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Russell Greenberg

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## THE ROLE OF NEOPHOBIA IN DETERMINING THE DEGREE OF FORAGING SPECIALIZATION IN SOME MIGRANT WARBLERS

RUSSELL GREENBERG

Department of Zoological Research, National Zoological Park, Smithsonian Institution,  
Washington, D.C. 20009

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Some animals are more specialized than others in where they search for food. The ultimate factors determining when animals should be specialists or generalists have been a focus of ecological theory (MacArthur and Levins 1967; Cody 1974; Roughgarden 1974), but the psychological basis of the specialist-generalist continuum has been largely ignored.

What are the proximate mechanisms that underlie the decision of which foraging sites to visit? Animals can often learn through experience where they can feed most profitably given the distribution of food and morphological constraints. Animals may not explore all possible foraging sites, however, and may be restricted to certain feeding microhabitats by some form of behavioral stereotypy (Klopfer 1965, 1967). Here I investigate the response of some migrant warblers to novel feeding places.

The factors that determine specialization versus generalization are particularly problematic in tropical migrant birds, which as young often arrive at unfamiliar winter habitats without parents and other conspecifics. These birds are faced with an array of microhabitats such as vines, epiphytes, leaf clusters, dead leaves, etc., with varying degrees of similarity to those encountered on their natal range.

Until recently, it was assumed that migrants display a high degree of plasticity in foraging behavior (Willis 1966; Morse 1971). Field studies indicate that migrant species have a range of foraging strategies; some species forage in a consistent manner, and in similar situations throughout the year, while others forage in a variable and generalized manner during the winter months (see papers in Keast and Morton 1980).

During three winters I studied the foraging ecology of chestnut-sided (*Dendroica pensylvanica*) and bay-breasted (*D. castanea*) warblers, two morphologically similar foliage-gleaning warblers, in the lowland tropical forest of Barro Colorado Island and the Canal Area of Panama. In the face of the same available resources, seasonal climatic regime, and habitat, bay-breasted and chestnut-sided warblers were distinctly different in their foraging behavior: bay-breasted was the most generalized and chestnut-sided warbler was the most specialized of eight species of foliage-gleaning birds that I studied (Greenberg 1979, in press). In

forests, bay-breasted warblers have a greater foraging height range, occur in a greater diversity of plant and foliage types, and feed off a greater diversity of foraging surfaces. The opportunistic behavior of the bay-breasted warbler is exaggerated in human-disturbed habitats, where they forage along roadsides, on lawns, from garbage cans, and on buildings, screens, and lights.

During the breeding season bay-breasted warblers are generally restricted to spruce-fir forest and the chestnut-sided warbler frequents broad-leaved second growth. The difference between the species reflects a general dichotomy among the *Dendroica* of eastern North America: More opportunistic winter behavior characterizes species that breed only in coniferous forests (Greenberg 1979).

In the following experiments I examine some psychological factors that could give rise to the different degrees of foraging specialization found in bay-breasted and chestnut-sided warblers during the winter. I have focused on these two species, since I have extensive field comparisons of their foraging behavior. I also include data from four other species of *Dendroica* to place the two species in broader context.

#### THE BIRDS

Thirty immatures of six species of *Dendroica* were captured at banding stations in Maryland during September and October 1981 and kept indoors in pyramidal (50 cm × 60 cm × 45 cm) soft mesh cages. The species included: chestnut-sided (7 individuals); bay-breasted (4); magnolia (*D. magnolia*, 4); black-throated blue (*D. caerulescens*, 3); Cape May (*D. tigrina*, 5); and yellow-rumped (*D. coronata*, 7). The warblers were offered mealworms and nutritious mash, ad libitum, in ceramic dishes (2.5 cm × 10 cm diameter) 7–12 h a day and kept at a constant 12/12 light regime 18° C–24° C. The experimental foraging situations were presented in their home cages (with 1 exception), since the warblers showed more fear when placed in a flight cage for short periods. None of the following experiments were conducted until the birds had been in captivity for at least 6 wk.

