DEVELOPMENT OF DEAD LEAF FORAGING IN A TROPICAL MIGRANT WARBLER[1]

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Abstract. The Worm-eating Warbler (*Helmitheros vermivorus*), a Neotropical migrant bird, specializes during the nonbreeding season in searching dead curled leaves that hang in the understory of tropical forest. How such a specialization might develop in individual warblers was investigated in an experimental study of hand-raised birds. In these experiments I measured the preference that juvenile warblers showed in visiting various microhabitats. The experiments produced the following results. (1) Juvenile warblers, prior to any self feeding, showed a highly stereotypic ranking of preference for exploring different "microhabitats," visiting dead leaf clusters nearly three times as frequently as the next most preferred microhabitat types. Such a strong stereotyped order of preference was not found in similar experiments using the ecologically less specialized Carolina Chickadee (*Parus carolinensis*). (2) The same individual Worm-eating Warblers showed consistent preferences for visiting certain microhabitats at the age when they would normally be arriving in the tropics. However, dead curled leaves were no longer strongly preferred over other foliage types. (3) With other factors held constant, Worm-eating Warblers spent significantly more time manipulating curled versus uncurled foliage, but did not respond to either texture or color differences between live and dead leaves. (4) Worm-eating Warblers spent over half of their active time manipulating substrates, particularly foliage; this activity varied little among birds and among experiments and was also not extinguishable through elimination of food reinforcement. (5) Preference for a particular foliage type (including dead leaves) increased with positive reinforcement with food. These results suggest that young Worm-eating Warblers enter the world with a rigidly determined preference for dead leaves during the period of unreinforced exploration. I suggest that this preference is relaxed when birds are self-feeding because, with their highly manipulative behavior, they can readily track changes in abundance of dead-leaf and live-leaf arthropods. In this case, a consistent and apparently species-typical foraging preference for dead curled leaves appears to be learned.

Key words: foraging specialization; Helmitheros; migrant bird; ontogeny of behavior; Parulinae; stereotypy; Worm-eating Warbler.

INTRODUCTION

Migrant birds encounter major changes in habitat on an annual basis. Some migrants are quite specialized in their foraging site selection in tropical habitats, even though their natal experience is in temperate woodlands. How does such foraging specialization develop in young birds during their first winter? Is it influenced by early learning? Is it based on some innate responses to particular habitat features, or does it result from exploration and trial-and-error learning? The determination of the relative role of these factors will allow the evaluation of the degree of foraging plasticity (Morse 1980).

The Worm-eating Warbler (*Helmitheros vermivorus*) has been widely reported in the nonbreeding season to be a specialist at searching for arthropods in aerial leaf litter (dead curled leaves that hang suspended from forest understory plants; Willis 1960, Lack

and Lack 1972, Rappole and Warner 1980). Visits to dead leaves comprised approximately 75–80% of the total visits and foraging time of Worm-eating Warblers at widely scattered localities in Jamaica, Belize, and Dominican Republic (Greenberg 1987). This specialization is shared by a number of resident species in Central and South America, particularly in the genera *Philydor, Myrmotherula, Automolus,* and *Thryothorus* (Gradwohl and Greenberg 1984, Remsen and Parker 1984). During the breeding season Worm-eating Warblers forage primarily by gleaning live foliage (Greenberg 1987, Bennett 1980). The shift from live leaf foraging during the breeding season to dead leaf foraging during winter is associated with a ten-fold greater relative biomass of arthropods in dead versus live leaves on a per leaf basis (Greenberg 1987).

Experimental evidence suggests that several processes influence the development of foraging site specialization in insectivorous birds. (1) Innate responses can predispose birds to be attracted to particular habitat features, such as foliage type, even in the absence

of prior reinforcement (Klopfer 1963, Partridge 1974). (2) Early experience can influence the habitat or foraging site selection of older birds (Klopfer 1965, Gluck 1984, Greenberg 1984a). Finally, (3) birds can restrict their foraging preferences through associative learning, concentrating on foraging sites that give them the highest return. Although a number of studies have demonstrated the ability of wild insectivorous birds to learn the location of food (Smith and Dawkins 1971, Alcock 1973, Smith and Sweatman 1974, Zach and Falls 1976), only a few have shown that birds can learn particular habitat features (e.g., foliage type and leaf damage) as cues (Heinrich and Collins 1983, Greenberg 1985). Birds can solve a wide range of visual discrimination and more complex learning problems (Sutherland and MacKintosh 1971).

Each of the above processes acts to promote foraging specialization, but they may vary in the permanence and lability that they impose on birds' foraging decisions. Curiosity and exploratory behavior (i.e., the tendency to investigate novel or previously unreinforced stimuli; Glickman and Sroges 1966) provide a creative force counteracting the tendency towards increasingly specialized foraging. Exploratory behavior has been virtually ignored as a subject for study in wild birds (but see Smith 1973).

To examine how dead leaf foraging develops in individual Worm-eating Warblers, I examined the responses of naive hand-raised Worm-eating Warblers to a set of experimental "microhabitats" (natural or artificial objects each of which approximated the size of a dead leaf cluster or a spray of foliage); all microhabitats presented in a set were matched in accessibility and in the presence or absence of food reinforcement. The microhabitats varied in intrinsic morphology and in their familiarity to the warblers. The following questions were asked both of exploratory juveniles (birds prior to the age of self-feeding) and of immatures at the age when they should be arriving on their wintering range: Do the warblers show a consistent ranking of preference for investigating the different microhabitats in the absence of differential reinforcement? Do the warblers show any tendency to prefer to visit familiar vs. novel microhabitats? What is the pattern of exploratory behavior in the absence of food reinforcement? Do warblers respond to particular leaf features by increasing their exploratory behavior? Can warblers learn to associate particular microhabitats with food?

Materials and Methods

Experiment 1: microhabitat exploration in juvenile Worm-eating Warblers

The purpose of this experiment was to observe any bias that juveniles might exhibit in exploratory and manipulative behavior under conditions where various microhabitats were equally accessible and juveniles were unrewarded by food.

I made 16 experimental microhabitats, some constructed of natural and some of synthetic materials, and all matched for overall size. Prior to the experiments each of the microhabitats was assigned to one of two groups randomly, with the constraint that each group had three foliage types; to each group was added a set of 10 (20 × 15 cm) dead curled chestnut oak (*Quercus prinus*) leaves. Oak leaves comprise much of the aerial leaf litter on the birds' breeding range (Greenberg 1987) and also are typical in size and shape for tropical dead curled leaves.

