FEEDING ECOLOGY OF THREE RESIDENT SYMPATRIC SPARROWS IN EASTERN TEXAS

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THE feeding ecology of two or more closely related organisms involves detailed observations of those organisms in their natural habitat. Of particular interest are ways in which competition for food is reduced between them. Moreau (1948) stated that whenever related species of birds overlap in range, they are either different in size or they use different methods of seeking food. Lack (1945) found that the sympatric Great Cormorant (*Phalacrocorax carbo*) and Shag (*Phalacrocorax aristotelis*) coexist by specializing on different foods. MacArthur (1958) and Morse (1973) reported that competition between closely related warblers was reduced, in part, by differences in vertical and horizontal feeding positions and behavior. Wiens (1969), in a study of seven grassland birds, and Hespenheide (1971), in a study of three eastern deciduous forest flycatchers, found preferences in habitat based on foliage density that would lead to a spatial distribution, thereby reducing competition for food.

The purpose of this study was to investigate the foraging behavior and food habits of the sympatric Bachman's Sparrow (Aimophila aestivalis), Field Sparrow (Spizella pusilla), and Chipping Sparrow (Spizella passerina) that have allowed them to coexist as permanent residents in eastern Texas.

METHODS AND MATERIALS

Field data were collected from 1 July 1971 to 29 February 1972, on two study tracts in Nacogdoches County, Texas. Field equipment consisted of a pair of 8 \times 35 binoculars, a clipboard with data sheets, and a folding aluminum chair. Observations were divided into summer (July and August), fall (September, October, and November), and winter (December, January, and February) seasons. An average of 15 h a month was spent in each study tract. Most observations were made during the first 4 h after sunrise. A total of 250 h was spent in the field.

Study tracts.—Study areas were located 14.3 km southwest (area I) and 6.5 km north (area II) from the junction of Highways 21 and 59 in Nacogdoches, and consisted of 10 and 8 ha, respectively. Area I was grazed land supporting an open stand of pine with a few hardwoods and a partial clearing with a small stock pond. Area II was an old brushy field with scattered bushes and small hardwoods, junipers, and pine trees.

The tree composition on area I was loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*), 79% (combined); persimmon (*Diospyros virginiana*), 7.5%; eastern red cedar (*Juniperus virginiana*), 6.5%; post oak (*Quercus stellata*), 3.5%; and sassafras (*Sassafras albidum*), 3.5%. Greenbriar (*Smilax* sp.) was abundant in certain areas. Some of the common grasses were little bluestem (*Schizocharium* sp.) and panicum (*Panicum* sp.).

On area II grew loblolly pine and shortleaf pine, 67.5% (combined); persimmon, 16%; eastern red cedar, 6%; sweetgum (*Liquidambar styraciflua*), 4.5%; and winged elm (*Ulmus alata*), southern red oak (*Quercus falcata*), post oak, and hercules club (*Zanthoxylum clava-herculis*), 6% (combined). Greenbriar was plentiful, and little bluestem and panicum were the most common grasses.

Food analysis.—A total of 29 Chipping Sparrows, 28 Field Sparrows, and 20 Bachman's Sparrows were collected away from the study tracts by shooting from August through February, in Nacogdoches, Angelina, and Jasper Counties. These birds were brought into the laboratory for measurement and stomach content analyses. Tarsus length, wing length, and bill length, width, and depth were measured to 0.1 mm with vernier calipers, and specimens were weighed on a triple beam balance. Sex (gonadal examination) and age (skull ossification) of all specimens were recorded. The gizzard and crop of each specimen were removed for seed and insect identification and seed measurements.

Seeds were segregated and counted, and measurements (to within 0.1 mm) were taken of their length, width, and depth with vernier calipers placed on the stage of a 0.7-3.0 adjustable power binocular microscope. The largest measurement was considered the seed length, the smallest measurement the seed depth, and the measurement between these two the seed width. Most of the seeds had already been hulled prior to consumption; therefore these measurements represent mainly those of the kernels. The number of seeds measured for each bird varied depending on how many seeds were found and their condition. In cases where 10 or more seeds of a particular kind were present, only five to 10 were measured, and average dimensions for this kind of seed were then calculated. If seeds were identifiable but badly fragmented no measurements were taken, but they were included in the total count. The mean length, width, and depth of seeds were calculated for every bird. Simple linear regressions were run with the various seed measurements as dependent variables and bill measurements as independent variables. All of the statistical analyses were performed on the WANG 700 Series Advanced Program Calculator with 702 output plotter at the Statistics Laboratory, Stephen F. Austin State University.

