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SPATIAL VARIATION IN FORAGING OF THE BLACK-THROATED GREEN WARBLER ALONG THE SHORELINE OF NORTHERN LAKE HURON[1]

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Abstract. The Great Lakes strongly influence local climate, vegetation, and animal communities, all of which are important to both migrating and breeding birds. This influence can be considerable during springtime in nearshore habitats, as onshore winds depress air temperatures, delaying development of shoreline vegetation relative to inland areas. These developmental differences also may affect abundance, distribution, activity, and growth of insect prey, resulting in spatially-related differences in foraging by birds. Here we test the hypothesis that northern Lake Huron influences the foraging behavior of Black-throated Green Warblers (*Dendroica virens*) during both migratory periods and the breeding season. We detected spatial variation in a number of variables we used to describe foraging, with most differences occurring during spring migration. We suggest that birds primarily varied foraging in response to spatial differences in prey resulting from microclimatic influences of nearby Lake Huron. We also suggest that emerging aquatic insects in shoreline habitats, primarily midges (Diptera: Chironomidae), are important to birds and propose that this abundant prey source has a primary influence on foraging.

Key words: Black-throated Green Warbler, Dendroica virens, *foraging behavior, Lake Huron, Michigan, migration, spatial variation.*

INTRODUCTION

Through their size, the Great Lakes strongly influence local climate, vegetation, and animal communities (Eichenlaub 1979, Albert et al. 1986), all of which are important to migrating as well as to breeding bird populations. Near the shoreline for example, temperature depression resulting from onshore winds delays phenological development of vegetation in spring (Ewert and Hamas, unpubl. data) and presumably the emergence and activity of potential prey species for passerine migrants, as both are dependent upon ambient air temperature (Williams 1961). Thus, lakeshore influence may result in spatial differences in both prey species activity and abundance between shoreline and inland areas.

Whereas climatic influence can be considerable in nearshore habitats, this effect declines with increasing distance from the lake. Inland ambient temperatures vacillate to a greater extent than along the shoreline (Albert et al. 1986). Diurnal temperatures in habitats away from the ameliorating effects of the lake tend to increase more rapidly during the day, stimulating a quicker rate of phenological development of vegetation (Ewert and Hamas, unpubl. data). This differential influence may result in spatially dependent, temperature driven microhabitats, which in turn may lead to differential prey types and abundances throughout the year. Ultimately, these influences may result in differential foraging by birds as the abundance and activity of principal prey items vary both spatially and temporally.

In this paper we describe the foraging behavior of the Black-throated Green Warbler (*Dendroica virens*), a relatively stereotypical foliage gleaner (Bent 1953, Morse 1976) that is abundant both as a migrant as well as breeding bird in Michigan's eastern Upper Peninsula. The forested landscape adjoining northern Lake Huron provided a unique opportunity to examine this species' foraging behavior as it relates to distance from the lakeshore during spring migration, the breeding season, and fall migration. We tested the hypothesis that proximity to the shore-

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line of northern Lake Huron influences Black-throated Green Warbler foraging behavior.

METHODS

STUDY AREA

Fieldwork was conducted along the shoreline of northern Lake Huron in Michigan's eastern Upper Peninsula. The study area included 80 km of shoreline, extending from Horseshoe Bay to DeTour State Park in Mackinac and Chippewa counties. Ewert and Hamas (unpubl. data) determined forest composition at 45 permanent 50-m fixed-radius bird census points throughout the study site using the point-centered technique (Cottam and Curtis 1956), and we use their results in this study. Sampling points were selected for uniformity, and we feel that this sampling methodology provides a reasonable representation of forest composition within the study area. We recognize the presence of heterogeneity within forest communities and note that some of our foraging observations were not necessarily confined to the community type as described by this vegetation analysis. However, we feel that by observing foraging behavior across such a large area, our sampling is representative, and any observed effects can be attributed largely to reasons other than habitat heterogeneity.

FORAGING OBSERVATIONS

Foraging data were partitioned seasonally as spring migration, breeding season, and fall migration. Observations of spring migrants were made when the first birds arrived in early May and continued through early June. Breeding season observations were obtained from 10 June 1993 and 14 June 1994 until 19 July of both years. Observations of fall migrants commenced on 15 August and continued until the last birds departed (24 September 1993, 1 October 1994). We based the cut-off date for migration vs. the breeding season on historical records of arrival and departure for birds in the area (Woods 1951, Ewert and Hamas, pers. observ.).

