encontrar condiciones climáticas adversas y baja disponibilidad de presas, pero los insectos acuáticos emergentes (e.g., mosquitos quironómidos) pueden brindar un recurso alimenticio importante en las áreas de humedales. Usamos i) análisis de isótopos estables de carbono ($\delta^{13}\text{C}$) de CO_2 exhalado como una indicación del consumo dietario reciente (contribuciones de las redes tróficas acuáticas o terrestres), ii) perfiles de metabolitos lipídicos del plasma como determinante del rendimiento del reabastecimiento y iii) muestreos de artrópodos para investigar a) si la dieta y el reabastecimiento difirieron entre la costa del lago Erie y los sitios de bosque tierra adentro y b) cómo la dieta, la condición y la disponibilidad de mosquitos (biomasa) se asociaron con el reabastecimiento a lo largo de la costa del lago en el noroeste de Ohio en la primavera de 2007 y 2008. La disponibilidad de mosquitos no se asoció con el rendimiento del reabastecimiento para *Dendroica coronata*, *D. magnolia* o *Zonotrichia albicollis*, pero *D. magnolia* tuvo un rendimiento del reaprovisionamiento mayor a medida que progresó el día. No detectamos una relación entre la dieta y el reabastecimiento para ninguna especie; sin embargo, *D. coronata* tuvo un valor de $\delta^{13}\text{C}$ acuático más fuerte en dos sitios costeros que en otros sitios. En los sitios de costa y de interior los migrantes usaron una combinación de artrópodos acuáticos y terrestres y tuvieron beneficios energéticos por este uso, incluso dentro de pequeños sitios de costa (1.18–2.86 ha) que frecuentemente tienen altas densidades de individuos migrantes pasajeros. Sugerimos que la conservación y la restauración de áreas costeras y de parches de bosque tierra adentro en los paisajes que contienen humedales pueden promover el reabastecimiento de las aves terrestres migratorias.

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MIGRATING LANDBIRDS HAVE high energetic demands and must use stopover sites en route to rest and replenish energy stores. During spring, migrant landbirds can encounter adverse weather and low prey availability (Moore et al. 2005). This is significant because the availability of high-quality habitats and food resources can strongly influence refueling performance (i.e., ability to gain mass; Schaub and Jenni 2001) and increase the chances of a successful migration (Moore et al. 1995). Refueling is an important determinant of arrival timing that can affect acquisition of high-quality breeding territories and mates (Alerstam and Lindström 1990, Schaub and Jenni 2000, Smith and Moore 2005). Despite the fact that early arrival is beneficial to migrants (Cristol 1995), inadequate attention has been focused on the energetic constraints and habitat requirements of landbirds during migratory stopover (Moore and Simons 1992, Moore et al. 1995, Petit 2000).

The ability of migrating birds to refuel is greatly influenced by dietary choice and can be assessed by using plasma lipid metabolite profiling, which evaluates the physiological state of an individual (Schaub and Jenni 2001). Plasma triglycerides (TRIG) are elevated during fat deposition, whereas glycerol (GLYC) and β -hydroxybutyrate (BUTY) are elevated during fasting and lipolysis. Plasma concentrations of these metabolites are directly correlated with daily gains and losses in body mass (Jenni-Eiermann and Jenni 1994, Jenni and Schwilch 2001) and can be used to distinguish songbirds that are fattening from those that are fasting (Jenni-Eiermann and Jenni 1996, 1997) and to assess refueling performance (Guglielmo et al. 2002, 2005; Ydenberg et al. 2002). Because the ability of a migrant to gain mass is considered an index of habitat quality (Dunn 2000, 2001), plasma TRIG can identify the diets and habitats that promote successful refueling by migrant songbirds (Guglielmo et al. 2005, Cerasale and Guglielmo 2010).

Stable isotope analysis has increasingly been applied to avian dietary and habitat studies because isotopic values in the tissues of consumers reflect dietary choices in a predictable manner (Pearson et al. 2003, Evans Ogden et al. 2005, Podlesak et al. 2005). Stable isotopes of carbon have been used to determine the relative contributions of marine and terrestrial sources to the diets of birds and other animals (e.g., Hobson 1990, Hobson and Sealy 1991, Angerbjörn et al. 1994, Hilderbrand et al. 1999, Roth 2003, Barrett et al. 2005, Hocking et al. 2007). And, although several studies have used stable isotopes to examine the relative contributions of terrestrial and aquatic carbon sources to aquatic food webs (see France 1995a, b, 1996; Doi et al. 2006; Grey 2006 and citations therein), few have examined the contribution of freshwater systems to terrestrial food webs (e.g., Kato et al. 2004, Briers et al. 2005, Paetzold et al. 2005, Walters et al. 2008). Depending on the tissue of interest, stable isotope analysis can also provide time-integrated dietary information because tissues differ in their metabolic rates (Hobson and Clark 1992). For instance, stable isotope analysis of whole blood was used to infer winter habitat use in Dunlin (*Calidris alpina*) during the previous 2–4 weeks (Evans Ogden et al. 2005). By contrast, stable carbon isotopes of exhaled CO_2 reflected the dietary choices of migratory songbirds during the previous 4.4 ± 2.1 h (Podlesak et al. 2005).

Refueling performance and dietary composition are particularly important to consider for spring migrant landbirds because they are likely to encounter lower prey availability as they

approach northern breeding grounds (Ewert and Hamas 1995). In the Great Lakes region during spring, shoreline habitat and associated food resources can be strongly influenced by their proximity to the Great Lakes because cool lake winds lower ambient temperatures and often delay phenological development of vegetation (i.e., lake effects; Eichenlaub 1979). As a result, the emergence and availability of lepidopteran larvae, an important food resource for insectivorous landbirds, may be delayed near shorelines. However, large swarms of emergent aquatic insects can occur at shoreline forest patches in spring, with midges (Diptera: Chironomidae) being the most abundant (Smith et al. 2007). Recent evidence suggests that midges provide an important food resource for spring migrant songbirds in the northern Great Lakes region. For example, differences in foraging behavior of migrant Black-throated Green Warblers (*Dendroica virens*) and American Redstarts (*Setophaga ruticilla*) between Lake Huron shoreline and inland forest in northern Michigan were attributed to high lakeshore concentrations of midges and their near absence farther inland (>0.4 km from shoreline; Smith et al. 1998, 2004). In a subsequent study, Smith et al. (2007) reported that early-spring migrants near shoreline also frequently consumed spiders, which were abundant because of their numerical response to immense numbers of prey (midges).