The group 1 microhabitats consisted of: Beech (*Fagus grandifolia*), 20–25 cm spray of 7–10 fresh green leaves; Vine Tangle, 20 cm diameter twisted wreath of ivy (*Hedera helix*); Box, 30 × 15 × 15 cm cardboard box open at one end and covered on outer and inner surfaces with black construction paper, glued so that the edges were free from the box surfaces; Big Leaves, 30 cm cluster of 6–8 10 × 15 cm green vinyl leaves; Bark, 25 × 15 cm slab of 5 cm thick oak bark with deep furrows; Tube, 30 × 10 cm open tube of brown laminated cardboard; Easter Grass, 25 × 15 cm of green pinkish plastic excelsior; Chenille Stems, eight 15-cm yellow pipe cleaners in a Plasticine base. The group 2 microhabitats included: Holly, 25-cm spray of 10–15 leaves of *Ilex*; Bamboo, 25 × 15 cm spray of Bamboo foliage (*Pseudosasa japonica*); Thin Leaves, 30-cm cluster of 6–8 8 × 20 cm vinyl leaves; Spanish Moss, 20-cm mound of Spanish Moss (*Tillandsia usneoides*), Orange Leaves, cluster of five 5 × 10 cm orange construction paper leaves connected to a Plasticine base with 5-cm orange pipe cleaners; White Moss, 20 cm diameter mound of white excelsior; Coconut, a hollow half of a 10 cm diameter coconut suspended from a wire; Sponge, 12 × 5 × 5 cm block of green artificial sponge.

During the summers of 1983–1984 I collected eight nestling Worm-eating Warblers from five broods. The birds were divided between two experimental groups; each was exposed to one of the sets of microhabitats. Within each group two birds were reared together and two in isolation. The nine microhabitats in each group (eight experimental ones plus the cluster of chestnut oak leaves) were randomly placed at set positions in each 2 × 2 × 1.5 m aviary (initial order was randomly selected for each of the three aviaries used for each group of microhabitats), and each day the microhabitats were rotated clockwise by one position (Fig. 1).

The warblers were introduced to the aviaries from smaller rearing cages (1.0 × 0.6 × 0.4 m) at 8–10 d after fledging and were exposed to the microhabitats for three complete rotations (27 d). The warblers were either hand fed or, after 20 d out of the nest, were offered food from a feeding station at the corner of the aviary farthest from the experimental microhabitats. They were kept on a 14:10 light : dark artificial light regime throughout the rearing process. Individual members of a team of 7–15 observers sat quietly in
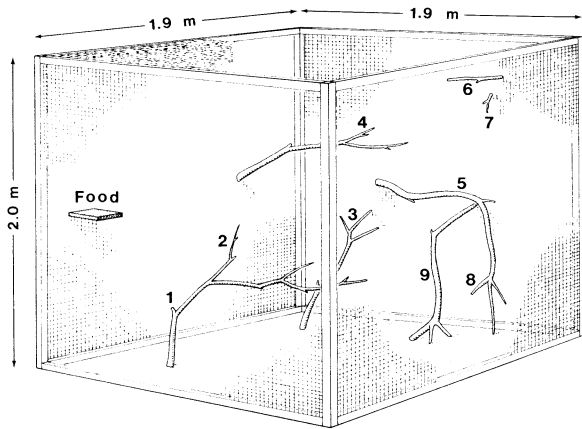
FIG. 1. A diagram of the aviary setup for Experiment 1. Numbers denote stations where microhabitats were placed. Microhabitats were shifted daily one station in the direction of increasingly large numbers (except the shift from station 9 to 1).

front of the aviary (the hand-raised birds showed no fear of people, so a blind was unnecessary) and recorded the number of visits to different microhabitats for 6–9 h/d for each warbler. An individual visit consisted of movement to an object that resulted in pecking, probing, or intense peering into a surface of the microhabitat. Two consecutive visits to the same microhabitat were counted only when the warbler moved to another object or to the cage floor in the interim. Although the number of hours of observation per day varied among birds, depending on the size of the observation team, each bird was watched for a constant time period per day, and, therefore, there should have been no systematic bias towards gathering data from a particular age or spatial configuration of microhabitats. Since birds varied greatly in their rate of behavioral development, I standardized the analysis to include data from the first completed rotation after we recorded 400 visits from a bird.

Experiment 2: a comparison of microhabitat exploration by juveniles of a generalist insectivore

This experiment further tested the hypothesis that the stereotyped preferences in exploratory visits in juvenile Worm-eating Warblers are related to their specialized foraging behavior as adults (in the nonbreeding season). I examined the juvenile exploratory behavior in the Carolina Chickadee (*Parus carolinensis*), a species that breeds sympatrically with Worm-eating Warblers. Chickadees were selected for comparison because of their highly generalized foraging behavior and adaptability (Robinson and Holmes 1982, Heinrich and Collins 1983). In addition, chickadees forage from dead leaves on occasion, but do not specialize in searching aerial leaf litter for long periods (Remsen and Parker 1984, Greenberg 1987).

The same microhabitat types were presented as were used in Experiment 1. In 1985, 10 chickadee nestlings were collected from two broods and hand-raised in a covered incubator until they were $\approx$18 d old. The juveniles spent 2 d in rearing cages and were then released into experimental flight cages. These were the same aviaries used in the experiments with the warblers. The experiment was identical in most respects to Experiment 1, except that the chickadees were reared in three groups (3, 3, and 4 individuals), which were all presented with group 1 microhabitats. The chickadees were all independent by the end of two complete rotations of the microhabitats (18 d).

Experiment 3: microhabitat preference in immature warblers

After the period of juvenile exploration I examined preferences for visiting microhabitats in 12–16 wk old warblers, at the age when they should be arriving on their wintering range. In addition, I compared their responses to microhabitats with which they were raised (natal) vs. those with which they had no prior experience (novel).

I presented the same microhabitats that were used in Experiment 1. In addition, I introduced a microhabitat known as Hemlock, a 25-cm spray of hemlock (*Tsuga canadensis*) foliage, a microhabitat not previously experienced by the hand-reared warblers, for comparison to dead leaves, which had been experienced by all warblers.

