

## AN EXPERIMENTAL TEST OF PREY DISTRIBUTION LEARNING IN TWO PARULINE WARBLERS<sup>1</sup>

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*Abstract.* Experiments conducted to examine the prey distribution learning of two paruline warbler species showed no significant effect of foliage structure. However, there was significant variation in learning abilities among individuals within each bird species, and between bird species. Black-throated Blue Warblers (*Dendroica caerulescens*) learned to locate prey more proficiently when prey were distributed on lower leaf surfaces, while Black-throated Green Warblers (*D. virens*) learned to locate prey more proficiently when prey were distributed on upper leaf surfaces.

*Key words:* Aviary experiment; foliage structure; foraging behavior; learning; paruline warbler; prey distribution.

### INTRODUCTION

Although little is actually known about the resource base for insectivorous forest birds (Wiens 1984), available information suggests that insect prey often vary dramatically in abundance and in spatial distribution over both short and long time periods (Hutto 1981, Graber and Graber 1983, Rodenhouse 1986, Holmes and Schultz 1988). To forage efficiently, therefore, insectivorous birds might be expected to modify their foraging behavior based upon their experience of this variable resource base. In other words, insectivorous birds should be able to learn about changing insect prey distributions and adjust their foraging efforts accordingly (Kamil and Yoerg 1982).

Several laboratory experiments have presented insectivorous birds with problems of spatial discrimination (e.g., Smith and Dawkins 1971; Alcock 1973; Zach and Falls 1976a, 1976b; Krebs et al. 1978). Greenberg (1985), however, argued that this approach to the role of learning in the foraging decisions of insectivorous birds may be inappropriate. Because many insectivorous birds do not revisit specific branches in site-restricted searches (Robinson and Holmes 1982, Greenberg 1985), rather than learning the location of a successful prey capture, these birds should learn habitat cues associated with the

presence of prey. In support of this hypothesis, Greenberg (1985) showed experimentally that both a generalist and a specialist species of paruline warbler were able to learn to discriminate between two types of artificial foliage that differed in foraging profitability. The ability to discriminate between different types of foliage, i.e., to recognize leaf shape, could allow birds to specialize their foraging on tree species with greater abundances of insect prey.

Besides the shape of foliage, other features of the habitat could serve as cues to the presence of insect prey. For example, Heinrich and Collins (1983) provided experimental evidence that Black-capped Chickadees (*Parus atricapillus*) can (1) use leaf damage by phytophagous insects as a cue to locate prey, and (2) discriminate between similar leaves of different tree species. Roland et al. (1986) similarly found that Pine Siskins (*Carduelis pinus*) also use leaf damage to locate prey. Because arthropods tend to be distributed differentially with respect to upper and lower leaf surfaces (Greenberg and Gradwohl 1980, Holmes and Schultz 1988), birds could also cue into particular leaf surfaces for finding prey. That is, I hypothesize that these birds can learn that prey are found in greater concentrations on, for example, lower leaf surfaces, focus their foraging efforts on those leaf surfaces, and thus increase their foraging efficiency. In addition, because foliage structure differs among tree species and affects where and how birds capture prey (Kendeigh 1945, Franzreb 1978, Holmes and Robinson 1981, Whelan 1987), I also hypothesize that foliage structure might influence the

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ability of foliage-foraging birds to learn about the distribution of prey on upper vs. lower leaf surfaces.

In this paper I compare the prey distribution learning abilities of Black-throated Green Warblers (*Dendroica virens*) and Black-throated Blue Warblers (*D. caerulescens*) on two tree species with contrasting foliage structures, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*). Sugar maple has large leaves held above the branch on long petioles, while yellow birch has smaller leaves held even with the branch on short petioles (Whelan 1987). My experiments address the following questions: (1) When prey distribution remains constant over time, will these species learn this prey distribution and increase their capture rates? (2) Will a change in prey distribution lead to a decrease in capture rates? (3) Does foliage structure influence these learning abilities? (4) Are there differences in learning abilities between these warbler species? and (5) Are there differences among individuals within these two warbler species in their learning abilities?

## METHODS

### SUBJECTS

Five adult male Black-throated Green Warblers and five adult male Black-throated Blue Warblers caught in mist nets between May and August 1986, near Hanover, New Hampshire, served as subjects. Each bird was held singly in an indoor flight cage (1.5 × 2.5 × 2.0 m) for up to 2 weeks, during which time experiments took place. When birds were not being used in experiments, they were fed an insectivorous bird diet modified from R. Greenberg (pers. comm.). After experimentation was completed, the birds were released near the site of capture.