In order to make spatial comparisons, data were partitioned into either shoreline or inland categories. All observations within 0.4 km of Lake Huron were categorized as shoreline. Inland observations extended 0.4–3.2 km from the lake.

To ensure independence of data, we adopted the protocol of Hejl et al. (1990). Only the first bird (per sex) detected in a flock was used as a subject. Additional data were recorded only after an observer traveled a minimum of 30 m or at least 10 min had elapsed since the previous observation. Thus, the likelihood of collecting data from the same individual was minimal. In order to reduce bias toward conspicuous maneuvers, an observer waited 5 sec after initial visual contact. Then, the next foraging maneuver utilized by the bird was recorded (Morrison 1984, Hejl et al. 1990).

Foraging behaviors were designated 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 insect and bird are in flight—which also has been termed as flycatching or hawking behavior (Sabo 1980, Petit et al. 1990).

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). Additionally, we recorded height for each foraging bout. A clinometer was used to measure the angle from the observer to the maneuver location. Then distance to the location was recorded using a rangefinder. These data were converted to an actual height in meters.

Additional data recorded for each foraging observation included: species of tree foraged in, where birds directed foraging (leaf, branch, air for deciduous species; needle, branch, air for coniferous species), whether the attack was directed at the top or bottom of a substrate, time of day, distance from the shoreline, and weather conditions.

STATISTICAL ANALYSIS

With the exception of tree species foraged in, we pooled data across year as there were no statistical differences in the other variables of interest. Additionally, after stratifying the data set to make the comparisons of interest (shoreline vs. inland during spring migration, the breeding season, and fall migration), the small number of females in our data set and the problems associated with categorical analysis when greater than 20% of cells have an expected frequency of less than 5 precluded analyzing sexes separately (Cochran 1954). Females were especially secretive during both spring migration and the breeding season—we observed six males for every female during both periods. During fall migration females were more evident and we collected two male observations for every female. We recognize that, given the differential sex-based constraints placed upon birds, there are very likely identifiable sex-related differences with respect to our variables of interest. Finally, the five most frequently used tree species were considered when analyzing tree species used for foraging. These were balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), northern white cedar (*Thuja occidentalis*), and white spruce (*Picea glauca*). Frequencies of use for all other vegetation resulted in expected cell values of less than 5. Therefore, these cells were collapsed into a single category for statistical analysis.

All data were analyzed using SAS (SAS Institute 1988). Statistical treatment of variables depended on whether data were continuous or categorical. The continuous variable (foraging height) was found to be normally distributed using the SAS procedure UNIVARIATE, so procedure GLM was used to test for spatial differences in foraging height, controlling for season (Sokal and Rohlf 1995). Log-likelihood ratio (G) tests (Sokal and Rohlf 1995) were used to analyze frequency data such as spatial differences in tree species use, maneuver use, horizontal position while foraging, and maneuver focus (branch, leaf/needle, or air) using the SAS procedure FREQ. Average foraging heights reported below are means ± SE. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Calculated importance values indicated that, on average, forest composition of the five tree species most frequently used by foraging Black-throated Green Warblers was similar in both shoreline and inland habitats (Ewert and Hamas, unpubl. data). Moreover, examination of tree densities, pooled across the study site, indicate a high degree of similarity between shoreline and inland. The dominant tree in the study area was northern white cedar, which had the same rank order in terms of importance value and density at both shoreline and inland sites. Forests along the shoreline contained primarily white spruce, balsam fir, quaking aspen, paper birch, and to a lesser extent white pine (*Pinus strobus*), and balsam poplar (*Populus balsamifera*). Inland sites had the same set of common species except that red maple (*Acer rubrum*) replaced balsam poplar. Canopy height across the study area averaged 13.5 m with an understory comprised of principally balsam fir and white spruce.