At 12 wk post-fledging (6 wk after the microhabitats were removed from aviaries) the Worm-eating Warblers were individually presented a choice test among all microhabitats. These tests were conducted in September and October, which corresponds to the arrival time of this species in Mexico (D. Warner, *personal communication*) and Belize (Greenberg 1987). Shortly after the juvenile period (>6 wk) the photoperiod was reduced from 14 h to 12 h. For each trial, three mi-
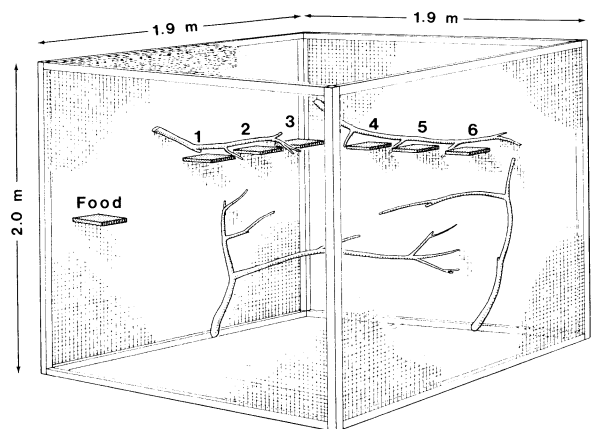

FIG. 2. A diagram of the aviary setup for Experiments 2 and 3. In Experiment 6 only stations 4–6 were used.

crohabitats were randomly selected from each group (see Experiment 1 for lists; Dead Leaves were added to group 1 and Hemlock to group 2) and assigned randomly to one of six stations. The stations were placed halfway up two sides of the rearing aviary (Fig. 2) and each consisted of a small (150-cm²) wooden platform with a natural perch resting on the upper surface. Warblers were placed in the test aviary at least 24 h prior to the experiments and were only removed to allow experiments on other individuals.

The feeding conditions in the experiments varied somewhat among birds: for the first six individuals, small bits of meat mash were placed on the perch near the feeding platforms during the first 50 (out of 150) trials to attract the warblers to the areas where microhabitats were placed. This had proved to be necessary for similar experiments conducted on other warbler species (Greenberg 1984a). A food attractant was apparently not needed for Worm-eating Warblers, however, and for the last two experimental birds run I presented no food reinforcement at all. No differences were observed in the quantity or quality of responses between these individuals and the others. Microhabitats were placed for easy access, within a run all feeding platforms were equally reinforced with food, and the microhabitats themselves never contained food.

Trials lasted 5 min and were run consecutively in two equal blocks, a total of 10–15 trials/d. Trial blocks were separated by at least 1 h. As in Experiment 1 the major measure of preference was the frequency of visits (see Experiment 1). Occasionally the warblers became alarmed and "froze," bathed, or fed for long periods. Any trial during which no exploratory activity was recorded was not included in the final analysis. Although all of the birds received the same program of 150 trials, the number of actual trials on which they performed differed among individuals (range: 121–140). To analyze the data I computed the number of visits to a microhabitat per presentation for trials in which a warbler visited any microhabitat. To compare individuals with different activity levels I divided each microhabitat score by the sum of the number of visits/trial of exposure to all microhabitats for a given bird; I refer to this value as the Standard Visitation Score (SVS; see Fig. 3 legend for calculation). One such score was calculated for each warbler–microhabitat combination.

Experiment 4: response to potential foliage cues

In this experiment (conducted in October and November) I examined in more detail the responses of Worm-eating Warblers to specific differences between dead–curled and live leaves. By proceeding in a hierarchical manner, I was able to examine the effect of different potential cues one at a time. All of the experiments were conducted on beech foliage. I initially compared the response of warblers to "fresh" vs. "green
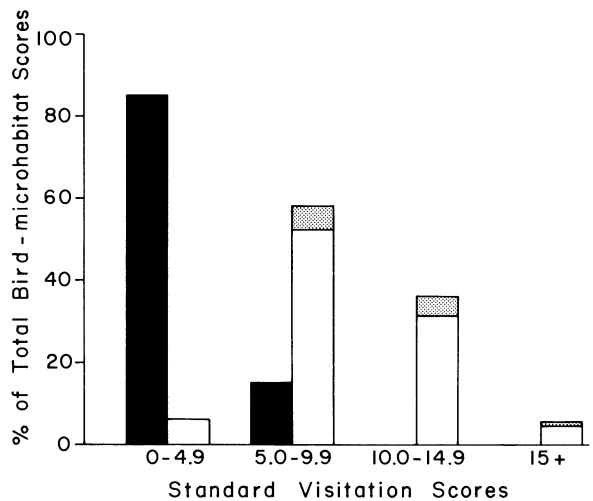

FIG. 3. A histogram of Standard Visitation Scores (SVS) for visits to foliage (open bars) and nonfoliage (solid bars) pooled for all eight warblers in Experiment 3. Stippled areas indicate proportion of SVS for foliage composed of dead leaves. The SVS_i is calculated as follows:

$$V_i/T_i \div \sum_i^j V_i/T_i,$$

where V_i is the total visits to microhabitat i, T_i is the total number of trials in which microhabitat i was presented, and j is the total number of microhabitats (18). One SVS is calculated for each bird–microhabitat combination. Sample size is 64 for foliage (8 birds × 8 microhabitats) and 80 for nonfoliage (8 × 10).

flat dried" sprays of leaves; I then examined the responses to "green flat dried" vs. "green curled" leaves; and finally contrasted reactions to "green curled" and "brown curled" leaves. In this way I examined the preference of warblers for the texture, curl, and color associated with fresh vs. dead–curled foliage.

For each comparison, sprays of foliage containing 10 leaves were selected from each tree and randomly assigned to each treatment group. "Fresh leaves" were cut immediately before experiments; "Green Flat Dried" leaves were placed in a plant press for 2 d prior to the experiment; "Green Curled" leaves were dried rapidly indoors; and "Brown Curled" leaves were allowed to dry on the tree (as part of natural fall color change). A much larger number of sprays was selected and prepared than the six required for each trial (three sprays of each of two types), and these alternates were rotated often, as the warblers damaged the leaves. These alternations also minimize the degree to which warblers could identify one particular spray.

Six sprays used in a trial ware assigned random locations among the six experimental platforms. For this experiment no food was presented at the experimental platform, but meat mash and mealworms were provided ad lib at the regular feeding station at the front of the aviary.

For each of the three comparisons (fresh vs dry; flat

TABLE 1. Percentage of visits to different microhabitats by two groups of four juvenile captive-raised Worm-eating Warblers.

