

INTRINSIC FACTORS IN THE SELECTION OF FORAGING SUBSTRATES BY PINE WARBLERS: A TEST OF AN HYPOTHESIS

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ABSTRACT.—This paper describes a test of an hypothesis recently proposed to explain a difference in foraging behavior observed in Pine Warblers (*Dendroica pinus*) on two neighboring Bahama islands. The hypothesis, that the members of the two populations were using different intrinsic preference patterns in selecting their foraging substrates, is supported by observations of different substrate responses in captive birds from the two islands in a common test situation. We interpret intrinsic preferences as expressions of stereotyped response patterns selected for during episodes of stress and active competition in fluctuating environments and becoming detectable as deviations from currently optimal patterns (matching the local resource distribution) during periods of resource abundance and reduced or suspended competition. Intrinsic preferences are difficult to recognize in nature, and we believe that they may be much more common than generally suspected. *Received 22 September 1980, accepted 16 December 1980.*

THE adaptive plasticity of foraging behavior in birds seen in recent studies of optimal foraging (Pyke et al. 1977, Krebs 1978) is, of course, invariably constrained by the morphological and physiological specializations of the species. The possibility that purely behavioral specializations may similarly constrain a bird in its foraging activities in nature has received little attention (but see Morse 1971) because of the difficulties inherent in detecting and identifying behavioral preferences and aversions outside of experimental contexts where extrinsic factors of food availability and interference can be controlled.

In a recent field study one of us (Emlen in press) demonstrated that during the breeding seasons of 1971, 1976, and 1978, Pine Warblers (*Dendroica pinus*) on Grand Bahama Island foraged almost exclusively on pine foliage, while those in closely similar situations on neighboring Andros Island divided their foraging activity about equally between foliage and bark. After measuring the distribution of insects on bark and foliage and examining the potential role of direct interference from community associates on the two islands, he concluded that the birds were not responding to the extrinsic factors of food abundance or substrate accessibility but to intrinsic factors of substrate preference, i.e. that the two populations were phenotypically different with respect to this behavioral characteristic. Emlen's hypothesis, paraphrased in more specific terms, states that: if presented with a choice of bark and foliage in a neutral setting, birds from Grand Bahama will confine their searching activity almost entirely to foliage, while those from Andros will search on both substrates.

In May 1980 we tested this hypothesis by presenting freshly caught Pine Warblers from each island with a choice of bark and foliage in a portable observation tent, timing the number of seconds each bird spent searching on each of the substrates in 30-min observation sessions. We also measured the bills and feet of all test birds on the premise that the divergent substrate preferences might reflect small and previously undetected differences in size or proportions.

METHODS

Birds of both sexes (10 from Grand Bahama and 12 from Andros) were lured into mist nets on their territories by play-backs of taped songs and, in most cases, by caged live birds serving as decoys. After capture the birds were held in small individual cages with food (meal worms plus a high-protein mash) and water. During transportation between islands they were held in small paper cones for up to 4 h at a time.

The portable observation tent, made from translucent, green-dyed bed sheets and measuring 1.6 m × 1.6 m × 2.3 m high, was set up in the forest with a foliage-bearing pine tree segment serving as the central tent pole. Bark/foilage ratios were roughly standardized for each setting by selecting trees with good foliage in the central portion and cutting the 2.3-m segment of trunk between the 6.0-cm and 3.5-cm diameter points. Foliage on the 10–15 lateral branches in these segments was trimmed to 46 needle clusters in all sets. Observations were made from a small darkened blind at one side of the tent through a one-way milar window.

Each bird was tested twice in the observation tent, first on sterile substrates (thoroughly sprayed with Diazinon insecticide) in order to control the possible effects of response reinforcement, and a few days later on untreated substrates (residual native insects intact) from the other island as a check against differences of potential significance in the two insect faunas. Released quickly into the tent from the hand after a 1–4-h period of food deprivation, each bird typically flew to the central or upper part of the tree, peered around, fluffed and preened, and started foraging within 3–10 min. Activity, categorized as searching in the needles, searching on the bark, searching on the ground, quietly resting, and restlessly flying about, was monitored with a stop watch in hand for 30 min or longer, and the number of seconds of each of the five activities was recorded. A few birds failed to search the substrates; these and those that spent less than 30 s of searching in the 30-min observation period were disqualified from the record.

RESULTS

The number of seconds of searching on needles and bark in the two tests is presented in Table 1. The results in both cases support the prediction of the hypothesis that the proportion of bark foraging would be appreciably higher in the Andros than in the Grand Bahama birds. The proportions in these tests were all lower than those obtained for free-ranging birds in the field, but this may simply reflect a lower availability of bark relative to foliage in the test situation and does not appear to invalidate in any way the conclusion of an island-specific preference difference.

Several additional insights on foraging behavior may be drawn from the observations of the birds in the tent:

1. Some of the birds searched the available foliage and bark surfaces, systematically working downward from the top or upward from the bottom with little or no backtracking, then stopped searching. Others were quite haphazard in covering the available surfaces and continued to search to the end of the observation session. Individuals tended to follow similar searching routines on successive tests.

2. Some birds moved almost continuously through the branches and foliage as though using a short visual search range; others advanced less frequently and in longer hops. The former pattern appeared to be more common in the Grand Bahama birds, the latter in the Andros birds.