SPRING MIGRATION

We found more shoreline/inland differences in the variables we used to characterize foraging of Black-throated Green Warblers during the spring migratory period than either the breeding season or fall migration. During spring migration, inland birds gleaned less (56.6% inland compared to 69.1% shoreline) while increasing use of sally hovers (23.0% inland compared to 14.12% shoreline) and sally strikes (20.5% inland compared to 16.8% shoreline). This difference was significant ($G_2 = 6.3$, $P = 0.04$). They did not, however, vary in where they foraged within a tree, either horizontally ($G_2 = 1.9$, $P > 0.3$) or vertically ($F_{1,382} = 0.1$, $P > 0.5$; shoreline = 9.51 ± 0.22 m, inland = 9.64 ± 0.36 m). There were significant shoreline/inland differences in use of trees in both 1993 ($G_5 = 32.2$, $P < 0.001$) and 1994 ($G_5 = 19.4$, $P < 0.01$) (Fig. 1). Inland birds used white cedar less and balsam fir, quaking aspen, paper birch, and white spruce more relative to birds foraging in shoreline habitat. The most notable difference in tree use was that of white cedar along the shoreline in both years. Birds foraged in this species substantially more than other trees in shoreline habitats during spring in addition to exhibiting a dramatic within year shoreline/inland difference in use. This difference was only present during spring migration (Fig. 2). Even though there were significant differences in tree use by year ($G_5 = 20.3$, $P = 0.001$), these spatial trends remained similar in both years (Fig. 1).

Because of the large shoreline/inland and seasonal differences in white cedar use (see Fig. 2), we performed the analysis again, omitting white cedar. This revealed no difference in 1993 ($G_4 = 8.2$, $P > 0.05$) or 1994 ($G_4 = 2.3$, $P > 0.5$), indicating that the observed differences were a result of birds' use of northern white cedar. During spring migration along the shoreline, birds did not depart significantly from random in their use of white cedar in 1993 ($G_1 = 2.7$, $P > 0.05$) or 1994 ($G_1 = 0.8$, $P > 0.5$). However, during both years, inland birds foraged in white cedar significantly less than expected (1993: G_1 =

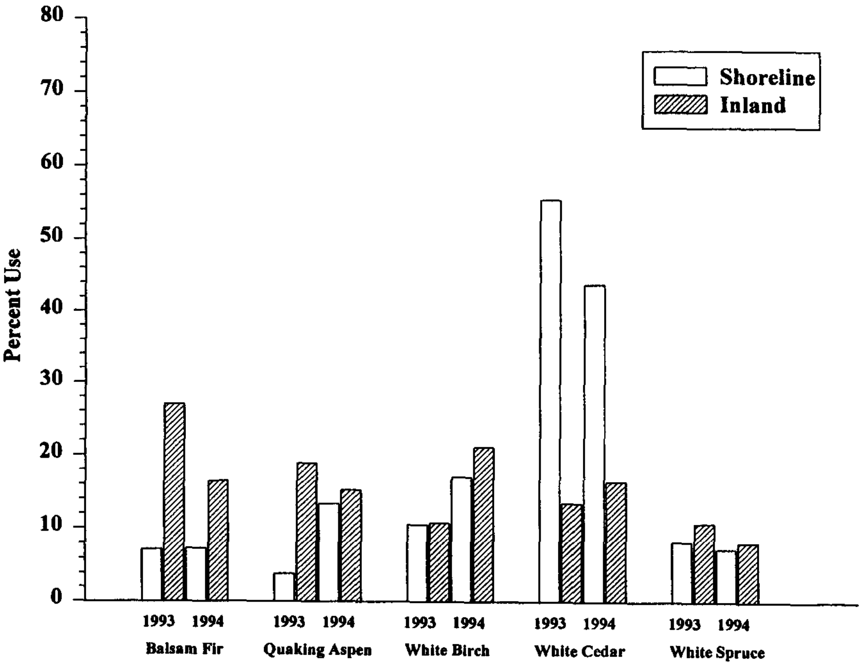

FIGURE 1. Black-throated Green Warbler spatial use of tree species during spring migration, 1993 ($n = 217$) and 1994 ($n = 167$).

