

SPATIAL FORAGING DIFFERENCES IN AMERICAN REDSTARTS ALONG THE SHORELINE OF NORTHERN LAKE HURON DURING SPRING MIGRATION

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ABSTRACT.—Lowland coniferous forests adjacent to northern Lake Huron provide important stopover habitat for landbirds during spring migration. Large numbers of aquatic insects emerging from nearshore waters of northern Lake Huron appear to be an important food source. In this study we compared the foraging behavior of a long-distance landbird migrant, the American Redstart (*Setophaga ruticilla*), in areas with high densities of emergent aquatic insects to areas with few or no emergent aquatic insects to assess the significance of these arthropods as an early spring food source. Redstarts foraged differently in shoreline habitats relative to inland habitats of similar vegetation composition. Both males and females gleaned significantly more in shoreline habitats as compared to inland areas of similar vegetation composition, and inland birds performed more sally strikes than birds at the shoreline. Both sexes also varied the use of tree species in which they foraged. Redstarts used northern white cedar (*Thuja occidentalis*) more at shoreline than inland, while inland redstarts foraged in deciduous trees more than at the shoreline. We suggest that differences in foraging between shoreline and inland locations were responses to differences in prey types and abundance, most notably the presence of emergent aquatic insects (Diptera: Chironomidae) in shoreline habitat. Our results complement those of previous work, suggesting that midges provide a critical early season resource for landbirds migrating through Michigan's eastern Upper Peninsula during spring. Received 30 September 2003, accepted 26 March 2004.

During spring and early summer in temperate North America, large numbers of aquatic insects that have metamorphosed into sexually mature adults often amass in terrestrial habitats adjacent to riparian and lacustrine systems (Armitage 1995, McCafferty 1998). These invertebrates are relatively weak fliers (e.g., Kovats et al. 1996) and tend to be restricted to nearshore terrestrial habitats. In Michigan's eastern Upper Peninsula, midges (Diptera: Chironomidae) are the predominant aquatic arthropods when migratory landbirds stop during spring migration. These invertebrates swarm profusely in shoreline areas while being virtually nonexistent inland (DNE unpubl. data).

Recent evidence suggests that lowland coniferous forests adjacent to northern Lake Huron provide important stopover habitat for spring migrants. More landbirds are found in

nearshore, midge-abundant habitats than inland habitats with comparable vegetation (DNE unpubl. data). Further, Black-throated Green Warblers (*Dendroica virens*) forage in and use habitat elements differently in midge-abundant habitats compared to inland, midge-depauperate habitats (Smith et al. 1998), and American Redstarts (*Setophaga ruticilla*) and Black-throated Green Warblers forage at higher rates in midge-abundant areas relative to habitats with no midges (Seefeldt 1997).

Here we describe shoreline/inland differences in the foraging behavior of a long-distance landbird migrant, the American Redstart, during spring migration in Michigan's eastern Upper Peninsula. By focusing on spring migration, we were able to examine bird behavior when shoreline/inland differences in arthropod abundances were most dramatic (Smith et al. 1998; DNE unpubl. data). We compared redstart foraging behavior in areas with high densities of midges to areas with few or no emergent midges to assess the significance of these arthropods as a food source during early spring.

METHODS

Study area.—The study area included approximately 80 km of shoreline, extending

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from Horseshoe Bay to DeTour State Park in Mackinac and Chippewa counties, respectively (45° 57' to 46° 04' N, 84° 00' W to 84° 44' W). Limestone and dolomite peninsulas define much of the shoreline, with sandy coves and marshes characterizing borders of intervening bays. Conifers, especially northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), eastern white pine (*Pinus strobus*), and deciduous species, including paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*), dominate the forest. Forest composition was relatively uniform throughout the study area, as determined by vegetation sampling performed in association with a bird census project that occurred in the same landscape (Smith et al. 1998; DNE unpubl. data). Using the point-centered technique of Cottam and Curtis (1956), DNE (unpubl. data) determined forest composition at 45 permanent, 50-m fixed-radius bird census points positioned on nine transects spaced uniformly across the study area. Sample points were positioned at 0, 0.4, 0.8, 1.6, and 3.2 km from the lake-shore. Canopy height ranged from 10 to 15 m. The understory was heavily browsed by white-tailed deer (*Odocoileus virginianus*) and consisted mostly of balsam fir and white spruce.

