

EXPERIMENTAL EVIDENCE FOR INTRINSIC MICROHABITAT PREFERENCES IN THE BLACK-THROATED GREEN WARBLER¹

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Abstract. Black-throated Green Warblers (*Dendroica virens*) use coniferous vegetation as foraging and perching substrates at coastal sites in Maine and predominantly deciduous vegetation at inland sites in interior New Hampshire, despite the availability of both substrates. I tested the hypothesis that these habitat use patterns result from intrinsic preferences (fixed behavioral choices independent of environmental influence) by quantifying coniferous and deciduous vegetation use by individuals from New Hampshire and Maine in "common-garden" aviary experiments with equal substrate and prey availability. I also determined the strength of these preferences by skewing experimental prey distributions toward the less preferred vegetation type of birds from each region and measuring resulting substrate use. Individuals from coastal sites showed significantly greater preferences for coniferous vegetation as both perching and foraging substrates than did inland birds, which preferred deciduous vegetation. In skewed prey distribution experiments, individuals maintained their regional preferences for perching substrates, but shifted foraging substrates typically after first capturing all prey from the preferred vegetation type. Significant morphological variation (larger maxillary width, tibiotarsi, tarsometatarsi, humeri, and radii in coastal birds) was found among Black-throated Green Warblers from the two regions that corresponded to morphology-habitat associations found in other mixed coniferous and deciduous bird assemblages. These data suggest that intrinsic factors may be influential as a proximate microhabitat selection mechanism in the Black-throated Green Warbler.

Key words: *Habitat selection; intrinsic preferences; behavioral stereotypy; Neotropical migrants; ecomorphology; Black-throated Green Warbler; Dendroica virens.*

INTRODUCTION

Numerous factors such as predation (e.g., Lindstrom 1990, Suhonen 1993), food supply (Holmes and Schultz 1988, Whelan 1989), competitive interactions (Morse 1973, 1989; Sherry and Holmes 1988), morphology (Winkler and Leisler 1985), and vegetation structure (Robinson and Holmes 1982, 1984; Parrish 1995) may serve as evolutionary mechanisms in avian habitat selection (Hildén 1965). However, we understand little of the proximate mechanisms that promote stereotyped habitat use patterns (Cody 1985, but see Greenberg 1990). Intrinsic preferences (i.e., phenotypic differences in behavior independent of external factors) for a particular microhabitat may serve as one such proximate mechanism (Emlen 1981, Emlen and DeJong 1981).

Differences in habitat selection behavior within a species present important opportunities to study the potential role of these intrinsic factors. The Black-throated Green Warbler (*Dendroica virens*), for example, occurs across Canada and the north-central and north-eastern United States

in coniferous, mixed coniferous-deciduous, and entirely deciduous forests (Sabo 1980, Morse 1993 and references therein). In coastal Maine this species spends over 90% of its foraging time in coniferous vegetation (Morse 1976; J. D. Parrish and D. H. Morse, unpublished data). However, in mixed coniferous-deciduous forests in New Hampshire it uses deciduous vegetation almost exclusively, with 90–95% of foraging observations in deciduous vegetation (Sabo 1980; Holmes and Sherry 1986; J. D. Parrish, unpublished data). In neither region do these birds use coniferous and deciduous vegetation in proportion to substrate availability (Morse 1976, Sabo 1980). Moreover, the Black-throated Green Warbler is socially dominant to sympatric *Dendroica* warblers in these regions (Morse 1971), suggesting that extrinsic competitive interactions are unlikely to influence habitat use in this species. Intrinsic preferences may therefore influence or maintain the habitat selection of these populations.