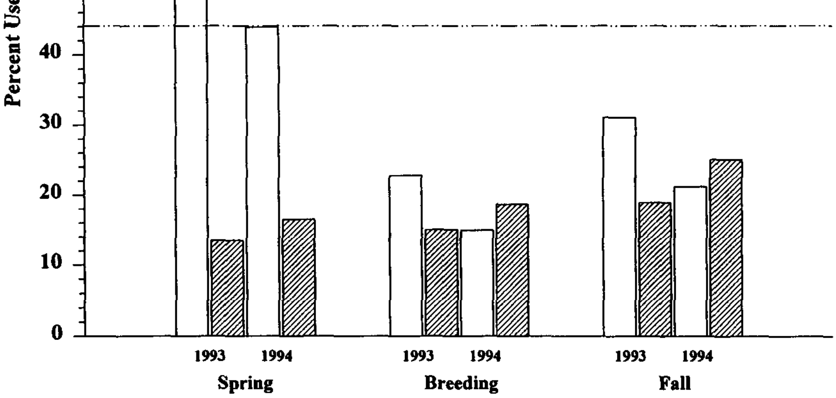

FIGURE 2. Black-throated Green Warbler spatial use of northern white cedar, by season, 1993–1994 (spring $n = 155$; breeding $n = 61$; fall $n = 63$). Reference lines indicate relative density of white cedar in shoreline (—) and inland (··——··) habitats.

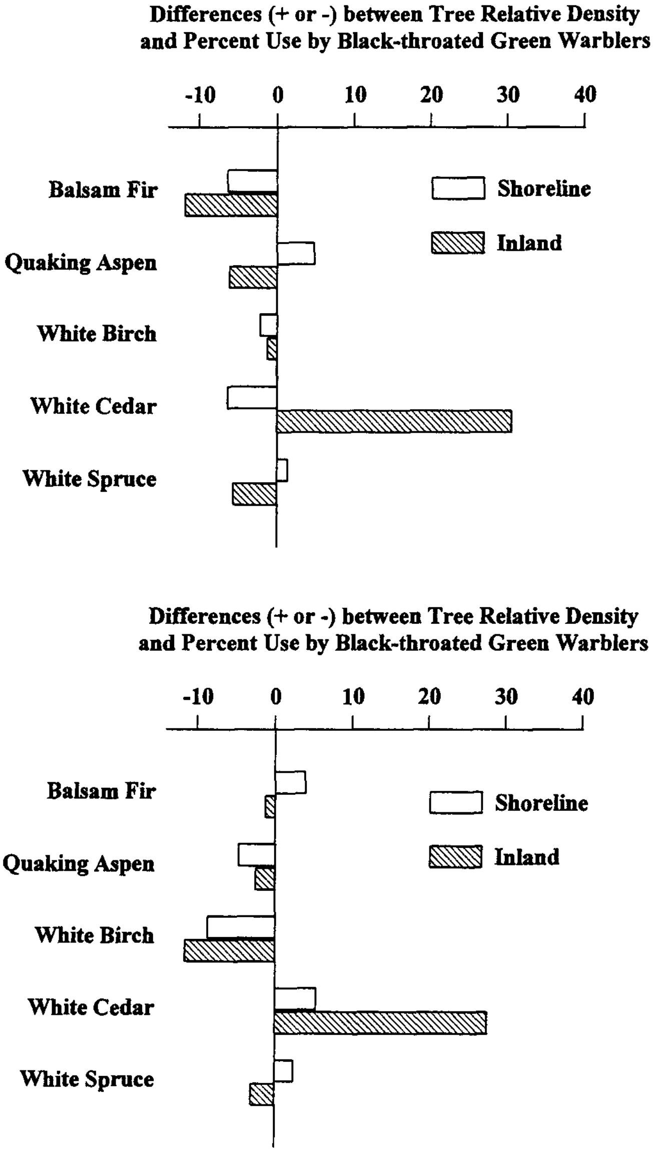

FIGURE 3. Use of five common tree species by foraging Black-throated Green Warblers. Bars represent the differences (+ or -) between relative density of tree species and percent use by birds during spring migration, 1993 (top) and 1994 (bottom).

15.3, $P < 0.001$; 1994: $G_1 = 27.6$, $P < 0.001$) (Fig. 3). This lack of use was evident during both the breeding season and fall migration in both shoreline and inland sites (Fig. 2).