Foraging observations.—We collected data on foraging American Redstarts during spring migration of 1993 and 1994. To avoid bias in our sampling effort, we spent equal amounts of time in shoreline and inland habitats while searching for foraging redstarts. Observations of spring migrants commenced when the first birds arrived in early May and continued through early June, the onset of breeding for birds in the area (Wood 1951; DNE and MJH pers. obs.; R. J. Smith and F. R. Moore unpubl. data). To compare foraging at shoreline and inland locations, observations made ≤ 0.4 km from Lake Huron were designated as shoreline, and observations made 0.4–3.2 km from the lake were designated as inland. We selected 0.4 km as the boundary between shoreline and inland because midge abundance drops precipitously beyond this point (DNE unpubl. data).

We used the protocol of Hejl et al. (1990) to minimize the likelihood of pseudoreplication. Only the first bird (of each sex) detected

in a flock was used as a subject. We recorded additional data only after an observer had traveled ≥ 30 m or ≥ 10 min had elapsed since the previous observation. To reduce discovery bias, we waited 5 sec after making initial visual contact, and then recorded the subsequent foraging maneuver performed by the bird (Morrison 1984, Hejl et al. 1990).

Foraging maneuvers were categorized as (1) glean, a 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 is attacked by a hovering bird; and (3) sally strike, a maneuver in which both the insect and bird are in flight—also known as fly-catching or hawking behavior (Sabo 1980, Petit et al. 1990a).

We described the location of a foraging maneuver both horizontally and vertically within a tree. To characterize horizontal position, we arbitrarily divided a tree into inner, middle, and outer thirds (MacArthur 1958, Remsen and Robinson 1990). We also recorded foraging height for each bout by using a clinometer to measure the angle from observer to the bird and an optical rangefinder to measure distance; these data were converted to height (m) using the appropriate trigonometric equation. At the end of each observation we also recorded the species of tree in which the bird was observed, time of day, distance from the shoreline, and weather conditions.

We pooled data across years to maximize sample sizes. Only the five most frequently used tree species were considered when analyzing tree species used during foraging: white spruce, balsam fir, northern white cedar, quaking aspen, and paper birch. All data were analyzed using SPSS (2000). Treatment of variables depended upon whether data were continuous or categorical (Zar 1996). We used a General Linear Model to resolve differences in foraging height by sex and observation location (shoreline versus inland). Log-likelihood ratio (G) tests were used to analyze frequency data such as spatial differences in use of tree species, maneuver used, and horizontal position while foraging. Log-likelihood ratio (G) tests also were used to compare actual to expected use of northern white cedar by foraging redstarts. If redstarts preferred to forage in (or avoided) cedar, then they would exhibit

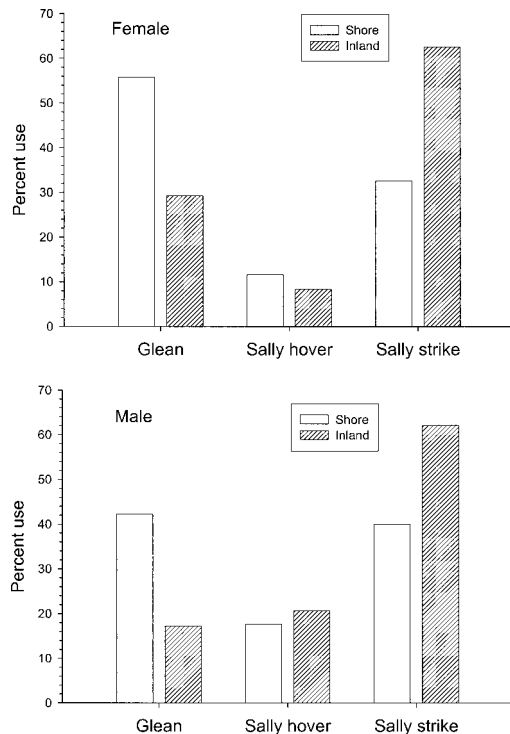


FIG. 1. Comparison of American Redstart foraging maneuvers at shoreline and inland habitats during spring migration 1993–1994, northern Lake Huron, Michigan (female $n = 67$, male $n = 379$).

a disproportionate use of cedar (Morrison et al. 1998). We used relative density estimates of cedar—calculated from vegetation sampling—to derive expected redstart use of cedar. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Males did not differ by age in foraging maneuvers used ($G = 4.89$, $df = 2$, $P = 0.087$, $n = 283$), nor did males differ from females in their use of foraging maneuvers ($G = 3.32$, $df = 2$, $P = 0.19$, $n = 333$). The type of foraging maneuver used, however, was dependent on habitat for both males ($G = 6.24$, $df = 2$, $P = 0.044$, $n = 379$) and females ($G = 6.22$, $df = 2$, $P = 0.045$, $n = 67$). Both sexes gleaned more at shoreline than inland locations (males: 42 versus 18%; females: 56 versus 29%) and used more sally strikes inland than at the shoreline (males: 64 versus 40%; females: 63 versus 32%; Fig. 1).