RESULTS

FORAGING BEHAVIOR

Height and time of foraging.—We found Bachman's Sparrows to be strictly ground feeders. Both Field and Chipping Sparrows foraged primarily within 1 m of the ground. They thus differed from Bachman's Sparrows by taking seeds that had not yet fallen to the ground, particularly grass and weed seeds. In this sense they inhabited a much wider niche than did the Bachman's Sparrow.

During the breeding season (July and August) all three species foraged during the first 5 h after sunrise and the last 2 h before sunset. Foraging during the nonbreeding season was not restricted to any particular time, but took place irregularly throughout the daylight hours. The hotter midday temperatures during the summer (breeding) season may explain these differences. Manner of foraging.—Although all three sparrows are predominately seed eaters, like other emberizines they feed their young insects and frequently supplement their own diet with insects when these are readily available. Insectivorous foraging was watched in all three species. The Field and Chipping Sparrows hunted by perching 30–40 cm above the ground and peering into the vegetation below. When a bird spotted a nonflying insect, it quickly descended from its perch and tried to catch it in its bill. In all cases seen, the insect was swallowed whole. Sparrows were relatively active when foraging for insects, at no time remaining on a particular perch for more than 10 sec; the almost constant movement apparently helped to flush insects. Chipping Sparrows were somewhat less active than were Field Sparrows.

Field Sparrows demonstrated the greatest variety of seed gathering techniques, and were the most acrobatic of all three species in procuring seeds. Flying to the tops of grasses, they let their weight carry both themselves and the stems to the ground where, still holding onto the grass stems, they ate the seeds, and then repeated the same procedure with new grass stems.

Field Sparrows spent more time foraging from low perches than did either of the other two species, and we never saw the Bachman's Sparrow feed above the ground at all. Field Sparrows often used brush piles, fallen trees, low shrubs, or barbed wire fences as perches from which to reach out and eat grass seeds off the tips of stems. Chipping Sparrows also occasionally foraged in the same manner.

Chipping Sparrows were more gregarious in their feeding behavior during the nonbreeding season than the other two species. Often they foraged in flocks of 25–50 birds. In area I, where this species was most common, they perched typically in the upper half of the taller trees (usually pines) and slowly, one-by-one, flew down to the ground and disappeared in the grass. After a while the birds flew back up into the trees and then moved on to another area, where they repeated this manner of group foraging. Field Sparrows were never seen in such large flocks, nor did their group foraging appear as well coordinated. It is difficult to postulate the adaptive significance of the gregarious feeding of Chipping Sparrows, but it may be a more efficient method of locating seeds from a rather large, relatively homogeneous habitat such as an open pine woods.

Bachman's Sparrows were shy and secretive and difficult to watch in the tall grasses among which they foraged. On one occasion (breeding season) in area I, I watched a Bachman's Sparrow for about 30 min foraging on the ground among some short grasses. It moved slowly and methodically, constantly searching the ground for food, and seldom

		Summer			Fall			Winter	
r amuy Genus	\mathbf{B}^2	н	C	В	F	c	В	н	C
Gramineae									
Digitaria sp.	0	92.2	77.5	4.5	42.6	42.9	0.8	29.1	35.2
Panicum sp.	95.2	0.5	0	67.8	10.7	8.2	89.5	2.5	1.7
Setaria sp.	4.8	0	8.9	11.2	28.2	9.2	0.4	0.2	6.5
Triodia sp.	0	0	5.3	4.1	9.8	0	2.5	5.1	0
Chloris sp.	0	0	0	0	0	0	6.3	3.1	5.2
Gramineae sp. 1	0	0	0	0	0	0	0	46.0	11.2
Gramineae sp. 2	0	0	0	0	0	13.9	0	14.0	36.9
Compositae	c	c	ע ע ע	04	c	20	C	c	С
1va sp.	5	2	C.O	t S	þ		>)	•
Leguminosae					c	¢		c	c
Galactia sp.	0	0	0	0	0	0	0.4	Ð	D
Cyperaceae									
Cyperus sp.	0	0	0	0	5.0	0	0	0	0
Euphorbiaceae									
Acalypha sp.	0	0.5	1.8	4.5	1.3	20.0	0	0	1.5
Euphorbia sp.	0	0	0	0	2.2	0	0	0	0
Unidentified	0	6.8	0	7.5	0.2	2.9	0	5.0	1.8
Total no. of seeds eaten	42.0	220.0	68.0	267.0	458.0	695.0	238.0	557.0	583.0
No. of birds examined	5 (3) ³	4 (4)	5 (5)	11 (10)	15 (13)	15 (15)	44 (4)	(6) 6	6) 6

KINDS OF SEEDS EATEN¹ BY BACHMAN'S, FIELD, AND CHIPPING SPARROWS TABLE 1

April 1975]

Sparrow Feeding Ecology

263

¹ Percent of total number. ² B = Bachman's, F = Field, C = Chipping. ³ Number of crops containing seeds is in parentheses.