Although emergent aquatic insects may provide an important food resource, little research has quantified the energetic contributions from freshwater food webs to the diet of migratory landbirds or the energetic consequences associated with the use of these resources. We investigated the importance of emergent aquatic insects as a food resource for two early-season (mid-April to early May) migrants, the Yellow-rumped Warbler (*D. coronata*) and White-throated Sparrow (*Zonotrichia albicollis*), and one late-season (early to late May) migrant, the Magnolia Warbler (*D. magnolia*), in the western basin of Lake Erie in northwestern Ohio during spring 2007 and 2008. Spring migrant landbirds concentrate along the southwestern shores of Lake Erie, and abundance is significantly greater at forest patches adjacent to the lakeshore than in forest patches 0.5 to 5 km inland (P. G. Rodewald unpubl. data). We used stable-carbon-isotope ($\delta^{13}\text{C}$) analysis of exhaled CO_2 as an indication of recent dietary intake (contributions from aquatic or terrestrial food webs), plasma lipid metabolite profiling to assess refueling performance, and arthropod sampling to investigate (1) the contribution of emergent aquatic insects to migrant songbird dietary intake, (2) whether early-season migrants utilize emergent aquatic insects differently than late-season migrants do, (3) whether dietary intake and refueling differ between Lake Erie shoreline and inland forest sites, and (4) how diet, condition, and midge availability (biomass) were associated with refueling. Midges are inactive during cool mornings (Armitage 1995, Dallman and Smith 1995) and respond slowly to the quick movements of foraging songbirds (Busby and Sealy 1979, Smith et al. 1998). Hence, we predicted that migrants with more aquatic $\delta^{13}\text{C}$ values would experience greater refueling performance than migrants with terrestrially based diets, given the high abundance of midges and their relative ease of capture. We predicted that midge availability would be higher along the shoreline and that $\delta^{13}\text{C}$ values for migrant landbirds at these sites would reflect greater use of emergent aquatic insects than at inland forest patches.

METHODS

Study area.—Our study was conducted within Ottawa National Wildlife Refuge (41°36'56"N, -83°12'58"W), Ottawa County, Ohio. The refuge is located within the western basin of Lake Erie, a region that has scattered and often isolated patches of deciduous forest because of agriculture and shoreline housing development. Ottawa National Wildlife Refuge is a matrix of wetlands, beach ridge forests, and patches of mature hardwood forest, with hedgerows that connect many of the forest patches. Beach-ridge forest sites adjacent to the shoreline (hereafter "shoreline sites") included Crane Creek (1.18 ha), Darby West (2.86 ha), and Lamb's Woods (1.87 ha) and had a high, open canopy dominated by Eastern Cottonwood (*Populus deltoides*) and Green Ash (*Fraxinus pennsylvanica*) in a 2:1 ratio, and a dense understory primarily composed of dogwood (*Cornus* spp.) shrubs. Mature inland forest sites, located 2–3 km from the shoreline (hereafter "inland sites"), included Butternut Woods (3.26 ha), Kurdy House (2.68 ha), and Shop Woods (1.29 ha). These had more continuous canopies and were composed predominantly of Green Ash and oaks (*Quercus* spp.), with lower amounts of maples (*Acer* spp.), hickories (*Carya* spp.), Common Hackberry (*Celtis occidentalis*), and willows (*Salix* spp.), and a relatively open understory. Composition and habitat structure were similar among shoreline sites, whereas among inland sites, Shop Woods was younger and had a greater representation of Eastern Cottonwood and willows than Kurdy House and Butternut Woods (P. G. Rodewald unpubl. data).

Sample collection.—From 11 April to 31 May 2007 and 2008, we sampled migrant Yellow-rumped and Magnolia warblers, and White-throated Sparrows (2008 only). All three species are non-breeding migrants (i.e., transient) in our study area. Migrants were captured daily using 2.6 × 12 m mist nets (30 mm mesh) over a 7-h period. On each day, we simultaneously sampled one shoreline site and one inland site, with pairings varying from day to day. Sampling was delayed until 1 h after sunrise to minimize effects of overnight fasting or migratory flight on plasma lipid metabolites (Jenni-Eiermann and Jenni 1991) and to allow migrants time to forage and assimilate food items from the stopover site. Two to five mist nets were closely monitored with a timer to accurately determine the time (in minutes) from initial capture to blood collection (hereafter "bleed time"), because circulating levels of plasma metabolites are affected by capture stress and short-term fasting (Jenni-Eiermann and Jenni 1991; Guglielmo et al. 2002, 2005). Blood samples (40–60 µL) were collected by brachial venipuncture with a sterilized 26-gauge needle into a heparinized microhematocrit capillary tube and stored on ice. Within 6 h of collection, blood samples were centrifuged at 6,000 rpm for 5 min and plasma was transferred to screw-top cryogenic tubes and stored at -20°C in a liquid nitrogen dry shipper for later analysis. Each individual was banded with a U.S. Geological Survey aluminum leg band, and aged and sexed (Pyle 1997). Location, date, and time were recorded, as were wing chord (±0.5 mm), tarsus length (±0.01 mm), and body mass (±0.1 g).

