

HABITAT SELECTION IN TWO SPECIES OF *SPIZELLA*: A CONCURRENT LABORATORY AND FIELD STUDY

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ABSTRACT.—Habitat selection in *Spizella passerina* and *S. pusilla* was studied in the laboratory and in the field at monthly intervals from December through June. The two species showed a significant difference in their responses to photographic transparencies of two habitats in the laboratory, *S. passerina* exhibiting a consistent though slight preference for a coniferous tree habitat in both morning and afternoon and *S. pusilla* showing a preference for the tree habitat in the morning and the field habitat in the afternoon.

In free-living populations the species both fed in the field habitat, mostly on the ground. There was a significant difference in non-feeding habitat preference, *S. passerina* preferring the tree habitat in both morning and afternoon and *S. pusilla* preferring the field habitat in both morning and afternoon. Field observations on a population of *S. pusilla* where *S. passerina* was not present showed a non-significant shift in preference similar to that seen in laboratory tests; the birds perched in trees in the morning and in fields in the afternoon. The non-feeding preferences shown in the field were considered most closely analogous to the laboratory results. *Received 15 July 1976, accepted 3 October 1977.*

SPATIAL segregation is one means by which closely related species may coexist (e.g. MacArthur 1958, Schoener 1974), but it is not always clear from field studies whether such segregation results from active habitat selection or some other mechanism (Klopfer and Hailman 1965). The term selection implies an ability to choose between two or more alternatives, yet field studies of habitat selection in birds have primarily emphasized correlations between habitat types and the presence or absence of a particular species (Wasilewski 1961, Hespeneheide 1971). Observations of what appeared to be active habitat selection have been reported by Niethammer (1940) for South African larks.

In his initial discussion of habitat selection as a psychological factor in bird distribution, Lack (1933) stated that the proximate factors to which a bird responds are not necessarily those that directly affect its survival in a given habitat. Klopfer (1963, 1965, 1967) and Oelke and Klopfer (1971) found that certain species of passerine birds could discriminate leaf size and shape and that this discrimination formed the basis of preferences exhibited in a two-choice situation in the laboratory. There is some evidence from the field that suggests that birds are also able to recognize more generalized habitat features. MacArthur et al. (1962) and James (1971) showed that gross features of the vegetation structure tended to be similar for different individuals of the same species on their breeding grounds. This implies that a *Gestalt* type of perception of the habitat is involved in selection (see Lack 1933, Klopfer and Hailman 1965).

One of the goals of the present study was to determine if Chipping Sparrows (*Spizella passerina*) and Field Sparrows (*Spizella pusilla*) would respond differently to photographic presentations of gross habitat types in the laboratory. These species are members of different but related species groups (Mayr and Short 1970) and are

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broadly sympatric in the eastern United States. They are morphologically similar, having a bill size ratio of 1.03 (Schoener 1965), and have extensive dietary overlap (Judd 1901, Evans 1964, Allaire and Fisher 1975). Species with such small differences in size and diet would be expected to show marked differences in habitat selection under conditions of resource limitation.

To aid in the interpretation of laboratory results, a further goal was to make simultaneous observations on habitat use in free-living populations of both species. Comparisons of laboratory and field results would be of value in assessing the validity of laboratory techniques and importance of habitat selection behavior in the patterns of spatial segregation observed in the field.

METHODS

Laboratory tests.—The test chamber consisted of a plywood box measuring 71 cm by 36 cm by 43 cm high with an incomplete partition in the center. On each end was a 24 cm by 19 cm high window and in the center of each compartment was a single perch mounted on a microswitch. A bird on a perch could see only the near window, the view of the far window being blocked by the central partition. Birds could move freely between chambers by passing through the space under the partition. Rectangular food and water dishes were recessed in the floor and centered on either side of the long axis of the box. The top of the apparatus had two symmetrically arranged hinged doors for introducing and removing birds and a centrally placed circular hole with a ventilation fan. Extensions on either end of the top supported clamp-type incandescent lamps with 100-watt bulbs. Display transparencies 25 cm by 20 cm high made from color slides were sandwiched between two plates of glass and were mounted in the windows. The transparencies were illuminated from outside by the lamps, which were connected to continuously-variable rheostats. Illumination was set at approximately three ft-c in each chamber using a Weston Model 707-67 ft-c meter. I placed a sheet of frosted acetate between the light sources and the transparencies to give uniform illumination. The inside of the boxes was painted flat white for the tests of December through May and for the June test was painted flat black to make the transparencies more distinct.

