Proc. Natl. Acad. Sci. USA
Vol. 81, pp. 3778–3780, June 1984
Ecology

Neophobia in the foraging-site selection of a neotropical migrant bird: An experimental study

(warbler/*Dendroica*/early experience/habitat selection/feeding behavior)

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Communicated by S. Dillon Ripley, February 10, 1984

ABSTRACT **I hand-raised chestnut-sided warblers (*Dendroica pensylvanica*) in a room with eight experimental microhabitats; the microhabitats were removed after 6 weeks. I then measured the response of the warblers to the eight "natal" and eight "novel" microhabitats in two experiments conducted 2 and 4 months after removal. Chestnut-sided warblers responded with decreased feeding latency (neophobia) and a greater preference for foraging at the natal microhabitats. I suggest that an ontogenetic increase in neophobia restricts chestnut-sided warblers to foraging at microhabitats most similar to those experienced as juveniles.**

While a number of experiments have examined how birds decide where to forage (1–5), these fine-tuned studies shed little light on the behavior of birds entering new habitats with unfamiliar microhabitats. Yet, this is precisely the problem that most temperate-zone birds face when they migrate.

The problem is particularly intriguing for studying temperate-breeding species that winter in structurally complex tropical forests. The young of these species often migrate without parents and other conspecifics, and they even defend territories during their first winter (6). They face the choice of where to search for food among myriad unfamiliar microhabitats, including unusual foliage types, dead leaf clusters, epiphytes, and displays of flowers and fruits. While innate preferences for some habitat features have been demonstrated for birds (7), the sheer number of potential cues facing a migrant seem to make foraging decisions too complex to be based solely on genetic factors (8). Here I report experiments that test the hypothesis that an ontogenetic increase in neophobia (the aversion to feeding at unfamiliar objects; see refs. 9–11) may restrict chestnut-sided warblers to foraging sites most similar to those experienced on their natal range.

Chestnut-sided warblers are highly migratory, breeding in temperate second-growth of eastern North America and wintering in lowland tropical forests and woodlands of Central America. Prior to migration, juveniles spend several weeks in close association with their parents and they are, like other passerines, curious and exploratory (12). Captive warblers at this age are attracted to novel objects that they often pick at or manipulate with their beaks. In captivity, chestnut-sided warblers >8 weeks old are hesitant to feed at novel foraging microhabitats even when preferred food is conspicuously presented (13). Thus, time spent in juvenile exploration may familiarize warblers with a set of microhabitats; the neophobia of older birds might tend to restrict them to foraging situations similar to those experienced as juveniles.

While there is a shift toward the use of more mature woodlands between temperate breeding and tropical non-breeding seasons, chestnut-sided warblers are consistent in their use of microhabitat features (e.g., foliage type, size and arrangement, branch distribution). In the forests of Panama, chestnut-sided warblers are specialized foliage-gleaning birds with respect to foraging substrate, foliage type, and other microhabitat variables (14).

In this report, I present the findings of two experiments that examine the response of warblers to novel microhabitats. One experiment measures the initial feeding latency at novel versus natal microhabitats presented one at a time. A second experiment examines the preference for familiar versus novel microhabitats over a large number of trials. Thus, the experiments examine the possibility of an initial bias toward approaching familiar sites and the stability of any resulting preference.

MATERIAL AND METHODS

General Methods. Before the experiments began, I prepared a master list of 16 microhabitats. From this list, 8 were randomly selected to be "natal" microhabitats and the remaining 8 were used in the experiments as "novel" microhabitats. The selection was balanced so that each list contained two live plants. The 8 natal microhabitats included the following: box, a 12 × 12 × 30 cm black box; moss, a 20-cm-diameter mound of Spanish moss (*Dendropogon usneoides*); Easter grass, a 20-cm mass of pink and chartreuse Easter grass; parasol, a 5-cm white disk on a 10-cm dowling planted in a 5 × 7.5 cm plasticine base; vine tangle, a 40-cm mass of woven honeysuckle (*Lonicera* sp.) and ivy (*Hedera helix*) vines; coconut, a half coconut shell; *Dracaena*, a 20-cm *Dracaena compacta* plant in a 7.5-cm green plastic pot; palm, a 45-cm palm (*Chamaedorea elegans*) in a 15-cm green plastic pot.

The 8 novel microhabitats included the following: tube, a 10 × 30 cm brown tube; dead leaf, a 15-cm brown curled leaf (*Platanus* sp.); pipe cleaner, six 15-cm-long yellow pipe cleaners in plasticine; holly, a 30-cm spray of holly (*Ilex* sp.); bamboo, a 35-cm tall clump of dried bamboo foliage; sponge, a 10 × 7.5 cm block of chartreuse sponge; fern, a 10-cm fern (*Nephrolepis exaltata*) in a 5-cm green plastic pot; *Dracaena*, a 30-cm *Dracaena marginata* plant in a 15-cm green plastic pot. The two species of *Dracaena* used in these experiments are morphologically dissimilar.

