

BEHAVIORAL ASPECTS OF HABITAT SELECTION: THE ROLE OF EARLY EXPERIENCE

PETER KLOPFER

IF we walk through a Piedmont (North Carolina) meadow in the month of June, it will not surprise us to find meadowlarks or bluebirds. We would not expect to find Pine Warblers, however, or other species that we might easily encounter were we to turn from the meadow into the surrounding loblolly pine. For each species of bird we recognize a characteristic habitat. The question on which we want to focus our attention is, "What determines a preference for a particular habitat?" That is to say, what factors assure that the young of a particular species will develop the same preferences as those of its parents?

The importance of being able to answer this question relates, in turn, to a hypothesis formulated by Klopfer and MacArthur (1961. *Amer. Nat.*, 95:223-226) that seeks to explain the enhanced avifaunal diversity of tropical regions in terms of an increase in the stereotypy of the behavior of tropical birds. The present study represents the first of a series on habitat selection in temperate zone and tropical birds.

METHODS

The purpose of the techniques described below was to measure the effect of certain kinds of early experience on the preference for particular perch sites of a north temperate zone passerine, the Chipping Sparrow (*Spizella passerina*).

Birds were obtained from mixed stands of loblolly pine and hardwood (in which the loblolly pine predominated) throughout various regions of Durham and Orange counties of the North Carolina Piedmont. Four groups of Chipping Sparrows were established as well as one additional group of White-throated Sparrows (*Zonotrichia albicollis*) trapped in the same area. These groups were as follows:

Group 1: wild-trapped adults (Chipping and White-throated Sparrows).—Ten birds of each species. These birds were captured in a funnel trap and held in large outdoor aviaries for from three to ten weeks prior to testing.

Group 2: wild-trapped adults (Chipping Sparrows).—These ten birds were obtained and treated as those in Group 1; for these the number of perches and amount of foliage in the pine-decorated half of the test chamber was reduced by one half.

Group 3: hand-reared nestlings (Chipping Sparrows).—This group of six birds, removed from the nest within 24 hours after the eyes opened, or, in most cases, before the eyes had opened, was reared in a cloth-covered cage kept within a house. They at no time in their lives saw any natural foliage, their vision being restricted to the sight of the experimenter who did the feeding, the cloth-covered interior of their cage and, occasionally, the furniture in the room where they were kept.

Group 4: hand-reared nestlings (Chipping Sparrows).—this group of eight birds, also collected either before their eyes had opened or within 24 hours after the opening of the eyes, was also reared by hand in a cloth-covered aviary which was decorated with a supply of freshly picked oak leaves. The leaves were from trees of various oak species native to the Piedmont, primarily red oak (*Quercus rubra*) and members of the white oak group. Both the hand-reared groups (Groups 3, 4) remained within the confines of their cloth-covered aviaries until the time of their tests. These tests began one to three months after the nestlings were fully fledged and feeding independently.

The experimental chamber within which the tests were conducted consisted of a room 12 feet long, 8 feet wide, and 8 feet high. Along the length of this room a light gradient was established by means of a series of six 40-watt day-light fluorescent bulbs which varied from a maximum intensity (at the perches) of 500 foot-candles to a minimum at the opposite end of the room of $<.8$ foot-candles. The placement of one of the lamps, midway along the length of the room caused the light intensity to fall off fairly abruptly halfway along the main axis, so that the room could be conveniently divided into a bright half and a dim half. In the center of the ceiling, just above the dividing light fixture, was a small exhaust fan that assured uniform circulation of air.

Along two opposite sides of the room were arrayed steel racks consisting of two parallel sets of bars stacked about 10 inches above one another and running the length of the room. These provided an abundance of perches of uniform position and size along the length of both sides of the room. To these racks were tied twigs from loblolly pines or, alternatively, from the various oaks. The purpose of tying the twigs to the racks was to assure that equal perch opportunities would be provided by both foliage types, a fact which is of course not the case in nature, where the difference in the perch opportunities afforded by a broadleaf tree and a pine tree is rather great. The significance of this feature will be apparent later. The position of the oak and pine (i.e., right or left of the chamber) was reversed for one-half of the birds.

The entrance to the room was closed by a panel on which was fastened a double layer of gauze painted with military camouflage pattern. Behind this was a darkened blind. Thus, it was possible for an observer to sit in the blind and watch the activities of the birds confined within the room without being seen. From the behavior of the birds, which frequently clung to the gauze directly in front of the observer, it was quite clear that the observer's presence was not detected by the birds. The observer had in his lap, in addition to note paper, a series of micro-switches, each of which was attached to a separate counter and timer. Thus, it was possible to record both the number of visits that a bird made to any particular section of the room as well as the duration of that visit. Food was available ad lib. near the center of the room.