Birds used in the initial laboratory tests were captured in late summer from sympatric local populations in Pickens County, South Carolina. I maintained 12 individuals of each species in an outdoor aviary exposed to natural photoperiod and temperature. Six *S. passerina* were lost after only one test and three *S. pusilla* were lost after three tests because of rodent predation in the outdoor aviary. I replaced these birds with freshly netted birds from local wintering populations in January and February. Ten fresh birds of each species were used in June trials in order to test for possible effects of prolonged confinement on the first group. These birds were maintained under conditions identical to those of the first group.

Testing began the second day of each month from December 1973 through June 1974. I placed two different color transparencies, one of a stand of pine (Fig. 1A) and one of a field habitat (Fig. 1B) in the windows of each of two test chambers. These photographs were taken at localities in Pickens County and no birds from either locality were used as test animals. Three different photographs showing similar views of the same field locality were used during the course of the study. The one used for the tests of December through February showed the field as it appeared in September. For the March and April tests a February view of the field was shown and for May and June an April view was used. The same pine photograph, taken in September, was used throughout the study.

I tested 2 individuals of the same species each day, *S. passerina* and *S. pusilla* on alternating days, until a total of 10 individuals of each species had been tested. Morning tests were begun between 0700 and 0900 EST and afternoon tests were begun between 1330 and 1430 EST. An individual was tested in one box in the morning and the other box in the afternoon, and was always introduced through the door on the west-facing side. Because of the staggered arrangement of the transparencies this was the "tree" side in one test chamber and the "field" side in the other. Birds were left in the boxes for 2.5 h during which time I made field observations. The first half hour of a laboratory test was considered an acclimation period and was not included in the analysis. Between morning and afternoon tests birds were housed in individual cages on tables near windows in the laboratory that looked out on the wall of an adjacent building.

Perch hops were registered by an Esterline-Angus event recorder. The records were quantified by placing a ruler along the record and counting the number of millimeter marks containing one or more perch registrations. This quantity is referred to in the following discussion as the *perch index*.

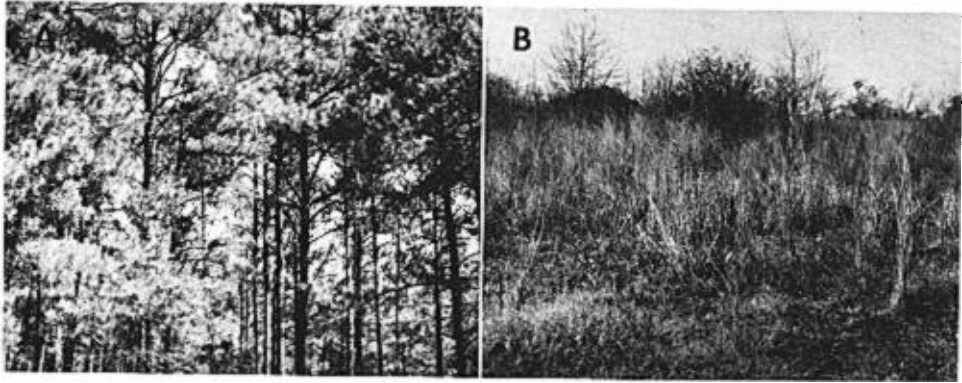


Fig. 1. Photographs used in laboratory test apparatus. A. Tree habitat. B. Field habitat.

Field observations.—The outdoor study area was located in a disturbed area consisting of an open garden of about 1 ha and surrounding stands of trees and shrubby areas in Pickens County, South Carolina. The trees were for the most part pines (*Pinus taeda*, *P. virginiana*, and *P. echinata*). The scattered deciduous trees included *Quercus falcata*, *Quercus nigra*, *Ulmus alata*, *Juglans nigra*, *Gleditsia triacanthos*, and *Liriodendron tulipifera*. In the shrub category were *Cercis canadensis*, *Juniperus virginiana*, *Prunus serotina*, *Conus floridana*, and *Salix* sp. Both *S. passerina* and *S. pusilla* utilized the area as breeding residents, transients, and winter residents.