	Group 1				
	A	B	C	D	$\bar{X}$
No. visits	648	993	770	800	
Dead Leaves*	22.6	37.4	32.8	29.2	30.5
Beech*	13.4	12.3	17.0	21.2	16.0
Vine Tangle*	15.4	14.9	19.4	12.0	15.4
Box	12.6	7.4	12.2	8.0	10.1
Big Leaves*	10.8	10.5	7.9	10.5	9.9
Bark	7.2	5.5	2.6	7.8	5.8
Tube	7.2	6.7	3.5	5.4	5.7
Easter Grass	5.4	3.5	3.2	5.4	4.3
Chenille Stems	4.8	1.7	1.3	0.8	2.2

	Group 2				
	E	F	G	H	$\bar{X}$
No. visits	503	605	431	842	
Dead Leaves*	32.8	35.2	33.8	24.5	32.2
Holly*	9.1	14.5	17.6	9.3	12.6
Bamboo*	11.9	10.2	8.3	17.8	12.0
Thin Leaves*	12.5	12.6	10.7	10.4	11.6
Spanish Moss	10.9	5.6	6.4	10.3	8.9
Orange Leaves	8.3	7.9	7.6	8.3	8.0
White Moss	5.2	4.8	5.8	8.1	5.3
Coconut	5.2	5.0	5.1	4.4	4.9
Sponge	3.8	4.1	4.4	6.8	4.1

* Foliage types.

vs. curled; green vs. brown) I conducted 25–30 5-min trials in blocks of 5–10 trials/d. Variation in trial number for the experiments was consistent for an entire comparison and was based on time constraints for lab work.

Experiment 5: midwinter retest of preference for dead curled vs. other foliage types

I conducted a retest of visitation frequency to several foliage types to determine if a preference for dead curled leaves might not be more pronounced after the initial fall period. I compared the response of the Worm-eating Warblers to dead leaves, vine tangle, and beech foliage, the three most preferred microhabitats in Experiment 2. I conducted this experiment in the second winter of the study (1984–1985) on birds raised during the previous summer (1984), and only on the four birds that had previously preferred either vine tangle or beech over dead leaves in Experiment 2. If a developmental change within winter is important, then the preference in these individuals should have shifted to dead leaves.

The three microhabitats were similar to those described for Experiment 1, except that I substituted dried green beech leaves (fresh leaves were no longer available). This substitution is justifiable because in Experiment 3 warblers consistently failed to show any preference for or behave differently in response to dried vs. fresh flat green leaves.

This experiment was conducted from 23 December 1984 to 5 January 1985. The birds had all been experiencing only 11.5 h of daylight since mid-October.

For each 5-min trial two clumps of each microhabitat were put in random locations at the six platforms. I conducted 25 trials in five 5-trial blocks over 2 d.

Experiment 6: the effect of food reinforcement on visitation preference among the most preferred foliage types

The experiments were run on three warblers within a few weeks of Experiment 4 with the same foliage types. The placement of each of the three microhabitats at one of three of the experimental platforms located in the rear of the experimental aviary was randomized for each trial. After placement the warblers were allowed to approach the microhabitats. For the initial phase of the experiment (trials 1–150), if the warblers approached Beech or Vine Tangle the other microhabitats were removed and the selected foliage clump was left on its platform for 90 s. If the warbler approached the dead leaves, then a small lump of meat mash (a preferred food) was placed under the leaves and the warbler was allowed to locate the food and feed. Each bird was deprived of food for 3 h prior to any trials. Trials were then presented in three blocks of 10 separated by 45 min. The initial phase was terminated when the warblers reached a level of performance (50% visit to dead leaves in first 5 trials of each trial block) that was stable for ≈100 trials. After this the warblers were presented 40 trials similar to those of the initial phase except that visits to Vine Tangle were rewarded.

RESULTS AND DISCUSSION

Experiment 1: microhabitat exploration in juvenile Worm-eating Warblers

All eight birds visited dead curled leaves much more often than any other microhabitat (Table 1): such visits made up 23–37% of the total, a percentage far greater than the random expected value of 11%. Each individual visited dead leaves more often than the next most preferred microhabitats (x^2 values ranged from 10.5 to 96.4; df = 1, $P < .001$ in each case). Dead leaves were followed in preference by various types of foliage. The preference for dead leaves was stable through the entire juvenile period; for example, visits to dead leaves comprised 28.8% of the visits after only one rotation of microhabitats was completed, and 31.0% of total visits.

Warblers showed great consistency in how they ranked (by number of visits) the nine microhabitats. Kendall's coefficient of concordance (W) was 0.96 for group 1 and 0.89 for group 2 (x^2 values: 30.8 and 28.9, df = 8, $P < .001$). This high degree of agreement was not an artifact of some of the birds being raised in the same aviaries: the mean Spearman rank correlation coefficient, r_s, for solitary birds vs. other birds in the same experimental group was 0.92 (SE 0.02, $N = 10$) and the mean value for r_s between birds reared in the same aviary was 0.92 ($N = 2$).

TABLE 2. The percentage of visits by hand-raised Carolina Chickadees to nine microhabitats during rearing (Experiment 2).

	Aviary 1			Aviary 2				Aviary 3			
	B	BY	Y	BW	R	OW	G	O	B	RW	$\bar{X}$
No. visits	635	583	627	544	562	749	483	415	422	434	
Bark	19.6	17.0	19.8	13.8	19.9	22.0	16.3	23.1	18.7	20.2	17.2
Box	14.5	11.7	10.8	15.6	18.9	13.2	18.2	15.9	16.0	14.5	15.6
Tube	16.2	16.8	16.6	15.3	12.6	9.9	8.8	12.9	13.7	13.8	13.9
Vine Tangle	10.4	7.3	5.9	13.8	19.9	22.0	16.3	16.6	16.1	13.6	13.8
Beech	6.5	5.0	8.9	9.2	6.9	12.1	10.7	12.5	13.9	13.8	10.0
Dead Leaves	11.3	11.7	10.8	6.8	8.1	7.3	6.2	7.7	9.0	10.5	9.9
Big Leaves	9.1	12.3	12.0	7.7	8.0	9.1	13.5	2.9	4.3	9.0	8.7
Chenille	6.5	6.5	6.7	9.1	6.6	7.5	7.9	8.7	7.3	2.3	6.8
Easter Grass	5.8	6.3	6.2	7.9	0.5	8.1	8.4	0.5	0.7	2.0	4.4

The overall consistent ranking suggests that the microhabitats varied in features upon which curious young Worm-eating Warblers based their choices, and that dead curled leaves were at the preferred end of the gradient (of those encountered). The Worm-eating Warblers spent most of their time probing into holes and crevices or prying between sheets of material. The order of preference probably reflects variation in surface structure in the microhabitats. For example, all of the foliage types provided abundant interfaces between leaf surfaces, which would explain the warblers' overall preference for these microhabitats. Dead curled leaves, however, have additional crevices formed by the curling of the leaves. Of the nonfoliage microhabitats (in group 1), Box, Bark, and Tube, each of which provided thin laminated sheets of material or ridges for prying, were preferred over all of the other more moss-like material (which the warblers tended to pull). In group 2, the two microhabitats with the lowest surface heterogeneity, Coconut and Sponge, were the least preferred in the nonfoliage class.