Exhaled CO₂ was collected for stable-carbon-isotope analysis to assess dietary intake during migratory stopover at the study sites. We defined dietary intake in terms of δ¹³C values, which can indicate contributions from aquatic or terrestrial food webs (Fry and Sherr 1984, Hobson 1990, Hobson and Sealy 1991). Stable



FIG. 1. Sampling unit used to collect breath samples from migrant landbirds as described in Hatch et al. (2002a). The breath sampling unit was composed of a three-way stopcock valve, face mask, and balloon collection chamber. The balloon was flushed and filled with pure oxygen, which the bird was allowed to breathe for 20 s. Collected CO₂ was immediately transferred to an evacuated Exetainer tube for future stable-carbon-isotope analysis.

carbon isotopes in exhaled CO₂ of Yellow-rumped Warblers reflect diet over the previous 4.4 ± 2.1 h (Podlesak et al. 2005). Breath samples were collected using a small facemask connected to a latex balloon with a three-way valve (Hatch et al. 2002a; Fig. 1). The balloon was flushed 5–6 times with pure oxygen and then filled with oxygen until just past taut. The edge of the mask was lined with a small bead of KY Jelly (Johnson & Johnson, New Brunswick, New Jersey) to minimize leakage and placed over the bird's bill and face. The birds were allowed to breathe the oxygen for ~20 s while exhaled CO₂ was collected in the balloon. After collection, breath samples were immediately transferred to an evacuated Exetainer tube (Labco, Buckinghamshire, United Kingdom) using an 18-gauge syringe needle and then stored at room temperature. This CO₂ sampling method has a power of 0.75 for detecting differences greater than 0.41‰ between birds reared on homogeneous diets (K. A. Hatch et al. unpubl. data).

Arthropods and phenology of vegetation (i.e., leaf development) were sampled on each morning that migrants were sampled at a site. We sampled arthropods at randomly selected heights (0.5–5.0 m) using a branch-clipping method at 10 locations per site (Smith et al. 2007). Midge availability was determined from branch clippings by weighing foliage to account for variation in the amount of vegetation between samples, and is reported as midge biomass (mg) per 100 g foliage. Captured invertebrates were preserved in 70% ethanol for baseline stable-carbon-isotope analysis (Hobson et al. 1997). We also visually estimated midge abundance within a 5-m radius at 15 previously established locations at each study site. Abundance of aerial midges was visually estimated using the following categories: (0) no midges, (1) 1–10 midges, (2) 11–100 midges, (3) 101–500 midges, (4) 501–1,000 midges, (5) 1,001–5,000 midges, and (6) >5,000 midges (Smith et al. 2007). We randomly selected and marked 15 focal trees and shrubs, which were representative of the forest composition at each of the six study sites. On each day that birds were sampled at a site, we visually scored the phenological development of leaves for

each focal plant using the following categories: (1) leaves in bud, (2) leaves emerging from bud, (3) leaves unfurled but not fully expanded, and (4) leaves fully expanded.

Laboratory analysis.—Breath samples were analyzed at the Department of Geological Sciences Stable Isotope Laboratory at Brigham Young University using a Gasbench II on-line gas preparation and introduction system in line with a Delta Plus isotope ratio mass spectrometer (Thermo Finnigan, San Jose, California). He₂ and CO₂ were isolated in the on-line gas preparation device and then carried to the mass spectrometer for isotopic analysis. The external precision for CO₂ in air was approximately ±0.2‰. Standards of lithium carbonate (LSVEC) and calcium carbonate (UCLA) were run with breath samples to assess the calibration of the mass spectrophotometer. Invertebrate samples were weighed to 1.0 ± 0.2 mg, packaged into pressed tin capsules, and sent to the University of California-Davis Stable Isotope Facility for isotopic analysis. Samples were combusted using a PDZ Europa ANCA-GSL elemental analyzer linked to a PDZ Europa 20–20 mass spectrometer (Sercon, Cheshire, United Kingdom). Results are reported in per mil (‰) deviation from the standard according to the equation $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C}_{\text{sample}}) / (^{13}\text{C}/^{12}\text{C}_{\text{standard}}) - 1] \times 1,000$.

Free TRIG and TRIG were assayed via sequential color endpoint assay (Trinder reagent A and B; Sigma-Aldrich, St. Louis, Missouri) in a microplate spectrophotometer (Labsystems Multiskan MCC/340; Thermo Fisher Scientific, Waltham, Massachusetts; Guglielmo et al. 2002). Assays were run in triplicate in 400- μL flat-bottom, 96-well polystyrene microplates. Free GLYC was measured using 5 μL of plasma with 240 μL of reagent A, with a reading taken at 540 and 750 nm after 10 min of incubation at 37°C. Total TRIG was measured after adding 60 μL of reagent B to all wells, with a reading taken at 540 and 750 nm after 10 min of incubation at 37°C. TRIG concentration (mmol L^{-1}) was calculated by subtracting free GLYC from total TRIG (Guglielmo et al. 2002). Each plate was run with a standard curve based on a serial dilution of 2.54 mmol L^{-1} glycerol (Sigma-Aldrich) and a sample standard (chicken plasma) pool to calculate interassay coefficient of variation.

Statistical analysis.—TRIG concentrations were $\log_{10} + 1$ transformed to normalize data; all other variables were normally distributed and were not transformed. We created an index of energetic condition (hereafter “condition”) using a principal component analysis (PCA) of wing chord and tarsus length. Body mass was regressed against scores from the first principal component, and residuals were used as an index of energetic condition (Green 2001). Individuals with positive condition scores (residuals) were considered to be in better-than-average energetic condition in relation to all individuals sampled for each species.

All statistical analyses were performed using R, version 2.6.2 (R Development Core Team 2008). Breath $\delta^{13}\text{C}$ was compared between shoreline and inland sites, among sites, and among capture dates for each species using analysis of covariance (ANCOVA), and least-squares means were calculated. Tukey’s post hoc test was used to control error rate for multiple pairwise comparisons among sites. For each species, we used simple linear regression to test the relationship between breath $\delta^{13}\text{C}$ and plasma TRIG concentration. Midge biomass (based on branch clippings) was compared between shoreline and inland sites using analysis of variance.

