Mazzoni, and D. Paullin read and improved earlier drafts of the manuscript, and D. Ehlers and A. Miller provided typing assistance. C. M. Kirkpatrick and L. Walkinshaw refereed the manuscript and provided suggestions, corrections, and comments for improvement. To them I am extremely grateful. Funds for the study have been provided primarily by the U.S. Fish and Wildlife Service.—CARROLL D. LITTLEFIELD, *Malheur Field Station, Box 260, Princeton, Oregon 97721.* *Received 27 Jan. 1984, accepted 2 Mar. 1985.*

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Diets of House Sparrows in urban and rural habitats.—The House Sparrow (*Passer domesticus*) is a familiar and important member of the urban avifauna. A close association with man has been a major factor in its success (Summers-Smith, The House Sparrow, Collins, London, England, 1967; Robbins, pp. 3–9 *in* A Symposium on the House Sparrow [*Passer domesticus*] and European Tree Sparrow [*P. montanus*] in North America, S. C. Kendeigh, ed., Ornithol. Monogr. 14, 1973). Despite its abundance and widespread distribution, relatively little is known of the ecology and behavior of the House Sparrow in urban habitats. Previous studies of food habits (Kalmbach, U.S. Dept. Agric. Tech. Bull. 711, 1940; Southern, Annals Appl. Biol. 32:57–67, 1945; Hammer, Danish Rev. Game Biol. 1: 3–59, 1948) generally have focused on agricultural populations. More recently, Seel (Ibis 111:36–47, 1969) reported diets of nestlings from suburban areas and agricultural villages in England.

The objectives of this study were to determine the food habits of urban House Sparrows during the breeding season, and to compare their diet with that of nearby rural sparrows. We also tested the reliability of tartar emetic (antimony potassium tartrate) as a technique for collecting food samples from sparrows.

Study area and methods.—The study area comprised separate urban and rural areas in Centre County, Pennsylvania. A 1.3-km^2 portion of the Borough of State College constituted the urban site, and included the business district plus neighboring residential areas. The urban area was arbitrarily divided into 15 blocks of approximately equal area, each containing one sparrow trap site. The rural area consisted of nine farms 8–16 km from State College. All were small family farms, 60–80 ha in size, raising dairy or beef cattle and crops primarily of corn and hay.

House Sparrows were captured in mist nets or unbaited Potter traps from 26 April through 28 July 1981 and were classified by age and sex. A trapping schedule of 2 days in the urban area to 1 day in the rural area was established to maintain fairly equal numbers of captures in each habitat throughout the study period. Also, a rotation of farms and urban trap sites was followed to ensure equal trapping pressure over the study areas. All trapping was done between 06:00 and 15:00 EDT.

Two methods were employed to obtain food samples from captured House Sparrows: (1) tartar emetic (antimony potassium tartrate), a local stomach irritant, was administered to all birds to stimulate regurgitation; and (2) a sample of sparrows was sacrificed and their stomachs removed. Each bird received an oral 0.4-cc dose of 0.5% solution of tartar emetic, and was placed in a darkened box lined with a plastic tray for 15 min. Regurgitated food was rinsed from the tray into storage vials containing 10% formalin solution. After treatment with the emetic, 322 birds were sacrificed. Stomachs and crops were removed and preserved in 10% formalin.

In the laboratory, food samples were rinsed on a nylon net sieve of 28 meshes/cm, and volumes of regurgitated and combined stomach and crop samples (hereafter called stomach samples) were measured by water displacement. Food items were identified with the aid of

TABLE 1

FREQUENCY OF OCCURRENCE (PERCENT) OF FOOD CATEGORIES AND FOOD ITEMS IN THE DIETS OF URBAN AND RURAL HOUSE SPARROWS IN CENTRE COUNTY, PENNSYLVANIA, 26 APR.–28 JUL. 1981