Experiment 2: a comparison of microhabitat exploration by a generalist insectivore

Dead curled leaves were not the preferred microhabitat among the chickadees (Table 2). The mean percentage visitation to dead leaves was 10%, which is considerably less than the corresponding value for Worm-eating Warblers (31%). Because aviary-mates showed a strong correlation in visitation preference, I tested the difference between chickadees and warblers using the mean value for each cage and found them to differ significantly (Mann-Whitney $U_{3,3} = 0$, $P < .05$). Overall, the preferences of Worm-eating Warblers and chickadees were poorly correlated; the Spearman rank correlation coefficient (r_s) between mean values for the two species was 0.29 ($P > .05$). Chickadees, on the average, preferred to visit Bark, Box, and Tube over the foliage microhabitats, a pattern opposite that found in the warblers.

Consistency of preferences among chickadees reared together was quite high: the values of Kendall's W were 0.76, 0.89, and 0.95 for the three flight cages ($P < .01$ in all cases). The overall W was lower (0.62), however,

because the concordance among birds reared apart was low (0.45, based on the mean value for each aviary). Also, the within-individual diversity of visitation was significantly higher for chickadees (Simpson Index, $\bar{X} \pm$ SE: 6.9 $\pm$ 0.07) than for warblers (5.4 $\pm$ 0.06; $U_{10,4} = 0$, $P < .01$).

These results support the idea that the stereotyped preferences found in juvenile Worm-eating Warblers are related to the specialized foraging behavior of adults. Warblers preferred dead leaves over live foliage and live foliage over other microhabitats, whereas chickadees showed weaker preference for certain nonfoliage microhabitats. Chickadees showed less specialization within individuals for any of the microhabitats presented in the experiment and more variation among individuals reared apart from each other. Chickadees reared together showed relatively high interindividual correlation, which may reflect a great potential for social facilitation in determining exploratory preferences. Warblers had such highly consistent preferences when
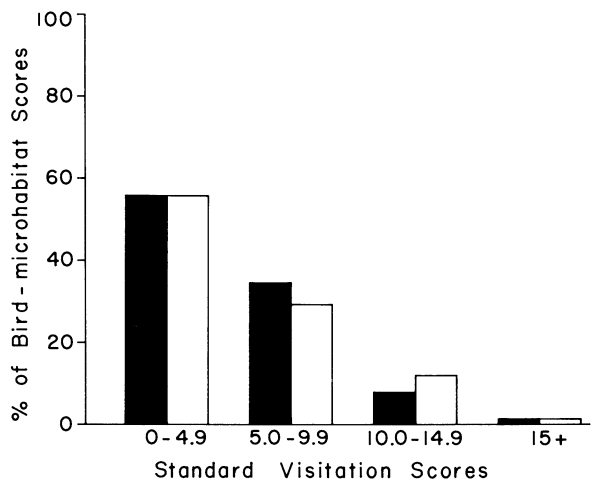

FIG. 4. Histogram of SVS (see caption for Fig. 3) for novel and natal microhabitats pooled for all eight birds. Dark bars indicate responses to novel microhabitats (e.g., group 1 warblers to group 2 microhabitats); light bars indicate responses to natal microhabitats (e.g., group 1 warblers to group 1 microhabitats). Total sample size for each class of microhabitats is 64 (8 warblers × 8 microhabitats).

TABLE 3. Response of Worm-eating Warblers to fresh vs. dried (flat green) beech leaves, in 5-min trials.

Bird	Visits		Manipulation time (s)		Trials in which dried leaves preferred*		Wilcoxon T
	% to dried	n	% on dried	n	%	n	
A	55	118	28	4683	22	27	NS
B	50	100	52	4791	56	23	NS
C	51	75	54	2181	50	22	NS
D	44	131	55	6100	54	28	NS
E	56	131	62	1453	60	23	NS
F	44	141	25	5462	37	30	NS
G	54	125	55	4837	53	30	NS
H	48	116	46	5100	54	28	NS
Mean ± SE	50 ± 2		47 ± 5		48 ± 4		
Wilcoxon T	NS		NS		NS		

* Preference based on seconds spent at foliage type per trial; sample size is the number of trials in which a preference could be determined. If values for the two foliage types fell within 5 s of each other no preference was assigned.

reared in isolation that for them the role of social facilitation appears to be much more limited.

Experiment 3: microhabitat preference in immature warblers

The Worm-eating Warblers strongly preferred to visit foliage, even artificial foliage, over the other microhabitats (Fig. 3, individual SVS are listed in the Appendix). The mean SVS (±SE) for natural foliage was 9.7 ± 0.45, for artificial foliage 7.0 ± 0.66, and for other microhabitats 2.8 ± 0.23; all differences are significant (Mann-Whitney U tests, P < .001). However, the foliage type that was preferred varied considerably among individuals. In contrast to their behavior during the fledgling period, these immature Worm-eating Warblers showed neither a strong nor a consistent preference for dead curled leaves. Although the overall SVS for dead leaves was higher than that for each of the other microhabitats, it was only the highest for three of the eight individuals. However, there was significant variation in preference for natural foliage types (Friedman's two-way ANOVA, birds vs. foliage type, $\chi^2 = 16$, P < .0001).

Overall, the Worm-eating Warblers showed a consistent ranking of microhabitats (Kendall's W = 0.69

within treatment groups and 0.73 overall, P < .001). However, the r_s values within groups averaged significantly lower than the r_s values within groups from Experiment 1 ($U = 7$, $n_1 = 12$, $n_2 = 12$, P < .001). The mean Spearman rank correlation of natal microhabitats in Experiments 1 vs. 2 was quite similar within warblers ($\bar{X} \pm$ SE: 0.77 ± 0.03, P < .05).