Refueling performance was analyzed using a linear mixed-effects model with maximum-likelihood estimation. The response variable was plasma TRIG concentration, and fixed effects included midge biomass (based on branch clippings) from the day the bird was captured, dietary intake (breath $\delta^{13}\text{C}$), condition, capture time, site, site type (shoreline or inland), year, age–sex class (second-year male, after-second-year male, second-year female, after-second-year female), and bleed time. Capture (Julian) date was set as the random effect to account for unbalanced sample sizes due to day-to-day variability in migrant abundance. This allowed the population inference to be independent of daily sample size. Individual migrants were treated as the experimental unit. If a bird was recaptured, only data from initial capture were used in the analysis. Year, age, and sex were excluded from the White-throated Sparrow analysis because they were sampled only during 2008 and were not reliably aged and sexed in the field. A set of 26 *a priori* candidate models was tested for Yellow-rumped and Magnolia warblers, and 20 *a priori* candidate models were tested for White-throated Sparrows. We used Akaike’s information criterion with a correction factor for small sample sizes (AIC_c) to rank candidate models (Burnham and Anderson 2002). When the difference in AIC_c (ΔAIC_c) between the top-ranked model and the model in question was <2.0, the model was considered to have substantial empirical support in relation to all models examined (Burnham and Anderson 2002). Models with $\Delta\text{AIC}_c < 5$ were averaged, and the relative variable importance (RVI) was calculated to obtain multimodel inference. Results are presented as means ± SE.

RESULTS

We sampled 116 Yellow-rumped Warblers, 58 Magnolia Warblers, and 64 White-throated Sparrows for breath stable-carbon-isotope analysis and for plasma lipid metabolite profiling from 11 April to 31 May in 2007 and 2008. Median passage date (based on captures) was 1 May for both Yellow-rumped Warblers (17 April–26 May) and White-throated Sparrows (17 April–24 May), and 16 May for Magnolia Warblers (6–28 May).

Midges were first detected during standardized visual surveys and in branch clippings in late April. Midges emerged synchronously across sites, and on a given day midge numbers (as recorded in visual surveys and branch clippings) were similar between shoreline and inland forest sites (Fig. 2). Mean biomass of midges was 3.8 ± 2.90 mg per 100 g vegetation (2007) and 5.3 ± 2.96 mg per 100 g vegetation (2008) at shoreline sites, and 5.1 ± 2.77 mg per 100 g vegetation (2007) and 5.6 ± 2.47 mg per 100 g vegetation at inland sites (2008; Table 1). There was no difference in midge biomass between shoreline and inland sites in either 2007 ($F = 2.98$, $df = 1$ and 32 , $P = 0.094$) or 2008 ($F = 0.02$, $df = 1$ and 48 , $P = 0.895$). Mean $\delta^{13}\text{C}$ value of midges was $-24.3 \pm 1.7\text{‰}$ ($n = 33$), which differed from that of terrestrial invertebrates (mean $\delta^{13}\text{C} = -29.0 \pm 2.1\text{‰}$, $n = 33$; $t = -10.26$, $df = 62$, $P < 0.001$).

By 26–30 April, leaves at inland sites had unfurled but were not fully expanded, whereas at shoreline sites most vegetation still had leaves emerging from buds. However, by 6–9 May, the phenology of shoreline and inland vegetation did not differ greatly (Fig. 2). Mean dates for full leaf-out (i.e., leaves of focal trees completely expanded) were 11 May 2007 (± 1.5 days) and 15 May 2008 (± 1 day) for shoreline sites, and 10 May 2007 (± 1.5 days) and 13 May 2008

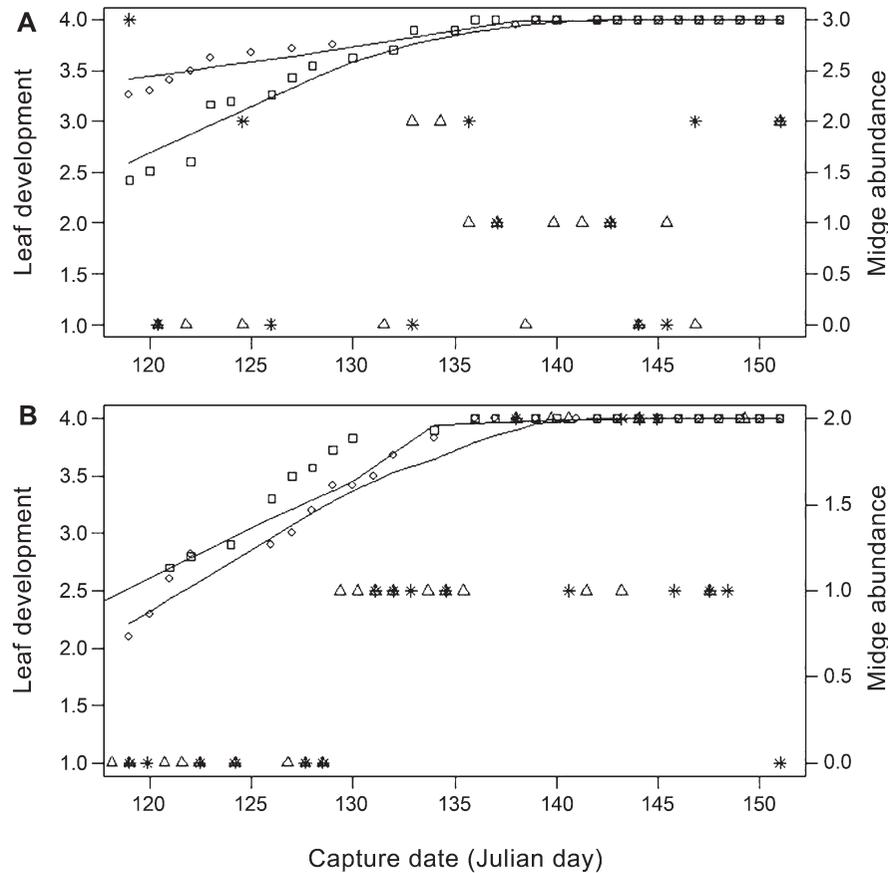


FIG. 2. Lowess analysis of visual estimates of leaf development and midge abundance (based on visual observations) in relation to capture date (Julian day) at shoreline (top line) and inland sites (lower line) in the western basin of Lake Erie in northwestern Ohio in April and May of (A) 2007 and (B) 2008. Abundance of aerial midges was visually estimated using the following categories: (0) no midges, (1) 1–10 midges, (2) 11–100 midges, (3) 101–500 midges, (4) 501–1,000 midges, (5) 1,001–5,000 midges, and (6) >5,000 midges. Phenological development of leaves was assessed using the following categories: (1) leaves in bud, (2) leaves emerging from bud, (3) leaves unfurled but not fully expanded, and (4) leaves fully expanded. Squares represent shoreline leaf development, and diamonds represent inland leaf development. Triangles represent midge abundance at shoreline sites, and asterisks represent midge abundance at inland sites. The Julian date for 1 May was 121 in 2007 and 122 in 2008.

