The Auk 124(1):1–XXX, 2007

STOPOVER HABITAT ALONG THE SHORELINE OF NORTHERN LAKE HURON, MICHIGAN: EMERGENT AQUATIC INSECTS AS A FOOD RESOURCE FOR SPRING MIGRATING LANDBIRDS

Robert J. Smith,[1,3] Frank R. Moore,[1] and Christopher A. May[2]

[1]*Department of Biological Sciences, The University of Southern Mississippi, Hattiesburg, Mississippi 39406, USA; and*
[2]*Grand Bay National Estuarine Research Reserve, 6005 Bayou Heron Road, Moss Point, Mississippi 39562, USA*

Abstract.—Recent work in Michigan's eastern Upper Peninsula suggests that terrestrial areas bordering northern Lake Huron provide important stopover habitat for spring migrating landbirds, principally because of the presence of emergent aquatic midges (Diptera: Chironomidae). Migrants were concentrated in lakeshore habitats abundant with midges during spring migration. American Redstarts (*Setophaga ruticilla*) and Black-throated Green Warblers (*Dendroica virens*) foraged and used habitat differently, depending on their distance from the lakeshore. Here, we describe results of an integrative study in which we sampled resources, quantified American Redstart foraging behavior, and estimated mass change in American Redstarts and five other common migrant landbird species to evaluate the importance of adult midges as an early season resource for spring migrants. Resource sampling and American Redstart foraging behavior suggested that more food was available in shoreline habitats than inland during spring migration. Furthermore, migrants gained mass in shoreline habitat during stopover, which supports the argument that nearshore areas provide important stopover habitat for spring migrants. Finally, resource sampling, mass change estimates, and American Redstart foraging behavior suggested that midges and spiders (Araneae: Arachnidae) provided an important early season resource for migrating landbirds. Evidence suggests that midges were responsible for elevated spider abundance at the shoreline and that birds foraged on both midges and spiders. Midges appear to play an important role in providing high-quality stopover habitat for landbirds migrating through Michigan's eastern Upper Peninsula. *Received 29 June 2004, accepted 12 January 2006.*

Key words: ~~xxx~~, xxxx, xxxx, xxxx.

Stopover Habitat along the Shoreline of Northern Lake Huron, Michigan: Emergent Aquatic Insects as a Food Resource for Spring Migrating Landbirds

Resumen.—Recent work in Michigan's eastern Upper Peninsula suggests that terrestrial areas bordering northern Lake Huron provide important stopover habitat for spring migrating landbirds, principally because of the presence of emergent aquatic midges (Diptera: Chironomidae). Migrants were concentrated in lakeshore habitats abundant with midges during spring migration. American Redstarts (*Setophaga ruticilla*) and Black-throated Green Warblers (*Dendroica virens*) foraged and used habitat differently, depending on their distance from the lakeshore. Here, we describe results of an integrative study in which we sampled resources, quantified American Redstart foraging behavior, and estimated mass change in

---

[3] Present address: Department of Biology, The University of Scranton, Scranton, Pennsylvania 18510, USA. E-mail: smithr9@scranton.edu

American Redstarts and five other common migrant landbird species to evaluate the importance of adult midges as an early season resource for spring migrants. Resource sampling and American Redstart foraging behavior suggested that more food was available in shoreline habitats than inland during spring migration. Furthermore, migrants gained mass in shoreline habitat during stopover, which supports the argument that nearshore areas provide important stopover habitat for spring migrants. Finally, resource sampling, mass change estimates, and American Redstart foraging behavior suggested that midges and spiders (Araneae: Arachnidae) provided an important early season resource for migrating landbirds. Evidence suggests that midges were responsible for elevated spider abundance at the shoreline and that birds foraged on both midges and spiders. Midges appear to play an important role in providing high-quality stopover habitat for landbirds migrating through Michigan's eastern Upper Peninsula.

MIGRATION IS A period of exceptional energy demand (Berthold 1975; Blem 1980, 1990; Alerstam and Lindström 1990; ~~Smith et al. 1998, 2004~~). To fuel this demand, birds deposit substantial fat stores, at times reaching 50% of total body mass among long-distance intercontinental migrants (Blem 1980, 1990). If migrants satisfy energy demands and meet *en route* exigencies in a timely manner (*sensu* Alerstam and Lindström 1990), they experience a successful migration. How well a migrant offsets *en route* exigencies has consequences not only for survival during migration (Moore et al. 1995), but also for subsequent reproductive performance (Smith and Moore 2003, Moore et al. 2005).

Within Michigan's eastern Upper Peninsula, nearshore waters of northern Lake Huron produce large hatches of emergent aquatic midges (Diptera: Chironomidae), which may create important stopover habitat for spring migrating landbirds (Ewert and Hamas 1996, Smith et al. 1998). Migrants were more abundant during spring migration in lakeshore habitats than in inland areas that had comparable vegetation (Ewert and Hamas 1996). Further, at least two species of intercontinental landbird migrants, the Black-throated Green Warbler (*Dendroica virens*; hereafter "green warbler") and the American Redstart (*Setophaga ruticilla*; hereafter "redstart"), foraged and used the habitat differently, depending on whether birds were observed within 0.4 km of the Lake Huron shoreline or >0.4 km from the shoreline (Smith 1995, Ewert and Hamas 1996, Seefeldt 1997, Smith et al. 1998).

Our primary objective was to assess the value of midges as a food resource during spring migration, a period when northerly migrants confront perhaps the most extreme weather and poorest food conditions they will encounter throughout the annual cycle (Slagsvold 1976, Nolan 1978, Perrins 1996, Nystrom 1997, Brown and Brown 2000, Smith 2003). We used an integrative approach, combining data describing foraging behavior and mass change of landbirds, along with temporal and spatial variation in resource abundance, to evaluate the significance of midges to migrating landbirds. Because birds adjust foraging behavior in response to prey type (Robinson and Holmes 1982), we used behavior to draw inferences about prey choice. Foraging rates should be proportional to food density until foraging rate is limited by satiation or handling limitations (Hutto 1990). Thus, predator foraging rates may provide an indication of food availability within a habitat (Morse 1981, 1989; Graber and Graber 1983; Kilgo 2005). We collected data describing redstart~~s~~ foraging to gain insight into prey abundance and choice during spring migration. Further, we estimated mass change in six species of landbirds using the shoreline as stopover habitat. Researchers commonly assess the quality of a stopover site by determining whether individuals spending time within that habitat gain or lose fat, as indicated by changes in body mass (Moore and

Kerlinger 1987, Loria and Moore 1990, Yong and Moore 1997, Dunn 2000). Mass change provides an index not only of food abundance but also of food availability, reflecting factors such as predation risk (Dunn 2000) or competition (Moore and Yong 1991).