The basic data on habitat distribution were collected in a manner similar to that described by MacArthur (1958). The study area was divided into "field" areas (including grasses, shrubs, brush piles, and garden) and "tree" areas (including both pines and hardwoods). The procedure involved searching the area until birds were encountered and then using a stopwatch to record the amount of time the birds spent in either habitat type. Care was taken not to alarm the birds during observations. On those occasions when birds were in an area that could not be clearly relegated to either the field or tree habitat, I assigned half the time to one type and half to the other. Notes were taken on the general activities of the birds under observation (e.g. feeding, maintenance activities, singing, etc.) and on interspecific and intraspecific interactions. An effort was made to equalize the amount of time spent searching the two types of habitat. Additional field observations were made on an allopatric population of *S. pusilla* in January and February 1974 at another locality in Pickens County. This site was similar to the main study area but lacked cultivated ground, and data were collected in a manner identical to that given above.

The field data were divided into two major categories for analysis: 1) feeding activities (any observations in which foraging movements were seen, not necessarily food-taking itself), and 2) non-feeding activities. The non-feeding observations were considered to be the most closely comparable to the laboratory data because they were indicative of perch site preference.

All data were tested with Analysis of Variance and the 0.05 level of probability or lower was accepted as significant in all statistical tests.

RESULTS

Laboratory tests

Considered independently, the data for each month's tests were too variable to reveal statistically significant relationships. There were no statistically significant differences among the monthly tests (including June), so the data for the entire period of study were combined and analyzed.

Spizella passerina exhibited significantly more perching activity than *S. pusilla* ($P < .001$). Overall, *S. passerina* perched most frequently in view of the pine photograph both in the morning and afternoon, while *S. pusilla* perched most frequently near the pine photograph in the morning, switching to the field photograph in the afternoon (Table 1). The shifting pattern of *S. pusilla* was evident in each month's

TABLE 1. Laboratory habitat preferences as expressed by perch indexes (all months combined). F = field habitat; T = tree habitat

	A.M.			P.M.		
	No. hours tested	F	T	No. hours tested	F	T
<i>S. passerina</i>	140	901	991	132	409	586
<i>S. pusilla</i>	138	342	876	138	422	257

test, excepting April. Neither of these preferences taken individually was statistically significant, but when the daily patterns of both species were compared with analysis of variance the differences were significant ($P < .05$).

Field observations of sympatric populations

Feeding.—There were no statistically significant differences between the two species in feeding habitat (Table 2). Both species fed primarily in the field habitat and almost always on the ground whatever the habitat. *Spizella passerina* was occasionally seen foraging briefly along pine branches and I recorded one instance of *S. pusilla* foraging among the emerging flowers of a low willow (*Salix* sp.). Both species were seen “flycatching” during the warmer months. *Spizella pusilla* engaged in flycatching much more than *S. passerina* and both did so almost invariably from the ground in the field habitat.

Some seasonal trends are evident in the monthly patterns of feeding habitat preferences shown in Table 2. The lack of selective preference in April deviated significantly ($P < .01$) from the other months because of an increased amount of feeding in the tree habitat by both species. This was correlated with a large influx of birds of both species, presumably transients. In June there were no feeding observations of *S. pusilla* in the study area though the number of non-feeding observations was not especially low (Table 3). *Spizella passerina* used the garden area not only for feeding in this month, but also for singing and copulation. Three recorded instances of interspecific aggression occurred in April and May. In two of these encounters *S. passerina* succeeded in driving off *S. pusilla* and in the other *S. pusilla* was dominant.

Non-feeding.—There was a significant ($P < .001$) difference between the two species with respect to non-feeding habitat use over the entire season (Table 3). *Spizella passerina* perched more frequently in the tree habitat and *S. pusilla* perched more

TABLE 2. Total number of seconds each species was observed in the two habitats at outdoor study sites (feeding activities) based on 209 h of observations. F = field habitat; T = tree habitat