TABLE 1. Mean (\pm SE) midge biomass (mg per 100 g vegetation) based on branch-clipping samples collected at shoreline and inland forest sites in the western basin of Lake Erie in northwestern Ohio in April and May, 2007 and 2008.

Site type	Site	Year	n	Midge biomass
Shoreline	Crane Creek	2007	20	3.63 \pm 2.36
		2008	20	5.20 \pm 2.83
	Darby West	2007	20	4.01 \pm 2.12
		2008	20	5.56 \pm 2.33
Inland	Lamb's Woods	2007	20	3.71 \pm 2.78
		2008	20	5.27 \pm 2.65
	Butternut Woods	2007	20	5.09 \pm 2.22
		2008	25	5.53 \pm 2.14
Inland	Kurdy House	2007	20	4.93 \pm 2.45
		2008	25	5.01 \pm 2.73
	Shop Woods	2007	20	5.34 \pm 2.72
		2008	25	6.42 \pm 2.54

(\pm 2days) for inland sites. There was no difference in full leaf-out between shoreline and inland sites in 2007 ($t = 1.60$, $df = 4$, $P = 0.184$) or 2008 ($t = 1.55$, $df = 3$, $P = 0.221$).

Dietary intake.—Breath $\delta^{13}C$ values became more enriched as spring progressed in Yellow-rumped Warblers ($\beta = 0.10$, $F = 11.72$, $df = 1$ and 114, $P < 0.001$, $n = 116$) and Magnolia Warblers ($\beta = 0.11$, $F = 5.17$, $df = 1$ and 56, $P = 0.027$, $n = 58$; Fig. 3), indicating an increasingly aquatic dietary composition within the spring migratory period for both species. On the other hand, we detected no association between breath $\delta^{13}C$ and capture date in White-throated Sparrows ($\beta = -0.02$, $F = 0.15$, $df = 1$ and 62, $P = 0.699$, $n = 64$).

Values of breath $\delta^{13}C$ in Yellow-rumped Warblers differed both between shoreline and inland habitats ($F = 16.26$, $df = 1$ and 108, $P < 0.001$) and among sites ($F = 6.61$, $df = 4$ and 108, $P < 0.001$) and showed a stronger aquatic signature with capture date ($F = 9.61$, $df = 1$ and 108, $P = 0.002$). Yellow-rumped Warblers at shoreline sites had $\delta^{13}C$ values indicative of a slightly more terrestrially

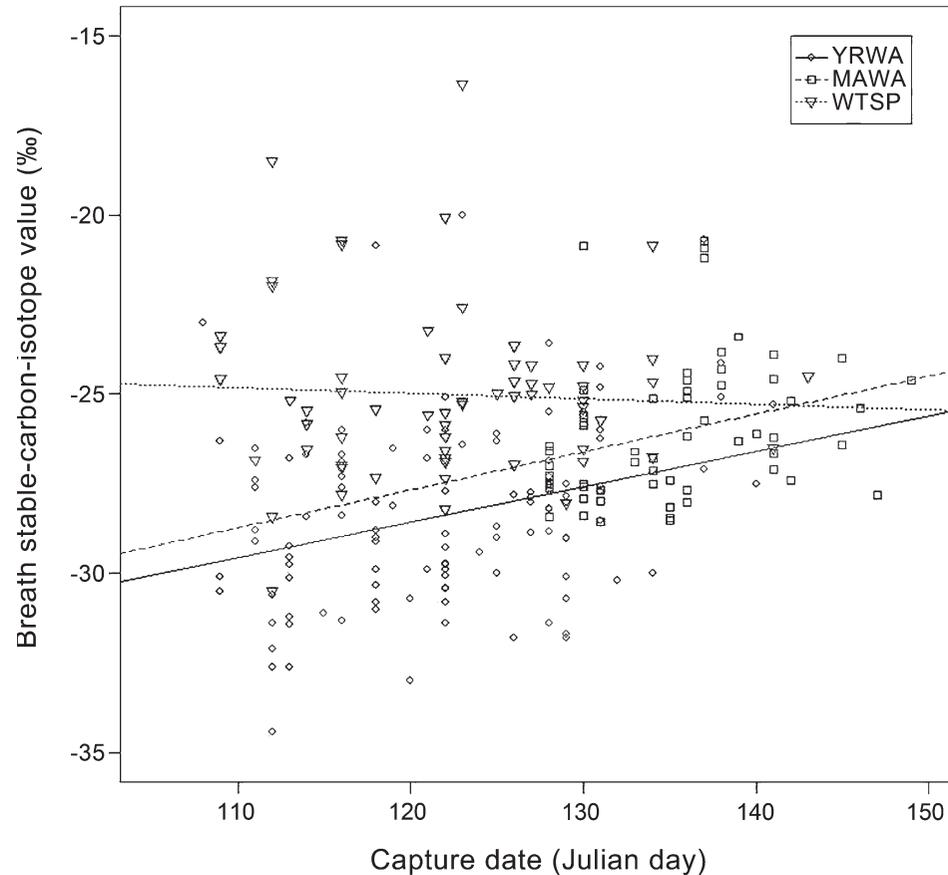


FIG. 3. Dietary composition (breath $\delta^{13}\text{C}$) in relation to capture date (Julian day) of Yellow-rumped Warblers (YRWA; solid line), Magnolia Warblers (MAWA; dashed line), and White-throated Sparrows (WTSP; dotted line) sampled in the western basin of Lake Erie in northwestern Ohio in April and May, 2007 and 2008.