	CHIPPING SPARROWS
	AND
	FIELD,
TABLE 2	BACHMAN'S,
	BΥ
	EATEN ¹
	ARTHROPODS
	OF
	KINDS

Order		Summer			Fall			Winter	
Class	B ²	ы	د ا	B	Ъ	ပ	 m	μ	C
Insecta									
Coleoptera	67.7	33.3	37.5	11.8	0	0	0	0	0
Isoptera	0	0	0	5.9	11.1	40.0	0	0	0
Orthoptera	0	16.7	62.5	11.8	0	0	0	0	0
Lepidoptera	13.3	25.0	0	41.1	88.9	0.09	0	0	0
Hemiptera	20.0	0	0	17.6	0	0	0	0	0
Homoptera	0	8.3	0	5.9	0	0	33.3	0	0
Diptera	0	0	0	0	0	0	33.3	0	0
Hymenoptera	0	8.3	0	0	0	0	0	0	0
Arachnoides									
Araneae	0	8.3	0	0	0	0	0	0	С
Unidentified	0	0	0	5.9	0	0	33.3	0	0
Total no. of arthropods eaten	15	12	00	17	0	15	~		
No. of birds examined	5 (3) ³	4 (3)	5 (2)	11 (8)	15 (4)	15 (4)	5 4 (2)	6 (0)	o) 6
¹ Percent of total number. ² $\mathbf{B} = \mathbf{B}$ achman's, $\mathbf{F} = \mathbf{F}$ ield, ³ Number of crops containing a	C = Chipping. arthropods is in p	arentheses.							

looked elsewhere. During this period it ate only seeds except for one grasshopper. This species appears to be more thorough and deliberate in its foraging than either the Chipping or Field Sparrows.

During the breeding season individuals of all three species foraged independently or in pairs, but in the nonbreeding season both Field and Chipping Sparrows foraged in flocks. These two species appeared to forage separately in the fall; but during the winter months we found both species together in mixed flocks, often also with Eastern Bluebirds (*Sialia sialis*), Cardinals (*Cardinalis cardinalis*), Dark-eyed Juncos (*Junco hyemalis*), Pine Warblers (*Dendroica pinus*), and Yellow-rumped Warblers (*Dendroica coronata*).

FOOD HABITS

Seeds and insects eaten.-The kinds of seeds eaten are shown in Table 1. All three species fed predominately on grass seeds. In general Field and Chipping Sparrows ate similar kinds of seeds throughout the period of this study, though their diets differed more in the winter than in the summer and fall. It could be that with an increase in winter residents competition for certain seeds was more intense and that alternative seeds (either size or shape) were utilized. Unlike the other two species, the Bachman's Sparrow ate mostly Panicum seeds throughout all three seasons. Table 2 shows the kinds of insects and spiders found in the crops and gizzards. Arthropods were eaten hardly at all in the winter months, and only in relatively small amounts (compared with seeds) during the summer and fall. Again Field and Chipping Sparrows were rather similar in the dietary items they chose (at the ordinal taxonomic level), and Bachman's Sparrows differed the most. As the variety and relative abundance of seeds and insects present in nature was not investigated, no statement can be made regarding preferences for different kinds of foods. Within a specific habitat (and possibly a preferred food size range) the three sparrows may have been eating merely what was available.

Correlations of seed size with bill size.—The hypothesis that food size is correlated with bill size and shape was tested (Table 3). In all cases, except when just seed length was used as the dependent variable, there was a statistically significant positive correlation (P = 0.001) of seed size with bill size. As bill size increased (length, width, depth, or a summation of these), so did seed size (width, depth, or a summation of these with length). The lack of correlations between bill size and seed length apparently results from the fact that Bachman's Sparrows have a much larger bill than Chipping or Field Sparrows have but they do not eat longer seeds (Fig. 1). Fig. 1 also shows that Field

X character (bill size)	Y character (seed size)	Correlation coefficient $(= r)$
		0.6562
D	D	0.678^{2}
\mathbf{L}	L	0.124
W + D + L	W + D + L	0.667 ²
W + D	W + D	0.685^{2}
W + D	W + D + L	0.619^{2}
$\mathbf{W} + \mathbf{D}$	L	0.102
L	W + D + L	0.682 ²
D	W + D + L	0.582 ²
W	W + D + L	0.645 ²
W + D + L	W	0.696 ²
$\mathbf{W} + \mathbf{D} + \mathbf{L}$	D	0.726 ²
W + D + L	L	0.121
W	W + D	0.682^{2}
D	$\mathbf{W} + \mathbf{D}$	0.660 ²
L	$\mathbf{W} + \mathbf{D}$	0.742 ²

 TABLE 3

 Regression Analyses of Seed Size on Bill Size¹

¹All specimens of all three species of sparrows with seeds in their crop are included (N = 34). The mean seed size for each bird is used. W = width; D = depth; and L = length. ²Significant at the 0.001 level of probability.

and Chipping Sparrows are very similar in all three seed and bill dimensions, though Chipping Sparrows tend to eat seeds very slightly larger than those consumed by Field Sparrows. This may be associated with the slightly longer bill of the Chipping Sparrow.

