HABITAT SELECTION: DIFFERENCES IN STEREOTYPY BETWEEN INSULAR AND CONTINENTAL BIRDS

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EVEN a casual visitor to an island must note the reduction in the number of species relative to adjacent continents. The whys and wherefores of this situation are not especially obscure, though it remained for MacArthur and Wilson (1963) to provide a quantitative statement of the causal relation between the diversity of an island's fauna on the one hand and its size, topography and distance from the mainland on the other. Nor have the evolutionary effects of island isolation been ignored, as witnessed by the testimony of biologists from Darwin (1859) to Mayr (1963). Ethologists have examined changes in bird song as related to a reduction in species diversity (see Thorpe, 1963), and ecologists have long been concerned with changes in food seeking or nesting activity coincident upon the absence of competitors (e.g., Crowell, 1962 and Grant, 1966). We have sought to enlarge upon one aspect common to these several themes: is there a reduction in the behavioral stereotypy of island species?

Consider the data of Crowell: on Bermuda, only three species of birds are common. While they appeared to him to behave in much the same way on Bermuda as in their habitats in the eastern United States, on the islands they occupied a greater variety of habitats. Klopfer (1967) found a similar situation for Bananaquits (*Coereba flaveola*) in Puerto Rico and Central America. The unanswered question is whether individual birds on Bermuda (or Puerto Rico) expanded their range of habitats or, alternatively, whether the expansion was of the species habitat, i.e., with each individual as restricted as ever, but with more varieties of individuals. This study reports on analysis of stereotypy in foliage preferences and feeding activity of a few individual Catbirds and Cardinals from Bermuda and the Durham area in the Piedmont of North Carolina.

METHODS

The feeding activity of wild Catbirds (*Dumetella carolinensis*) and Cardinals (*Richmondena cardinalis*) was recorded at 10 second intervals and feeding height and distribution were recorded where the bird was first seen and again where it was last seen. Feeding activity included foraging (searching) movements as well as actual feeding and, thus, the data are not strictly comparable with those of Crowell (1962) who recorded only active pecking. The definition of vegetation layers depended upon the general configuration of the vegetation in any particular habitat. For example, the maximum height of the shrub layer varied between 2.5 and 6.5 meters. The radial

position of the bird was recorded as trunk (main stem of tree), intermediate, or terminal (branches reduced to less than 1 cm in diameter).

Foliage preferences were tested in two rooms, each divided into two equal chambers by netting. The chambers in each room were identical except for the foliage. Fluorescent lighting was provided continuously and identical perches consisting of parallel bars were placed in each chamber. Connecting the chambers in each room was a small box, open at each end with a battery of three photocells at each opening. The photocells were connected to counters and the length of time that the bird spent in each chamber was automatically recorded. Food was placed in the center of the box and water was provided in each chamber. The rooms were identical with the first and second rooms used by Klopfer (1965) and previously described.

Before experiments were begun, the birds were trained, in groups of three, to move from one chamber to the other. In addition, before each trial, the bird was permitted a habituation period of 8–24 hours. In actual trials birds were tested singly for at least three days. The chamber into which the bird was first introduced was alternated with each trial.

To test foliage preferences, artificial leaves were offered in the following combinations: large oak-large elm, large oak-small elm, small oak-large elm. The lengths of the artificial leaves were as follows: large oak—24 cm, large elm—14 cm, small oak—14 cm, small elm—8 cm. The leaves were suspended from the perches, walls and ceiling with masking tape. Arrangement of leaves in each chamber was identical.

For each trial, the proportion of time spent by the bird in each chamber was calculated and a discrimination index (H) derived using the graph presented by Klopfer (1965). This graph is a modification of the expression of diversity, $\Sigma P_i (- \log_e P_i)$ (MacArthur and MacArthur, 1961).