Food category or item	Urban (N = 218)		Rural (N = 267)	
Commercial cereal grains	66.5[a]	(19.3)[b]	97.3	(73.0)
Corn (*Zea mays*)	42.7	(6.9)	86.1	(49.4)
Oats (*Avena sativa*)	0.0	(0.0)	8.9	(4.1)
Wheat (*Triticum aestivum*)	5.0	(3.2)	7.8	(3.7)
Unidentified grains	40.8	(11.5)	60.3	(15.7)
Commercial birdseed	61.9	(25.7)	2.9	(0.7)
Millet (*Panicum miliaceum*)	35.8	(9.6)	1.8	(0.3)
Milo (*Sorghum vulgare*)	49.5	(14.7)	2.9	(0.3)
Sunflower (*Helianthus annuus*)	7.3	(1.4)	0.3	(0.0)
Other seeds	81.2	(21.6)	47.9	(1.8)
Grass and weed seeds	45.9	(3.2)	32.2	(1.8)
Compositae	2.8	(0.5)	1.4	(0.3)
Oxalis spp.	17.9	(0.0)	3.4	(0.0)
Panicum spp.	0.0	(0.0)	0.3	(0.0)
Polygonum spp.	18.8	(1.8)	12.4	(0.0)
Setaria spp.	8.7	(0.0)	1.4	(0.3)
Stellaria spp.	10.6	(0.5)	16.8	(1.1)
Unidentified grass seed	9.6	(0.0)	3.7	(0.0)
Unidentified seeds	25.7	(0.9)	21.7	(0.0)
Elm mast (*Ulmus americana*)	56.4	(18.3)	2.2	(0.0)
Plant fragments	47.2	(2.7)	62.9	(2.2)
Anthers	5.9	(0.0)	8.9	(0.3)
Flower parts	3.2	(0.4)	2.6	(0.0)
Grass fragments	26.1	(0.4)	46.1	(0.0)
Leaf fragments	19.7	(1.3)	17.6	(1.4)
Unidentified plant fragments	8.7	(0.4)	4.1	(0.3)
Insects and arachnids	93.1	(10.5)	94.3	(6.7)
Coleoptera	79.8	(6.4)	82.0	(5.6)
Carabidae	0.0	(0.0)	1.1	(0.3)
Curculionidae	3.6	(0.0)	4.4	(0.3)
Unidentified Scarabidae	0.0	(0.0)	1.4	(0.3)
Japanese beetle (*Popillia japonica*)	30.2	(3.6)	20.2	(1.8)
Unidentified Coleoptera	55.0	(2.7)	64.4	(2.6)
Insect larvae and pupae	26.6	(3.2)	26.2	(1.1)
Gypsy moth (*Lymantria dispar*)	4.1	(0.9)	0.3	(0.0)
Unidentified larvae	22.4	(2.2)	24.7	(1.1)
Unidentified pupae	0.9	(0.0)	2.9	(0.0)
Other insects	49.5	(0.9)	41.2	(0.0)
Collembola	3.6	(0.0)	1.4	(0.0)
Diptera	1.3	(0.0)	1.1	(0.0)

TABLE 1

CONTINUED

Food category or item	Urban (N = 218)		Rural (N = 267)	
Hemiptera	0.9	(0.0)	0.0	(0.0)
Unidentified Homoptera	2.7	(0.0)	4.4	(0.0)
Aphididae	4.1	(0.0)	3.7	(0.0)
Unidentified Hymenoptera	3.2	(0.0)	2.2	(0.0)
Formicidae	4.1	(0.4)	1.8	(0.0)
Orthoptera	0.0	(0.0)	1.1	(0.0)
Insect eggs	1.8	(0.0)	0.7	(0.0)
Unidentified insects	37.1	(0.4)	34.8	(0.0)
Arachnida	0.9	(0.0)	0.3	(0.0)
Miscellaneous items				
Parasites	30.2	(0.0)	26.5	(0.3)
Acarina	29.3	(0.0)	25.8	(0.0)
Cestoda	6.8	(0.0)	4.1	(0.3)
Mallophaga	0.4	(0.0)	0.3	(0.0)
Siphonaptera	0.4	(0.0)	0.7	(0.0)
Bread	5.0	(2.2)	0.3	(0.0)

[a] Includes all samples (regurgitated, stomach) obtained from a bird.
[b] Numbers in parentheses are the percentage of times the food category or item was the volumetrically most important item in a regurgitated sample.

a reference collection and seed and insect keys, and were ranked visually in order of volume. The efficiency of the emetic was evaluated by comparing the volume and composition of regurgitated samples with the birds' total stomach contents.