Individuals in a roomful of warblers show cycles of activity that are coordinated. When one warbler starts to move, all others in the room become active. These periods of activity are halted by periods of complete stillness (when a warbler becomes alarmed). Periods of stillness were not counted in the timing of the experiments.

#### EXPERIMENT 1

##### *Methods*

In this experiment I examined whether chestnut-sided warblers approach or feed from fewer novel microhabitats containing hidden mealworms. A series of 10 objects, each with one hidden mealworm, was placed in the cage one or two at a time. All birds were offered the same objects in the same order and combination during a 6-wk period, November to December, 1981. The objects were placed near perches or on the floor of the cage so that no special foraging maneuvers were

required to obtain the prey. Birds were deprived of food for 2 h prior to the experiment.

Mealworms had to be alive and whole for warblers to show any interest. To restrict the movements of mealworms, I fastened them to objects by placing them on masking tape or fine-gauged insect pins.

Trials lasted 20 min during which I watched from a distance of 5 m or from behind an opaque screen (aviary experiments only) and scored approach behavior. An approach to an object was accompanied by several motions that made the bird's interest in foraging unambiguous: sudden crouching with fanned tail, peering, craning of the neck, pecking at the object. Approaches were close ( $<7.5$  cm) or far ( $>7.5$  cm). While most persistent warblers could remove a worm from its attachment, birds were considered successful at foraging if they tugged at the mealworm. The objects containing the live mealworms included: (a) a flat dead leaf (*Acer*) on the cage floor with a worm hidden under the raised lips; (b) a curled dead leaf (*Platanus*) suspended from a cage perch with a worm on the inside near the lower lip; (c) a section of branch ( $7.5 \times 15$  cm) with worms glued into two 0.5 cm diameter holes with a peanut-butter paste; (d) a leaf cluster from the spider plant (*Chlorophytum elatum*), which resembles a small epiphyte, into which a mealworm was pinned; (e) a cardboard tube ( $5 \times 12$  cm) taped to a perch in the cage corner. The worm was placed in the cup bottom and could not be seen without a close approach; (f) a cardboard tube ( $5 \times 12$  cm) suspended from a perch in which a worm was taped 1 cm from the lower end; (g) a shallow gray cardboard cup (5 cm diameter  $\times$  2 cm) taped to a perch in the cage corner. The worm was placed in the cup bottom and could not be seen without a close approach; (h) small sections of plastic drinking straw were taped perpendicularly to the perches in the upper half of a large flight cage (2 m  $\times$  2 m  $\times$  3 m). Worms were placed in the tubes; (i) clusters of three spiny spherical seed capsules (from *Liquidambar*) with the worm pinned on the top and between the three capsules; (j) a cardboard box (10 cm  $\times$  10 cm  $\times$  10 cm) placed on its side on the cage floor with the worms placed at the back end of the box; (k) an inflorescence of bottlebrush (*Melaleuca* sp.) with a worm pinned among the red stamens was taped to the cage side next to a perch.

#### RESULTS

Bay-breasted and chestnut-sided warblers differed in their response to and success at the foraging stations (table 1). Chestnut-sided warblers rarely attempted to seize hidden prey ( $\bar{X} = 1.0$ ). Bay-breasted warblers showed greater success ( $\bar{X} = 4.3$ ) and the difference is significant ( $U_{4,7} = 4.5$ ,  $P < .05$ ). Both species, however, approached the objects with similar frequency ( $U = 14$ , NS), but the proportion of approaches that led to feeding was higher in the bay-breasted warbler ( $\bar{X} = 0.8$ ) than the chestnut-sided warbler ( $\bar{X} = 0.2$ ,  $U = 0$ ,  $P < .01$ ). The approaches of chestnut-sided warblers were timid and ambivalent, alternating between approaches and flights, and a significantly greater number of approaches were far approaches (BBW  $\bar{X} = 0.9$ , CSW  $\bar{X} = 1.7$ ,  $U = 3.5$ ,  $P < .05$ ).