RESULTS AND DISCUSSION

Crowell (1962) found that Bermuda Catbirds and Cardinals spent a greater proportion of their time in ground-feeding than did their North American counterparts and this observation is confirmed by results presented here (Table 1). The indices of diversity (H values) obtained by Crowell did not support the hypothesis that island birds, apparently living under conditions of reduced inter-species competition, are less stereotyped in their feeding activity. However, Crowell's mainland comparisons were based on birds scattered widely over the eastern seaboard. In contrast, H values obtained in the present study (Table 1) are slightly higher for Bermuda Catbirds and Cardinals, suggesting that the island birds are slightly less stereotyped with regard to feeding activity.

Analysis of the vertical (layer) and radial distribution of feeding activity

TABLE 1
FEEDING ACTIVITY OF BERMUDA AND MAINLAND CATBIRDS AND CARDINALS

	Bermuda Catbirds		N.C. Catbirds		Bermuda Cardinals		N.C. Cardinals	
Feeding activity	n	H	n	H	n	H	n	H
Ground	289	0.315	266	0.293	607	0.243	164	0.309
Trunk	83	0.150	10	0.046	8	0.046	1	0
Foliage	1,127	0.223	1,267	0.155	230	0.354	753	0.171
Fruit/flower	8	0.046	0	0	2	0.023	0	0
Hawk/hover	17	0.046	21	0.046	3	0.023	10	0.046
Totals	1,524	0.78	1,564	0.54	850	0.69	928	0.53

(Table 2) also produced consistently higher H values for Bermuda birds. The field data suggest that Bermuda Catbirds and Cardinals are less restricted in their feeding activities than North American birds. This can be interpreted to mean that the food niches occupied by these species are larger on the Bermudas than on the mainland, and that while Crowell's treatment of his data, which take foliage density profiles into consideration, may seem more precise than ours, this is not necessarily the case. When the chance of observing birds is less in one layer than another, the method of simply recording the position of the bird, rather than limiting observations to the actual taking of food (as did Crowell), may be more meaningful. Often the position of the bird can be detected in dense foliage, even when actual feeding cannot. In any case, our data are suggestive of greater plasticity in the foraging behavior of Bermuda birds.

As a group, Bermuda Catbirds did appear to be slightly less stereotyped in their artificial foliage preferences than did North Carolina Catbirds

TABLE 2
FEEDING DISTRIBUTION OF BERMUDA AND MAINLAND CATBIRDS AND CARDINALS

	Bermuda Catbirds		N.C. Catbirds		Bermuda Cardinals		N.C. Cardinals	
	n	H	n	H	n	H	n	H
Vertical distribution								
Ground	72	0.322	61	0.309	29	0.365	48	0.328
Shrub	224	0.306	273	0.171	44	0.352	153	0.274
Canopy	73	0.322	5	0.046	19	0.328	29	0.265
Totals	369	0.95	339	0.53	92	1.04	230	0.87
Radial distribution								
Trunk	17	0.169	3	0.046	3	0.150	0	0
Intermediate	118	0.367	28	0.230	33	0.340	64	0.367
Terminal	162	0.333	248	0.104	27	0.363	118	0.280
Totals	297	0.87	279	0.38	63	0.85	182	0.65

TABLE 3
ARTIFICIAL FOLIAGE PREFERENCES OF BERMUDA AND NORTH CAROLINA CATBIRDS

Choice of artificial foliage	Bermuda Catbirds			North Carolina Catbirds		
	No. of birds	% of time in Oak	Mean H	No. of birds	% of time in Oak	Mean H
Large Oak-Large Elm	6	57	0.19	6	61	0.28
Small Oak-Large Elm	6	44	0.09	6	34	0.17
Large Oak-Small Elm	6	69	0.19	8	65	0.21

(Table 3). Mean H values for Bermuda Catbirds are consistently lower (weak preference) for each pair of discriminanda, though none of the differences can be shown to be statistically significant given the smallness of the sample and the need for relying upon relatively weak nonparametric tests.