Food items in each sample were combined for statistical analysis into five categories: commercial cereal grains, commercial birdseed, other seeds, plant fragments, and insects and arachnids. To ensure that no food items present in a bird were missed, only combined stomach and regurgitated samples from sacrificed birds were used. Loglinear analysis (Bishop et al., Discrete Multivariate Analysis: Theory and Practice, MIT Press, Cambridge, Massachusetts, 1975) was used to determine differences in food habits of urban and rural House Sparrows. The method uses a contingency table to detect interactions among variables under the null hypothesis of independence. Each contingency table included habitat (urban or rural), sex, age (juvenile or adult), and presence or absence of a food category. To examine significant interactions in more detail, log-odds of presence versus absence of a food category were calculated for each sex and age class in each habitat. Standard errors and approximate 95% simultaneous confidence intervals were calculated according to Haberman (Analysis of Qualitative Data, Vol. 1, Academic Press, New York, New York, 1978).

Analysis of diets.—Food samples were collected from 218 urban and 267 rural House Sparrows; 322 of these birds (158 urban, 164 rural) were sacrificed to obtain stomach contents after being treated with tartar emetic. Commercial cereal grains (97.3% of samples) and insects (94.3%), primarily coleopterans, were the most frequently occurring foods of rural House Sparrows (Table 1). Insects (93.1%), other seeds (81.2%), cereal grains (66.5%), and commercial birdseed (61.9%) were important foods of urban birds. Birdseed in urban birds and cereal grains in rural birds were the most important food categories by volume in regurgitated samples.

TABLE 2
LOGLINEAR MODELS AND GOODNESS-OF-FIT STATISTICS FOR PRESENCE OR ABSENCE OF FOOD CATEGORIES IN HOUSE SPARROWS

Food category	Model[a]	df	G^2	P[b]
Commercial cereal grains	Y = FH + AH + AS + E	8	13.06	0.109
Commercial birdseed	Y = FH + AS + FA + E	8	4.86	0.772
Other seeds	Y = FH + AH + AS + E	8	11.45	0.177
Plant fragments	Y = FH + AH + AS + E	8	9.84	0.276
Insects and arachnids	Y = AH + AS + F + E	9	9.00	0.437

[a] Y = ln(expected cell count), F = presence or absence of food category, H = habitat, A = age, S = sex, E = error term.
[b] Nonsignificant ($P > 0.05$) test statistic indicates good model fit.

The simplest loglinear model predicting the presence or absence of cereal grains in House Sparrows included interactions between grains and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). The only significant difference in consumption of grains was between urban and rural juvenile males (Table 3). All rural birds, however, were more likely than urban birds to consume grain, and adults were more likely to do so than juveniles.

The presence of commercial birdseed in House Sparrows was affected by interactions between birdseed and habitat, age and sex, and birdseed and age ($P < 0.05$) (Table 2). Among adult sparrows, urban birds consumed birdseed significantly more often than rural birds (Table 3). All categories of urban sparrows ate more birdseed than rural birds did, and urban adults ate more than juveniles.

The simplest model describing the presence of other seeds in House Sparrows included interactions between seeds and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). Urban birds consumed other seeds more frequently than did rural sparrows, with juvenile males being most likely to include other seeds in their diets ($P < 0.05$) (Table 3). Significant differences also existed between rural adult males and urban adults, and between rural adult females and urban adult males.

The model describing the occurrence of plant fragments in House Sparrows included interactions between plant fragments and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). No differences were detected in log-odds ($P > 0.05$) (Table 3); however, rural birds were generally more likely to eat plant fragments than were urban birds.