DISCUSSION

Birds appear to partition the food resources of a community in several different ways, thereby reducing competition. One way is in their foraging behavior (Lack 1954, MacArthur 1958, Orians and Horn 1969, Snow and Snow 1971). In this study Field Sparrows tended to utilize higher perches (brush piles, fallen trees, etc.) to obtain seeds than did either of the other species. Chipping Sparrows were gregarious and more organized in their manner of foraging. Such behavior may result in a more efficient form of locating food. Bachman's Sparrows, on the other hand, were not so gregarious as either of the other two species, and they foraged only on the ground. They also differed from Field and Chipping Sparrows in their more deliberate and thorough foraging techniques.

Another way in which food resources were partitioned was in the kind of food chosen. Field and Chipping Sparrows were very similar in the kinds of seeds and insects they ate in all three seasons (Tables 1 and 2), but Bachman's Sparrows differed considerably from these two species in the dietary items. The variety of foods eaten indicates

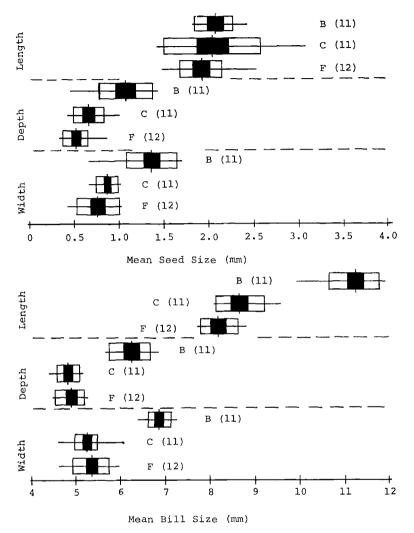


Fig. 1. Seed and bill dimensions of Chipping (C), Field (F), and Bachman's (B) sparrows. Sample size in parentheses. Vertical line = mean (\bar{x}) ; solid bar = standard error of the mean $(\pm S\bar{x})$; open bar = standard deviation $(\pm SD)$; horizontal line = range.

that the food habits of all three species are flexible. Such flexibility enhances their chances for survival should a particular kind of food become scarce. Evans (1964) in a similar study with Field, Chipping, and Vesper Sparrows (*Pooceetes gramineus*) found no evidence of significant differences in the kinds of foods eaten by the different species of sparrow and no indication of a food shortage. He concluded that the three species were able to breed sympatrically without competing for food because of its abundance.

Finally, a third way in which competition for food was reduced was by differences in sizes and shapes of seeds eaten. Studies (Hespenheide 1966, Newton 1967, Ashmole 1968, Pulliam and Enders 1971) support the idea that food size is correlated with bill size and shape in some birds. The data gathered (Fig. 1) showed that Bachman's Sparrow, which has a larger bill, ate larger (but not longer) seeds than did the other two species. It could be that longer seeds cannot be efficiently manipulated (Kear 1962, Willson 1971), or that a particular seed shape, L. Tinbergen's "searching image" (*in* Klopfer 1973), is desired. Competition for seeds of a particular size was more severe between Field and Chipping Sparrows. Both species ate long, thin, narrow seeds that were similar in size (Fig. 1). This may be a result of their similarly sized bills.

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SUMMARY

Differences in the feeding ecology of Bachman, Field, and Chipping Sparrows that permitted sympatric coexistence in eastern Texas consisted of differences in foraging behavior among all three species. Field and Chipping Sparrows had a wider niche, in a sense, than did the Bachman's Sparrow, because they foraged slightly above the ground as well as on the ground. Bachman's Sparrows were more deliberate in their feeding than were the other two species, and Field Sparrows were the most adept at obtaining seeds on the heads of tall grasses. Chipping Sparrows usually fed in well-organized groups.

Food habits were not the same. Bachman's Sparrows ate larger and different kinds of seeds than did the other two species, and also ate different kinds of insects. Bill size showed a significant positive correlation with seed size (except length). Field and Chipping Sparrows ate very similar foods and therefore competed for food in habitats where they occurred together.

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