Differences between these two species reflect a pattern of variation of all *Dendroica* species tested (table 1). Overall, the six species showed significant

TABLE 1  
NUMBER OF APPROACHES AND FEEDING ATTEMPTS AT THE TEN OBJECTS  
PRESENTED TO WARBLERS IN EXPERIMENT 1

SPECIES	NO. OF FORAGING ATTEMPTS	NO. OF APPROACHES	NO. OF WEAK APPROACHES
Chestnut-sided warbler .....	1.0 (.4 SE)	5.6 (1.0)	1.7 (.3)
Bay-breasted warbler .....	4.0 (1.1)	5.5 (1.8)	.3 (.3)
Magnolia warbler .....	3.0 (.7)	7.0 (.4)	.9 (.5)
Cape May warbler .....	1.8 (.6)	4.2 (.9)	.8 (.4)
Black-throated blue warbler ....	3.7 (.9)	4.7 (1.3)	0
Yellow-rumped warbler .....	3.4 (.3)	5.3 (1.0)	.4 (.1)

variation in the number of successful foraging attempts (Kruskal Wallis,  $\chi^2 = 23$ ,  $df = 5$ ,  $P < .001$ ). This did not result so much from variation in the number of objects approached (Kruskal Wallis = 9.5,  $df = 5$ , NS) as from the proportion of approaches leading to feeding (Kruskal Wallis = 18.5,  $df = 5$ ,  $P < .01$ ). Chestnut-sided warblers ranked among the most timid and bay-breasted warblers ranked among the least timid and most successful warblers.

## EXPERIMENT 2

### Methods

This experiment tests the idea that chestnut-sided warblers are more hesitant to approach novel foraging microhabitats, even when the reward is familiar and conspicuous. Warblers were trained to take mealworms from small plastic cups by feeding them from these cups for 2 days. These cups, filled with their conspicuous mealworm reward, were embellished with accessories to make model microhabitats. The purpose of the model microhabitat design was not to mimic explicitly natural objects, but to present novel objects that could be varied in specific features (color, size, shape, and orientation). Warblers were observed for up to 20 min of activity, after 1 h of food deprivation; the primary performance criterion was the time the warbler first peered at or approached the microhabitat to the time of first feeding. If a bird failed to feed from the model microhabitat, the cup was offered without its embellishment. In all cases of nonfeeding from the experimental cup, birds fed immediately from the ordinary cups. In addition, four replicate times were obtained from birds feeding from the plain cups after 1 h food deprivation; for all birds mean values fell well below 60 s.

The model microhabitats were as follows: (1) *Spines*—Six sections of toothpicks (2.5 cm) attached to the lip of the cup with plasticine. (2) *Opaque spines*—Spines similar to those of 1 but connected with masking tape. (3) *Long yellow spines*—Eight yellow chenille stems (15 cm) attached to the base of cup in a vertical orientation. (4) *Horizontal tube*—Cardboard tube (5 × 7.5 cm) filled in center with paper and placed 2.5 cm from cup. (5) *Horizontal cylinder*—Similar to 4 but taped at both ends to form an apparently solid object. (6) *Vertical tube*—Similar to 4 but suspended by wire with bottom 7.5 cm from cup. (7) *Vertical cylinder*—Similar to 5 but suspended over cup as in 6. (8) *White moss*—A

semicircular mound of finely shredded white paper in which the cup was placed. (9) *Small green leaves*—Four ( $5 \times 7.5$  cm) elliptical green leaves of construction paper on green chenille stems (1 cm). The leaves were arranged planar to the lip of the cup. (10) *Small red leaves*—Similar to 9 but with vermilion paper. (11) *Large green leaves*—Similar to 9 but with  $7.5 \times 12$  cm leaves. (12) *Large erect green leaves*—Similar to 11 with leaves perpendicular to the mouth of the cup. (13) *Large curled green leaves*—Similar to 11 with leaves curled into 2.5 cm diameter tubes. (14) *Large fanned leaves*—Similar to 11 with leaves finely dissected with palmately arranged cuts at approximately 1 mm intervals. (15) *Small clustered green leaves*—Similar to 9 but with three rows with four leaves each.