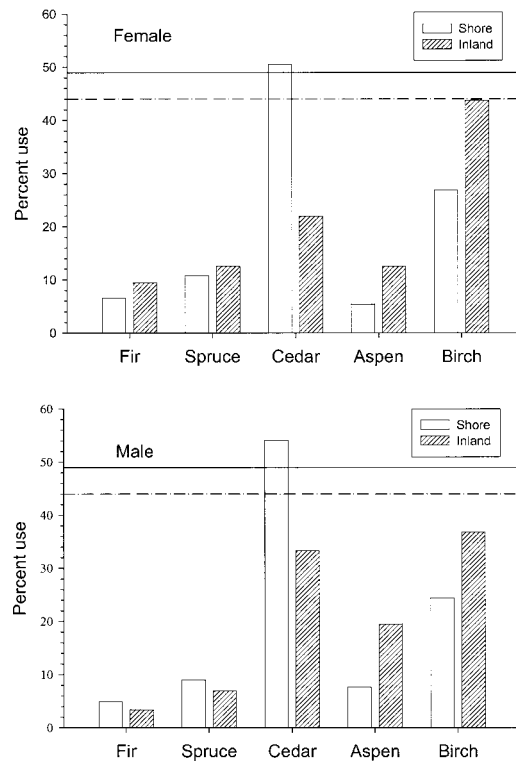


FIG. 2. American Redstart tree use in shoreline and inland habitats during spring migration 1993–1994, northern Lake Huron, Michigan (female shoreline $n = 93$, female inland $n = 32$; male shoreline $n = 590$, male inland $n = 87$). The solid reference line indicates relative density of northern white cedar in shoreline habitats and the dashed line indicates relative density of cedar inland.

There was no relationship between tree species selected for foraging and age of males ($G = 4.85$, $df = 4$, $P = 0.30$, $n = 229$) or gender ($G = 4.35$, $df = 4$, $P = 0.36$, $n = 363$). Males used tree species for foraging differently in shoreline habitats as compared to inland ($G = 21.23$, $df = 4$, $P < 0.001$, $n = 677$); the relationship was not significant in females ($G = 9.06$, $df = 4$, $P = 0.060$, $n = 125$). In shoreline habitats, both males and females foraged more in northern white cedar than in other tree species (males 55%, females 52%), but they were observed more in aspen and birch inland relative to the shoreline (Fig. 2). Redstarts foraging in shoreline habitats did not use northern white cedar disproportionately (male: $G = 0.16$, $df = 1$, $P = 0.66$, $n = 590$; female: G

= 0.033, $df = 1$, $P = 0.81$, $n = 93$), but inland they did use cedar significantly less than expected (male: $G = 4.54$, $df = 1$, $P = 0.038$, $n = 87$; female: $G = 4.33$, $df = 1$, $P = 0.042$, $n = 32$; Fig. 2).

Foraging height was not related to male age ($F_{1,374} = 2.60$, $P = 0.11$), and male foraging height did not differ between shoreline and inland habitats ($F_{1,374} = 0.02$, $P = 0.89$); there was no male age by habitat interaction for foraging height ($F_{1,374} = 0.14$, $P = 0.71$). Foraging height of the sexes did not differ ($F_{1,441} = 2.27$, $P = 0.13$), nor did foraging height differ between shoreline and inland habitats ($F_{1,441} = 0.24$, $P = 0.63$); there was no sex by habitat interaction for foraging height ($F_{1,441} = 0.01$, $P = 0.99$). We found no shoreline/inland differences in horizontal position of males and females within trees (male: $G = 2.16$, $df = 2$, $P = 0.34$, $n = 378$; female: $G = 0.36$, $df = 2$, $P = 0.84$, $n = 67$).