3. None of the birds searched the three available substrates (foliage, bark and ground) sequentially with indications of an order of preference. Some did considerable ground searching; others did none. Bark searching was interspersed with foliage searching as the birds moved about.

The behavioral differences between the Andros and Grand Bahama populations were associated with slight differences in morphology. The Andros birds in the test series averaged significantly smaller than the Grand Bahama birds in five of the

TABLE 1. Proportion of bark searching to total searching in two test situations: A—on sterile (insecticide-treated) native substrates, and B—on untreated foreign substrates. Values are seconds of searching activity for each bird.

A—TESTS ON STERILE (NATIVE) SUBSTRATES ^a							
Grand Bahama birds				Andros birds			
Bird number	Bark	Foliage	Prop on bark	Bird number	Bark	Foliage	Prop on bark
1	0	340	0.00				
2	0	440	0.00	1	39	41	0.4875
3	5	650	0.0076	3	20	59	0.2532
6	13	313	0.0399	4	30	330	0.0833
7	2	233	0.0085	7	14	60	0.1892
8	0	367	0.00	8	52	259	0.1672
				10	37	75	0.3304
				11	1	65	0.0152
				12	4	293	0.0135
(\bar{x} = 0.0093 ± 0.0155)				(\bar{x} = 0.1924 ± 0.1629)			
B—TESTS ON UNTREATED FOREIGN SUBSTRATES ^a							
Bird number	Bark	Foliage	Prop on bark	Bird number	Bark	Foliage	Prop on bark
2	5	707	0.0071	1	15	33	0.3125
5	0	153	0.00	3	14	203	0.0645
6	25	375	0.0625	4	37	151	0.1968
7	15	180	0.0769	5	43	261	0.1414
8	5	190	0.0250	6	2	55	0.0351
9	3	161	0.0183	8	21	9	0.7000
10	0	154	0.00	12	17	72	0.1910
(\bar{x} = 0.0286 ± 0.0309)				(\bar{x} = 0.2345 ± 0.2249)			

^a Differences significant at 5% level (*t*-test).

seven measurements recorded (Table 2). Although not recognized as taxonomically distinct, the Andros population has been suspected of being slightly smaller (James Bond pers. comm.). At this time we see no basis for a functional relationship between these morphological divergencies and the behavioral divergencies under consideration.

DISCUSSION

These results confirm our prediction that captive representatives of the Pine Warbler populations of Grand Bahama and Andros islands would retain their distinctive response characteristics both in a neutral choice situation (sterile substrate) and when

TABLE 2. Bill and foot measurements (cm) for the test birds captured on Grand Bahama and Andros islands. (Culmen measurements are omitted for six birds with cage-damaged foreheads, foot measurements for one bird with diseased feet.)

	Grand Bahama	Andros
Culmen ^a	1.23 ± .030 (5)	1.18 ± .029 (7)
Gonys	0.78 ± .044 (7)	0.78 ± .036 (11)
Gape ^a	1.62 ± .085 (7)	1.52 ± .051 (11)
Nostril to tip	0.86 ± .075 (7)	0.82 ± .042 (11)
Tarsus ^a	2.02 ± .047 (6)	1.87 ± .089 (11)
Hind toe + claw ^a	1.21 ± .033 (6)	1.12 ± .047 (11)
Hind claw ^a	0.62 ± .019 (6)	0.55 ± .028 (11)

^a Differences significant at 5% level (*t*-test).

presented with the natural substrates of the opposite island. This, in turn, supports our underlying hypothesis that the substrate responses observed in the field in these two populations reflected intrinsic response tendencies (genetically or culturally inherited) rather than extrinsic factors.

As with habitat selection (Lack 1937, Hildén 1965), or foliage selection (Klopfer 1965, Partridge 1974), any expression of substrate preference will, according to prevailing evolutionary theory, be maladaptive unless it coincides with the currently optimum response. A preference that would restrict a bird's freedom to exploit portions of otherwise available resources, as appears to be the case in the Grand Bahama birds that bypassed bark insects and the Andros birds that bypassed foliage insects, would, on this basis, be maladaptive and untenable. Departure from the current optimum may be adaptive, however, where environmental conditions fluctuate and specialization on a subset of the available substrates is advantageous during critical phases of the fluctuations (Wiens 1977). Species living in fluctuating environments thus have a choice between two evolutionary strategies: plastic responsiveness to the changing conditions, or stereotyped specialization for conditions encountered during the most critical phase of the fluctuations. We propose that the apparent maladaptions in the substrate selections of Pine Warblers in this study reflect stereotyped response patterns adapted for conditions of intense competition and observed by us only during periods of reduced or suspended competition when food supplies exceeded the local community's demands. On Grand Bahama, where the Pine Warblers occurred with two species of bark-gleaning specialists (Emlen 1977), competition during food crises would presumably favor foliage-gleaning specialists over generalists, while on Andros, where there were no bark-gleaning specialists, no such selective pressure for specialization would occur.

The direct observational techniques that enabled us to detect these differences in foraging behavior in the Pine Warblers on the two islands also revealed significant foraging differences in the two Blue-gray Gnatcatcher (*Polioptila caerulea*) populations (Emlen in press). We suspect that further studies of this type would reveal additional examples of local foraging specialization attributable to intrinsic factors wherever environmental conditions fluctuate and resources are incompletely exploited during periods of resource superfluity.

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