To examine the response to natal vs. "novel" microhabitats (novel microhabitats were defined as those to which the warblers had not been exposed as juveniles), I examined the distribution of the SVS among the 16 microhabitats for the trials in which they were novel microhabitats vs. the trials in which they were natal microhabitats (dead leaves and hemlock leaves were not included since the latter was always novel and the former was always natal). A detectable effect of early experience should have produced a difference in the two distributions even though the exact same microhabitats were involved. However, the two distributions are very similar (Fig. 4), and are not significantly different overall (Kolmogorov-Smirnov statistic = 0.06, P > .05) nor in their means (4.7 vs. 4.9). I conducted a two-way ANOVA to examine the relative effect of microhabitat type and familiarity on visitation rate (SVS). Microhabitat type accounted for

TABLE 4. The response of warblers to curled vs. uncurled (green–dried) beech leaves, in 5-min trials.*

Bird	Visits		Manipulation time (s)		Trials in which curled leaves preferred		Wilcoxon T
	% to curled	n	% on curled	n	%	n	
A	41	80	43	2185	47	19	NS
B	60	110	66	2504	80	20	P < .05
C	54	57	60	3789	55	22	NS
D	58	167	53	4607	64	28	NS
E	60	93	77	2900	84	19	P < .005
F	61	97	76	3298	75	20	P < .005
G	63	102	73	2325	89	19	P < .005
H	62	143	70	6035	72	25	P < .05
Mean ± SE	57 ± 2.5		65 ± 4.2		71 ± 5.1		
Wilcoxon T	P < .025		P < .01		P < .001		

* See footnote for Table 3.

TABLE 5. Response of warblers to dried, green curled leaves vs. dried, brown curled leaves, in 5-min trials.*

Bird	Visits % to brown	n	Manipulation time (s) % on brown	n	Trials in which brown leaves preferred %	n	Wilcoxon T
A	47	81	31	3323	16	19	$P < .01$
C	60	67	55	3323	60	20	NS
E	45	95	51	2721	47	19	NS
F	51	84	54	2962	55	20	NS
G	48	71	48	2014	53	19	NS
Mean ± SE	49 ± 2		48 ± 4		46 ± 8		
Wilcoxon T	NS		NS		NS		

* See footnote for Table 3.

71% of the total variance ($F_{15,112} = 19.3$, $P < .001$); familiarity explained 0.3% of the variance ($F_{1,112} = 1.0$, $P = .38$); and there was no significant interaction.

It could be argued that warblers can imprint on certain microhabitats more readily than others, as appears to be true for two other forms of early learning in birds: song learning (Kroodsma 1982) and filial imprinting (Bateson 1979). To examine this, I analyzed the percentage of visitation to natal vs. novel natural foliage types, since these microhabitats were the most preferred and are the most species-typical in the wild. I found a preference for visiting foliage types that were natal, although the magnitude of the preference was small (mean SVS was 10.6 vs. 9, median 11.2 vs. 7.1; Mann Whitney U test: $T = 1.47$, n = 32, $P = .075$).

Experiment 4: response to potential foliage cues

Worm-eating Warblers showed no consistent preference for dried vs. fresh flat beech foliage ($\bar{X} = 50\%$ of visits were to dried leaves; Table 3), nor for brown vs. green curled foliage ($\bar{X} = 49\%$ of visits to brown leaves; Table 5). But they did show a significant preference for curled vs. uncurled dried leaves ($\bar{X} = 57\%$ of visits to curled leaves; overall Wilcoxon $T = 3$, $n = 8$ birds, $P < .025$; Table 4). The preference based on the proportion of trials during which more time was spent at curled vs. uncurled leaves was even stronger ($\bar{X} = 71\%$ of trials). In addition, seven of eight birds showed a preference for visiting curled leaves, and for five of them the preference was significant (based on within-bird Wilcoxon test).

TABLE 6. The number of visits to three foliage types during 25-trial simultaneous choice tests in late December and early January.

Warbler	Vine Tangle	Beech	Dead Leaf*	Chi-square
A	60	33	24	20.8 $P < .001$
C	28	35	26	1.0 NS
H	47	33	35	3.0 NS
D	68	48	33	12.1 $P < .01$

* Dead curled chestnut oak leaves as in Experiments 1 and 2.

Experiment 5: midwinter retest for preference of dead leaves vs. other foliage types

None of the four warblers tested visited the dead curled leaves more than the other two foliage types (Table 6). Three warblers preferred vine-tangles and one beech leaves. In general their response was similar to that of the fall experiment (Experiment 2) and therefore showed no increase in preference for dead leaves as the winter progressed.

Experiment 6: the effect of food reinforcement on visitation to the preferred foliage types

When visits to dead leaves were reinforced with food, the three birds showed the same basic pattern of response (Fig. 5): an increase in visits to dead leaves after three trial blocks (30 trials) that was most strongly expressed in the opening five trials of each block. If these trials alone are analyzed, then all three birds visited dead leaves in ≈50% of the trials. These values are significantly different from the relative frequencies of visitation during the first 30 trials (26%, 20% and 3%; χ^2 range 6.5–25.1, df = 1, $P < .05$) and those in Experiment 5 (20%, 26%, 31%; $\chi^2 = 6.1$–17.1, df = 1, $P < .05$). The reversal was both rapid and strong. Visitation to dead leaves declined from 48% to 5%, from 51% to 28% and from 51% to 5%. This occurred with essentially no identifiable transition period. It appears that the reversal was learned much more rapidly than the initial problem.