derived diet compared with inland forest sites (mean inland $\delta^{13}\text{C} = -26.9 \pm 2.8\text{‰}$, $n = 28$; mean shoreline $\delta^{13}\text{C} = -28.8 \pm 2.3\text{‰}$, $n = 88$). However, breath $\delta^{13}\text{C}$ in Yellow-rumped Warblers differed among shoreline sites ($F = 12.2$, $df = 2$ and 85 , $P < 0.001$), because birds at Lamb's Woods (mean $\delta^{13}\text{C} = -29.0 \pm 2.0\text{‰}$, $n = 33$) and Crane Creek (mean $\delta^{13}\text{C} = -30.0 \pm 1.8\text{‰}$, $n = 30$) had more terrestrially derived breath $\delta^{13}\text{C}$ values than birds at Darby West (mean $\delta^{13}\text{C} = -27.3 \pm 1.8\text{‰}$, $n = 25$; $P = 0.009$ and $P < 0.001$, respectively); migrants at Lamb's Woods did not differ from those at Crane Creek ($P = 0.095$; Table 2). There was no difference in breath $\delta^{13}\text{C}$ among inland sites for Yellow-rumped Warblers (Butternut Woods: mean $\delta^{13}\text{C} = -26.6 \pm 0.91\text{‰}$, $n = 4$; Kurdy House: mean $\delta^{13}\text{C} = -24.1 \pm 5.7\text{‰}$, $n = 2$; Shop Woods: mean $\delta^{13}\text{C} = -27.4 \pm 2.7\text{‰}$, $n = 22$; $F = 1.31$, $df = 2$ and 25 , $P = 0.288$) (Table 2).

We found that breath $\delta^{13}\text{C}$ of Magnolia Warblers did not differ between shoreline (mean $\delta^{13}\text{C} = -26.2 \pm 1.8\text{‰}$, $n = 42$) and inland habitat (mean $\delta^{13}\text{C} = -25.4 \pm 2.2\text{‰}$, $n = 15$; $F = 1.98$, $df = 1$ and 51 , $P = 0.165$) or among sites ($F = 0.98$, $df = 4$ and 51 , $P = 0.427$) (Table 2). Values of breath $\delta^{13}\text{C}$ in Magnolia Warblers indicated an increasingly aquatic dietary composition as spring progressed ($F = 4.04$, $df = 1$ and 51 , $P = 0.050$). Similarly, breath $\delta^{13}\text{C}$ of White-throated Sparrows did not differ between shoreline (mean $\delta^{13}\text{C} = -25.3 \pm 2.2\text{‰}$, $n = 42$) and inland habitat (mean $\delta^{13}\text{C} = -24.3 \pm 2.7\text{‰}$,

$n = 22$; $F = 2.59$, $df = 1$ and 57 , $P = 0.113$), among sites ($F = 1.04$, $df = 4$ and 57 , $P = 0.406$), or across the season ($F = 0.00$, $df = 1$ and 57 , $P = 0.989$) (Table 2).

Refueling performance.—Mean bleed time was 7 min 16 s (± 3 min 39 s) for Yellow-rumped Warblers, 6 min (± 3 min 13 s) for Magnolia Warblers, and 7 min 51 s (± 3 min 51 s) for White-throated Sparrows. Plasma TRIG concentration was weakly associated with bleed time for Magnolia Warblers ($\beta = -0.02$, $F = 4.92$, $P = 0.031$, $r^2 = 0.08$, $n = 58$), but there was no relationship between bleed time and plasma TRIG for either Yellow-rumped Warblers ($\beta = 0.003$, $F = 0.26$, $P = 0.609$, $r^2 = 0.002$, $n = 116$) or White-throated Sparrows ($\beta = -0.009$, $F = 1.87$, $P = 0.176$, $r^2 = 0.03$, $n = 64$).

Among the models considered, the model that best described plasma TRIG concentrations in Yellow-rumped Warblers included midge biomass and an interaction between condition and capture time ($\omega_i = 0.379$; Table 3); the model including midge biomass and condition also had some empirical support ($\omega_i = 0.252$). Despite high relative variable importance for condition (RVI = 0.78) and midge biomass (RVI = 0.74), the average linear mixed model revealed that 95% confidence intervals for both condition ($\beta = 0.140 \pm 0.125$) and midge biomass ($\beta = 0.023 \pm 0.014$) included zero. However, the top two models, which both included midge biomass, together accounted for 0.63 of the Akaike weight, well

Table 2. Least-squares mean breath $\delta^{13}\text{C}$ (\pm SE) and mean plasma triglyceride (TRIG) concentration (\pm SE) and sample sizes for migrant songbirds at six stopover sites in the western basin of Lake Erie in northwestern Ohio, April and May, 2007 and 2008. Crane Creek, Darby West, and Lamb's Woods are shoreline forest sites; Kurdy House, Butternut Woods, and Shop Woods are inland forest sites.

Species	Site	<i>n</i>	Mean $\delta^{13}\text{C}$	Mean TRIG
Yellow-rumped Warbler	Crane Creek	30	-30.0 ± 1.8	1.26 ± 0.22
	Darby West	25	-27.3 ± 1.8	1.45 ± 0.12
	Lamb's Woods	33	-29.0 ± 2.0	1.42 ± 0.15
	Kurdy House	2	-24.1 ± 5.7	1.13 ± 0.04
	Butternut Woods	4	-26.6 ± 1.0	1.38 ± 0.19
	Shop Woods	22	-27.4 ± 2.7	1.37 ± 0.18
Magnolia Warbler	Crane Creek	18	-26.0 ± 1.9	1.40 ± 0.20
	Darby West	7	-26.0 ± 2.0	1.46 ± 0.17
	Lamb's Woods	18	-26.4 ± 1.4	1.44 ± 0.16
	Kurdy House	3	-26.1 ± 0.7	1.30 ± 0.07
	Butternut Woods	4	-26.3 ± 0.6	1.36 ± 0.23
	Shop Woods	8	-24.9 ± 2.3	1.49 ± 0.17
White-throated Sparrow	Crane Creek	22	-25.8 ± 2.4	1.15 ± 0.21
	Darby West	7	-24.1 ± 2.4	1.36 ± 0.20
	Lamb's Woods	13	-25.2 ± 1.3	1.14 ± 0.22
	Kurdy House	1	-25.3	1.16
	Butternut Woods	16	-24.0 ± 3.1	1.21 ± 0.20
	Shop Woods	5	-25.3 ± 1.0	1.29 ± 0.22

above the third-ranked model ($\omega_i = 0.059$). For this reason, we also averaged only the top two models and found that the model that included midge biomass ($\beta = 0.027 \pm 0.011$, RVI = 0.63) best described plasma TRIG concentration in Yellow-rumped Warblers. This suggested that even though the relationship was not

strong, refueling performance by Yellow-rumped Warblers was positively related to a condition-dependent response to midge biomass. The null model had a ΔAIC_c value of 9.75 ($\omega_i = 0.003$), which suggests that the top candidate models were different from random.