The data can be further broken down to reveal the relative importance of leaf size and shape as possible cues in habitat selection (Table 4). When offered a choice of large and small leaves, most birds of both groups preferred large leaves. North Carolina Catbirds spent 63 per cent of their total time among large leaves compared with 62 per cent for Bermuda Catbirds. Oak foliage was only slightly preferred to elm; North Carolina birds spent 52 per cent of their total time in oak and Bermuda birds 56 per cent. The slight preference for oak could be related entirely to the larger size of the artificial oak leaves. Mean H values again indicate that Bermuda Catbirds are slightly, but consistently, less stereotyped in their artificial foliage preferences.

Catbirds used in the preference tests showed considerable variation between individuals in the relative importance of leaf shape and size as discriminanda. Nevertheless, individual birds tested with all three pairs of artificial foliage tended consistently to select one particular type of artificial foliage. Of five North Carolina birds tested, three consistently selected large leaves and two consistently chose leaves of a particular shape (one chose oak and one elm). Similarly, of the six Bermuda birds tested, three consistently selected large

TABLE 4
RELATIVE IMPORTANCE OF LEAF SIZE AND SHAPE IN SELECTION OF ARTIFICIAL FOLIAGE BY CATBIRDS

	Number of birds selecting:							
	Large leaves		Small leaves		Oak		Elm	
	n	Mean H	n	Mean H	n	Mean H	n	Mean H
North Carolina Catbirds	11	0.20	3	0.18	10	0.24	10	0.20
Bermuda Catbirds	9	0.17	3	0.04	10	0.21	8	0.09

leaves and two consistently selected leaves of a certain shape (again, one chose oak and one elm). One Bermuda Catbird did not show a consistent preference for either leaf shape or leaf size.

The data presented here lend support, though tenuous, to the hypothesis that niche size and behavioral stereotypy are directly related. Species living on islands or in temperate habitats where numbers of species are reduced and average niche size is, presumably, larger should be less stereotyped in their behavior than species living on continents or in the tropics where niches are presumed smaller. Those aspects of behavior related to food and space (generally the most important niche parameters), in particular, should vary directly with niche size.

It is unlikely that most birds use only one cue in selecting their habitat. In the case of a bird responding to a single cue, all other discriminanda would be irrelevant and, though the bird might be highly stereotyped for the appropriate cue, this would not be detected if irrelevant discriminanda were offered. It is possible that discriminanda used in the present study were completely irrelevant but, since most of the birds exhibited consistent preferences, this does not seem to be the case.

A related problem, less easy to resolve, is whether the artificial foliage choices were of equal relevance to Bermuda and North Carolina birds. If the cues were of less relevance to Bermuda birds, this would account for the slightly lower H values of these birds without necessarily being related to a difference in niche size. Oak and elm are abundant in North Carolina but not on the Bermudas. Thus, one would expect oak and elm leaves to be of less significance to Bermuda birds. The only evidence that can be offered to refute this is, again, the consistency with which both groups of birds selected leaves of a particular size or shape.

The possibility that leaf size and shape are of minor importance as cues should also be considered. For example, the apparent preferences of Catbirds for large leaves could be related to light intensity and preference for leaves of a certain shape could be related to light pattern. Experiments to test these possibilities are continuing.

The idea that niche size and behavioral stereotypy are interrelated is an attractive one and the data presented here do offer some evidence of such a relationship. Perhaps a more detailed approach, such as completely defining the food and space components of each niche and relating these to habitat cues, should be used.

SUMMARY

Indices of diversity indicate that Bermuda Catbirds and Cardinals may be slightly less stereotyped in their feeding activities than North Carolina birds of the same species. Bermuda Catbirds were also slightly less stereotyped in their artificial foliage preferences.

Some support is presented for the hypothesis that Bermuda birds, living under reduced interspecies competition, may occupy larger niches with an associated reduction in behavioral stereotypy.

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