I infer from the results of the experiment that Worm-eating Warblers can rapidly learn to associate food with a particular foliage type. The lack of a higher asymptotic performance probably resulted from the Worm-eating Warblers not responding to the experimental stimuli with disinterest when they were not hungry. I suggest that the warblers were searching for food in the earlier trials and responding to preferences for manipulating particular leaf types in later trials. In a similar finding Inglis and Ferguson (1986) reported that Starlings (*Sturnus vulgaris*) continued to forage for prey hidden in covered holes in the presence of easily exploited food in a dish; furthermore, they increased foraging for the hidden prey after they had fed. In the
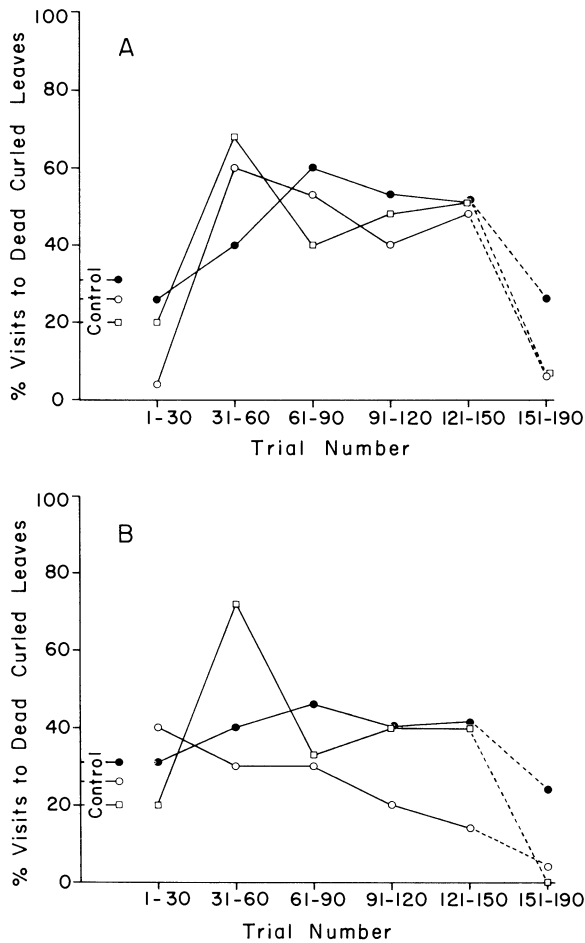
FIG. 5. Percentage visits to dead curled leaves by three warblers in a three-way choice test with vine tangle and beech leaves (each line and symbol denote the performance of one warbler). In Fig. 5A only the responses during the first 5 trials of each 10-trial block are plotted; in Fig. 5B the second 5 trials are shown. For the first 15 trial blocks, visits to dead leaves were rewarded with food. In trial blocks 16–19, vine tangle was reinforced with food. "Controls" are based on the unrewarded visits in Experiment 5 with the same three birds.

wild, reinforcement for pecking at any particular microhabitat is much lower and the energy required to visit a microhabitat much greater. Therefore, free-living warblers may always be operating with a higher feeding motivation than that of my experimental birds.

MANIPULATIVE AND EXPLORATORY BEHAVIOR

One of the most striking features of the performance of Worm-eating Warblers in these experiments was their persistence at manipulating and pecking at the various microhabitats, even under conditions of ad lib food and no reinforcement associated with the experimental objects. The mean time spent manipulating the microhabitats per 300-s trial was 153 s (SE = 15 s) and the correlation coefficient of trial number vs. the

amount of time spent at microhabitats averaged close to zero ($r = -0.0015$). The amount of time spent manipulating objects was consistent among individuals; the F ratio for interindividual variation/within-individual variation (measured in seconds of manipulation per trial) was 0.35 (df = 31, 1122, $P > .05$). When deprived of any specific objects to explore, the birds spent most of their active time pecking at branch tips, probing into holes, and sliding their bills under and gaping at, paper and strapping tape. This intense manipulative behavior was not observed in other species of hand-raised warblers presented similar experimental tasks (Hooded Warblers, *Wilsonia citrinea,* and Chestnut-sided Warblers, *Dendroica pensylvanica;* R. Greenberg, *personal observation).*

THE EFFECTS OF INNATE BIAS, FAMILIARIZATION, ASSOCIATIVE LEARNING AND EXPLORATION ON DEAD LEAF SPECIALIZATION

Innate biases

I define innate biases as those preferences that develop in the absence of any differential reinforcement or experience. Innate biases play several important roles in the development of dead leaf foraging. The hand-raised warblers when young (<6 wk) showed a strong preference for visiting and manipulating dead curled leaves over a variety of other microhabitats (Table 1); this preference occurred in the context of an overall highly consistent response to all microhabitats in terms of preference ranks. Such a stereotyped response was not found in juvenile Carolina Chickadees (Table 2), a less specialized user of aerial leaf litter. When the warblers were at an age when they should be arriving at their tropical wintering grounds (>10 wk), they showed a reduced interindividual consistency in microhabitat preference. Although foliage of all types was visited more frequently than nonfoliage microhabitats, dead leaves were visited more often than other foliage types by only three of the eight birds tested. This lack of a clear preference for dead curled oak leaves was stable through early January (Table 6). The hand-raised warblers showed no preference for visiting brown vs. green, or dried vs. fresh beech leaves, but did show an overall significant preference for curled vs. uncurled leaves, all other factors being equal (Tables 3–5). Therefore, innate biases appear to play a complex, but not omnipotent role in shaping the winter foraging specialization.

Early learning

Unlike Chestnut-sided Warblers (Greenberg 1984a), hand-raised Worm-eating Warblers showed no significant tendency to visit microhabitats experienced as juveniles. However, the Worm-eating Warblers did seem to visit familiar foliage more often than novel foliage. This interspecies difference in response to nov-

elty agrees with field observations that show that the Worm-eating Warblers prefer to forage at dead leaf types (even in the fall observation period), such as large palm and epiphyte rosettes. I found that Chestnut-sided Warblers avoided unusual tropical foliage types (Greenberg 1984*b*), indicating a greater potential role for early learning in this species.

Associative learning

Because hand-raised Worm-eating Warblers showed no strong preference for visiting dead leaves when they were older, the seasonal shift between live and dead leaves may be facilitated by the sampling of changes in resource distributions. Consistent with this, three Worm-eating Warblers tested showed a greater preference for visiting dead leaves when the leaves were reinforced with food.

Curled leaf foraging, however, is the most physically demanding behavior in the foraging repertoire of Worm-eating Warblers, and critical for over-winter survival. If the manipulative behavior of pre-independent young Worm-eating Warblers is practice for adult behavior (as was shown for prey handling in Reed Warblers, *Acrocephalus scirpaceus*; Davies and Green 1976), then this is a period when hanging, gaping, and other maneuvers associated with dead leaf foraging should occur. It is also a time, however, when fledglings are receiving little or no food reinforcement for their behavior and the parents are foraging from live, not dead leaves. I suggest that the need for practice and the lack of any external attractant associated with dead leaves select strongly for an innate preference to manipulate dead leaves when the birds are young. In older birds, this preference can be relaxed since economic factors can direct their attention to dead leaves or away from them to other food sources.