In this study, I tested the hypothesis that intrinsic factors influence microhabitat and foraging-site selection differences of Black-throated Green Warblers from two separate regions. I de-

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terminated the substrate preferences of solitary, wild-caught adults from inland New Hampshire and coastal Maine using "common-garden" experiments in aviaries with equal quantities of coniferous and deciduous vegetation and equal abundances and distributions of prey. If habitat selection observed in the wild were a result of intrinsic factors, solitary birds in aviaries with equal resource availability should exhibit significant preferences for a substrate type in either their overall use of vegetation (an index of microhabitat choice) or in the location where foraging occurs (an index of foraging-site selection). To investigate further the strength of these preferences, I skewed prey densities away from each population's preferred substrate in a subsequent experiment. Morphological measurements were also taken from birds from each geographic region to test for a possible correlation between differences in habitat selection behavior and morphological variation, factors potentially associated with population divergence (Hespenheide 1973, Miles and Ricklefs 1984, Winkler and Leisler 1985).

METHODS

CAPTURE AND MAINTENANCE OF EXPERIMENTAL BIRDS

I captured birds and conducted experiments between 15 June and 5 August, 1992 and 1993. Individual birds were taken from two sites approximately 175 km apart, where previous field observations of geographic differences in microhabitat selection had been documented (Morse 1976; Holmes and Sherry 1986; J. D. Parrish, unpublished data). I captured six individuals at altitudes of 600–750 m at the base of Mt. Osceola, Carroll County, New Hampshire. This forest is composed predominantly of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), white ash (*Fraxinus americana*), white birch (*Betula papyrifera*), red spruce (*Picea rubens*), white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*). I also captured 11 individuals from coastal sites in Bremen, Lincoln County, Maine. Deciduous vegetation at the Maine sites was primarily white birch, with some red maple. Morse (1976) described the coastal Maine sites in further detail.

I captured all individuals in 12 m mist nets with playback recordings of Black-throated Green Warbler songs (Morse 1967) and use of a decoy.

Only males were used in experiments, because of the relative difficulty of capturing females using playback recordings. After capture all individuals were maintained for 72 hr in 2 m × 2 m × 2 m holding cages. Each cage included leafless branches as perches so as not to influence vegetation substrate familiarity during acclimation. Birds were maintained in these cages on a diet of mealworms and protein mixture (dog food, egg, and mineral supplement) presented in dishes, and all tested individuals maintained or gained mass in captivity. Upon completion of experiments, I released birds not retained for skeletal measures.

PREFERENCE EXPERIMENTS

Two deciduous and two coniferous branches, each approximately 1 m long, were placed in a field-deployed experimental aviary identical to acclimation cages. One red spruce and one white spruce branch represented coniferous vegetation, whereas deciduous vegetation was represented in experiments by white birch and red maple branches. The latter two species were representative of the most common deciduous physiognomies. The four branches were suspended from one side of the cage with monofilament line and small wire hooks (two branches in the upper half and two branches on the lower half). I randomized the configuration of experimental branches for each bird, with the constraint that one branch of each vegetation type (deciduous and coniferous) was always placed in an upper and lower region of the cage since birds could show preferences for high or low cage areas. I distributed ten, one-half mealworm (*Tenebrio molitor* larvae) pieces evenly along the main branch and large side branches of each coniferous bough, and secured them with small amounts of vegetable shortening (Whelan 1989). I also distributed ten mealworm pieces in the two deciduous branches, but five mealworm pieces were placed along the bare central branch, and five were placed on upper and lower leaf surfaces. Mealworms were spaced evenly along the branches in each experiment.

Birds were acclimated for three days prior to the commencement of experiments. After withholding food on experiment days for 2 hr to prevent satiation, I tested 11 different birds from Maine and six different individuals from New Hampshire with preference trials of 30 min in the prepared experimental aviary. I released one

bird into the aviary and recorded observations from behind a blind 4 m from the cage. Observations included the location and duration (in seconds) of perching, locomotory and foraging movements in the vegetation (hereafter referred to as "vegetation time"), and the substrate from which prey were taken. By separating perching activity (vegetation time) and foraging efforts, special attention could be given to foraging-site selection as well as perching-site selection, which preliminary experiments had shown could differ.