	<i>Spizella passerina</i>				<i>Spizella pusilla</i>			
	A.M.		P.M.		A.M.		P.M.	
	F	T	F	T	F	T	F	T
Dec.	0	0	3,668	0	694	0	929	0
Jan.	910	151	1,234	155	1,081	0	464	0
Feb.	1,334	0	553	0	401	0	515	50
Mar.	5,641	0	1,491	0	4,448	45	4,943	10
Apr.	3,138	3,557	3,156	6,047	4,863	3,734	3,203	3,412
May	3,534	59	4,018	861	2,369	27	2,992	701
Jun.	3,628	91	591	0	0	0	0	0
TOTAL	18,185	3,858	14,711	7,063	13,856	3,806	13,046	4,173

TABLE 3. Total number of seconds each species was observed in the two habitats in the field (non-feeding activities) based on 209 h of observation

	<i>Spizella passerina</i>				<i>Spizella pusilla</i>			
	A.M.		P.M.		A.M.		P.M.	
	F	T	F	T	F	T	F	T
Dec.	0	1,700	130	2,104	1,962	30	1,729	0
Jan.	775	1,168	129	825	790	921	570	201
Feb.	0	1,363	106	1,642	1,243	411	3,839	1,477
Mar.	82	2,404	34	2,462	1,032	526	3,330	850
Apr.	1,108	1,616	27	3,094	3,934	2,093	20	1,287
May	1,249	2,005	335	2,582	2,245	836	1,859	447
Jun.	2,109	3,168	278	1,243	940	321	1,578	817
TOTAL	5,235	13,424	1,039	13,952	12,146	5,139	12,925	5,080

frequently in the field habitat. Furthermore, there was a significant ($P < .05$) three-way interaction in the data among the variables: species, time (A.M. or P. M.), and habitat; the preference of both species for their respective habitats was more pronounced in the afternoon than in the morning. This effect was only slight for *S. pusilla*, but was marked for *S. passerina*, whose use of the tree habitat increased by 21% in the afternoon.

Field observations of allopatric *S. pusilla*

The data on non-feeding habitat utilization for this population were combined for January and February for analysis. The pattern shown in the combined data for January and February was not statistically significant (Table 4). A pattern of daily shift is suggested, however, and is similar to that obtained in the laboratory.

The majority of feeding in the allopatric population was done on or close to the ground, but birds were frequently observed to forage among the needles of pine trees. This is in marked contrast to the behavior observed in the sympatric population, even though the proportion of time spent foraging in the tree habitat was about the same for both populations.

DISCUSSION

Orians (1971) stated that the proximate factors determining habitat selection behavior consist of those environmental features that evoke a settling reaction. The equivalent of this settling reaction in the laboratory tests of this study was a bird's sitting on one of the two perches in the test apparatus. The only reinforcement for choosing one side of the test chamber over the other was visual input from one of the two transparencies. Therefore, the proportion of time a bird spent perching in either half of the test apparatus could be considered an index to the attractiveness

TABLE 4. Total number of seconds allopatric *S. pusilla* were observed in the two habitats at outdoor study sites, based on 54 h of observation

	A.M.		P.M.	
	F	T	F	T
Feeding	12,062	990	3,916	3,107
Non-feeding	2,241	2,872	3,465	1,403

of the habitat independent of possible repelling forces such as competition or predation. Among the more obvious differences between the two transparencies was the greater amount of open sky in the photographs of the field habitat. Another was the stronger vertical orientation of the trees in the pine photograph contrasted with the more horizontal elements in the photographs of the field habitat. Future tests with this type of apparatus might involve the use of more simplified patterns if the mode of perception is to be investigated further.

Non-feeding habitat preferences of *S. passerina* and *S. pusilla* in free-living populations generally supported laboratory findings. The daily shift in preference of *S. pusilla* seen in the laboratory was not evident in the sympatric population though there was a suggestion of such a shift in allopatric populations. Free-living populations are faced with a wide array of stimuli, both physical and biological, that would be expected to modify patterns shown in the much-simplified laboratory environment.

My findings and those of other workers suggest that visual discrimination of habitat types can occur on at least two levels. Long-distance selection as shown by migratory birds in their landing behavior (Gauthreaux 1972) and by birds in the laboratory in this study must involve recognition of rather generalized habitat features. Within-habitat selection is probably based on such characteristics as light intensity or leaf size and shape (see Oelke and Klopfer 1971). Among the numerous other factors that determine the suitability of a habitat or microhabitat are thermal conditions (Calder 1973) and the presence of intraspecific or interspecific competitors (Fretwell 1968, 1972; Cody 1974).

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