This experiment was conducted from December 1981 through January 1982 and microhabitats were presented to all the warblers in the same order (no more than 2 trials were conducted on the same bird in a day). A complete survey of all 15 microhabitats was conducted on three species (15 individuals, bay-breasted, chestnut-sided, and magnolia warblers) and supplemented by a series of seven microhabitats (1,3,4,8,11,13) presented to Cape May, yellow-rumped and black-throated blue warblers.

#### RESULTS

Bay-breasted and chestnut-sided warblers differed in their approach and feeding at the model microhabitats. Bay-breasted warblers approached quickly and fed with little hesitation, whereas the chestnut-sided warbler fed only after repeated approaches or not at all. The median feeding times (table 2) were 0 s for bay-breasted and 175 s for chestnut-sided warblers. The mean feeding times, excluding nonfeeding, were 48 s and 250 s, respectively ( $U_{4,7} = 0$ ,  $P < .001$ ). In addition, every chestnut-sided warbler failed to feed at some microhabitats, whereas all bay-breasted warblers fed at all microhabitats. The frequency of nonfeeding averaged 4.0 for chestnut-sided warblers.

Magnolia warbler, the third species tested on all 15 microhabitats, performed intermediate to the other species (median = 68 s). The mean ranks for individual performance on 15 microhabitats were 5.7–8.4 for magnolia, 3.3–5.6 for bay-breasted, and 9.9–12.8 for chestnut-sided warbler (overall Kruskal Wallis = 23.2,  $P < .001$ ). Magnolia warblers failed to feed at an average of 0.75 trials. The performance of individual warblers was fairly consistent across all of the microhabitats Kendall's  $W$  of concordance = 0.49,  $\chi^2 = 102.9$ ,  $df = 14$ ,  $P < .001$ ).

How an individual warbler ranked on 15 microhabitats was correlated with its mean ranking on a smaller set of seven microhabitats ( $r_s = 0.87$ ,  $df = 14$ ,  $P < .05$ ) used to compare all six species of *Dendroica*. In this broader survey individual warblers ranked consistently across all microhabitats (Kendall's  $W = 0.46$ ,  $\chi^2 = 83.8$ ,  $df = 25$ ,  $P < .01$ ). In addition, overall interspecific variation in feeding latency was significant (table 2, Kruskal Wallis = 25,  $df = 5$ ,  $P < .001$ ) with bay-breasted warblers having the lowest and chestnut-sided warblers the highest feeding latencies.

The latency in feeding by the warblers was not for want of interest. The long feeding times reflect a large number of approaches and withdrawals. Even war-

TABLE 2

MEDIAN LATENCIES FOR WARBLERS FEEDING AT MODEL MICROHABITATS PRESENTED IN EXPERIMENT 2

SPECIES	15 MICROHABITATS		7 MICROHABITATS	
	Overall Median Feeding Times (s)	Range*	Overall Median Feeding Times (s)	Range
Chestnut-sided warbler . . . .	175	109–no feed	416	130–no feed
Bay-breasted warbler . . . . .	0	0–5	17	0–79
Magnolia warbler . . . . .	68	5–120	70	5–300
Black-throated blue warbler . . . . .			220	240–470
Cape May warbler . . . . .			270	35–no feed
Yellow-rumped warbler . . .			127	30–312

NOTE.—Experiments were arbitrarily ended at 20 min; a warbler that failed to feed during a trial was scored as “no feed.” Since these trials cannot be assigned an integer value I present median values.