Finally, we sampled shoreline and inland invertebrates throughout the time migrants arrived on the study site. If midges are as important as previously hypothesized (Ewert and Hamas 1996, Smith et al. 1998), we expected redstarts to forage in a manner consistent with midge use. For example, because midges are restricted to shoreline areas (Smith 2003) and midge flight is temperature-dependent (Armitage 1995, R. J. Smith and F. R. Moore unpubl. data), redstarts should vary foraging behavior between shoreline and inland areas while increasing aerial foraging later in the day, reflecting increased midge flying as habitats warm.

Methods

The work was conducted during the spring migratory and breeding periods in habitat within 3.2 km of the northern Lake Huron shoreline (46°2′N, 84°35′W). Forest vegetation at the site was a mixture of conifers, including balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), eastern white pine (*Pinus strobus*), red pine (*P. resinosa*), and deciduous species including paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*). Relative densities of each species (estimated using the methodology of James and Shugart 1970) were as follows: northern white cedar (61%), balsam fir (10%), quaking aspen (7%), white spruce (5%), paper birch (2%), eastern white pine (1%), red pine (<1%), and balsam poplar (<1%). Vegetation composition and structure within the study area were representative of the lowland coniferous forests common to shoreline habitats throughout the eastern Upper Peninsula of Michigan (Smith et al. 1998, R. J. Smith pers. obs.).

We sampled arthropod abundance and redstart foraging behavior at both shoreline and inland sites. We defined inland habitats as those >0.4 km from the shoreline because (1) this met the definition of Ewert and Hamas (1996) and (2) midge abundance drops precipitously beyond this point (Smith 2003). We controlled for differences in vegetation by sampling inland areas that had vegetation composition similar to the shoreline site (Smith et al. 1998).

For logistical reasons, we were able to trap birds only in shoreline habitat. Birds were trapped daily using mist nets (12 × 2.6 m, 30-mm mesh) from 7 May to 6 June 1997, from 4 May to 28 June 1998, from 30 April to 23 July 1999, from 27 April to 29 July 2000, and from 27 April to 26 July 2001. Except for 1997, when we actively employed 10 mist nets, we used 25–30 permanently positioned mist nets to sample avifauna.

Nets were opened shortly before sunrise, remained open through early afternoon, were reopened in early evening, and closed at dusk. Nets were closed when temperatures dropped below 3°C or in the event of high wind or rain. Standard measurements were taken from birds, including body mass (g), tarsus length (mm), and unflattened wing chord (mm). All measurements were performed by trained individuals who were periodically tested to ensure validity and repeatability. Each bird was aged and sexed according to protocol outlined in Pyle (1997), fitted with a federal aluminum band and, if a redstart, individually color banded. All recaptures were measured without reference to previous records.

Arthropod sampling.—We sampled shoreline and inland arthropods every six days in 1997–1999 and every three days in 2000–2001 using a "grab" sampling technique modified from Cooper and Whitmore (1990). During each sampling round, three locations were randomly selected in shoreline habitat and three inland. At each location, we collected one sample of each common tree species (white cedar, balsam fir, quaking aspen, white spruce), resulting in 24 samples per round. We chose these species for arthropod sampling because trees with relative density estimates of <5% rarely occurred at randomly chosen sampling locations. Because most quaking aspens within the shoreline study site were fully mature (average height = 15.1 m), we collected samples from a young aspen stand 7.2 km east of the study area (average height = 3.0 m). We chose this aspen stand because it was a similar distance from the lakeshore as our shoreline site. Furthermore, there was no obvious difference in phenology of leafout between the sites (R. J. Smith pers. obs.).

Sample height was randomly selected, ranging from 1 to 5 m above ground. A bag was quickly placed over the selected branch, the bag sealed, the branch clipped, and the contents fumigated with insecticide. All arthropods were collected and sorted to size and order, except for dipterans, which were differentiated as Chironomidae (midges) or other Diptera. For the present study, we grouped arthropods into three categories: "midges," "spiders," and "other." The "other" category comprised all sampled arthropods (including nonmidge dipterans) except midges or spiders.

We used the equations of Hódar (1996) to estimate biomass for each arthropod group. To correct for differences in amount of vegetation between samples, we weighed clipped branches and report biomass estimates as biomass (mg) per 100 g foliage. Arthropod data did not meet parametric assumptions, so we used Spearman's *r* to assess relationships between midge and spider biomass, and Wilcoxon-Mann-Whitney tests to make shoreline and inland comparisons of invertebrate biomass.

We separated analyses describing foraging behavior and mass change into "early-season period" and "late-season period," as indicated by temporal changes in invertebrate abundance and diversity. Subdividing our data in this manner allowed examination of redstart behavior and migrant mass change when the major prey types available to birds were principally flight-capable midges or substrate-dwelling spiders (early season; see Fig. 1). The late-season period encompassed the spring migratory period from 16 May (Julian day 136) to the end of each bird species' migration. We operationally delineated the end of migration for each species as the day after the capture rate for that species declined to ≤30% of the average of the three days with the highest capture rate (Fig. 2). This definition coincides with the onset of breeding for birds in the area (Wood 1951, R. J. Smith and F. R. Moore unpubl. data, M. J. Hamas pers. comm.).

Foraging behavior.—We used a focal sampling approach (Altmann 1974) to collect data on redstarts in both shoreline and inland habitats. We waited 5 s after first contact before recording