SKewed PREY DISTRIBUTION EXPERIMENTS

To confirm the strength of any existing regional preferences, an additional experiment in which prey distributions were skewed in favor of less preferred substrates was performed on nine of the coastal Maine birds and three of the inland New Hampshire birds used in the previous preference experiments. Sample sizes differed between the two experiments because of the use of some individual birds in additional experimental studies (Parrish 1995). These skewed prey distribution experiments were identical to preference experiments, except 18 mealworm pieces were placed in the less preferred substrate (conifers for inland birds, and deciduous branches for coastal birds) and two in the preferred vegetation type. I conducted these skewed prey distribution experiments subsequent to preference experiments for all individuals, and according to identical methodology as used in preference experiments.

MORPHOLOGICAL MEASUREMENTS

Because population differentiation or morphological variation between coastal and inland populations are possible explanations for intrinsic behavioral differences, I collected 19 individuals from Maine and eight individuals from New Hampshire for morphological measurements. I measured the following morphological characters after skeletal preparation: femur, tibiotarsus, tarsometatarsus, humerus, radius, proximal phalanx of the hallux, second phalanx of the second digit, third phalanx of the third digit, and the fourth phalanx of the fourth digit. The following bill measurements were also taken: culmen length, maxillary width, and bill depth. Measurements were taken according to standards from Proctor and Lynch (1993). Collecting morphological data from birds originating from the exact region as

the experimental individuals allowed investigating the possibility of population divergence.

DATA TREATMENT AND STATISTICAL ANALYSES

One preference experiment per bird is presented in these analyses, although often two or three preference (equal prey distribution) experiments were performed on any individual bird. Birds frequently perched repeatedly on the cage netting rather than on the vegetation substrates when first captured and typically decreased this nervous behavior with acclimation time. To remove the potential bias of these unacclimated trials, I analyzed only that preference experiment for each bird with the lowest proportion of time spent perching on the cage rather than on experimental branches.

Time spent on each substrate was expressed as a proportion of the total time spent on any vegetation during the experiment. The number of prey items taken from each substrate was presented as a proportion of total prey taken during an experiment. All proportions were arcsine transformed (Sokal and Rohlf 1981), which resulted in data fitting normal distributions. I used a two-factor design ANOVA for each experiment to determine whether perching substrate use or foraging substrate use was best explained by origin of the bird (substrate \times origin interaction). General linear models were used in the analyses of variance to account for the unequal sample sizes of samples from each origin (Zar 1974; S. D. Gaines, pers. comm.).

Morphological measurements were individually compared with one-way analysis of variance using general linear models. Furthermore, a multivariate analysis of variance (MANOVA) was used to test for overall differences in morphology between birds from the two geographic regions given all morphological measurements.

RESULTS

PREFERENCE EXPERIMENTS

Coastal Maine Black-throated Green Warblers spent more time perching in coniferous branches than in deciduous branches (significant origin \times substrate interaction, Table 1, Fig. 1A). Conversely, inland New Hampshire birds used deciduous substrates during a greater proportion of their vegetation time than they used coniferous substrates (significant origin \times substrate interaction, Table 1, Fig. 1A). Birds from coastal