Black-throated Green Warblers also varied in where they directed foraging maneuvers during spring migration in both coniferous ($G_2 = 15.0$, $P = 0.001$) and deciduous vegetation ($G_2 = 8.3$, $P = 0.02$). Birds foraging in conifers directed maneuvers more to needles and less to the air and branches in shoreline habitats relative to inland, whereas inland birds foraged substantially more on leaves while reducing maneuvers directed to air and branches in deciduous vegetation (Fig. 4). Furthermore, birds exhibited differences in use of top/underside of foraging substrates. During spring, birds foraging in deciduous trees utilized the top of leaves more at the

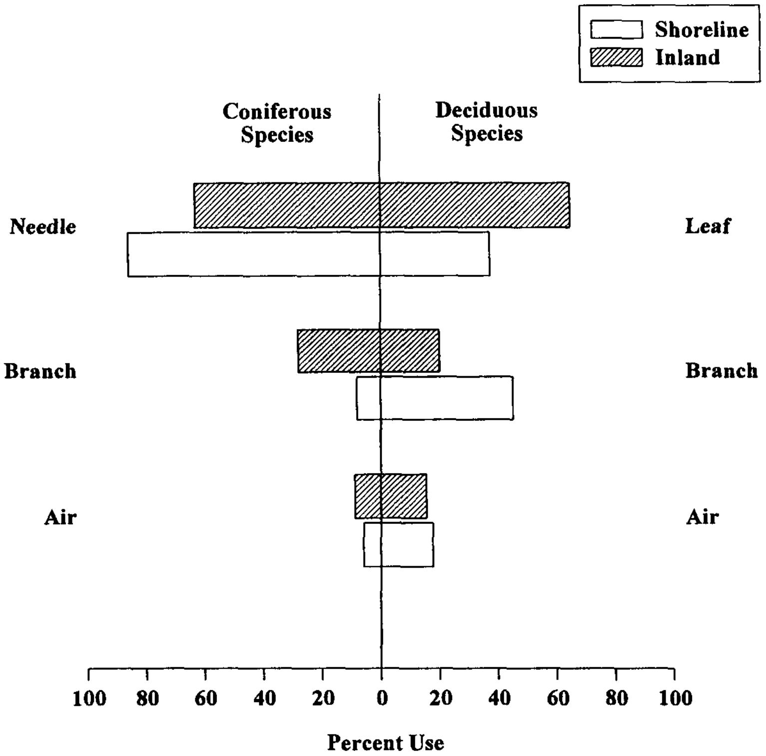

FIGURE 4. Black-throated Green Warbler spatial variation in foraging maneuver focus in coniferous (n = 243) and deciduous (n = 243) tree species inland and at the shoreline, during spring migration 1993–1994.

shoreline (72.4% of leaf directed maneuvers) than inland (43.8% of leaf directed maneuvers) ($G_1 = 5.2$, $P = 0.02$).

BREEDING SEASON

We identified no significant differences between shoreline and inland habitats during the breeding season in birds' use of foraging maneuvers ($G_2 = 0.0$), horizontal position ($G_2 = 1.3$, $P > 0.5$), foraging height ($F_{1,310} = 0.7$, $P > 0.5$; shoreline = 11.83 ± 0.29 m, inland = 12.28 ± 0.44 m), tree species foraged in during 1993 ($G_5 = 9.7$, $P > 0.05$) or 1994 ($G_5 = 10.3$, $P > 0.05$), or where they directed foraging maneuvers when foraging in coniferous ($G_2 = 0.5$, $P > 0.3$) or deciduous ($G_2 = 0.8$, $P > 0.3$) vegetation. However, birds did exhibit significant variation in use of top/underside of foraging substrates in coniferous tree species ($G_1 = 5.0$, $P = 0.03$), favoring the top of substrates more in shoreline habitats than inland (67.1% compared to 46.5%) and the bottom of substrates more inland than at the shoreline (53.4% compared to 32.9%). This difference was not evident when examining only deciduous species ($G_1 = 0.1$, $P > 0.8$).

FALL MIGRATION

The only spatial difference detected for foraging height occurred during fall migration, in which average height was 9.34 ± 0.37 m inland and 8.34 ± 0.33 m along the shoreline ($F_{1,273} = 4.1$, $P < 0.05$). Further analysis indicated that this difference was attributable to shrub use, principally serviceberry (*Amelanchier arborea*) and witchhazel (*Hamamelis virginiana*) ($F_{1,15} = 4.8$, $P < 0.05$; shoreline = 3.18 ± 0.82 m, inland = 5.7 ± 0.66 m), and that birds did not vary foraging height in any of the five most frequently used tree species ($F_{1,267} = 2.9$, $P < 0.10$).