Finally, additional observations were made of ten other wild-trapped, adult

individuals of Chipping and White-throated Sparrows separately confined in outdoor aviaries measuring $20 \times 8 \times 8$ feet (Groups 5 and 6). Within each of these aviaries there was available a coniferous tree, a broad-leaved tree, and a small pile of tangled vines and brush as well as some open unshaded grass.

Each bird was separately observed for a total of ten hours. Observations commenced only after the bird had been allowed to habituate to the test chamber or aviary for a period of 72 hours. No more than three hours of observation were made in any one day, and generally the observations were spread over four to five days. Whenever a bird failed to move for 45 consecutive minutes it was assumed to be asleep and the record for that period was rejected and replaced by another hour's observation made later in the day or the following day. Observations were made at all hours of the day which began at 6 AM and lasted until 10 PM (for the indoor trials); These 16 hours of light were provided by an automatic time clock. The aviary birds, of course, were subjected to the normal diurnal rhythm.

The data recorded on the graphs represent the percentage of the time spent in one or the other of the foliage types or light intensity areas, as calculated from the ratio of the number of seconds spent in portion A of the cage to the number of seconds spent in portions A plus B.

RESULTS

Group 1.—The preferences of adult Chipping and White-throated Sparrows are depicted in Fig. 1. The Chipping Sparrow group, it will be noted, was divided almost equally between birds favoring the light half of the chamber and birds favoring the dark half. All of the white-throats but one spent more than 50 per cent of their time in the darker half of the chamber. With respect to foliage preferences, the Chipping Sparrows clearly spent most of their time in the pine—only one bird spent less than 50 per cent of the recorded observation period in the pine foliage. The white-throats, on the other hand, were fairly evenly divided between pine and oak, four birds being predominately in the pine and six in the oak.

Group 2.—This group of birds was tested in a chamber with twice the volume of oak foliage as pine and twice the number of perches in oak as in pine and showed much the same distribution (Fig. 2) for light preferences as did those of Group 1. Their foliage preferences, however, are clearly distinct. Six birds of the ten spent more than 50 per cent of their observation period in the oak.

Group 3.—These six birds had never seen foliage of any sort prior to their introduction into the test chamber. All but one spent most of the observation period in the lighter half of the room (Fig. 3), and all but one preferred the pine. In this last respect, at least, these birds resembled the Group 1 controls.

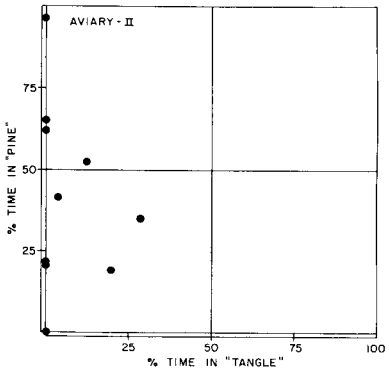
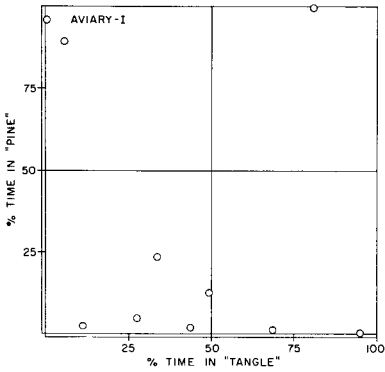
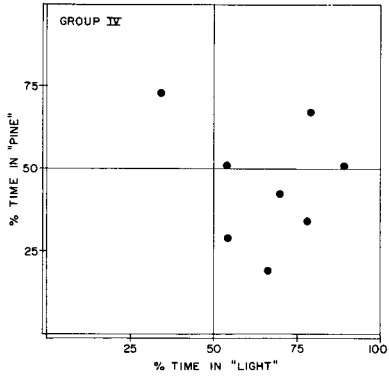
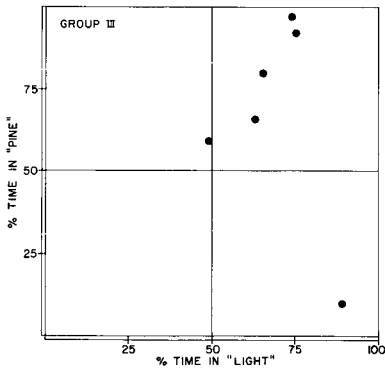
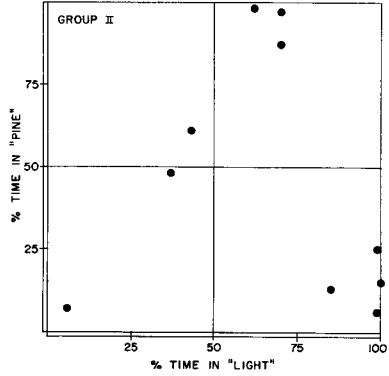
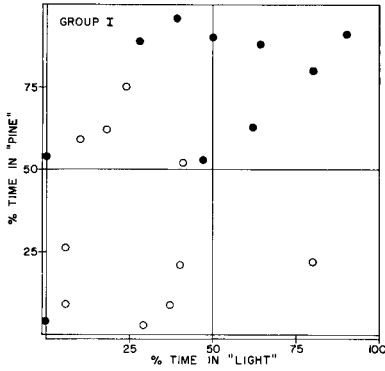