\* Range of individual medians.

blers that failed to feed always fed from plain cups placed in their cage after the experiment. All birds fed from the cups rapidly during control trials.

What features of microhabitat design caused the greatest feeding latencies in warblers? In order to evaluate this I have made some specific comparisons among sets of similar microhabitats. I presented seven types of “leaves” (microhabitats 9–15) to bay-breasted, chestnut-sided, and magnolia warblers. The 15 warblers fed at certain leaf types consistently more slowly than others. All warblers fed quickly at stations with small green leaves. Dense green leaves, red leaves, and large leaves were presented after small green leaves and produced greater feeding latencies. Pairwise comparisons of feeding times of individual warblers, using a Wilcoxon signed rank statistic ( $T$ ), were all significant: red versus small green ( $T = 7$ ,  $P < .001$ ), dense green versus small green ( $T = 4$ ,  $P < .001$ ), large green versus small green ( $T = 5$ ,  $P < .001$ ). Similarly, long yellow ( $T = 3$ ,  $P < .001$ ) and opaque spines ( $T = 20$ ,  $P < .05$ ) were more aversive than short spines.

More natural foraging microhabitats were presented to the warblers to see if results were consistent with those outlined above. I gave warblers large clustered leaves (*Magnolia*) and small planar leaves (*Ilex* with the spines removed). For this experiment, order was controlled: half (11) of the 21 warblers were presented with the larger leaves first and the order was reversed for the other 10 warblers. Warblers visited the large clustered leaves far more slowly (median time = 300 s) than the small leaves (30 s) and the difference was significant comparing the performance of individual warblers at each leaf type with a Wilcoxon signed rank test ( $T = 4$ ,  $P < .001$ ). The result is in accord with the warbler’s greater hesitancy to approach large erect versus small planar model leaves.

#### DISCUSSION

Variation in hesitancy to approach novel microhabitats may produce variation in foraging specialization, such as is found between bay-breasted and chestnut-

sided warblers. In experiment 1, bay-breasted and chestnut-sided warblers approached a similar number of objects but differed in the number of successful foraging attempts. Chestnut-sided warblers approached in an ambivalent manner suggesting flight-approach conflicts. While other warbler species were similar to bay-breasted warblers in the number of successful foraging attempts, magnolia warblers often showed the same behavioral conflicts that marked the approaches of chestnut-sided warblers.

The second experiment showed that in the face of a strong positive foraging stimulus (a familiar cup full of mealworms) warblers often showed reluctance or refusal to approach a novel stimulus to feed. The variation had a species-specific component with bay-breasted warblers showing the least hesitation, and chestnut-sided warblers showing the greatest hesitation.

The role of aversion in determining foraging specialization is suggested by the correlation of individual performances in the two experiments (fig. 1). Warblers that obtained more hidden prey from foraging objects in experiment 1 tended to be those that ranked lowest in feeding time in experiment 2 (15 warblers–15 microhabitats  $r_s = .84$ ,  $df = 14$ ,  $P < .01$ ; 26 warblers–7 microhabitats  $r_s = .71$ ,  $df = 26$ ,  $P < .001$ ).

The feeding latency of experiment 2 was probably largely a response to the novelty of the microhabitats. The objects were diverse in shape, form, orientation, and color, so their major unifying feature is their probable unfamiliarity to wild-caught, immature warblers. For example, the most aversive “leaf” types were large, clustered, and red leaves; the small green leaves had little effect. Similarly, the opaque and long yellow spines were more aversive than the simple spines. In addition, in a series of experiments I report elsewhere (Greenberg, MS) I have shown that warblers habituate to and feed readily from the most aversive of the microhabitats. Neophobia has been shown to be an important factor in the feeding behavior of rats (Barnett 1958; Mitchell 1976; Cowan 1977). It may be an important component of the response of insectivorous birds to aposematic prey (Coppinger 1970).

