

BEHAVIORAL ASPECTS OF HABITAT SELECTION: A
PRELIMINARY REPORT ON STEREOTYPY IN FOLIAGE
PREFERENCES OF BIRDS

PETER H. KLOPFER

WE previously advanced the view that the great faunal diversity of tropical regions is due largely to a stereotypy in behavior that is characteristic of tropical species. In essence, we proposed that tropical animals are "masters-of-one-trade," in contrast to the "jacks-of-all-trades" that we believe occupy temperate regions. A community of "masters-of-one-trade," of specialists, should be able to accommodate many more different kinds of animals, even while the number of individuals of each kind must be reduced (Hutchinson, 1959). Our preliminary observations supported this contention (Klopfer, 1962; and Klopfer and Hailman, 1965) although we were never able to provide more than indirect and inconclusive evidence. One major problem has been the actual measurement of "behavioral stereotypy."

The term behavioral stereotypy was intended to refer to both perceptual and motor stereotypy. Perceptual stereotypy involves a sensitivity to, or an awareness of, or preference for, a limited range of a much larger complex of stimuli. An animal that responds only to a narrow band of wavelengths, for example, would be considered perceptually more stereotyped than one responding to a wider band. It should be noted that stereotypy can thus be due either to filters in the peripheral sensory field, which, for instance, transmit only wavelengths of a given value, or to central nervous mechanisms. These last may be of many different types, but their nature, although of evolutionary importance, need not concern us here.

Motor stereotypy refers to the availability of only a small variety of movements by means of which an animal can accomplish a given act. Here, too, the constraints may be peripheral, in terms of muscle attachments, of limb shapes, or central. The precise nature of these constraints is also tangential to the purpose of this inquiry (cf. Klopfer, 1962). Both motor and perceptual stereotypy, may also be a phenotypic or a genotypic characteristic. Gause (1942) has provided an enlightening discussion of the apparent inverse relation between the flexibility of soma and germ plasm, a theme more recently developed by Bateson (1963). I return to this facet of the problem in the discussion of the data.

We have begun our study of behavioral stereotypy by examining *preferences* for particular types of foliage in tropical and temperate zone birds, under conditions where leaf shape, size, or leaf density were the only variables. Our most recent results are given below. It will be apparent that we have

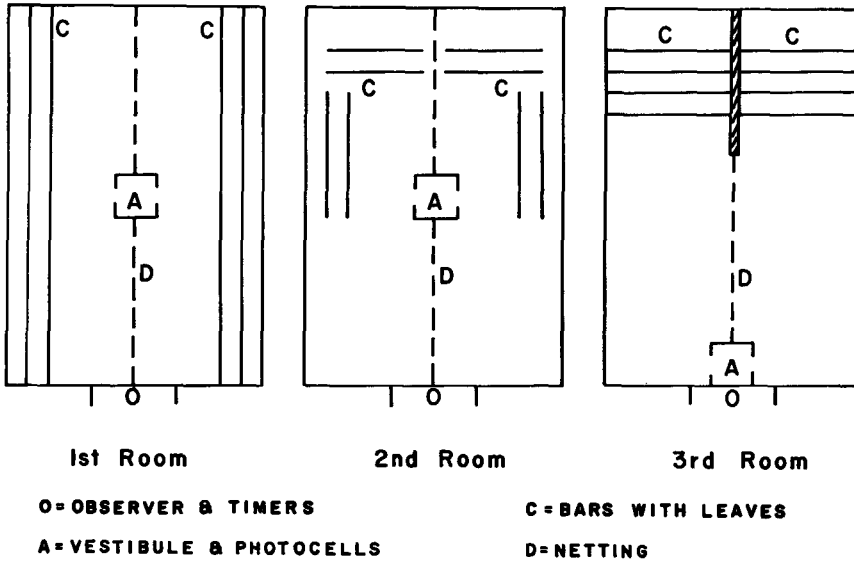


FIG. 1. Floorplan of test chambers.

yet to demonstrate a link between perceptual stereotypy, as measured by preference tests of the sort described below, and motor stereotypy. For the present time, we merely assume that there is such a correlation, leaving an empirical test to the future.

METHODS

The three test rooms averaged about 3 m × 3 m × 4 m, along the length of which a light gradient was established by means of an array of daylight fluorescent bulbs which were lit continuously for 24 hours of each day. (It may be noted that preliminary trials with a 12-hour day showed identical results.)