FIG. 1 (UPPER LEFT). Perch preference of Chipping (●) and White-throated Sparrows (○) in test chamber.

FIG. 2 (UPPER RIGHT). Perch preference of Chipping Sparrows in test chamber with one-half of the pine removed.

TABLE 1
LIGHT CHAMBER TESTS

Groups*	Group means % of time in:		Individuals with 50% or more of their time spent in:	
	Pine	Light	Pine	Light
Group 1 (Chipping Sparrows)	71	46	90	50
Group 1 (White-throated Sparrows)	34	29	40	10
Group 2	46	67	40	70
Group 3	67	69	83	83
Group 4	46	66	50	70

* See text.

Group 4.—These eight birds had been exposed to oak leaves since the opening of their eyes. Four of them subsequently preferred the oak to the pine (Fig. 4). All but one preferred the light to the dark half of the chamber.

Groups 5 and 6.—Unlike the birds of Group 1, the Chipping Sparrows tested within the confines of the large test aviary (Aviary II) did not show a marked preference for pine. Only four of the ten birds spent more than half their perching time in the pine tree, which, it should be noted, had a much reduced volume per foot of height than the broadleaved tree. The white-throats were generally similar (Aviary I), though they spent more of the time when they were on the ground within a dense tangle (rather than open grass) than did the Chipping Sparrows.

DISCUSSION

Relevant measures and cues.—A fundamental stumbling block to many studies of animal behavior lies in the determination of the appropriate measure for a particular trait or preference. In this case, one must ask whether the amount of time spent in a particular side of the apparatus represents an accurate measure of the preference for the foliage of that side. Would the selection of sleeping perches or nesting sites as the preference criteria have led to different conclusions? We have no data that would allow a clear answer. One can but surmise that since perch opportunities, micro-climatic conditions, and food were uniformly distributed, the non-uniform nature of the movements of the birds probably reflects an effect of the different foliage or light intensities.

FIG. 3 (CENTER LEFT). Perch preference of hand-reared Chipping Sparrows in test chamber.

FIG. 4 (CENTER RIGHT). Perch preference of hand-reared Chipping Sparrows (reared among oak leaves) in test chamber.

FIG. 5 (LOWER LEFT). Perch preference of White-throated Sparrows in outdoor aviary.

FIG. 6 (LOWER RIGHT). Perch preference of Chipping Sparrows in outdoor aviary.

TABLE 2
AVIARY TESTS

Groups*	Group means % of time in:		Individuals with 50% or more of their time spent in:	
	Pine	Tangle	Pine	Tangle
Group 1 (White-throated Sparrows)	33	41	30	40
Group 2	41	6	40	0

* See text.

The fact that the foliage was lighted on two sides to reduce shadows, further suggests that it is an attribute of leaf size or shape that is the relevant cue and not merely the shadow pattern cast by the leaves.

Effect of rearing conditions.—If we wish to compare the choices made by two groups of birds we may consider the group means, or, as is preferable in the case of small samples, the intragroup differences. Considering the means first, it can be seen (Table 1) that the wild-trapped Chipping Sparrows, on the average, chose the pine foliage over the oak 71 per cent of the time, contrasting with the white-throats, which selected pine 34 per cent of the time. Nine of the ten Chipping Sparrows spent half or more of the total observation period in the oak, while this was true for only five of the ten white-throats. An interspecific difference is thus apparent, though a statistical evaluation of the degree of difference is rendered difficult by the small size of the samples.