DISCUSSION

Landbirds are known to vary their foraging in response to a number of factors, including structural differences in habitat (Collins 1983, Holmes and Schultz 1988), inter- and intra-specific competition (Rappole and Warner 1976, Laursen 1978, Morse 1980), including gender (Morse 1968, Holmes 1986, Ornat and Greenberg 1990, Petit et al. 1990b) and age (Woodrey 1995) interactions, weather (Pinkowski 1977), ambient temperature (Ford et al. 1990), thermoregulatory requirements (Martin and Karr 1990), and distribution, diversity and abundance of prey species (Holmes and Schultz 1988, Ford et al. 1990, Szaro et al. 1990, Smith et al. 1998). While the observed shoreline/inland differences in redstart foraging might be attributable to one or more of these factors, our results most likely reflect shoreline/inland differences in the abundance and activity of arthropods.

The observed variation in redstart foraging is likely not a consequence of differences in forest composition because our equal sampling effort, distributed across such a large landscape, should have eliminated any spurious effects between shoreline and inland. Moreover, vegetation sampling performed at the same scale as behavior sampling indicated little shoreline/inland difference in density of

tree species throughout our study area (Smith et al. 1998; DNE unpubl. data).

It is possible that differences in migrant densities between shoreline and inland (DNE unpubl. data) may have caused birds to vary their foraging by creating a situation in which shoreline birds experienced enhanced competition. Consequently, migrants in shoreline locations may have altered their foraging relative to those inland as they sought to alleviate enhanced competition associated with higher numbers of competitors. While our data are insufficient to rule this out, we point out that the shoreline/inland differences observed in redstarts were very similar to foraging differences previously documented in Black-throated Green Warblers (Smith et al. 1998). As with redstarts, during spring migration Black-throated Green Warblers gleaned more at the shoreline while exhibiting more sally hovers and sally strikes inland. Furthermore, Black-throated Green Warblers foraging in shoreline locations used cedar more than other tree species, while birds observed inland dramatically reduced their use of cedar, instead foraging more in deciduous species such as paper birch and quaking aspen.

Differential distribution by age or sex also could have influenced foraging, if there were age or sex differences in how redstarts foraged at our site. Age- and/or sex-mediated habitat segregation has been demonstrated among redstarts on the wintering grounds (Marra et al. 1993, Parrish and Sherry 1994), during migration (Woodrey 1995), and during the breeding season (Sherry and Holmes 1997). However, we found no age or gender effect in how birds foraged or used tree species.

There were obvious microclimate differences between shoreline and inland areas within our study site (DNE unpubl. data). Shoreline habitats were, on average, cooler and remained cooler longer. Redstarts may have varied foraging in response to these temperature differences. Martin and Karr (1990) found that a number of warbler species increased flying maneuvers during the colder periods of early spring and late fall migration. They suggested that use of aerial maneuvers during cold periods may be more efficient than nonflying maneuvers because of increased heat production by flight muscles. However, we found that redstarts performed more nonflying ma-

neuers (gleans) in cooler shoreline habitats and more aerial maneuvers (sally hovers and sally strikes) in warmer, inland areas. These results are contrary to what would be expected if birds increased aerial maneuvers to enhance thermoregulatory efficiency, but they correspond with expectations if birds were responding to increased activity of flying invertebrates in warmer habitats (see below).

The Great Lakes' influence on local climate, vegetation, and animal communities is especially apparent in nearshore terrestrial habitats (Eichenlaub 1979). Temperature depression resulting from onshore winds delays the phenological development of vegetation (Albert et al. 1986; DNE unpubl. data) and presumably the emergence and activity of arthropods, as both are dependent upon ambient air temperature (Williams 1961). Shoreline microclimate differs from inland and likely results in unique abundance and distribution patterns of arthropods.

Evidence for differences in arthropod abundance between shoreline and inland areas is suggested by differing foraging maneuvers in the two areas. Inland, away from the cooling influence of the lake, redstarts performed more sally strikes and fewer substrate-directed gleans. Black-throated Green Warblers also increased their use of sally strikes at inland sites in Michigan's eastern Upper Peninsula (Smith et al. 1998). Increases in aerial maneuvers such as sally strikes suggest that either flying insects were more abundant inland, flying insects were more active inland, or some combination of the two. Because of the influence of temperature on invertebrate development and activity, any temperature differential between shoreline and inland may have resulted in disparities in activities and abundances of prey, thereby influencing foraging behavior. Birds also may have altered foraging behavior in response to shoreline/inland differences in the kinds of arthropods that were available within a habitat.