I obtained five nestling chestnut-sided warblers 6–7 days old (shortly after their eyes opened) and reared them in a small room (2 × 2 × 3.5 m). After fledging (9 days old), the warblers resided in a small cage, but the door was left open 3–5 hr per day to allow the birds to explore the room and the set of eight natal microhabitats, which were placed next to branches at scattered localities around the room and shifted in position twice per day. When hand feeding was no longer needed (4 weeks old), mealworms and meat mash were placed in small cups either near the natal microhabitats or directly on their surfaces. Six weeks after the birds fledged, the microhabitats were removed, and the warblers were moved from the rearing room into flight cages (2 × 2 × 2.5 m).

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Experiment 1. Warblers were housed solitarily in smaller cages (0.6 × 0.6 × 1.0 m) for 2 weeks prior to this experiment. Prior to the experimental trials, each warbler was extensively trained to feed from the isolated food cup; experimental trials were initiated only after each warbler fed from the cup within 30 sec on four consecutive trials (after 1 hr of food deprivation). After 13–15 weeks, the 8 novel microhabitats were presented, one at a time, for 10 min at the bottom front corner of the home cage adjacent to a dowling perch. Four days after the initial exposure, each microhabitat was presented in experimental trials in the same location adjacent to a small white cup (2 × 2 cm) filled with mealworms and meat mash. For each trial, I recorded the time it took for the warbler to feed from the cup after it was placed in the cage. Warblers were deprived of food for 1 hr prior to the experiment, and the trials were terminated after 20 min. Since the warblers fed immediately from the food cups, I attribute the long latencies obtained on experimental trials to a response to the associated microhabitats.

After 16–18 weeks, the natal microhabitats were presented in the same sequence outlined above for the novel microhabitats.

Experiment 2. Four months after the natal microhabitats were removed from the 7-week-old birds, I presented combinations selected from six of the natal and six of the novel microhabitats in simultaneous choice tests. Live plants were excluded from both sets for logistical reasons. The experiment was conducted on all five birds simultaneously in their home flight cage after 1 hr of food deprivation. They had been housed together for 2 months and displayed no aggression or mutual disturbance when feeding. In each trial, two microhabitats were selected randomly from each set and assigned random locations at four feeding stations located midway on the sides of the aviary. Cups with mealworms and meat mash were placed next to perches adjacent to each microhabitat. Ten 10-min trials were run each day for 10 consecutive days (100 trials), and the number of trials in which a particular microhabitat was visited for feeding was summed for each bird.

RESULTS

Experiment 1. The warblers fed with greater hesitancy from the novel microhabitats (median time for novel, no feeding; median time for natal, 330 sec; Table 1). The null hypothesis of equal latency was rejected using a Friedman's 2-way analysis of variance [warbler versus microhabitat class—i.e., natal versus novel—with different microhabitats treated as multiple observations per cell; $\chi^2 = 13.9$; degrees of freedom (d.f.) = 1; $n = 90$; $P < 0.001$]. This greater latency must be a result of aversion to feeding at novel microhabitats.

The consecutive presentation of the two groups of microhabitats does not appear to have contributed to the decreased latency at the natal microhabitats. A previous series of experiments (14) presenting 15 microhabitats to chestnut-sided warblers over a shorter time period produced no increased speed of feeding in later trials. If feeding latency decreases on repeated presentation of microhabitats, one would expect a negative correlation between the order of presentation and feeding time within the blocks of 8 microhabitats; in fact, I found a weakly positive relationship, indicating that birds fed slightly more slowly on later trials; the mean Spearmann rank coefficients for the five birds were 0.20 (±0.90 SEM) for novel and 0.14 (±0.07 SEM) for the natal microhabitats.

Experiment 2. All five birds fed more frequently at the natal microhabitats (60% of the total visits, $\chi^2 = 18.5$; d.f. = 1; $n = 420$; $P < 0.001$). Individuals fed from the natal microhabitats on 56–75% of their total visits (Table 2). I conducted a 2-way analysis of variance using microhabitat class (i.e., natal versus novel) versus individual bird, with different microhabitats within each cell. The results of this analysis indicate that the variation in the number of visits between birds was not significant ($F_{4,50} = 1.46$), nor was the interaction between bird and microhabitat type ($F_{4,50} = 0.23$), but the variation between microhabitat class was significant ($F_{1,50} = 5.54$; $P < 0.05$). This performance was stable over 100 trials; 65% of all feeding visits were made to natal microhabitats during trials 1–25, and 63% of feeding visits were to natal microhabitats for trials 75–100. When I summed visits of all birds, the six natal microhabitats were visited for feeding an average of 42.6 times (±6.0 SEM) versus 27.6 times (±8.4 SEM) for the novel microhabitat (Student's t test = 1.50; one-tailed test; $P < 0.10$). Despite considerable variation in feeding rate at microhabitats within the novel and natal