### EXPERIMENTAL PROCEDURE

All birds were used in four experiments. Each experiment consisted of four foraging trials. In the first three trials, hereafter referred to as the acquisition period, prey distribution (all on upper or on lower leaf surfaces) remained identical (although prey were placed arbitrarily on different leaves in each trial). In the fourth trial, hereafter referred to as the transfer period, the prey distribution was switched to the opposite leaf surface. Trials were separated by 1.5 hr, during which time the bird was deprived of food. Before

the first trial the bird was given a single mealworm (at 06:30) and then deprived of food for 1.5 hr. In two experiments the birds foraged among the foliage of a sugar maple sapling. In the other two experiments the birds foraged among the foliage of a yellow birch sapling. Each sapling had approximately 400 leaves. Prey in all experiments consisted of a single mealworm (*Tenebrio* sp.) larva cut into six equal-sized pieces. Mealworm pieces were attached to the leaf surfaces with a small amount of vegetable shortening. I measured the time taken to capture the first four of the six prey items present in each trial. Measurement began when the bird landed on the sapling. Increased rate of prey capture and decreased time to first capture during the acquisition period were considered evidence of prey distribution learning.

All Black-throated Green Warblers were allowed to forage first on sugar maple, and all Black-throated Blue Warblers were allowed to forage first on yellow birch. Tree species were alternated in successive experiments, which were separated by 1 day. Whether prey were first on upper or lower leaf surfaces was determined by coin toss for each tree species.

### STATISTICAL ANALYSIS

*Acquisition period.* Capture rates (captures/second) for the three trials of the acquisition period were plotted and the least squares regression line fitting these points was calculated for each individual bird in each experiment (i.e., 40 regression lines were calculated). The slopes of these lines were used in two ways. First, the mean slope of the five individuals of each bird species was calculated for each experiment (e.g., Black-throated Green Warblers foraging on sugar maple with prey all on upper leaf surfaces). Whether each of these mean slopes was significantly different from zero was determined with a one sample *t*-test. A positive, nonzero slope indicates that the birds were foraging significantly faster in progressive foraging trials.

Second, a four-way factorial analysis of variance (ANOVA, GLM procedure, SAS 1985) was performed that examined simultaneously the effects of tree species, leaf surfaces, bird species, and individual birds nested within bird species, as well as interactions between tree species and leaf surfaces, tree species and bird species, and bird species and leaf surfaces.

Decreasing time to first capture can also pro-

TABLE 1. Results of analysis of means of capture rate slopes during the acquisition period for each of four experiments for Black-throated Green Warblers (GW) and Black-throated Blue Warblers (BW).

Tree species	Prey distribution	Bird species	Slope <sup>1</sup>	Different from zero?	
				<i>t</i>	<i>P</i>
Sugar maple	Upper	GW <sup>2</sup>	0.042 ± 0.002	20.02	<0.0005
		BW <sup>2</sup>	0.009 ± 0.011	0.72	>0.25
	Lower	GW	0.020 ± 0.01	2.099	=0.051
		BW	0.042 ± 0.012	3.374	<0.025
Yellow birch	Upper	GW	0.045 ± 0.004	5.03	<0.005
		BW	0.021 ± 0.004	4.80	<0.005
	Lower	GW	0.026 ± 0.012	2.12	=0.050
		BW	0.021 ± 0.012	1.77	=0.075

<sup>1</sup>  $\bar{x} \pm 1$  SE.<sup>2</sup> *n* = 5.

vide evidence of learning. To test whether time to first capture decreased during the three trials of the acquisition period, times to first capture were analyzed similarly to capture rates.

*Transfer period.* Actual capture rates in the transfer period were compared to the capture rates predicted by the regression lines described above with Wilcoxon's Rank-Sum test (Bhattacharyya and Johnson 1977).

## RESULTS

### ACQUISITION PERIOD: CAPTURE RATE SLOPES

When prey were distributed on upper leaf surfaces of sugar maple, Black-throated Green Warblers increased their foraging rate over successive trials (i.e., they had positive, nonzero slopes, Table 1), but Black-throated Blue Warblers did not (Table 1). Both bird species, however, increased their foraging rates over successive trials when

prey were distributed on lower leaf surfaces of sugar maple (Table 1).