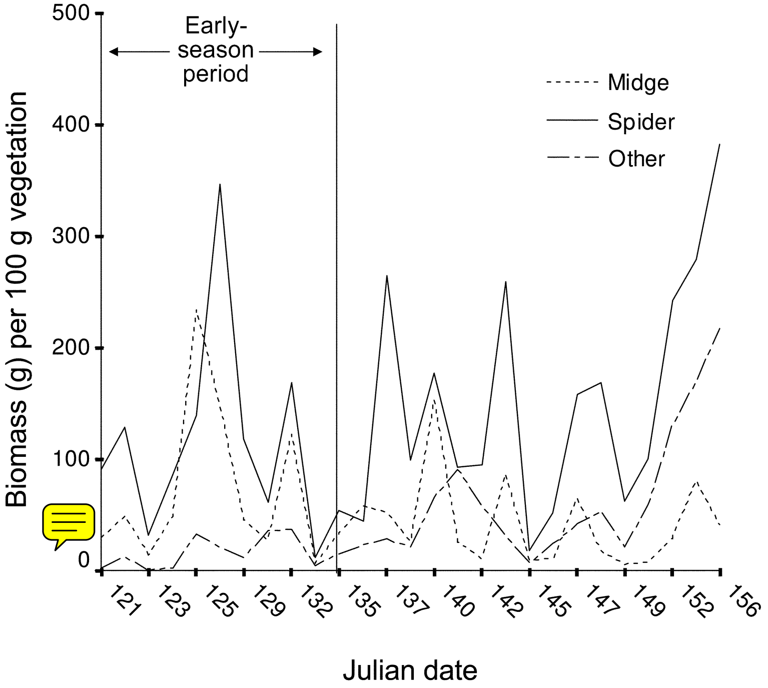

Fig. 1. Mean daily arthropod biomass at Pontchartrain Shores, Michigan, 1997–2001. Lines represent biomass (mg) of midges, spiders, and other (i.e., remaining arthropods excluding midges and spiders), per 100 g vegetation.

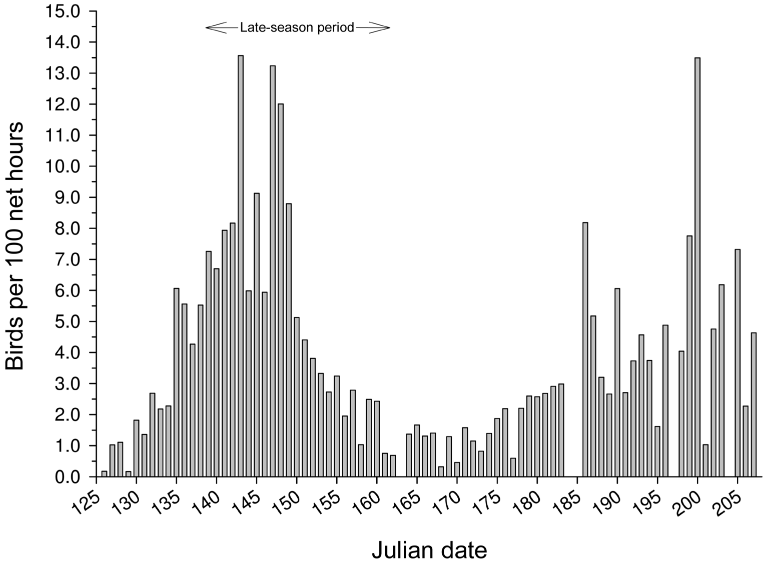

FIG. 2. Determination of the extent of spring migration for American Redstarts using capture data for the period 1997–2001 (see text for details). The y-axis (birds per net hour) refers to the number of newly captured individuals from all nets per day, corrected for sampling effort, summed across years.

data to reduce discovery bias (Morrison 1984, Hejl et al. 1990); foraging behavior was sampled for as long as a bird remained in sight. Foraging behaviors were classified as (1) "glean," a nonflying maneuver directed at a prey item on a substrate while the bird was either perched or hopping; (2) "sally-hover," a maneuver in which a stationary prey item on a substrate was attacked by a hovering bird; and (3) "sally-strike," a maneuver in which both insect and bird were in flight (Sabo 1980, Petit et al. 1990).

For each observation, we recorded date, time, temperature, wind direction and wind speed. Four aspects of foraging behavior were monitored: (1) foraging rate, (2) movement rate and (3) pattern while foraging, and (4) microhabitat use. Movement rate and pattern were quantified by recording estimated flight or hop lengths and number of foraging maneuvers (Remsen and Robinson 1990). We collected data to describe microhabitat use after losing a bird from sight. These data included tree species last foraged in, foraging height, and tree height. We also subjectively quantified midge abundance within a 5-m radius (sphere) around each bird's last observed location using the following scores: (0) no midges present, (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) >5,001 midges.

To reduce bias, we made efforts to search for inland redstarts during the same periods as we searched shoreline habitats. However, because more birds were present in shoreline habitat (R. J. Smith and F. R. Moore unpubl. data), we collected substantially fewer observations of inland redstarts. For unbanded individuals, we recorded data after traveling ≥30 m or when ≥10 min had elapsed since the previous observation. We restricted analyses to behavioral sequences of ≥20 s, because variance in foraging rates stabilized after this minimum period (R. J. Smith and F. R. Moore unpubl. data). When a banded bird was observed multiple times, we used the first observation (≥20 s in our analyses). Rates were estimated by dividing the number of each maneuver within a foraging sequence by the length (in seconds) of that sequence. We made spatial comparisons of maneuver use via log-likelihood G tests. Rate comparisons were made using Wilcoxon-Mann-Whitney tests. We used Spearman's r and Kendall's partial t to examine relationships between time–temperature and maneuver rates (Siegel and Castellan 1988). Results are presented as means ± SE.

Mass change.—Capture times were converted to minutes since sunrise as recommended by Dunn (2000). Analyses of mass change were limited to first captures of individuals during the late-season period or the early-season period. We investigated mass change in six species of insectivorous landbird migrants: redstart, Yellow-rumped Warbler (*D. coronata*), green warbler, Magnolia Warbler (*D. magnolia*), Black-and-white Warbler (*Mniotilta varia*), and Blackburnian Warbler (*D. fusca*). Mass change was evaluated using a general linear mixed-modeling approach (PROC MIXED in SAS, version 8.0; Littell et al. 1996). Year, Julian date, sex, breeding status, and minutes since daylight were considered fixed effects. The primary focus of this analysis was short-term mass change (i.e., minutes-since-daylight effect). Therefore, we controlled for year and Julian date by modeling them as classification variables, and we considered combinations of year and Julian date to be the treatment levels. Wing chord and tarsus length were considered random effects (i.e., covariates that could account for variation in mass gain but could not be controlled experimentally). Variables were introduced into models according to a hierarchy to limit the number of variables in the models. Sex and breeding status were introduced first and retained in subsequent models if significant. Then, all other effects were introduced and second-order and higher interactions were evaluated. Finally, any nonsignificant interactions were removed from the model and main effects were evaluated. If birds gain mass during stopover, there should be a positive relationship between first captures of birds and the time elapsed since daylight (Winker et al. 1992, Dunn 2000). Residuals were screened for agreement with model assumptions using techniques available in SAS. We used the effects in the final mixed model for each species to calculate mass change. The general form of the model for all species, except redstarts, was: mass = $b0$ + $b1$(year) + $b2$(date) + $b3$(wing length) + $b4$(tarsus) + $b5$ (minutes since daylight).