Just as neophobia may restrict a warbler from feeding at some microhabitats, variation in neophobia may be important in determining the level of specialization of different warbler species. An increase in neophobia will reduce the number of microhabitats that a bird will explore for food. Change in intensity of neophobia, however, is only a proximate mechanism. The ultimate factors that select for different levels of neophobia are probably those that select for different levels of foraging specialization.

In this case, I have suggested (Greenberg 1979, in press) that bay-breasted warblers are more generalized insectivores (and more omnivorous) than chestnut-sided warblers because as coniferous forest breeding birds, they are less well adapted for broad-leaved insectivory during the winter. Their increased plasticity allows them to exploit a wider range of possible resources and capitalize on shifts in insect abundance. By this argument, I expect that species that breed in coniferous forests should show less neophobia than those that breed in broad-leaved habitats. In fact, individuals of coniferous breeding species (bay-breasted, magnolia, Cape May, and yellow-rumped warblers) were significantly less neophobic



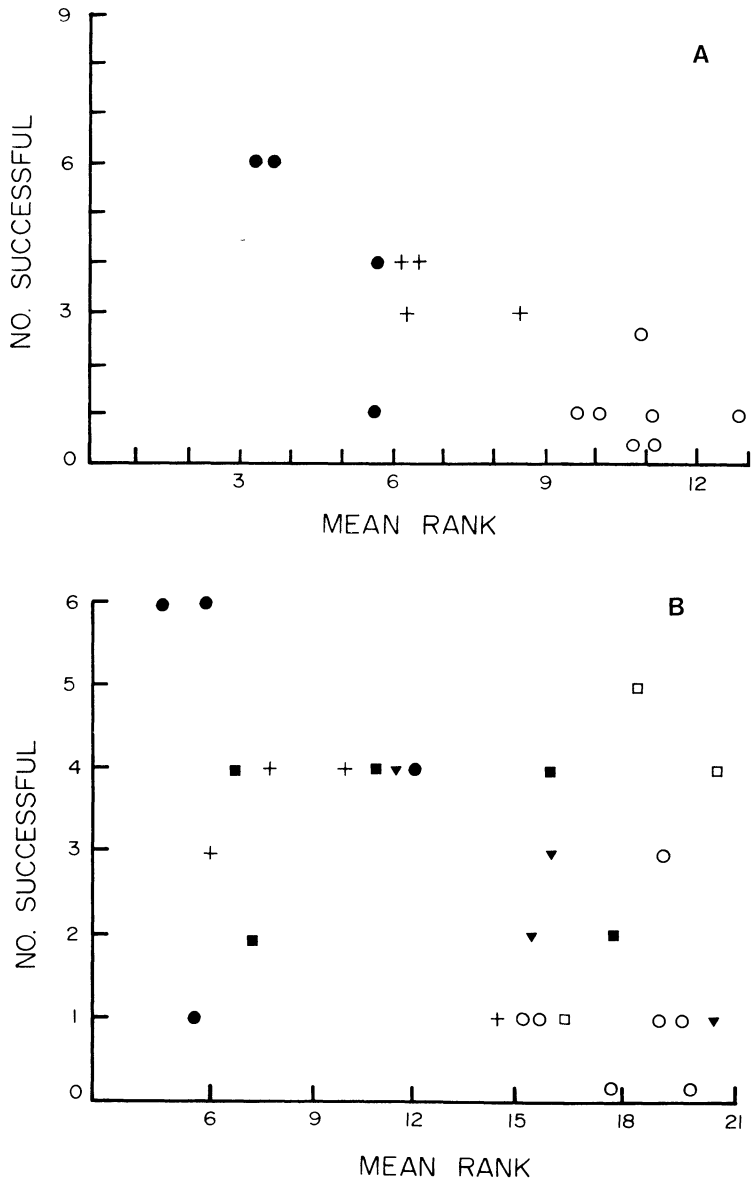


FIG. 1.—Mean rankings of individual warblers based on their feeding latencies at microhabitats presented in experiment 2 plotted against the number of foraging attempts for the 10 trials of experiment 1: *a*, included are 15 individuals (magnolia = +, chestnut-sided = ○, bay-breasted = ●) that were tested in 15 trials in experiment 2 ( $r_s = 0.84$ ,  $n = 15$ ,  $P < .01$ ); *b*, included are 22 individuals (symbols the same as in fig. 1*a*, in addition: Cape May = ▼, yellow-rumped = ■, black-throated blue = □) that performed on 7 trials in experiment 2 ( $r_s = 0.71$ ,  $n = 26$ ,  $P < .01$ ). Clear symbols are broad-leaved and dark symbols are conifer breeding species.

in experiment 2 than individuals of species breeding in deciduous vegetation (chestnut-sided and black-throated blue warblers,  $U = 14$ ,  $P < .001$ ).

But the neophobia hypothesis also suggests that alternative factors might select for foraging specialization. Species that are more susceptible to predation may show greater fear of approaching unfamiliar situations (Glickman and Sroges 1966). The foraging plasticity of island birds (Yeaton and Cody 1973; Terborgh and Faaborg 1973), for example, may be the indirect result of reduced predation pressure. Similarly, the supposed high foraging stereotypy of tropical forest birds (Klopfer and MacArthur 1961) may result from a high and diverse predator community selecting for increased neophobia. In the case of bay-breasted and chestnut-sided warblers, differences in search behavior and sociality may make bay-breasted warblers less vulnerable to predation; chestnut-sided warblers forage solitarily (with respect to conspecifics), searching the undersurfaces of leaves intently, whereas bay-breasted warblers occur in single species flocks and peer about in all directions when foraging.