In both years birds foraging in shoreline habitats used trees differently from inland habitats. During 1993 birds foraged in balsam fir, white cedar, and white spruce more in shoreline habitats, whereas quaking aspen and paper birch were used more inland ($G_5 = 14.0$, $P = 0.02$). In 1994 this trend, with the exception of paper

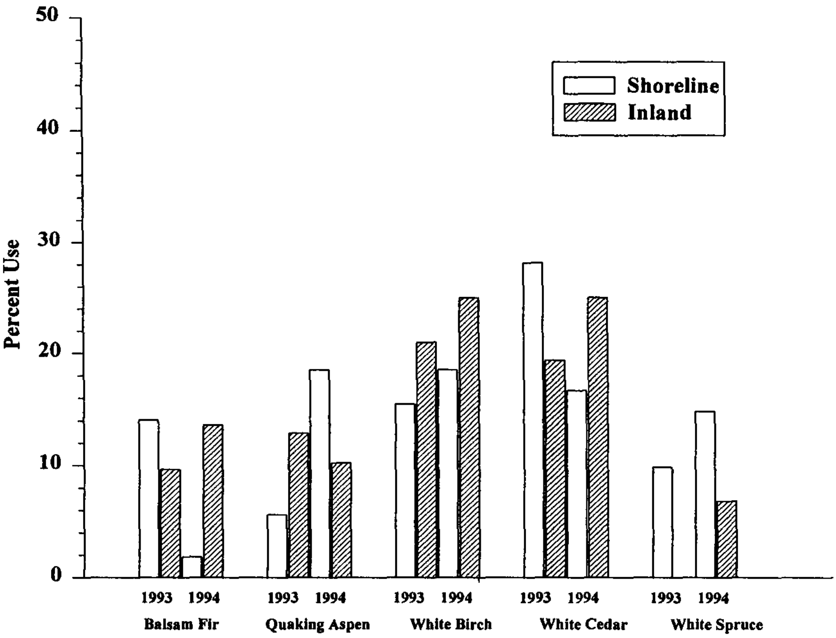

FIGURE 5. Black-throated Green Warbler spatial use of tree species during the fall migratory period, 1993 ($n = 133$) and 1994 ($n = 142$).

birch and white cedar, was nearly opposite of 1993; birds foraged in balsam fir, white cedar, and paper birch more inland, and quaking aspen and white spruce more along the shoreline ($G_5 = 13.4$, $P = 0.02$) (Fig. 5). We detected no significant spatial differences in birds' use of foraging maneuvers ($G_2 = 1.1$, $P > 0.5$), horizontal position within the tree when foraging ($G_2 = 0.4$, $P > 0.8$), where they directed foraging maneuvers in conifers (needle, branch, air; $G_1 = 1.2$, $P > 0.4$) or deciduous vegetation (leaf, branch, air; $G_2 = 2.9$, $P > 0.1$), or whether they foraged on the top or underside of substrates in coniferous ($G_1 = 0.0$) or deciduous ($G_1 = 0.1$, $P > 0.8$) vegetation.

DISCUSSION

Black-throated Green Warblers exhibited a number of shoreline/inland differences in the variables we used to describe foraging. We feel that our data indicate that birds were responding primarily to differences in arthropod types, abundance, and activity. Any influence that microscale differences in forest tree composition may have had on foraging can be effectively ruled out for a number of reasons. For one, we attempted to uniformly sample bird behavior across the entire study area, and our sampling design, by encompassing such a large area, should eliminate any such effect that may have occurred between shoreline and inland. Additionally, vegetation sampling, performed at the same scale as the behavior sampling, indicates little shoreline/inland difference in the common tree species (Ewert and Hamas, unpubl. data). Finally, if birds were varying foraging in response to floristics, we would expect spatial differences to have remained more constant with the passage of seasons. Birds should have been more conservative in their response as forest composition itself remains relatively constant. We detected more spatial differences in foraging during spring migration than either the breeding or fall migratory period.