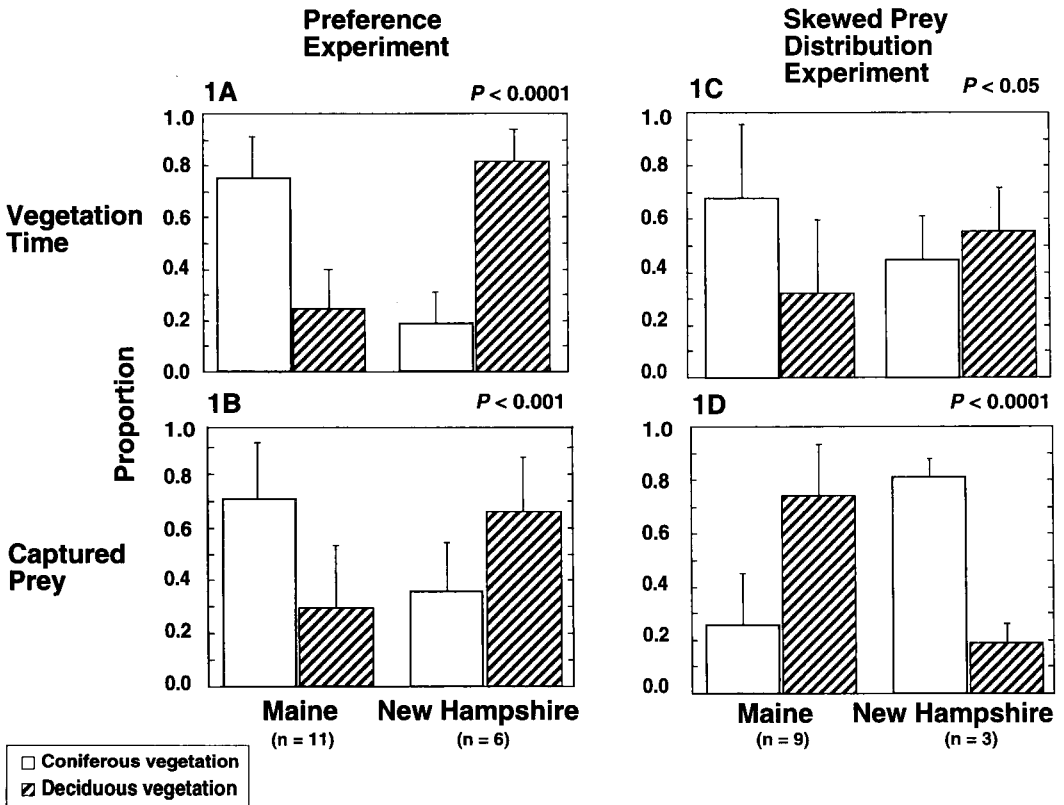


FIGURE 1. Coniferous and deciduous substrate use by Black-throated Green Warblers from coastal Maine and from inland New Hampshire in preference experiments (A–B) and skewed prey distribution experiments (C–D). Skewed prey distribution experiments were manipulations with greater prey densities in the less preferred substrates of a bird’s origin. Substrate use was measured as the proportion of time spent in the vegetation (A, C) and the proportion of the captured prey taken from substrates (B, D). *P* values given are for the substrate x origin interactions from two-way ANOVA which demonstrate significant different use of coniferous and deciduous substrates by birds from the two geographic origins.

Maine preferred conifers as the substrate from which to capture prey, while New Hampshire birds foraged upon significantly greater proportions of prey from deciduous than from coniferous substrates (substrate x origin interaction, Table 1, Fig. 1B).

SKewed PREY DISTRIBUTION EXPERIMENTS

In experiments distributing prey densities away from the preferred substrate of birds from each origin, inland New Hampshire and coastal Maine Black-throated Green Warblers maintained their significant preferences for deciduous and coniferous vegetation, respectively, as perching substrates (Table 1, Fig. 1C). However, birds of both origins shifted their use of substrates from which

prey were captured. A significant substrate x origin interaction showed significant foraging substrate preferences in the skewed prey distribution experiments (Table 1, Fig. 1D). However, these preferences were reversed; birds from New Hampshire now captured higher proportions of prey from coniferous vegetation than from deciduous vegetation in skewed prey distribution experiments, and Maine birds captured more prey from deciduous than from coniferous vegetation (Fig. 1D). Despite this reversal of foraging substrate use under skewed prey density, most birds first captured all prey available from the originally preferred substrate before beginning to forage in less preferred vegetation. Before switching to deciduous branches, five of nine (55.56%) coastal Maine birds first took all prey (both meal-

worm pieces) from the coniferous branches, while all five (100%) of tested inland New Hampshire birds captured all prey from deciduous substrates before foraging in coniferous branches.