When the number of pine-decorated perches is reduced by one-half, the apparent preferences of Chipping Sparrows shift, too. The percentage of time spent in pine drops from 71 to 46, and the proportion of individuals spending more than 50 per cent of their time in pine drops from $\frac{9}{10}$ to $\frac{4}{10}$. This suggests these birds have an opportunistic nature, a suggestion corroborated by the aviary tests. Under aviary conditions, in which the number of perches provided by the oak tree was considerably greater than that provided by the less intensely branched pine, the Chipping Sparrows (Table 2) spent 41 per cent of their perching time in the pine (four of ten individuals chose pine more often than oak). In this test, the Chipping Sparrows were scarcely to be differentiated from the white-throats (Table 1), although the two species can be sharply differentiated by the amount of time spent in dense, dark tangles of vegetation as opposed to the open, grass areas. Thus, the first consideration in the selection of a suitable perch site is apparently the physical structure and quantity of the perches. Only where these conditions are equal do the foliage preferences become decisive.

The Chipping Sparrows that were reared without sight of any foliage can not be distinguished from their wild-trapped counterparts except in their

greater preference for the higher of the light intensities proffered. This is probably due to their having been exposed to rather similar wave lengths and intensities of artificial light during rearing.

The group of Chipping Sparrows hand reared with oak foliage, however, shifted their preferences in the direction of the oak. Their mean time in the pine was only 46 per cent (compared to 71 per cent for the wild birds), with but five of ten individuals selecting pine more than 50 per cent of the time. It would seem, therefore, that Chipping Sparrows are, first of all, rather opportunistic in their selection of perch sites, choosing them for their availability and, perhaps, density and size. Second, their preferences for particular foliage types, manifested only when other conditions are equal, can be altered through exposure to a different foliage type during the first two to three months of their life. We do not know, at present, how stable these artificially created preferences will prove to be.

Intra-clutch differences.—The eight hand-reared Chipping Sparrows were taken from a total of three nests located (a) about 1.5 meters up in a *Ligustrum* hedge, (b) 5–6 meters up in a *Thuja*, and about 3 meters up in a *Juniperus virginiana*. All three sites were in fairly open country, among rows of other trees and shrubs, but not in deep woods. No systematic differences between birds from different clutches were apparent.

Thus, the variability in behavior found among a small population of Chipping Sparrows, at least insofar as foliage preferences are concerned, does not appear to be merely a consequence of the locus of the parental home or nest. A genetically determined variability seems considerably more likely.

General considerations.—Obviously, preferences for a particular shape of leaf represent but a small fraction of the preferences that totally determine the choice of habitat. Nonetheless, the behavior of the Chipping Sparrows used in these experiments accords well with what one would expect of a bird that must be equipped to deal with a varied and varying environment. The temporal changes in the stimulus fields of temperate zone birds would favor a fair degree of opportunism over absolutely rigid preferences for particular stimulus objects, and a fair degree of genetically imposed variability in preferences as well. It will be recalled that these are just the reverse of the characteristics postulated for the birds of tropical areas (Klopfer and MacArthur, *ibid.*). These, it is assumed, are less opportunistic, and thus, while highly adapted to a stable environment, are quite incapable of meeting the demands of changing seasons. A repetition of these tests described above, using representative tropical species should allow a closer scrutiny of this hypothesis.

SUMMARY

The foliage preferences of Chipping Sparrows were measured under conditions that sought to minimize the effects of other variables such as perching opportunities, food,

and light intensity. Wild-trapped adults indicated a preference for pine over oak leaves, as did the two- to four-month-old *Kaspar Hauser* birds that were reared without sight of any foliage. Isolates that were reared in the presence of oak foliage showed a decreased preference for pine. Studies of the stability of this shifted preference are in progress.

ACKNOWLEDGMENTS

Support for this study came from NIH Grants M 4453 and M 2850. I am much indebted, as always, to Dr. R. H. MacArthur. For their patient and conscientious assistance, I also wish to thank Miss Torrie Lowenbach, Miss Trudie Lowenbach, C. Hamilton, and C. M. Barnard.

ZOOLOGY DEPARTMENT, DUKE UNIVERSITY, DURHAM, NORTH CAROLINA, 1 MAY
1962

NEW LIFE MEMBER



C. Brooke Worth, a staff member with the Rockefeller Foundation in Port of Spain, Trinidad, West Indies, is a new Life Member of the Wilson Ornithological Society. He received his baccalaureate degree from Swarthmore College, and his M.D. degree from the University of Pennsylvania. Dr. Worth's publications include "A Manual of Tropical Medicine," with Mackie and Hunter, and "The Nature of Living Things," with Enders, as well as numerous papers.

His principal interests in ornithology are bird banding and the relationships of birds to human disease; other allied interests include entomology, mammalogy, parasitology, and popular nature writing. He is also a member of the AOU, Bombay Natural History Society, South African Ornithological Society, etc., and was president of the Eastern Bird Banding Association, and editor of the journal of the Delaware Valley Ornithological Club.