We used parameter estimates to calculate mass change. Both hourly gain estimates and 24-h mass-change estimates are included in the results for comparisons with other studies. Parameter estimates for treatment levels (year, date) are not reported because of the many levels in the analyses and because our focus was on the covariate effects and the effect of minutes since daylight.

For each species, we estimated a minimum threshold value that birds needed to exceed to show a net positive 24-h gain. Mass gain was assumed to have continued at some average rate over all daylight hours, and overnight mass loss of a bird stopping over equaled 4.5% of average body mass (see Winker et al. 1992, Dunn 2000). The threshold value represents the mass a bird must gain during daylight hours to break even energetically over a 24-h period with no migration (Dunn 2001). We converted overnight loss to grams lost over 24 h to estimate net 24-h mass change. We subtracted this loss from the estimated 24-h gain derived from the mixed-model analyses. Net mass change was then divided by the average mass of each species.

We were able to classify redstarts as either breeders or nonbreeders because we were monitoring color-banded individuals through both spring migration and the breeding season. We conducted daily searches of the study area as well as adjacent areas (+2 km) for color-banded birds. We used several types of evidence to identify individuals as local breeders: capture or observation during the breeding season, morphological evidence of breeding on recapture (brood patch or obvious cloacal protuberance), or evidence of nest attendance. Classification as breeders or nonbreeders allowed creation of a dummy variable (breeder), which was evaluated for its effect on mass change.

We point out that breeding individuals in species other than redstarts were likely contained in our analyses. However, using first-capture mass to estimate mass change resulted in a data set containing mostly migrating individuals. For all species included in the mixed-model analyses, many more birds passed through the study area than subsequently stayed to breed (e.g., Fig. 2). Therefore, local breeders make up only a small percentage of captures, especially given that only first captures were included in the analyses (Dunn 2002, Jones et al. 2002).

Results

Arthropods.—During the early season period, biomass of midges, spiders, and total arthropods was higher in shoreline habitats (Fig. 3A). There was no spatial difference in biomass of other arthropods (Fig. 3A). Finally, midge biomass correlated with spider biomass ($r = 0.307$, $P < 0.0001$, $n = 115$) in shoreline habitats, though not inland ($r = 0.084$, $P = 0.564$, $n = 49$).

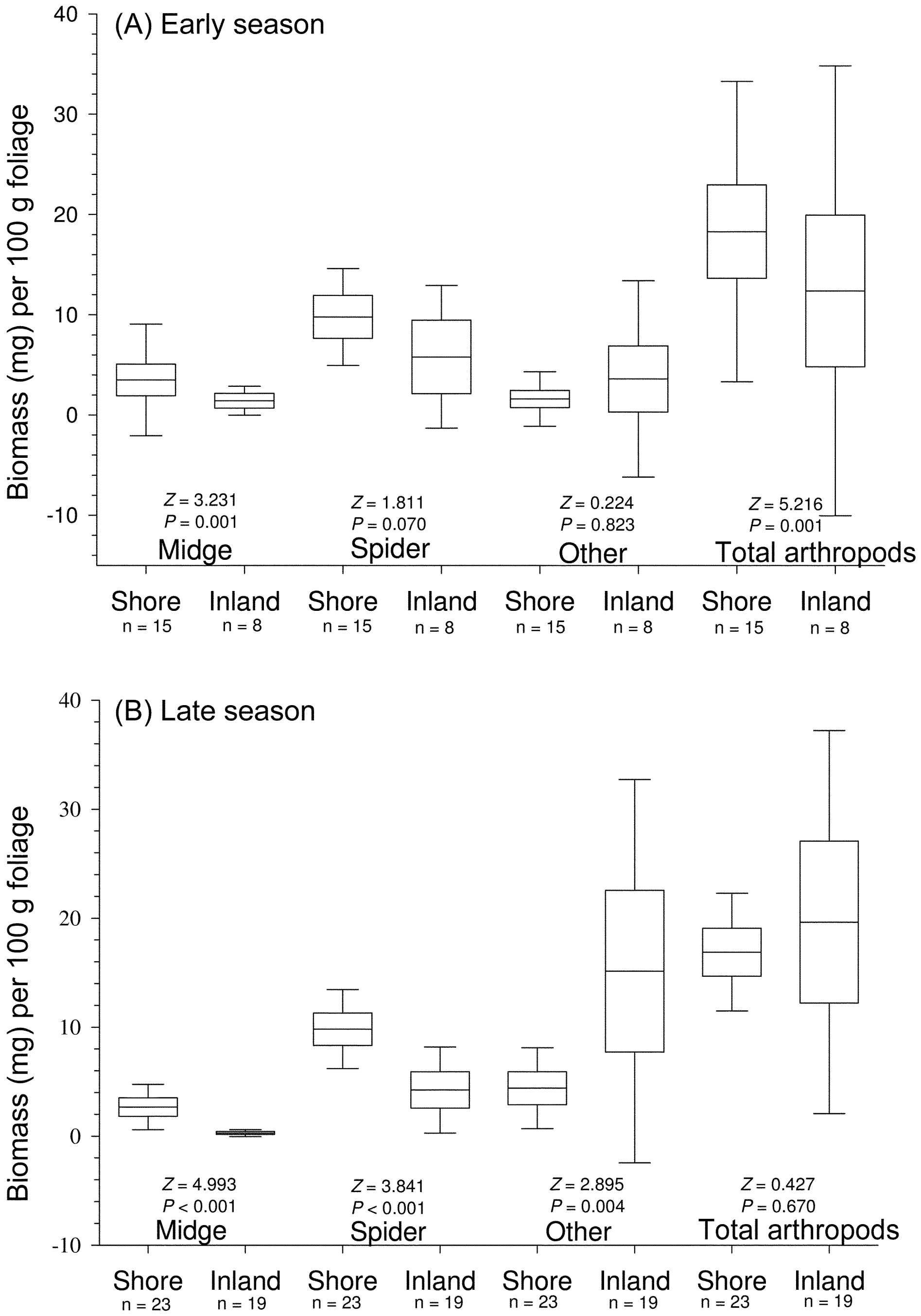

Fig. 3. Spatial comparisons of arthropod biomass as measured via grab sampling, years pooled. Sampling period is through 12 June (late-season period) for (A) and through 15 May (early-season period) for (B). Lines represent median, boxes indicate the 25th and 75th percentiles, and whiskers indicate the 10th and 90th percentiles. "Other" category includes all arthropods except midges and spiders.