TABLE 3. Rankings of linear mixed-effects models describing refueling performance ($\log_{10} + 1$ transformed TRIG concentration [mmol L^{-1}]) of migrant Yellow-rumped and Magnolia warblers sampled in the western basin of Lake Erie in northwestern Ohio in April and May, 2007 and 2008. Variables tested included $\delta^{13}\text{C}$ (breath stable-carbon isotopic value), site, site type (inland or shoreline), bleed time (number of minutes from initial capture to blood collection), age*sex (age and sex class [second-year male, after-second-year male, second-year female, after-second-year female]), year (2007 or 2008), capture time (number of minutes after sunrise), condition (index of energetic condition), condition|capture time (condition + capture time + condition*capture time), midge (midge biomass [branch clippings]). Models are ranked by Akaike's information criterion corrected for small sample size (AIC_c), where *k* is the number of parameters in the model, ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question, and ω_i is the Akaike weight, which reflects the relative likelihood of the model. Models with ΔAIC_c scores <2.0 are shown in bold and were considered to have substantial empirical support in relation to all models examined.

Species	Rank	Model	<i>k</i>	AIC_c	ΔAIC_c	ω_i
Yellow-rumped Warbler	1	Midge + condition capture time	5	-78.8	0	0.379
	2	Midge + condition	3	-77.9	0.8	0.252
	3	Condition capture time	4	-75.1	3.7	0.059
	4	Midge	2	-74.9	3.9	0.054
	5	Condition capture time + $\delta^{13}\text{C}$	5	-74.7	4.1	0.049
	6	Midge + site type	3	-74.6	4.2	0.046
	7	Condition	2	-74.3	4.5	0.040
Magnolia Warbler	1	Capture time	2	-33.8	0	0.378
	2	Condition capture time	4	-33.1	0.7	0.269
	3	Condition capture time + midge	5	-32.1	1.7	0.159
	4	Condition capture time + $\delta^{13}\text{C}$	5	-30.7	3.1	0.082
	5	Bleed time	2	-30.0	3.8	0.057

TABLE 4. Rankings of linear mixed-effects models describing refueling performance ($\log_{10} + 1$ transformed TRIG concentration [mmol L^{-1}]) of migrant White-throated Sparrows sampled in the western basin of Lake Erie in northwestern Ohio in April and May, 2008. Variables tested included $\delta^{13}\text{C}$ (breath stable-carbon-isotope value), site, site type (inland or shoreline), bleed time (number of minutes from initial capture to blood collection), capture time (number of minutes after sunrise), condition (index of energetic condition), condition|capture time (condition + capture time + condition*capture time), midge (midge biomass [branch clippings]). Models are ranked by Akaike's information criterion corrected for small sample size (AIC_c), where k is the number of parameters in the model, ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question, and ω_i is the Akaike weight, which reflects the relative likelihood of the model. Models with ΔAIC_c scores < 2.0 are shown in bold and were considered to have substantial empirical support in relation to all models examined.

Rank	Model	k	AIC_c	ΔAIC_c	ω_i
1	Midge + condition	3	-31.1	0.0	0.195
2	Midge	2	-30.2	0.8	0.129
3	Midge + $\delta^{13}\text{C}$	3	-29.7	1.3	0.100
4	Midge + bleed time	3	-29.7	1.3	0.100
5	Midge + condition capture time	5	-29.0	2.1	0.069
6	Bleed time	2	-28.6	2.4	0.057
7	Midge + site type	3	-28.5	2.6	0.054
8	Null	1	-28.5	2.6	0.053
9	$\delta^{13}\text{C}$	2	-28.2	2.8	0.047
10	Condition	2	-27.7	3.4	0.036
11	$\delta^{13}\text{C}$ + condition	3	-27.3	3.8	0.030
12	Site type	2	-27.3	3.8	0.029
13	Capture time	2	-27.0	4.1	0.025
14	$\delta^{13}\text{C}$ + site type	3	-26.7	4.3	0.023
15	Condition capture time	4	-26.4	4.6	0.019
16	$\delta^{13}\text{C}$ + condition capture time	5	-26.1	5.0	0.016

Plasma TRIG concentration of Magnolia Warblers was most parsimoniously described by the model that included only capture time ($\omega_i = 0.378$; Table 3). The second-ranked model included the interaction of condition and capture time ($\omega_i = 0.269$), and the third-ranked model included midge biomass and the interaction of condition and capture time ($\omega_i = 0.159$). On the basis of model averaging, plasma TRIG concentration of Magnolia Warblers was best described by capture time ($\beta = 0.0008 \pm 0.0003$, $\text{RVI} = 0.89$), which had a 95% confidence interval that did not include zero (0.000–0.001). These results suggest that migrant Magnolia Warblers experienced greater refueling performance later in the day. The null model had a ΔAIC_c value of 9.03 ($\omega_i = 0.003$), which suggests that the top candidate models were different from random.

For White-throated Sparrows, the top model in the candidate set describing plasma TRIG concentration included condition and midge biomass ($\omega_i = 0.195$; Table 4). Although the four models with ΔAIC_c scores < 2.0 each had low weight, the fact that midge biomass was included in six of the first seven models offers additional support for the importance of midges in relation to refueling performance. However, the averaged linear mixed model

revealed that 95% confidence intervals for condition ($\beta = -0.06 \pm 0.07$) and midge biomass ($\beta = 0.03 \pm 0.02$) both included zero, despite high relative variable importance for the latter ($\text{RVI} = 0.65$). These results suggest that plasma TRIG concentration in White-throated Sparrows was only weakly associated with the variables in our set of *a priori* models.