The shoreline delay in foliage development very likely influenced the abundance and distribution of foliage-clinging arthropods such as lepidopteran larvae—an important prey source for Black-throated Green Warblers (Morse 1993). As a result of advanced leaf-out inland, foliage insect abundance may have peaked sooner than along the shoreline. Moreover, as invertebrate development and activity is temperature dependent (Williams 1961), any temperature differential between shoreline and inland may have further resulted in disparities in activities and abundances of prey, thereby influencing foraging. Inland prey may have been, on average, more abundant and/or active at a given time during spring migration. An increase in insect activity may have resulted in the observed increase in aerial maneuvers inland. Disparities in prey abundance also are suggested from the variation in tree use during spring, substrate focus, and differential use of top/underside of leaves in deciduous vegetation during spring and top/underside of coniferous species during the breeding season, and possibly the fall migration differences in tree use. For instance, during spring migration, birds foraged more on leaves inland. Furthermore, birds directed foraging more to the underside of leaves inland as well as increasing use of sally hovers. Higher percentages of arthropods such as lepidopteran larvae typically are found on lower rather than upper leaf surfaces (Greenberg and Gradwohl 1980, Holmes and Schultz 1988). The increased use of the underside of leaves may have been in response to an increase in foraging on these larvae, which likely were more abundant inland during spring due to the temperature and phenology differential. Finally, as birds direct foraging more to the underside of substrates, they are apt to increase their use of sally hovers, a maneuver often used by Black-throated Green Warblers to remove prey from the underside of a leaf.

Although the difference we observed in birds foraging more on leaves inland may be an artifact of differential leaf development (more leaves inland at a given time during spring migration), we feel it is more likely a response to prey differences. The majority of our observations of birds foraging on leaves took place later in the spring, when the average phenological stage did not differ significantly between shoreline and inland (R. Smith, unpubl. data). Moreover, there were differences in those maneuvers directed at leaves during spring, with birds foraging on the underside significantly more inland. Thus, any difference in leaf abundance is being controlled for by comparing only maneuvers of birds foraging on leaves—this differential use suggests that birds are responding to prey.

Even as the shoreline/inland difference in fall tree use suggests that arthropod differences may have persisted into the fall migratory period, the difference in foraging height is more ambiguous. Unfortunately, our data set is not sufficiently large enough to determine if the observed difference in fall foraging height is biologically significant or not. Additional analyses revealed this difference to be attributable to shrub use, and that birds did not vary height during fall migration in any of the five principal tree species. We observed more than twice as many birds foraging in shrubs inland as compared to shoreline ($n = 5$ shoreline vs. $n = 12$ inland), although sample sizes for both habitats are small. Because of the small sample sizes, it is impossible to rule out the observed result being an outcome of a skewed mean that acted to enhance the observed difference in foraging height between shoreline and inland habitats.

Birds also may have altered their foraging in response to spatial differences in kinds of arthropods available within a habitat. For instance, during spring large hatches of aquatic midges (Diptera: Chironomidae) occurred in areas along the shoreline. These insects remained strongly associated with the lakeshore; abundance dropped to near zero within 0.40 km of the shoreline during all seasons (Ewert and Hamas, unpubl. data, R. Smith, unpubl. data). This difference, in conjunction with the spatial differences in foraging exhibited by Black-throated Green Warblers suggests that midges were an important resource to early arriving migrants. Whereas the use of emergent aquatic insects including chironomid adults as prey is perhaps best known for early arriving Tree Swallows (*Tachycineta bicolor*) (Hobson and Sealy 1987, McCarty 1997), other workers have demonstrated these small arthropods to be an important part of the diet for passerines during both migration (Laursen 1978) and the breeding season (Busby and Sealy 1979, Biermann and Sealy 1982, Gray 1993).