During the late-season period, midge and spider biomass estimates were higher in shoreline habitats than inland, whereas biomass of arthropods, excluding midges and spiders (other category), was significantly higher inland (Fig. 3B). There was no difference in total arthropod biomass between shoreline and inland. There was a significant association between midge and spider biomass in shoreline habitat ($r = 0.167$, $P = 0.002$, $n = 339$) that was not present inland ($r = -0.026$, $P = 0.742$, $n = 165$).

Body mass change.—Captures from the early-season period resulted in sufficient samples to perform analyses on redstart, Yellow-rumped Warbler, green warbler, and Black-and-white Warbler. Mixed modeling indicated significant mass gain throughout the day in all species (Table 1). Gain rates exceeded the minimum threshold value calculated for each species (Table 2). Twenty-four-hour estimated mass change ranged from 5.2% in green warblers to 13.0% in Black-and-white Warblers. Birds gained mass when arthropod sampling showed that insectivorous migrants had little other than midges and spiders available as prey.

Sex showed a significant effect on mass gain only for redstarts during the late-season period (Table 1). There was no difference in estimated mass gain in redstarts depending on breeding status (early-season period: $F = 0.02$, df = 1 and 84, $P = 0.878$; late-season period: $F = 0.00$, df = 1 and 89, $P = 0.963$); thus, this effect was not retained in subsequent analyses. For each species, all second-order and higher interactions among year, Julian date, sex, breeding status, and minutes since daylight were nonsignificant and removed from the models.

Analyses of captures during the late-season period suggested that all study species, except Black-and-white and Yellow-rumped warblers, gained mass during stopover (Table 1). Comparison of gain rates to minimum threshold values suggested that redstarts, green warblers, Magnolia Warblers, and Blackburnian Warblers gained mass at rates sufficient to overcome overnight losses (Table 2). Net 24-h mass change ranged from a low of 8.7% in green warblers to a high of 18.9% in Blackburnian Warblers (Table 2). There was no difference in estimated mass gain in redstarts, depending on breeding status (Table 1).

American Redstart foraging behavior.—Small sample sizes limited analyses to only males observed in shoreline habitat during the early-season period. Shoreline males decreased sally-strikes with time ($r = -0.309$, $P = 0.012$, $n = 35$) while increasing gleans with number of swarming midges ($r = 0.422$, $P = 0.045$, $n = 23$). There was no relationship between temperature and sally-strike rate ($r = 0.054$, $P = 0.793$, $n = 26$) nor temperature and glean rate ($r = -0.173$, $P = 0.399$, $n = 26$).

Foraging rates for both male and female redstarts differed between shoreline and inland habitats during the late-season period. Both sexes foraged at higher rates at the shoreline (female maneuvers min^{-1}: shoreline: $\bar{x} = 3.06 \pm 0.20$, $n = 122$; inland: $\bar{x} = 1.42 \pm 0.46$, $n = 9$, $Z = -2.007$, $P = 0.045$; male maneuvers min^{-1}: shoreline: $\bar{x} = 1.88 \pm 0.11$, $n = 231$; inland: $\bar{x} = 1.21 \pm 0.17$, $n = 54$, $Z = -2.905$, $P = 0.004$). Shoreline females increased sally-hovers with time of day ($r = 0.223$, $P = 0.014$, $n = 120$). There was no relationship between female sally-hover rate and temperature ($r = 0.166$, $P = 0.090$, $n = 106$), nor sally-hover rate and number of flying midges ($r = 0.110$, $P = 0.269$, $n = 102$). Females decreased sally-strikes with temperature ($r = -0.270$, $P = 0.005$, $n = 106$). Shoreline males increased gleaning with temperature ($r = 0.157$, $P = 0.019$, $n = 222$) while decreasing sally-strikes with both time ($r = -0.110$, $P = 0.089$, $n = 240$) and temperature ($r = -0.193$, $P = 0.004$, $n = 222$). Males significantly decreased sally-strikes with temperature, after statistically controlling for the influence of time of day on temperature (Kendall's partial $T = -2.666$, $P = 0.008$, $n = 220$). We were able to examine foraging maneuver use spatially only in males, because so few females were observed inland. Males foraged differently depending on whether we observed them at the shoreline or inland (Fig. 4). Shoreline males gleaned more, whereas inland males used more sally-hovers and sally-strikes ($G = 7.620$, df = 2, $P = 0.022$, $n = 214$).

Discussion

Food resources during migration.—Our results are consistent with the hypothesis that shoreline areas in Michigan's eastern Upper Peninsula are resource-rich during spring migration (Ewert and Hamas 1996, Smith et al. 1998). Arthropod biomass estimates suggested that more food was available in shoreline habitats than inland during spring migration, and

Table 1. Mixed-model analyses of mass change for six common species of insectivorous landbird migrants arriving at Pontchartrain Shores, Michigan, 1997–2001. Shown are parameter estimates (β), their standard errors (SE), and *F*-statistics with the associated degrees of freedom and probability values (*P*). Late-season period encompasses all captures from 16 May through the end of each species' migration (see text), whereas the early-season period is restricted to captures before 15 May.

	Mixed-model analysis				
Parameter	β	SE	*F*	df	*P*
American Redstart, early-season period (*n* = 101)					
Year			1.51	3 and 86	0.217
Date			0.34	8 and 86	0.946
Minutes since daylight	0.0007	0.0001	15.03	1 and 86	0.0002
Wing	0.0804	0.020	16.80	1 and 86	< 0.0001
Tarsus	0.1692	0.072	5.50	1 and 86	0.021
American Redstart, late-season period (*n* = 927)					
Year			6.47	4 and 892	<0.0001
Date			1.04	26 and 892	0.407
Minutes since daylight	0.0007	0.000111	158.20	1 and 892	<0.0001
Wing	0.0814	0.009	89.93	1 and 892	<0.0001
Tarsus	0.1497	0.024	39.16	1 and 892	<0.0001
Sex	–0.0722	0.031	5.55	1 and 892	0.019
Yellow-rumped Warbler, early-season period (*n* = 131)					
Year			1.03	3 and 108	0.384
Date			1.27	16 and 108	0.228
Minutes since daylight	0.0009	0.0003	8.04	1 and 108	0.006
Wing	0.0500	0.031	2.56	1 and 108	0.113
Tarsus	0.1878	0.112	2.83	1 and 108	0.096
Yellow-rumped Warbler, late-season period (*n* = 74)					
Year			0.64	4 and 43	0.636
Date			0.80	23 and 43	0.713
Minutes since daylight	0.0010	0.000	2.58	1 and 43	0.116
Wing	0.0176	0.056	0.10	1 and 43	0.752
Tarsus	0.068	0.222	0.09	1 and 43	0.759
Black-throated Green Warbler, early-season period (*n* = 56)					
Year			2.70	3 and 36	0.060
Date			1.26	13 and 36	0.284
Minutes since daylight	0.0006	0.000	7.47	1 and 36	0.010
Wing	0.0665	0.030	4.83	1 and 36	0.035
Tarsus	0.0801	0.113	0.51	1 and 36	0.481
Black-throated Green Warbler, late-season period (*n* = 130)					
Year			2.91	3 and 95	0.039
Date			0.89	28 and 95	0.633
Minutes since daylight	0.0008	0.000	22.57	1 and 95	<0.0001
Wing	0.1188	0.024	24.06	1 and 95	<0.0001
Tarsus	0.1940	0.095	4.18	1 and 95	0.044
Magnolia Warbler, late-season period (*n* = 189)					
Year			2.04	4 and 154	0.092
Date			1.35	27 and 154	0.132
Minutes since daylight	0.0008	0.000	17.42	1 and 154	<0.0001
Wing	0.0622	0.023	7.02	1 and 154	0.009
Tarsus	0.1449	0.081	3.21	1 and 154	0.075