Along two sides of the room were arrayed horizontal, parallel, 1 cm diameter bars spaced about 20 cm above one another (Fig. 1). These bars provided an abundance of perches of uniform position and size. To these bars were tied the test leaves, a different type on the bars of each side. Some leaves were also placed directly against the wall and hung from the ceiling. The purpose of tying leaves to the racks was to assure that equal perch opportunities would be provided among both foliage types, a fact which is of course not the case in nature where the difference in the perch opportunities afforded by e.g., a broadleaf tree and a pine is rather great. (Klopfer, 1963). The leaves themselves were commercially made of a glossy green plastic. The following were used with their maximum lengths indicated: large oak: 24 cm, small oak: 14 cm, large elm: 14 cm, and small elm: 8 cm.

Altogether, 3 different chambers were used for each bird (Fig. 1) so as to eliminate totally position or other effects. The test with foliage pairs was replicated in different

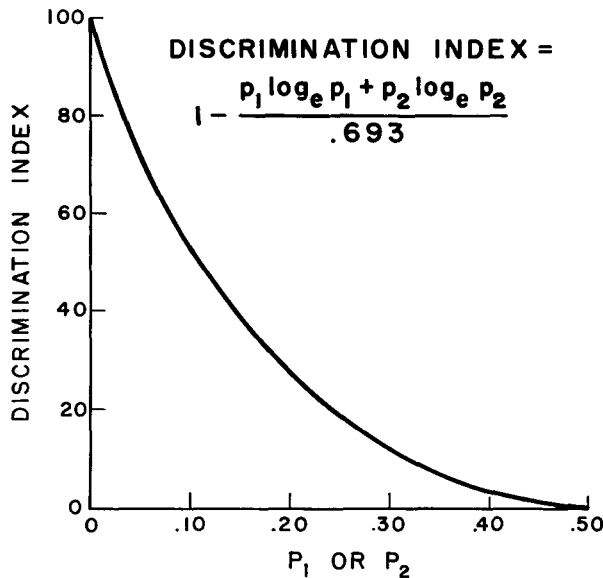


FIG. 2. Mathematical relation between discrimination index (H) and per cent preference for any given member of a pair of discriminanda.

rooms. In two of the chambers a partition was arranged so the bird could see both foliage types wherever it perched. In the third chamber, a bird perching amidst one foliage type could not see the other.

The rooms were divided into the two equal and symmetrical chambers by means of 0.4-cm netting. Passage from one section to the other was only possible through an approximately 20 cm × 20 cm × 20 cm "vestibule," within which food was provided ad libitum. Passage to and from the vestibule was monitored by a series of paired photo cells which automatically recorded the duration of visits to one side of the chamber or the other. The measure of a preference was the proportion of a three- to five-day period spent in one or the other side, following a 24-hour habituation period.

The four foliage types were offered in all possible pairs, although, because of escapes or mortality, every bird was not tested with every pair. For each pair of foliage types, the proportion of time spent amidst one or the other type was calculated and a "discrimination index" read from the graph (Fig. 2).

The graph represents a form (modified by R. H. MacArthur) of the now commonly used expression $\sum p_i (-\log_e p_i)$ (cf. MacArthur and MacArthur, 1961). The rationale for its use can be summarized as follows: the more stereotyped the preferences of an organism, the more marked will be the preferences among an array of discriminanda. If the discriminanda are paired, a completely plastic (nonstereotyped) individual should select each member of each pair 50 per cent of the time, i.e., evidence no preference. A

TABLE 1
DISCRIMINATION INDICES OF BIRDS TESTED WITH ARTIFICIAL FOLIAGE

Species	Rearing conditions	Individual values of H, based on 3 or more trials	Mean H
<i>Thraupis cana</i> (Blue Tanager)	hand-reared,		
	without sight of foliage	0.06;0.09	0.08
	with pine needles	0.12;0.28;0.31; (0.08) *	0.24
<i>Ramphocelus dimidiatus</i> (Crimson-backed Tanager)	hand-reared		
	without sight of foliage	0.08;0.14;0.28	0.17
<i>Spizella passerina</i> (Chipping Sparrow)	hand-reared		
	without sight of foliage	0.13;0.19;0.32	0.21
		(0.08;0.13;0.13;0.13;0.13; 0.30;0.30;0.38) *	(0.19)

* Trials with less than 3 or more pairs of foliage.

highly stereotyped individual will tend to select one member of many pairs to the exclusion of the other. The greater the stereotypy, the higher the proportion of pairs for which the choice should deviate from 50 per cent. In essence, the index may be thought of as representing the proportion of choices that deviates from 50 per cent. (A similar method for assessing preferences has been employed by J. P. Hailman [In press], in multichoice situations.) The more discriminating the bird, the larger the index. Of course, if a bird selects its habitat using *one* clue only (e.g., light intensity) it would be very stereotyped but not be so labeled on the basis of tests with many (irrelevant) discriminanda. We deem this possibility unlikely in birds although it cannot be ignored. Some behavioral evidence for believing leaf shape and size to be relevant are reported in Klopfer (1963).