MORPHOLOGICAL ANALYSES

Birds from coastal Maine and from inland New Hampshire differed in several morphological measurements important to locomotion and foraging (Table 2). Coastal Maine birds were larger than inland birds in humeri, radii ($P = 0.057$), tibiotarsi, tarsometatarsi ($P = 0.051$), and maxillar width. There were no differences in foot measurements between birds from inland assemblages and those from coastal Maine. Coastal Maine birds were significantly larger than birds from inland New Hampshire when all morphological measurements were considered together (MANOVA; Wilk's Lambda value = 0.265, $P = 0.02$).

DISCUSSION

INTRINSIC MICROHABITAT PREFERENCES

Black-throated Green Warblers from coastal Maine spruce forests and inland hardwood forests in New Hampshire maintained their use of coniferous and deciduous vegetation, respectively, when placed in aviaries with equal abundance of substrates and prey. The perching substrate preferences for coniferous branches by Maine birds (measured as the proportion of time spent in each vegetation type) and for deciduous branches by New Hampshire birds remained significantly different even when prey distributions were skewed in favor of the less preferred substrate. However, birds demonstrated the ability to shift foraging-sites; the location of prey capture in skewed prey distribution experiments was opposite that of preference experiments. The differential substrate use reported here in preference experiments and in the vegetation time of the skewed prey distribution experiments suggests that intrinsic preferences exist in these populations and that they can proximately influence microhabitat selection by Black-throated Green Warblers.

The results of this study indicate the pattern of stereotyped differences in behavior among Black-throated Green Warblers from these two regions; however, the exact cause of these intrinsic differences remains undetermined. Early experience and population divergence (and, therefore, genetic inheritance) are two potential ex-

TABLE 1. Results from two-way factorial analysis of variance for preference experiments and for experiments in which prey distribution was skewed in favor of the less preferred substrate of birds from a particular origin. Dependent variables (proportions of vegetation time and captured prey) were arcsine transformed before analyses.

Source	Preference experiments				Skewed prey distribution experiments								
	Vegetation time		Captured prey		Vegetation time		Captured prey						
	df	F value	P	df	F value	df	F value	P					
Substrate ¹	1	0.047	0.831	1	2.048	1	0.163	1	0.75	1	0.609	0.442	
Origin ²	1	0.006	0.940	1	0.274	1	0.605	1	0.096	1	0.001	0.976	
Substrate × Origin	1	30.571	0.0001***	1	15.912	1	0.0004***	1	4.871	1	0.039*	35.603	0.0001***
Residual	30			30		20		20					

* $P < 0.05$.
 *** $P < 0.001$.
¹ Coniferous or deciduous vegetation.
² From coastal Maine or inland New Hampshire regions.

TABLE 2. Morphological measurements (mean \pm SD in mm) of eight inland New Hampshire and 19 coastal Maine Black-throated Green Warblers. Measurements were compared with one-way ANOVA. Coastal Maine birds were also significantly larger than inland New Hampshire birds when all measurements were compared together by MANOVA ($F = 3.3$, $P < 0.05$).

	Origin		F-value	P
	New Hampshire	Maine		
Wing				
humerus	12.94 \pm 0.68	13.49 \pm 0.33	8.19	0.008*
radius	15.70 \pm 0.42	16.24 \pm 0.71	3.97	0.057†
Leg				
femur	12.36 \pm 0.42	12.54 \pm 0.30	1.47	0.236
tibiotarsus	22.86 \pm 0.51	23.73 \pm 0.67	10.80	0.003*
tarsometatarsus	16.25 \pm 0.86	16.76 \pm 0.45	4.22	0.051†
Phalanges				
of hallux	5.08 \pm 0.30	5.29 \pm 0.46	1.46	0.238
of second digit	3.51 \pm 0.40	3.57 \pm 0.53	0.09	0.773
of third digit	3.69 \pm 0.39	3.77 \pm 0.25	0.48	0.494
of fourth digit	2.20 \pm 0.31	2.30 \pm 0.18	0.98	0.332
Bill				
culmen length	12.68 \pm 0.52	12.76 \pm 0.41	0.17	0.686
maxillar width	4.64 \pm 0.32	4.92 \pm 0.22	7.21	0.013*
bill depth	3.85 \pm 0.16	3.89 \pm 0.26	0.03	0.857

* $P < 0.05$.