The most obvious spatial disparity in prey for migrants was the abundance of adult midges in shoreline habitats. These insects were strongly associated with the lakeshore; beyond 0.40 km from shoreline, midge abundance dropped to near zero (DNE unpubl. data). Midges commonly rest on nearshore vegetation in high densities, and both field obser-

vations and our results suggest that birds foraged heavily on these insects. In temperate habitats, mating swarms of midges are temperature dependent (R. J. Smith and F. R. Moore unpubl. data); depending on the species, they begin to swarm at a critical minimum temperature of about 10° C (Armitage 1995).

Redstart foraging preferences corresponded with the activity and presence/absence of midges. For instance, redstart foraging activity was most intense during early morning when temperatures often were below 10° C. Lower shoreline temperatures may have delayed swarming until later in the day, resulting in high densities of substrate-bound (resting) midges. Thus, resting midges may have elicited, at least in part, the more-frequent glean-ing observed in shoreline areas than inland areas. Furthermore, the differential use of northern white cedar suggests that midges may be an important food resource; redstarts used cedar significantly more at the shoreline compared to inland, even though there was no significant shoreline/inland difference in cedar density across the study area (DNE unpubl. data). Moreover, shoreline redstarts did not depart from random use of cedar while inland birds foraged in cedar less than expected. This differential use of cedar may reflect differential midge abundance. Birds shifted foraging away from cedar inland, where few midges occurred. This reduction in use of inland cedar suggests that suitable prey items, other than midges, were not abundant in cedar.

Similar results were documented in Black-throated Green Warblers foraging in cedar in the same area (Smith et al. 1998). Birds used cedar as expected at the shoreline during spring migration and less than expected inland. During the breeding season and fall migration, when midges were not abundant in shoreline habitats (DNE unpubl. data), Black-throated Green Warblers used cedar significantly less. The shoreline/inland differences in cedar use by both redstarts and Black-throated Green Warblers, and the decline in shoreline use by Black-throated Green Warblers during the breeding season and fall migration, suggest that birds foraged in cedar in response to the presence of midges and that prey items other than midges were not abundant in cedar.

Constructive replication in the behavioral

sciences is rare (Martin and Bateson 1993). We have identified concordant results between two warbler species that are rather disparate foragers. Black-throated Green Warblers include a high percentage of gleaners as part of their foraging repertoire (Morse 1993), whereas American Redstarts use relatively fewer gleaners and more aerial-directed foraging maneuvers (Sherry and Holmes 1997). Similarities in foraging between these two species reduce the likelihood that our results are spurious, and they provide additional support for the hypothesis that aquatic insects are a critical early season resource for landbirds during spring migration in Michigan's eastern Upper Peninsula.

Intercontinental landbird migrants often outpace the phenological development of vegetation and terrestrial invertebrates as they move north during spring migration (Slagsvold 1976, Ewert and Hamas 1995), arriving on their breeding grounds well before vegetation is fully leafed out and food becomes abundant (Slagsvold 1976, Nolan 1978, Perrins 1996, Nystrom 1997). Arrival of migrants breeding in northern Michigan may precede completion of leaf development by up to 4 weeks (RJS unpubl. data). Early arrival also increases exposure to inclement weather, including late season snowstorms, low temperatures, or extended periods of rain (Whitmore et al. 1977, Zumeta and Holmes 1978, Ewert and Hamas 1995, Aebischer et al. 1996, Merkle and Barclay 1996). Midges may provide the energy necessary for survival during severe weather or, under better conditions, energy for fat deposition, allowing a timely return and beginning of breeding (Alerstam and Lindström 1990, Rowe et al. 1994, Smith and Moore 2003). The quality of nearshore areas in Michigan's eastern Upper Peninsula appears to be augmented by the presence of adult aquatic insects, which provide a critical food source prior to the appearance of leaves and emergence of phytophagous insects.

ACKNOWLEDGMENTS

We thank three anonymous reviewers for constructive comments on a previous version of this manuscript. Funding for this work was provided by the National Fish and Wildlife Foundation, R. E. Ransom Fidelity Company, Dr. and Mrs. Lewis Batts, Central Michigan University, and The Nature Conservancy. Phil and Margaret Pittman generously provided hous-

ing during both field seasons. We thank Hiawatha National Forest, Michigan Department of Natural Resources, and M. Twining for permission to conduct this work on their properties. This manuscript benefited significantly from discussions with F. R. Moore and members of The University of Southern Mississippi Migratory Bird Group.

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