A generalized aversion to a range of unfamiliar situations may restrict birds to foraging in microhabitats to which they are best adapted and prevent from approaching dangerous sites. Since it is a general psychological phenomenon and not a specific foraging strategy, neophobia may be difficult to model. Novel microhabitats are not necessarily less profitable or more dangerous than familiar ones. Because of this decoupling of fear from any rationally inferred environmental variables, foraging models will have to rely on some knowledge of the experience of animals. Alternatively, foraging studies can continue to concentrate on generalist species that may have reduced neophobia; or studies can focus on the range of resources for which individuals show little or no aversion. However, by concentrating on these species and situations, behavioral ecologists may miss opportunities to relate behavioral mechanisms to community patterns.

#### SUMMARY

I conducted experiments to examine the psychological basis of foraging specialization in *Dendroica* warblers. The focus of the experiments was a comparison of wild-caught, immature bay-breasted and chestnut-sided warblers; I have studied the foraging ecology of these species during the winter in Panama. During the nonbreeding season, the bay-breasted warbler is a generalized forager compared to the chestnut-sided warbler. Individuals of four other species of *Dendroica* were tested in similar experiments to see how bay-breasted and chestnut-sided warblers compared with the genus as a whole.

Consistent with field observations, chestnut-sided warblers obtained hidden mealworms from fewer unfamiliar objects than did bay-breasted warblers. They approached a similar number of objects, but were more timid and ambivalent. When offered a variety of "model microhabitats" with a conspicuous and familiar reward, chestnut-sided warblers were far more hesitant to approach and would often not feed from novel microhabitats. Individuals of all six species of *Dendroica* had consistent rankings in how rapidly they fed at the model microhabitats. This variation had a species-specific component, with bay-breasted warblers

feeding most rapidly and chestnut-sided warblers feeding most hesitantly. These results suggest that the number of microhabitats visited by a warbler is the result of a dynamic interaction of attraction and fear. Individuals and species with greater aversion to novel foraging situations may be more specialized than less neophobic warblers. Shifts in a neophobia threshold may provide a relatively simple mechanism for varying foraging specialization among closely related species.

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