DISCUSSION

During spring landbird migration, midges are often found in immense numbers along coastal areas of the Great Lakes and other wetlands and are reported to be an important resource for migrants (Ewert and Hamas 1995, Smith et al. 2007). Nonetheless, associations between midge biomass and refueling performance in our study were moderate (not strong) for Yellow-rumped Warblers and White-throated Sparrows and not detected for Magnolia Warblers. This finding contrasts with results reported for fall migrant Sedge Warblers (*Acrocephalus schoenobaenus*) in Europe, which experienced higher refueling performance during emergences of mayflies (Ephemeroptera) and aphids (Aphididae) than when insects were scarce (Schaub and Jenni 2000). In our study, the relationship was more detectable for the two early-season (mid-April to early May) migrants (Yellow-rumped Warbler and White-throated Sparrow), which are more likely to experience variation in the availability of terrestrially derived food resources (e.g., lepidopteran larvae). Furthermore, our results indicate an increased seasonal use of aquatically derived food resources, because breath $\delta^{13}\text{C}$ values of both Yellow-rumped and Magnolia warblers became more enriched over the spring migration period. Midge emergences are temperature-sensitive and increase in frequency as spring weather and water temperatures become more favorable (Armitage 1995), which suggests that migrant warblers opportunistically supplemented their diets with midges as the availability of swarms increased.

Although midge biomass was not strongly associated with refueling performance in any of the three focal species, there was high relative variable importance of midge biomass for Yellow-rumped Warblers and White-throated Sparrows. The lack of even a weak relationship between midge biomass and refueling performance of Magnolia Warblers could be because this species has a narrow migratory window through our study area later (early to late May), when terrestrially derived food resources should be more available. Refueling performance of Magnolia Warblers was positively associated with capture time, which suggests that refueling was influenced more by foraging opportunities during the day than by the availability of midges. Plasma TRIG concentrations are often low in the early morning hours (Jenni-Eiermann and Jenni 1991, Jenni and Jenni-Eiermann 1996) and increase over the day as foraging opportunities become available (Jenni and Jenni-Eiermann 1996).

Despite moderate associations between midge biomass and refueling, we detected no relationship between breath stable-carbon-isotope values ($\delta^{13}\text{C}$) and plasma TRIG concentrations for any of the three species sampled. Utilization of emergent aquatic insects by migrant songbirds could be difficult to discern using stable carbon isotopes because $\delta^{13}\text{C}$ values of some aquatic ecosystems, such as forested headwater streams, may overlap those of some terrestrial systems (see France 1995b, 1997; Hebert et al.

1999). However, in other aquatic ecosystems, such as lakes and open streams, $\delta^{13}\text{C}$ values are enriched (less negative) than in terrestrial habitats (Fry and Sherr 1984; France 1995a, 1996; Doucett et al. 1996) and, thus, can provide information on a consumer's utilization of different food webs. In addition, chironomids feed primarily on epiphytes or detritus and often selectively feed on diatoms (James et al. 2000, Doi et al. 2006), even in mesotrophic lakes (Ingvason et al. 2004) such as Lake Erie. This is significant because diatoms differ significantly from terrestrial plants in their $\delta^{13}\text{C}$ values (James et al. 2000, Doi et al. 2006).

In our study system, midges that emerged from the surrounding marshland and Lake Erie had stable-carbon-isotope values between -24‰ and -21‰ , which was distinct from the values in terrestrial invertebrates ($\delta^{13}\text{C}$ range: -30 to -27‰). Consequently, we believe that stable-carbon-isotope analysis of bird breath allowed us to assess dietary contributions from aquatic and terrestrial food webs. The high variation in breath $\delta^{13}\text{C}$ values that we observed is not easily explained but could result from rapid movement of migrating birds among sites and from $\delta^{13}\text{C}$ values that reflect diet in previously used habitats. However, a radiotelemetric study of 32 Yellow-rumped Warblers in our study area indicated that mean stopover duration was 5.9 days (A. Buchanan and P. Rodewald unpubl. data), so it is more likely that our $\delta^{13}\text{C}$ values reflected local diet. In addition, metabolic state can influence the $\delta^{13}\text{C}$ of exhaled breath. Birds that are catabolic will exhibit breath $\delta^{13}\text{C}$ values that reflect their diet during lipogenesis, whereas those in an anabolic state will have $\delta^{13}\text{C}$ values consistent with their current diet (Hatch et al. 2002a, b). For these reasons, future work should consider the metabolic state of migrant birds (Hatch et al. 2002a) and sample additional tissues to facilitate detection of recent dietary shifts in migrants (Podelsak et al. 2005).

We found that the majority of migrant songbirds had breath $\delta^{13}\text{C}$ values that were consistent with the use of both aquatic and terrestrial arthropods, rather than specialization on one group ($\delta^{13}\text{C}$ range: -27.7 to -25.0‰). Contrary to our predictions, breath $\delta^{13}\text{C}$ values indicated that dietary composition did not differ between shoreline and inland forest sites for migrant Magnolia Warblers and White-throated Sparrows. In contrast to the northern Great Lakes, where shoreline areas may have delayed leaf development and far greater abundance of midges compared with areas 2–5 km inland (Ewert and Hamas 1995, Smith et al. 2007), lake effects appeared to be less pronounced in our study. Indeed, we found no difference in leaf development or midge biomass between shoreline habitat and inland sites, possibly owing to the extensive marshland adjacent to the inland forest sites and the presence of standing water within the forests, particularly during early spring.

Assessing refueling performance and the dietary choices that lead to successful mass gain can help in identifying high-quality stopover sites for bird conservation. Migrant landbirds occur in higher abundance in beach ridge forest along the Lake Erie shoreline than in inland forest patches (P. G. Rodewald unpubl. data). Such high use may be of some concern if high densities of migrants result in increased competition for food in stopover areas (Moore and Yong 1991, Moore et al. 1995). However, we found no difference in refueling performance of migrants between small shoreline forest sites (0.22–0.28 ha) and larger inland forest sites (0.69–1.74 ha), which suggests that these patches were of comparable habitat quality. We suggest that conservation and restoration

of shoreline and inland forest patches within landscapes that contain wetlands is warranted in the western basin of Lake Erie, and possibly in similar areas in the Great Lakes region, given the high concentrations of migrant songbirds in these habitats, the limited availability of forest habitat in the landscape, and the ability of migrant landbirds to successfully refuel in these locations.

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