Table 1. Continued.

	Mixed-model analysis				
Parameter	β	SE	*F*	df	*P*
Black-and-white Warbler, early-season period (*n* = 54)					
Year			0.97	3 and 32	0.418
Date			1.20	15 and 32	0.318
Minutes since daylight	0.0012	0.000	12.92	1 and 32	0.001
Wing	0.0192	0.032	0.36	1 and 32	0.551
Tarsus	–0.0921	0.197	0.22	1 and 32	0.643
Black-and-white Warbler, late-season period (*n* = 75)					
Year			1.12	4 and 43	0.361
Date			1.06	24 and 43	0.418
Minutes since daylight	0.0003	0.000	1.34	1 and 43	0.254
Wing	0.1006	0.031	10.60	1 and 43	0.002
Tarsus	0.2282	0.136	2.81	1 and 43	0.101
Blackburnian Warbler, late-season period (*n* = 46)					
Year			0.88	3 and 16	0.470
Date			0.60	23 and 16	0.870
Minutes since daylight	0.0016	0.001	6.09	1 and 16	0.025
Wing	0.0150	0.051	0.09	1 and 16	0.774
Tarsus	–0.1069	0.249	0.18	1 and 16	0.674

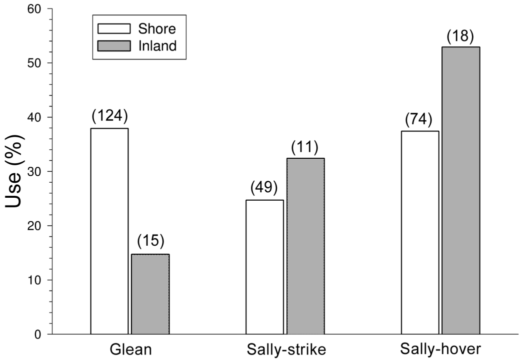

Fig. 4. Spatial comparison of male American Redstart maneuver use during the late-season period, Pontchartrain Shores, Michigan, 1997–2001.

foraging behavior of redstarts reflected greater food abundance at the shoreline. Seefeldt (1997), working in the same area, also showed elevated foraging rates among redstarts and green warblers during spring migration in shoreline habitats.

We cannot rule out the possibility that spatial differences in foraging rates were attributable to factors other than prey abundance. For instance, shoreline areas may have differentially attracted individuals with depleted fat stores. Fat-depleted migrants forage at higher rates and expand their foraging repertoire (Loria and Moore 1990, Wang and Moore 2005). Furthermore, inland habitats may have contained more breeders, whereas shoreline habitats contained more migrants. Thus, migratory–breeding status may have caused the observed rate differences. Because we were unable to capture birds inland to assess fat load and mass change, we are unable to evaluate whether birds in shoreline habitats were fat-depleted compared with inland birds.

Regardless, we believe that our results, especially when viewed in conjunction with previous work in the area, support our contention that differences in resource abundance and diversity are a reason for the observed differences in foraging. Numerous species of spring migrating landbirds are attracted to shoreline areas containing aquatic insects (Ewert and Hamas 1996), and both green warblers and redstarts forage at different rates and use foraging maneuvers and tree species differently, depending on whether they are observed in shoreline or inland habitats (Seefeldt 1997; Smith et al. 1998, 2004).

Midges appeared to be responsible for creating high-quality stopover habitat along the northern Lake Huron shoreline. Adult midges

Table 2. Estimated mass change in landbird migrants captured at Pontchartrain Shores, Michigan, 1997–2001. Estimates are from nonstandardized coefficients (β weights) calculated from the appropriate mixed models. Estimated hourly gain represents the mixed-model estimate of hourly mass gain during daylight hours. Percentage of mass change is based on average mass of captured birds during the appropriate period. Estimated losses are calculated assuming a 4.5% overnight loss (see text for explanation). The late-season period encompasses all captures from 16 May through the end of each species' migration (see text), whereas the early-season period is restricted to captures before 15 May.

	Early-season period		Late-season period	
	Hourly	24 h	Hourly	24 h
American Redstart				
Estimated gain (g)	0.042	1.008	0.042	1.008
Estimated loss (g) (threshold value)	0.015	0.355	0.013	0.312
Net change (g)	+0.027	+0.653	+0.028	+0.696
Mass change in 24 h (%)		+8.3		+9.1
Yellow-rumped Warbler				
Estimated gain (g)	0.054	1.296	Effect not significant	
Estimated loss (g) (threshold value)	0.022	0.526		
Net change (g)	+0.032	+0.770		
Mass change in 24 h (%)		+6.6		
Black-throated Green Warbler				
Estimated ain (g)	0.036	0.864	0.048	1.152
Estimated loss (g) (threshold value)	0.017	0.401	0.016	0.384
Net change (g)	+0.019	+0.463	+0.032	+0.768
Mass change in 24 h (%)		+5.2		+8.7
Magnolia Warbler				
Estimated gain (g)	Sample size precludes		0.048	1.152
Estimated loss (g) (threshold value)	early-season calculation		0.016	0.348
Net change (g)			+0.032	+0.804
Mass change in 24 h (%)				+9.4
Black-and-white Warbler				
Estimated gain (g)	0.072	1.728		
Estimated loss (g) (threshold value)	0.018	0.442	Effect not significant	
Net change (g)	+0.054	+1.286		
Mass change in 24 h (%)		+13.0		
Blackburnian Warbler				
Estimated gain (g)	Sample size precludes		0.096	2.304
Estimated loss (g) (threshold value)	early-season calculation		0.018	0.441
Net change (g)			+0.078	+1.859
Mass change in 24 h (%)				+18.9

restricted mating swarms to nearshore terrestrial areas, as shown by arthropod sampling and anecdotal observations. Spiders were also more abundant in shoreline habitat. The shoreline–inland differences in midge and spider biomass held during both the early- and late-season periods. Further, there were positive relationships between shoreline midge and spider biomass estimates during both periods that were not evident inland.