Both bird species increased their foraging rates over successive trials when prey were distributed on upper leaf surfaces of yellow birch (Table 1), but only Black-throated Green Warblers did when prey were on lower leaf surfaces (Table 1). Black-throated Blue Warblers showed a trend toward increased capture rates when prey were distributed on the lower leaf surfaces of yellow birch (Table 1).

The ANOVA model of the capture rate slopes was significant (Table 2). Analysis of main effects and interaction terms shows that individual birds nested within bird species ( $P = 0.053$ ) and the interaction of bird species with leaf surfaces ( $P = 0.0055$ ) were significant (Table 2; see also Fig. 1). The interaction between bird species and leaf surfaces reflects that the capture rate slopes of Black-throated Green Warblers were greater when foraging on upper than on lower leaf surfaces,

TABLE 2. Results of four-way factorial analysis of variance of slopes of capture rates of Black-throated Green Warblers and Black-throated Blue Warblers during acquisition period.

Source	df	Sum of squares	Mean square	<i>F</i> value	<i>P</i>
Model	14	0.01214695	0.00086764	2.33	0.0314
Error	25	0.000930282	0.00037211		
Corrected total	39	0.02144978			

Source	df	Type I sum of squares	<i>F</i> value	<i>P</i>
Tree species	1	0.00000203	0.01	0.9418
Leaf surfaces	1	0.00003062	0.08	0.7766
Bird species	1	0.00107123	2.88	0.1022
Individual (bird species)	8	0.00685280	2.30	0.0530
Tree species × leaf surface	1	0.00058522	1.57	0.2214
Tree species × bird species	1	0.00016402	0.44	0.5128
Leaf surfaces × bird species	1	0.00344103	9.25	0.0055

TABLE 3. Analysis of interaction between bird species and leaf surface from ANOVA presented in Table 2.

Bird species	Leaf surfaces <sup>a</sup>	
	Upper	Lower
Black-throated Green Warblers	0.044 ± 0.004	0.023 ± 0.007
Black-throated Blue Warblers	0.015 ± 0.006	0.032 ± 0.009

<sup>a</sup> Mean slope of capture rates ± 1 SE.

while the opposite was the case for Black-throated Blue Warblers (Table 3).

#### TIME TO FIRST CAPTURE

Only Black-throated Blue Warblers foraging on upper leaf surfaces of sugar maple had decreased the time to first capture over successive trials (i.e., they had negative, nonzero slopes, Table 4). Black-throated Green Warblers foraging on upper leaf surfaces of sugar maple, however, showed a nonsignificant trend toward decreased times to first capture (Table 4). All other mean slopes of times to first capture did not differ significantly from zero (Table 4).

The ANOVA model of the slopes of times to first capture was not significant (Table 5). No main effects and no interaction terms of this model were significant.

#### TRANSFER PERIOD

Observed capture rates of Black-throated Green Warblers during the transfer period were significantly less than predicted for three prey distribution switches: when prey was switched from upper to lower leaf surfaces on sugar maple, and for both distribution switches on yellow birch (Table 6). The least significant difference for Black-throated Green Warblers was when prey

distribution was switched from lower to upper leaf surfaces on sugar maple (Table 6).

For Black-throated Blue Warblers, there were no significant differences in capture rates for two prey distribution switches: when prey distribution was switched from upper to lower leaf surfaces of sugar maple, and when prey distribution was switched from lower to upper leaf surfaces of yellow birch (Table 6). The observed capture rates following the other prey distribution switches, from lower to upper leaf surfaces on sugar maple, and from upper to lower leaf surfaces on yellow birch, were significantly less than predicted (Table 6).

#### DISCUSSION

##### PREY DISTRIBUTION LEARNING

Both Black-throated Green and Black-throated Blue warblers displayed evidence of learning where prey are distributed. Capture rates during the acquisition period increased in all four experiments with Black-throated Green Warblers, and in two of four experiments with Black-throated Blue Warblers, with a strong tendency to increase in a third.

There was only one significant and one nonsignificant decreasing trend in time to first capture. Thus there seems to be no relationship be-

TABLE 4. Results of analysis of means of slopes of times to first capture during acquisition period for each of four experiments for Black-throated Green Warblers (GW) and Black-throated Blue Warblers (BW).