The degree to which adult preferences are innate should depend upon the stability of the resource distribution. The underlying abundance of dead and live leaf arthropods changes too much to select for a stereotypic preference for either microhabitat. On the other hand, leaf curls appear to be productive microhabitats at all times of the year. During winter, leaf curls are usually associated with dead leaves and have large numbers of potential prey. In the breeding season, leaf curls are found commonly on live foliage and have exceedingly high densities of caterpillars. Live-leaf curls represented the microhabitat that provides the greatest success rate per visit for Worm-eating Warblers (Greenberg 1987). It is, therefore, not surprising that the only innate bias found among all immature Worm-eating Warblers was for leaf curl in Experiment 3. The preference, however, was expressed most strongly in amount of time spent manipulating clusters of curled leaves, rather than the number of visits. This suggests that the curls did not act as a strong attractant to the warblers.

Exploratory behavior

Perhaps the most unusual aspect of Worm-eating Warblers is their high level of manipulative and exploratory behavior, particularly compared with other warbler species. This behavior is probably critically linked to the learning mechanism for the development of dead leaf foraging. It is important to contrast the types of cues available to a leaf surface forager vs. an insurface forager (Heinrich and Collins 1983, Gradwohl and Greenberg 1984). Leaf surface arthropods are directly observable, whereas curled-leaf insects remain hidden and must be located by active examination of hiding places and manipulation of crevices and crannies. Such behavior is time-consuming and often difficult to perform, and may be extinguished rapidly in the presence of little food reinforcement. Once lost, these are also the behavior patterns that are least likely to appear spontaneously in response to an increase in abundance of insurface arthropods. To continuously track the relative abundance of insurface and surface arthropods, the exploratory behavior associated with insurface foraging should be relatively impervious to the mechanisms of associative learning. By this logic, the amount of manipulation should be independent of hunger and food search. I suggest that it is the hunger-feeding system that directs Worm-eating Warblers to visit a location and that object exploration maintains the high degree of manipulation at whatever microhabitat is visited. Therefore, exploratory behavior in conjunction with learning allows Worm-eating Warblers to track resource distribution changes associated with moving between habitats.

Glickman and Sroges (1966) suggested that species that need to monitor a range of resources for food should display the greatest amount of "curiosity." However, most of the variation they detected was on rather broad taxonomic or ecological scales (carnivores vs. rodents, omnivores vs. insectivores). Results of this study and other recent observations (Terborgh 1983) suggest, however, that variation in the degree of manipulative behavior may characterize very closely related and ecologically similar species that differ only in the amount of insurface foraging they do.

The adult behavior of the hand-reared Worm-eating Warblers was largely indistinguishable from the exploratory behavior of juveniles both in intensity and in the objects at which this behavior was directed. In other warblers, juvenile exploration and neophilia end abruptly at about 6–8 wk of age (Greenberg 1984*a*). Therefore it is possible that adult manipulative behavior by Worm-eating Warblers is some form of behavioral neoteny.

These experiments provide evidence that even the most specialized foraging behavior may result from a complex interplay of innate bias, exploration, and learning. Innate biases and perhaps early experience appear to set the range of resources that are monitored

for economic benefit through trial-and-error learning. In this species, as well as others specializing on hidden prey, manipulative and exploratory behavior appears to be consistent, unextinguishable and independent of food reinforcement.

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APPENDIX

The *SVS* of the eight Worm-eating Warblers for the 18 microhabitats presented to two different groups of warblers in Experiment 2. (*SVS* = the proportion of total visits, standardized to the number of visits per presentation; see legend for Fig. 3.)

Microhabitat*	Group 1					Group 2					Grand $\bar{X}$
	A	B	C	D	$\bar{X}$	H	G	E	F	$\bar{X}$	
Total visits	494	411	295	324	381	257	292	560	449	389	385
Dead Leaves[1,2]	9.8	9.9	8.6	9.3	9.4	19.2	14.8	11.6	11.2	14.2	11.8
Vine Tangle[1]	11.0	8.9	14.5	12.2	11.7	9.9	11.4	9.3	10.5	10.3	11.0
Beech Leaves[1]	7.8	10.4	13.3	17.0	12.1	10.7	4.2	9.7	10.7	9.3	10.7
Bamboo[2]	10.4	11.9	8.8	8.3	9.2	8.3	8.8	10.4	11.9	9.9	9.6
Holly[2]	5.6	6.1	6.5	11.2	7.3	10.2	7.0	6.9	11.6	8.9	8.1
Hemlock	6.0	4.3	9.6	7.4	6.8	6.2	6.4	5.7	10.8	7.3	7.1
Big Leaves[1]	4.5	9.6	7.5	3.4	6.3	8.6	12.1	9.1	5.4	9.2	7.8
Thin Leaves[2]	3.9	4.4	7.7	5.1	5.3	7.7	9.7	6.9	4.8	7.3	6.3
Box[1]	7.0	6.1	7.1	1.4	5.4	1.4	3.9	6.2	4.2	3.9	4.7
Tube[1]	3.0	5.2	3.6	4.7	4.1	1.4	1.7	3.6	0.9	3.9	4.0
Easter Grass[1]	4.1	0.8	2.7	2.0	2.4	3.8	4.7	2.6	5.4	4.1	3.2
Spanish Moss[2]	5.4	5.4	3.1	2.6	4.1	1.8	1.6	1.9	2.5	2.0	3.1
Coconut[2]	4.7	4.2	1.7	2.7	3.3	1.9	4.3	1.9	0.7	2.2	2.8
Bark[1]	5.2	8.5	0	1.2	3.7	0	0	7.1	0.5	1.9	2.8
White Moss[2]	3.0	2.5	2.0	2.2	2.4	1.6	3.7	3.0	3.3	2.9	2.7
Chenille Stems[1]	5.2	1.8	0.4	1.1	2.1	0	0.3	0.9	6.4	2.0	2.1
Orange Leaves[2]	3.0	2.7	1.5	0.5	1.9	0	2.0	2.5	4.3	2.0	2.0
Sponge[2]	0.5	3.0	0.4	0.1	1.0	3.2	1.8	3.0	0.5	2.1	1.6

[1] is a natal microhabitat (one experienced by the birds when they were juveniles) for group 1 and [2] is a natal microhabitat for group 2.