Mass change.—How well a migrant satisfies the energetic demand of migration and meets *en route* exigencies depends largely on habitat quality (Moore et al. 1995, Dunn 2000). Individuals that can restore fat loads quickly minimize time spent *en route* and presumably arrive earlier at the breeding grounds (Cristol 1995, Aebischer et al. 1996, Lozano et al. 1996, Smith and Moore 2003) and in better condition (Sandberg 1996, Sandberg and Moore 1996, Smith and Moore 2003). Mass-change estimates are consistent with the argument that nearshore areas provide important stopover habitat for spring migrating passerines (Ewert and Hamas 1996, Smith et al. 1998). Moreover, in comparison to other studies that have calculated rates of mass change (e.g., Moore and Kerlinger 1987, Kuenszi and Moore 1991, Woodrey and Moore 1997, Jones et al. 2002), our estimates suggest that birds gain mass quickly while stopping over in Michigan's eastern Upper Peninsula. Moreover, mass gains during the early-season period were similar to estimates from the late-season period for most species, which suggests that birds gained mass quickly, even early in the migratory period when only midges and spiders were available.

Midges as a resource.—Seefeldt (1997) and Smith et al. (1998, 2004) have argued that redstarts and green warblers gleaned more in shoreline habitats in response to high midge density. Cool temperatures common during morning hours throughout the spring migratory period depress flight activity of chironomids, concentrating them on vegetation. Our results suggest an elaboration on that scenario. Not only do migrants feed on midges, but they also feed on spiders, which in turn prey on midges.

During the late-season period, both male and female redstarts decreased use of foraging maneuvers directed at flying prey while increasing use of substrate-directed foraging maneuvers as ambient temperature increased. Both results suggest that birds were increasingly focused on substrate-clinging arthropods, even as numbers of swarming midges increased. Further, shoreline and inland comparisons of maneuver use indicated that males gleaned more at the shoreline and used more sally-strikes and sally-hovers inland. These differences likely reflected spatial differences in arthropod prey. Arthropod data showed more spiders present at the shoreline, which explains the large number of gleans. Inland, away from the lake's delaying influence on vegetation development (Albert et al. 1986), foliage arthropods such as lepidopteran larvae may have peaked sooner than at the shoreline. Higher percentages of lepidopteran larvae are typically found on lower leaf surfaces (Greenberg and Gradwohl 1980, Holmes and Schultz 1988), which may explain the increased use of sally-hovers inland. As birds direct more foraging to the underside of substrates, they are apt to increase use of sally-hovers, a maneuver often used to remove a prey item from the underside of a leaf (Remsen and Robinson 1990).

Data from the early-season period also support the hypothesis that redstarts were foraging on spiders in addition to midges. Males decreased aerial maneuver use with time and increased gleaning with increasing number of midges in the air column. Both females and males were foraging in a manner opposite of expectations had they been focusing on midges alone.

By foraging on spiders, migrants may have been more efficient in meeting the energy demands of migration. Spiders were, on average, larger (spider: $\bar{x} = 10.67 \pm 0.52$ mg; midge: $\bar{x} = 3.50 \pm 0.26$ mg) and likely provided more energy per prey item than midges. Finally, by foraging on substrate-dwelling prey, whether spiders or midges, birds may have enjoyed a higher net energy gain by using fewer energetically costly aerial-foraging maneuvers. The reduction in energy used to forage may have enhanced fat deposition rates for birds at the shoreline.

Our results, coupled with earlier work (Dallman and Smith 1995, Smith 1995, Ewert and Hamas 1996, Seefeldt 1997, Smith et al. 1998), strongly suggest that shoreline areas in Michigan's eastern Upper Peninsula provide important stopover habitat for spring migrating landbirds. Adult aquatic insects appear to be a major reason that these nearshore areas are attractive to spring migrants (Ewert and Hamas 1996). Evidence presented here suggests that midges are an important early-season resource for migrating landbirds and that midges also represent a food source for spiders. Further, birds appear to benefit from midges both directly and indirectly. Midges feed spiders, midges feed birds, and spiders feed birds.

Acknowledgments

We are grateful to members of The University of Southern Mississippi Migratory Bird Group, both past and present: J. Buler, D. Cimprich, J. Clark, C. Dwyer, J. Farrington, S. Mabey, J. Owen, C. Szell, S. Woltman, and M. Woodrey all contributed significantly to this work. The comments of D. Lank, D. Beckett, D. Ewert, T. Sherry, S. Walls, and two anonymous reviewers significantly improved the manuscript. This research was supported by the National Science Foundation, Dissertation Improvement Award (DEB-0073190), the Animal Behavior Society, Eastern Bird Banding Association, Sigma Xi, the Frank M. Chapman Memorial Student Research Fund, the Kalamazoo Audubon Society, U.S. Fish and Wildlife Service, and B. and G. Meyers. We thank Hiawatha National Forest for permission to perform this research on Forest Service property, and we are grateful to The Nature Conservancy (notably D. Ewert) and M. Hamas of Central Michigan University for logistical help. Finally, we thank our field crews for their dedicated efforts.

Literature Cited

Aebischer, A., M. Perrin, M. Krieg, J. Studer, and D. R. Meyer. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*. Journal of Avian Biology 27:143–152.

Albert, D. A., S. R. Denton, and B. V. Barnes. 1986. Regional Landscape Ecosystems of Michigan. School of Natural Resources, University of Michigan, Ann Arbor.

Alerstam, T., and A. Lindström. 1990. Optimal bird migration: The relative importance of time, energy and safety. Pages 331–351 *in* Bird Migration: Physiology and Ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin.

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227–267.

Armitage, P. D. 1995. Behaviour and ecology of adults. Pages 194–224 *in* The Chironomidae: Biology and Ecology of Non-biting Midges (P. D. Armitage, P. S. Cranston, and C. V. Pinder, Eds.). Chapman and Hall, New York.