Midges were observed resting on nearshore vegetation in high densities, and both field observations as well as our results suggest that birds foraged heavily on these insects, especially during early spring. For instance, birds restricted their use of maneuvers along the shoreline, performing gleans more and sally hovers and sally strikes less than at inland sites. Midge mating swarms in temperate habitats are strongly temperature dependent, generally not beginning until reaching a critical minimum temperature, which, while species dependent, tends to be around 10°C (Armitage 1995). During spring, foraging activity was most intense during early morning, when temperatures were often below 10°C. Thus, the influence of temperature, by delaying swarming activity until later in the day, presented birds with high densities of substrate bound midges, making them easily captured by gleaning. These resting midges may have been at least partially responsible for the differential use of gleans between the shoreline and inland areas. Resting midges are relatively slow to react to rapid movements (Busby and Sealy 1979, R. Smith, pers. observ.) which, in conjunction with low temperatures present during early spring, may have made them easier to capture than other flight capable insects during this time. As a result of the high densities of midges, along with their ease of capture, there may be little need for birds to use other, more energetically expensive foraging maneuvers, especially during spring migration when energy requirements are high.

The differential use of northern white cedar during both years provides evidence that birds were foraging on midges. Birds used white cedar significantly more along the shoreline than inland during spring migration, even though there is no significant shoreline/inland difference in average density of cedar across the study area (R. Smith, unpubl. data). Moreover, there also were significant seasonal differences in use along the shoreline; use of white cedar during both the breeding season and fall migration dropped significantly (R. Smith, unpubl. data). These spring spatial differences coincide with high densities of midges. This, in conjunction with the drop in use in shoreline habitats outside of spring, suggests that suitable prey items other than midges may not have been present in cedar in abundant numbers at other times or places, and that Black-throated Green Warblers were foraging in white cedar in response to midge abundance.

Evidence of the importance of midges to spring migrants also was noted in other species of migratory birds observed within the study area. Dallman and Smith (1995), working within the same study site, documented Palm Warblers (*Dendroica palmarum*) and Yellow-rumped Warblers (*D. coronata*) foraging extensively on midges resting on boulders projecting from a protected bay during early spring. Additionally, we observed a number of other species, including American Redstarts (*Setophaga ruticilla*), Black-throated Green Warblers, Common Yellowthroats (*Geothlypis trichas*), and Chestnut-sided Warblers (*D. pensylvanica*) taking midges. Finally, Ewert and Hamas (unpubl. data) demonstrated a significant spatial difference in migrant abundance with respect to distance from the shoreline of northern Lake Huron; more birds were found in shoreline habitat during spring migration than inland. They suggest that these differences may be attributable to large hatches of midges.

Many spring migrants arrive in northern temperate habitats prior to leaf-out, and as a result, populations of foliage-clinging arthropods may be limiting (Slagsvold 1976, Busby and Sealy 1979, Martin and Karr 1990, pers. observ.). Moreover, even though early arrival may have positive reproductive consequences (Dhondt and Olaerts 1981, Nilsson 1994, Barba et al. 1995), it increases the potential for exposure to poor weather conditions such as late season snowstorms or low temperatures (Hamas 1982, Aebischer et al. 1996, Merkle and Barclay 1996). This is especially evident in northern Michigan, where passage birds, as well as those staying to breed, may precede completion of leaf-out by up to four weeks (Ewert and Hamas, unpubl. data), and exposure to inclement weather can be common. As a result, early arrivals may be faced with depressed populations of prey insects other than midges, which may be further exacerbated in areas of high densities of passage birds. Evidence from this study, in conjunction with results of other work within the area (Dallman and Smith 1995, Smith 1995, Seefeldt, pers. comm.), suggests that early arriving birds are foraging heavily on midges and that these insects may be a critical resource during an otherwise prey depauperate time.

It is evident from our results that foraging behavior does vary with respect to distance from the Lake Huron shoreline, and that much of this variability appears to be attributable to the influence of the nearby lake. We suggest that birds were varying foraging principally in response to spatial prey differences resulting from microclimatic influences of nearby Lake Huron on both vegetation as well as invertebrate activity and development. We further suggest that emergent aquatic insects may be an important prey source during spring migration for birds passing through Michigan's eastern Upper Peninsula.

These results demonstrate the importance of gaining a thorough understanding of a bird's foraging ecology, especially relative to potentially influential ecological features like Lake Huron. Black-throated Green Warblers varied their foraging in relation to a previously undocumented factor—the existence of a nearby large body of water. Although future work is necessary to more closely examine the midge/bird relationship, these results suggest that midges may be an important resource both to passage as well as breeding birds. Future studies which attempt to identify critical habitat components for conservation efforts need to take into account the potential effects such a feature may have on nearby habitats and ultimately how it may affect the species in question.

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