Tree species	Prey distribution	Bird species	Slope <sup>a</sup>	Different from zero?	
				<i>t</i>	<i>P</i>
Sugar maple	Upper	GW <sup>b</sup>	-3.21 ± 1.82	-1.763	<0.10
		BW <sup>b</sup>	-1.99 ± 0.67	-2.974	<0.025
	Lower	GW	-1.34 ± 0.87	-1.53	>0.10
		BW	-0.47 ± 1.32	-0.35	>0.10
Yellow birch	Upper	GW	-8.43 ± 6.02	-1.39	>0.10
		BW	-0.66 ± 1.32	-0.50	>0.10
	Lower	GW	-1.15 ± 0.98	-1.17	>0.10
		BW	-0.25 ± 1.12	-0.22	>0.40

<sup>a</sup>  $\bar{x} \pm 1$  SE.  
<sup>b</sup> *n* = 5.

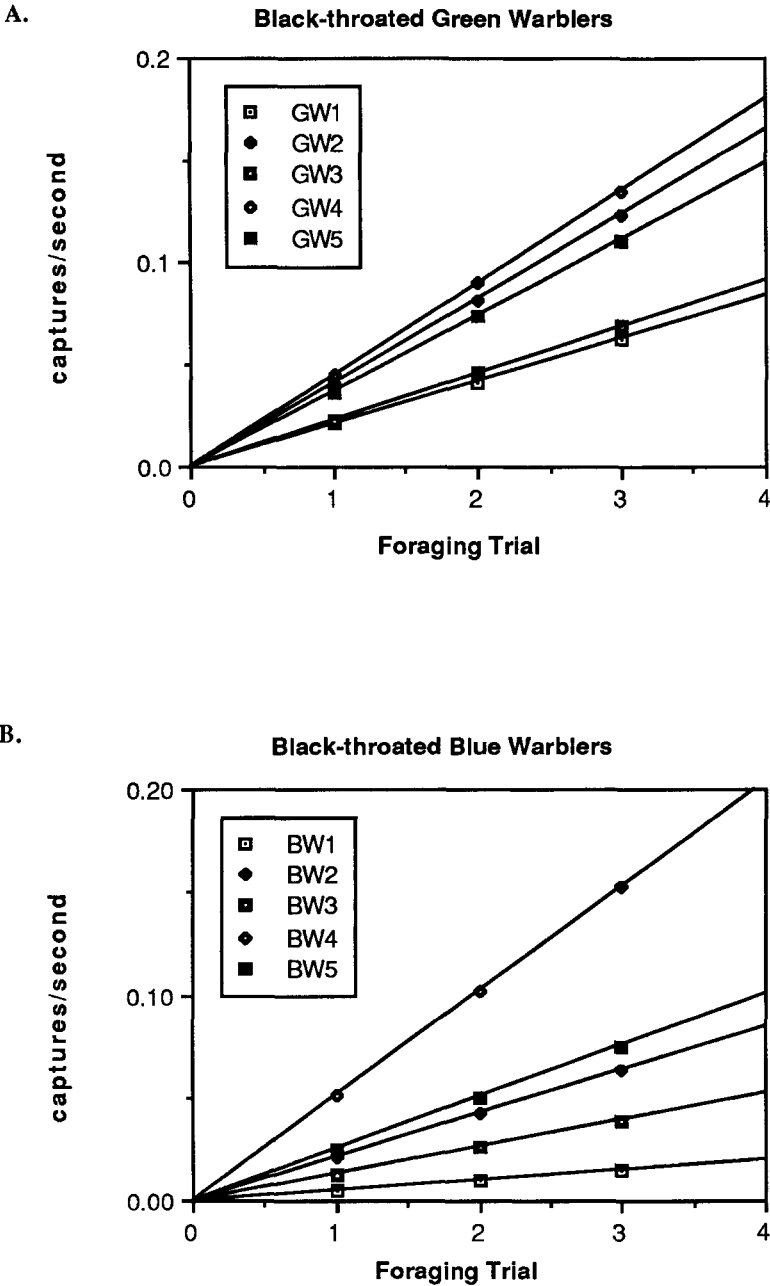


FIGURE 1. Learning curves based on mean slopes of capture rate vs. foraging trial of four experiments for (A) five individual Black-throated Green Warblers (GW) and (B) five individual Black-throated Blue Warblers (BW).

tween increasing capture rates and the time to first capture. In other words, the increased rate of foraging must have occurred after the first prey capture. These findings suggest that at the begin-

ning of each foraging trial, these birds were still searching both leaf surfaces, and they then focussed their foraging on a particular leaf surface after the first prey capture.