Berthold, P. 1975. Migration: Control and metabolic physiology. Pages 77–128 *in* Avian Biology, vol. 5 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

Blem, C. R. 1980. The energetics of migration. Pages 175–224 *in* Animal Migration, Orientation, and Navigation (S. A. Gauthreaux, Jr., Ed.). Academic Press, New York.

Blem, C. R. 1990. Avian energy storage. Pages 59–113 *in* Current Ornithology, vol. 7 (D. M. Power, Ed.). Plenum Press, New York.

Brown, C. R., and M. B. Brown. 2000. Weather-mediated natural selection on arrival time in Cliff Swallows (*Petrochelidon pyrrhonota*). Behavioral Ecology and Sociobiology 47: 339–345.

Cooper, R. J., and R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Pages 29–37 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

Cristol, D. A. 1995. Early arrival, initiation of nesting, and social status: An experimental study of breeding female Red-winged Blackbirds. Behavioral Ecology 6:87–93.

Dallman, M., and R. J. Smith. 1995. Avian predation on chironomids along the nearshore waters of Lake Huron. Michigan Birds and Natural History 2:201–204.

Dunn, E. H. 2000. Temporal patterns in daily mass gain: Assessing the quality of migration stopover sites from Magnolia Warblers (*Dendroica magnolia*). Auk 117:12–21.

Dunn, E. H. 2001. Mass change during migration stopover: A comparison of species groups and sites. Journal of Field Ornithology 72: 419–432.

Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368–379.

Ewert, D. N., and M. J. Hamas. 1996. Ecology of migratory landbirds during migration in the Midwest. Pages 200–208 *in* Management of Midwestern Landscapes for the Conservation of Neotropical Migratory Birds (F. R. Thompson, Ed.). U.S. Department of Agriculture, Forest Service, General Technical Report NC-187, North Central Forest Experiment Station, Detroit.

Graber, J. W., and R. R. Graber. 1983. Feeding rates of warblers in spring. Condor 85:139–150.

Greenberg, R., and J. Gradwohl. 1980. Leaf surface specializations of birds and arthropods in a Panamanian forest. Oecologia 46:115–124.

Hejl, S. J., J. Verner, and G. W. Bell. 1990. Sequential versus initial observations in studies of avian foraging. Pages 166–173 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

Hódar, J. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Ecologica 17:421–433.

Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: Effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology 66:720–728.

Hutto, R. L. 1990. Measuring the availability of food resources. Pages 20–28 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

James, F. C., and H. H. J. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Jones, J., C. M. Francis, M. Drew, S. Fuller, and M. W. S. Ng. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. Condor 104:49–58.

Kilgo, J. C. 2005. Harvest-related edge effects on prey availability and foraging of Hooded Warblers in a bottomland hardwood forest. Condor 107:627–636.

Kuenszi, A. J., and F. R. Moore. 1991. Stopover of Neotropical landbird migrants on East Ship island following trans-gulf migration. Condor 93:869–883.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina.

Loria, D. E., and F. R. Moore. 1990. Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1:24–35.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164–170.

Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: Important link in conservation. Pages 121–144 *in* Ecology and Management of Neotropical Migratory Birds (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

Moore, F. R., and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

Moore, F. R., R. J. Smith, and R. Sandberg. 2005. Stopover ecology of intercontinental migrants: *En route* problems and consequences for reproductive performance. Page 466 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (P. P. Marra and R. Greenberg, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Moore, F. R., and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86:146–150.

Morse, D. H. 1981. Foraging speeds of warblers in large population and in isolation. Wilson Bulletin 93:334–339.

Morse, D. H. 1989. American Warblers: An Ecological and Behavioral Perspective. Harvard University Press, Cambridge, Massachusetts.

Nolan, V., Jr. 1978. Ecology and Behavior of the Prairie Warbler, *Dendroica discolor*. American Ornithologists' Union, Washington, D.C.

Nystrom, K. G. K. 1997. Food density, song rate, and body condition in territory-establishing Willow Warblers (*Phylloscopus trochilus*). Canadian Journal of Zoology 75:47–58.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138:2–15.

Petit, D. R., K. E. Petit, and L. J. Petit. 1990. Geographic variation in foraging ecology of North American insectivorous birds. Pages 254–263 *in* Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

Pyle, P. 1997. Identification Guide to North American Birds, Part 1: Columbidae through Ploceidae. Slate Creek Press, Bolinas, California.

Remsen, J. V., and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Pages 133–160 *in* Avian Foraging: Theory, Methodology, and

Applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). Studies in Avian Biology, no. 13.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

Sabo, S. R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecological Monographs 50:241–259.

Sandberg, R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. Ibis 138:514–524.

Sandberg, R., and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: Reproductive consequences for passerine migrants. Oikos 77:577–581.

Seefeldt, N. 1997. Attack rates of Black-throated Green Warblers (*Dendroica virens*) and American Redstarts (*Setophaga ruticilla*) along the shoreline of northern Lake Huron. M.S. thesis, Central Michigan University, Mt. Pleasant.

Siegel, S., and N. J. Castellan, Jr. 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw Hill, Boston, Massachusetts.

Slagsvold, T. 1976. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. Ornis Scandinavica 8: 197–222.

Smith, R., M. Hamas, M. Dallman, and D. Ewert. 1998. Spatial variation in foraging of the Black-throated Green Warbler along the shoreline of northern Lake Huron. Condor 100:474–484.

Smith, R. J. 1995. Foraging ecology of the Black-throated Green Warbler along the northern Lake Huron Shoreline. M.S. thesis, Central Michigan University, Mt. Pleasant.

Smith, R. J. 2003. Resources and arrival of landbird migrants at their northerly breeding grounds: Linking *en route* with breeding season events. Ph.D. dissertation, The University of Southern Mississippi, Hattiesburg.

Smith, R. J., M. J. Hamas, D. N. Ewert, and M. E. Dallman. 2004. Spatial foraging differences in American Redstarts along the shoreline of northern Lake Huron during spring migration. Wilson Bulletin 116:48–55.

Smith, R. J., and F. R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134: 325–331.

Svensson, E., L. Råberg, C. Koch, and D. Hasselquist. 1998. Energetic stress, immunosuppression and the costs of an antibody response. Functional Ecology 12:912–919.

Wang, Y., and F. R. Moore. 2005. Long-distance bird migrants adjust their foraging behavior in relation to energy stores. Acta Zoologica Sinica 51:12–23.

Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853–862.

Wood, N. A. 1951. The Birds of Michigan. University of Michigan Museum of Zoology, Ann Arbor.

Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707.

Yong, W., and F. R. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263–278.

Associate Editor: D. B. Lank