Table 1. Time to feeding at microhabitats presented in experiment 1

	Warbler no.					Median time
	1	2	3	4	5	
Natal microhabitat						
Easter grass	120	nf	120	0	30	120
Coconut	nf	nf	320	70	120	320
Vine tangle	nf	380	330	220	510	380
Moss	180	nf	120	0	20	120
Box	480	nf	nf	450	105	480
Parasol	150	nf	350	60	420	350
Palm	nf	nf	60	60	nf	nf
D. compacta	40	nf	130	120	nf	130
Median time	330	nf	225	65	270	330
Novel microhabitat						
Bamboo	nf	nf	190	nf	510	nf
Dead leaf	1158	nf	210	150	nf	1158
Sponge	nf	nf	nf	nf	nf	nf
Pipe cleaner	nf	nf	nf	nf	nf	nf
Tube	820	nf	nf	nf	nf	nf
Holly	nf	nf	1150	nf	750	nf
Fern	600	780	nf	160	nf	780
D. marginata	nf	nf	nf	nf	nf	nf
Median time	nf	nf	nf	nf	nf	nf

Times are in sec. nf, No feeding.

Table 2. Number of trails during which a microhabitat was visited in experiment 2

	Warbler no.					Total
	1	2	3	4	5	
Natal microhabitat						
Easter grass	9	7	4	9	12	41
Coconut	11	5	8	13	9	46
Vine tangle	15	14	13	12	9	63
Moss	12	10	13	10	7	52
Box	5	6	5	4	1	21
Parasol	11	2	2	7	10	32
Total	63	44	45	55	48	256
Novel microhabitat						
Bamboo	16	7	8	10	14	55
Dead leaf	4	1	7	5	6	23
Sponge	15	0	0	22	2	39
Pipe cleaner	0	0	0	0	0	0
Tube	1	0	4	0	5	10
Holly	12	5	9	3	10	39
Total	48	13	28	40	37	166

classes (perhaps reflecting innate biases) an overall preference for natal microhabitats was demonstrated.

DISCUSSION

The first experiment demonstrated a difference in the initial aversion to feeding at novel versus natal microhabitats. This alone might suffice to discourage further exploration of unfamiliar foraging sites. In addition, the second experiment showed that the warblers prefer to feed at the natal microhabitats, and this bias was stable despite repeated exposure to the novel microhabitats in the replicate trials. The effect persisted for at least 4 months, long enough to influence habitat selection of wintering migrant birds.

Since the experimental microhabitats were randomly assigned to either the novel or natal class, the decreased aversion and increased preference to feed at the natal microhabitats is probably related to the early exploratory experience rather than to any intrinsic feature of the objects. While preferences can be associated with any specific microhabitat in either the natal or novel sets, the significantly greater preference for the entire set of natal microhabitats is most parsimoniously attributed to an emergent property of that set (i.e., familiarity) rather than to any fortuitous preference to features of one set over another.

The preference that chestnut-sided warblers show for foraging near familiar microhabitats provides a simple mechanism for a common observation: migrants tend to forage at microhabitats during migration and winter that are most similar to those used on their breeding grounds (15, 16). The value of this is probably to maintain migrants foraging in situations to which they are best adapted and most practiced, while decreasing the amount of potentially dangerous exploration in predator-rich tropical forests. I do not suggest that this process of familiarization occurs to the exclusion of associative learning; along with innate preferences, early familiarization may determine the range of resources and microhabitats for which trial-and-error learning can occur.

Neophobia itself may vary in an ecologically important manner. The degree of neophobia varies considerably between *Dendroica* warblers (13, 17). The bay-breasted warbler (*Dendroica castanea*), for example, winters in the same forests as the chestnut-sided warbler in Panama, and it is a more generalized and plastic forager (14). In the laboratory, immature bay-breasted warblers are much less hesitant in feeding at novel microhabitats than are chestnut-sided warblers. The intensity of neophobia may contribute to the degree of foraging specialization in the non-breeding foraging niche of migrant birds.

I am indebted to J. Dein, E. S. Morton, and particularly J. Gradwohl for help and advice in obtaining, raising, and maintaining warblers. J. Gradwohl, E. S. Morton, R. Mumme, K. Redford, E. Reese, J. M. N. Smith, and D. Winkler commented on earlier drafts. The manuscript was prepared by Teresa Cummings. The research was supported by postdoctoral fellowships from the Smithsonian Institution and Friends of the National Zoo.

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