TABLE 5. Results of four-way factorial analysis of variance of times to first capture of Black-throated Green Warblers and Black-throated Blue Warblers during the acquisition period.

Source	df	Sum of squares	Mean square	F value	P
Model	14	483.85073875	34.56076705	1.23	0.3168
Error	25	704.03550562	28.16142022		
Corrected total	39	1,187.88624437			

## RESPONSE TO PREY DISTRIBUTION SWITCH

Although I attempted to control the motivational state of each bird by providing it with the same amount of food and the same period of food deprivation before each foraging trial, it was still possible that motivation due to hunger, and concomitantly, capture rates, could have increased from the first to the fourth trial. However, the finding that capture rates decreased after the prey distribution switch in five of eight experiments suggests that the increased capture rates during the acquisition period were due to learning, as opposed to some other factor, e.g., increasing motivation due to hunger. In addition, in two of the three trials in which the capture rate did not decrease significantly following the switch, the prey distribution switch was to the leaf surface on which the bird species was better able to learn about prey distribution.

## EFFECT OF FOLIAGE STRUCTURE

The analysis of variance of capture rate slopes showed that there was no effect of tree species on the learning abilities of these warblers. Furthermore, tree species did not interact with any other effect to influence the learning abilities of these bird species. This suggests that the contrasting foliage structures of these tree species do not affect the ability of these bird species to learn

about the distribution of prey on upper and lower leaf surfaces. This result is rather surprising because several studies have suggested (Holmes and Robinson 1981, Holmes and Schultz 1988) or demonstrated (Whelan 1987) that foliage structure affects the ability of birds to locate, attack, and capture prey on these leaf surfaces. However, this may simply reflect that both tree species were abundant in the understory and canopy where the birds were captured, and that the birds had experience foraging on them. Nevertheless, this suggests that these birds should be able to respond to prey distribution changes equally well on both tree species.

## BIRD SPECIES DIFFERENCES

Greenberg (1985) found no differences in the foliage discrimination learning abilities of two species of paruline warbler. In contrast, the two species tested here showed differences in their prey distribution learning. While Black-throated Green Warblers displayed better learning abilities on upper leaf surfaces, Black-throated Blue Warblers had better learning abilities when prey were distributed on lower leaf surfaces. These results are consistent with field observations of the foraging behavior of these two bird species. In a study of the foraging behavior of these species at the Hubbard Brook Experimental Forest, Holmes and Schultz (1988) found that Black-

TABLE 6. Results of comparison with Wilcoxon's Rank-Sum test of observed capture rate following prey distribution switch to predicted capture rate (based on regression line of capture rates during the acquisition period, see text for details; Methods: Transfer period).

Bird species	Tree species	Prey distribution switch	$W_{obs}$	P
Black-throated Green Warblers	Sugar maple	Upper to lower	19	0.048
		Lower to upper	20	0.075
	Yellow birch	Upper to lower	19.5	<0.075
		Lower to upper	17	0.016
Black-throated Blue Warblers	Sugar maple	Upper to lower	22.5	>0.111
		Lower to upper	16	0.008
	Yellow birch	Upper to lower	16	0.008
		Lower to upper	25.5	>0.111

throated Green Warblers tended to forage proportionately more often from upper leaf surfaces, while Black-throated Blue Warblers tended to forage more frequently from lower leaf surfaces.

#### INDIVIDUAL DIFFERENCES

The analysis of variance of the capture rate slopes also revealed considerable variability in the learning abilities among individuals within both bird species. These individual differences could be due to actual differences in the innate learning abilities of these birds, or they could be the result of different histories and prior experiences of these wild-caught birds. Such differences were uncontrollable in this study.

In conclusion, this study shows that two species of paruline warbler can cue into particular leaf surfaces for finding prey. The results are similar to Heinrich and Collin's demonstration that chickadees can discriminate between similar leaves of different tree species and between leaves damaged and not damaged by insects. Studies in the future may examine whether warblers can also use other habitat cues, such as leaf damage, to locate phytophagous insects. Such studies would not only contribute to our knowledge of how these birds perceive their environments, but also help elucidate the kinds of selective pressures these visual hunters may exert on their insect prey (Heinrich 1979).

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