DATA AND DISCUSSION

The data are summarized in Tables 1 and 2. The unequal (and small) number of birds in each group is attributable to the high mortality initially encountered in efforts to hand-rear birds under unnatural conditions. (In addition, we had our fair share of escapes and human blunders.) As this work progresses, we expect sufficient data to allow use of statistical tests of significance. This point is still several seasons distant, hence the comments that follow must necessarily refer to apparent differences in group scores.

First of all, one may note that the discrimination indices for Chipping Sparrows (*Spizella passerina*) are similar whether the animals are wild-trapped adults (normally reared), or hand-reared without sight of foliage. Rearing Chipping Sparrows in the less-preferred oak foliage reduces the value of the index by a large amount (from 0.35 or 0.37 to 0.10), i.e., the birds

TABLE 2
DISCRIMINATION INDICES OF BIRDS TESTED WITH NATURAL FOLIAGE

Species	Rearing conditions	Individual values of H, based on single trials (data from Klopfer, 1963)	Mean H
<i>Spizella passerina</i> (Chipping Sparrow)	wild-trapped adults	0;0;0;0.3;0.5;0.5;0.5;0.5; 0.7;0.17	0.37
	hand-reared		
	without sight of foliage	0.05;0.06;0.3;0.5;0.5;0.7	0.35
	with oak leaves	0;0;0;0.1;0.1;0.2;0.2;0.2	0.10
<i>Zonotrichia albicollis</i> (White-throated Sparrow)	wild-trapped adults	0;0.04;0.04;0.2;0.2;0.2;0.2; 0.5;0.5;0.7	0.25

become less discriminating. This accords with the interpretation previously given (Klopfer and Hailman, 1965).

Secondly, the indices of the hand-reared Blue Tanagers (*Thraupis cana*) are apparently raised (from 0.08 to 0.24) by rearing in a particular type of foliage.

Finally, of the birds raised without sight of foliage, the Chipping Sparrows have generally higher scores than any of the tanagers (means of 0.21 or 0.35 to 0.08 or 0.17).

This suggests that the hand-reared sparrows appear to evince more stereotyped preferences than the hand-reared tanagers. On the other hand, the early visual experience with a particular foliage type appears to be much more of a constraint for the tanagers than the sparrows. Under natural conditions, of course, visual experience is not denied either young tanagers or young sparrows. Whatever the absolute differences in the range of preferences, it appears that a particular visual experience may limit the tanagers to a much greater degree than it does the sparrows. This constitutes a difference, not so much in the stereotypy of perceptual preferences themselves, but one secondarily imposed by differences in learning mechanisms.

CONCLUSIONS

Our data suggest that among hand-reared foliage-deprived birds, the Chipping Sparrows are more stereotyped in their visual preferences than are the tanagers. On the other hand, a particular visual experience serves to constrain the tanagers, but not the Chipping Sparrows. The tropical tanagers, as a consequence, can under normal conditions of rearing be expected to show a greater degree of stereotypy than the Chipping Sparrows. These experiments are continuing.

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LITERATURE CITED

- BATESON, G.
1963 The role of somatic change in evolution. *Evolution*, 17:529-539.
- GAUSE, C. F.
1942 The relations of adaptability to adaptation. *Quart. Rev. Biol.*, 17:99-114.
- HAILMAN, J. P.
In press. The ontogeny of an instinct. *Behaviour Supplement*.
- HUTCHINSON, G. E.
1959 Homage to Santa Rosalia, or Why are there so many kinds of animals. *Amer. Nat.*, 93:145-159.
- KLOPPER, P. H.
1962 Behavioral Aspects of Ecology. Prentice Hall, Englewood Cliffs, N. J.
1963 Behavioral aspects of habitat selection: the role of early experience. *Wilson Bull.*, 75:15-22.
- KLOPPER, P. H., AND J. P. HAILMAN
1965 Habitat selection in birds. In: *Advances in the Study of Behaviour*. Hinde, Lehrman, and Shaw, Eds. Academic Press, New York.
- MACARTHUR, R. H., AND J. W. MACARTHUR
1961 On bird species diversity. *Ecology*, 42:594-598.

ZOOLOGY DEPARTMENT, DUKE UNIVERSITY, DURHAM, NORTH CAROLINA, 14 JANUARY 1965