† $P < 0.10$.

planations for the ontogeny of intrinsic preferences (Hildén 1965, Emlen 1981). Intrinsic preferences may result from the preferred habitats being learned or imprinted upon earlier in life, an idea for which there is experimental supporting evidence (Klopfer 1965, Partridge 1974). Intrinsic preferences in habitat selection may also be genetically inherited, and therefore the result of birds being members of different populations (Emlen 1981). Further experimental studies are required to illuminate the cause of the intrinsic patterns reported here.

The role of intrinsic preferences in habitat selection has received relatively little attention. Partridge (1974, 1976a) showed that two closely related species (Coal Tits *Parus ater* and Blue Tits *P. caeruleus*) reared in the laboratory with no previous vegetation experience showed intrinsic differences in their selection of coniferous and deciduous trees. Emlen (1981) demonstrated that allopatric populations of Pine Warblers (*Dendroica pinus*) and Blue-gray Gnatcatchers (*Polioptila caerulea*) residing on two different Bahamian islands preferred different substrates within Carib pine (*Pinus caribae*) forests that could not be explained by differences in prey abundance or by interference competition. Emlen and DeJong (1981) found these substrate

preferences remained in subsequent experiments with captive Pine Warblers exposed to equal substrate availability. They concluded that intrinsic factors were important in determining differences in foraging substrate use by the two populations of this species.

Here I have shown that similar intrinsic preferences influenced coniferous and deciduous vegetation preference by conspecifics of the Black-throated Green Warbler from two nearby geographic origins. The habitat structures of coniferous and deciduous vegetation are functionally very different for arboreal foragers such as *Dendroica* warblers (Morse 1989). The tips of conifers can generally support foraging passerines easily, whereas distal tips of deciduous branches allow foraging only if the bird is clinging to the petiole or is attacking prey in flight. Furthermore, the dense and near-complete distribution of needles on coniferous branches requires passerines to perch directly on the vegetation, while only stems and petioles are usually used for perching in deciduous trees. Thus the vegetation structures of these habitats differ such that a species' behavioral response (e.g., microhabitat use and selection of foraging sites) should vary widely between the two vegetation types. Such differences may, in turn, exert selection pressure for

morphological and/or behavioral stereotypy in birds using the two contrasting vegetation types (Partridge 1976a, b).

MORPHOLOGICAL VARIATION

Morphology can constrain habitat selection (Winkler and Leisler 1985), and several studies have found significant correlations between morphology and habitat use (e.g., Partridge 1976b, James 1982, Winkler and Leisler 1985, Carrascal et al. 1990, Keast and Saunders 1991). Individuals sampled from coastal Maine sites had significantly larger humeri and tibiotarsi and wider bills than inland New Hampshire birds, tended to have larger tarsometatarsi and radii, and were significantly larger when all measures were combined. European passerines using conifers in mixed forests also had relatively longer tarsometatarsi than birds using deciduous trees (Carrascal et al. 1990). Long tarsometatarsi can enhance the range of leg motion while searching for prey among the long, dense needles of coniferous foliage (Carrascal et al. 1990).

Black-throated Green Warblers along the Maine coast are regularly confronted with extremes in wet weather from oceanic low pressure systems and coastal fog, which can substantially dampen needle foliage upon which coniferous foliage-gleaning warblers must perch. During these inclement periods, hover-gleaning is a frequently observed foraging maneuver (J. D. Parrish and D. H. Morse, unpublished data). Hovering when foraging within wet vegetation prevents extensive wetting of the bird, maintaining plumage insulation capabilities (Lustick and Adams 1977) and preventing the need to redirect time from foraging and parental care to preening of moist plumage (Morse 1976). The longer radii and humeri of coastal Maine birds compared to birds from inland New Hampshire facilitate hovering behavior by modifying wing shape to reduce wing-loading (Partridge 1976b, Norberg 1979). Strong selection for such behavior and correlated morphology probably exists in this coastal region during wet periods, as passerines suffer significant reduction in reproductive success during breeding seasons dominated by inclement weather (Morse 1976). Similar morphological and behavioral relationships have been found in the coniferous-dwelling Coal Tit, which has hovering abilities superior to deciduous forest congeners (Partridge 1976a, b). However, the strength of this selection force on wing

shape is likely balanced for birds of each geographic region by both the need for flight maneuverability within the arboreal canopy and selection for migratory flight efficiency (Winkler and Leisler 1985). Though it is unclear whether they are cause or consequence of the microhabitat use differences between inland New Hampshire and coastal Maine birds, these morphological differences are congruent with the hypothesis that birds from the two regions are members of different populations.

RESPONSE TO PREY DENSITY VARIATION

Redistributing prey densities in favor of less preferred substrates did not cause Black-throated Green Warblers to relax their regional substrate preferences (measured as the proportion of vegetation time) exhibited in earlier experiments using equal prey availability. However, birds showed the ability to shift foraging sites (where prey were captured) to less preferred substrates, tracking experimentally altered prey availability. It is possible that individual birds might have later learned the redistributed prey patterns if skewed distribution experiments were repeated, and therefore potentially relaxed their regional preferences for perching substrates. However, further repeated skewed prey distribution experiments on the same individual were not possible since most birds were also used in additional habitat selection experiments (Parrish 1995). Nevertheless, that regional preferences for perching substrates were maintained is in contrast with results from several studies that have concluded birds select microhabitats in proportion to their availability (Klopfer 1963) or the availability of the prey items they contain (Smith and Dawkins 1971, Holmes and Schultz 1988, Whelan 1989).

Experimental birds did not change perching time within the different vegetation types as a result of the skewed prey distribution manipulation, but they did shift away from preferred substrates in choosing where prey were taken, demonstrating plasticity in foraging-site selection (Greenberg 1990). However, most individuals captured all prey from preferred substrates first before switching to the less preferred vegetation type. Moreover, the experimental manipulation was an extreme reduction of food availability on the preferred substrate (from a 1:1 preferred to non-preferred ratio, to 1:9). All birds were deprived of food prior to experiments to

insure foraging activity would not be suppressed by satiation, and they were therefore under induced energy deficits that may have forced them to shift preferences despite intrinsic stereotypy in microhabitat selection. Morse (1971) also noted that Black-throated Green Warblers possessed a high degree of foraging and habitat selection stereotypy, which he suggested was a result of the species' dominant status within those communities. Similarly, in experiments with the amount of skewness in prey distribution necessary to reverse foliage preferences, Black-throated Green Warblers required significantly greater prey biomass in less preferred vegetation to alter preferences than did sympatric Black-throated Blue Warblers (*D. caerulescens*). This difference further suggests the species' relatively high behavioral stereotypy (Whelan 1989).

Black-throated Green Warblers show interpopulation variability in microhabitat selection on regional scales (Collins 1983, Petit et al. 1990, Morse 1993, this study). This study suggests that such variation in habitat selection between populations of the Black-throated Green Warbler in coastal Maine and inland New Hampshire is maintained, at least in part, by intrinsic proximate mechanisms. The ontogeny of these intrinsic preferences is unclear and requires further investigation through the use of rearing experiments and population genetic studies to determine if early experience or population divergence influence these preferences. Intrinsic factors, such as demonstrated here in the Black-throated Green Warbler, should be considered in future habitat selection studies as a proximate cause for observed habitat selection patterns.

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