Consumption of insects and arachnids by sparrows was influenced by interactions between age and habitat, and between age and sex ($P < 0.05$) (Table 2). There was no significant effect of habitat on presence of this food category in sparrows. There were also no differences in log-odds of the presence of insects and arachnids in different groups of sparrows ($P > 0.05$) (Table 3). However, urban birds, except for juvenile males, were somewhat more likely to consume insects and arachnids than were rural birds.

Efficiency of the emetic.—Of 485 birds treated with tartar emetic, 93% regurgitated food. The 322 sparrows that were sacrificed following treatment with the emetic regurgitated an average of 58.3% (range 0–100%) of the total volume of food in the stomach and crop. Food remained in the crops of only 9.3% of those sparrows.

Not all food in a sparrow was regurgitated; therefore, it was necessary to determine if the regurgitated sample was representative of the composition of the total stomach contents in a bird. To do this, the number of food categories present in a bird was compared with the number of categories in the regurgitated sample. Twenty-seven percent (N = 322) of the birds were missing one or more categories in the regurgitated sample.

TABLE 3

LOG-ODDS[a] OF THE PRESENCE OF FOOD CATEGORIES IN HOUSE SPARROW STOMACHS

Food category	Habitat	Age	Sex	Log-odds ± SE	95% confidence interval[b]
Commercial cereal grains	Urban	Adult	Female	0.759 ± 0.282	−0.014, 1.532
			Male	1.141 ± 0.292	0.341, 1.940
		Juvenile	Female	2.120 ± 0.864	−0.247, 4.490
			Male	−0.232 ± 0.395	−1.310, 0.848
	Rural	Adult	Female	4.533 ± 1.420	0.643, 8.420
			Male	4.533 ± 1.420	0.643, 8.420
		Juvenile	Female	3.664 ± 1.432	−0.256, 7.580
			Male	3.555 ± 0.828	1.290, 5.830
Commercial birdseed	Urban	Adult	Female	0.456 ± 0.269	−0.281, 1.193
			Male	0.681 ± 0.265	−0.045, 1.407
		Juvenile	Female	−0.143 ± 0.536	−1.610, 1.330
			Male	−0.903 ± 0.433	−2.090, 0.287
	Rural	Adult	Female	−4.533 ± 1.420	−8.420, −0.643
			Male	−3.412 ± 0.830	−5.680, −1.142
		Juvenile	Female	−3.662 ± 1.432	−7.580, 0.256
			Male	−4.673 ± 1.420	−8.560, −0.783
Other seeds	Urban	Adult	Female	1.630 ± 0.355	0.660, 2.600
			Male	1.876 ± 0.368	0.866, 2.880
		Juvenile	Female	1.526 ± 0.698	−0.384, 3.440
			Male	3.932 ± 1.428	0.022, 7.840
	Rural	Adult	Female	0.000 ± 0.292	−0.800, 0.800
			Male	−0.522 ± 0.302	−1.350, 0.308
		Juvenile	Female	0.731 ± 0.477	−0.579, 2.040
			Male	0.037 ± 0.272	−0.713, 0.787
Plant fragments	Urban	Adult	Female	0.313 ± 0.267	−0.419, 1.045
			Male	−0.220 ± 0.252	−0.910, 0.470
		Juvenile	Female	−0.747 ± 0.572	−2.320, 0.823
			Male	0.077 ± 0.393	−1.000, 1.160
	Rural	Adult	Female	0.522 ± 0.302	−0.305, 1.350
			Male	0.171 ± 0.293	−0.629, 0.974
		Juvenile	Female	0.511 ± 0.462	−0.759, 1.780
			Male	1.099 ± 0.314	0.239, 1.960
Insects and arachnids	Urban	Adult	Female	3.100 ± 0.647	1.330, 4.870
			Male	3.730 ± 0.826	1.470, 5.990
		Juvenile	Female	3.296 ± 1.440	−0.654, 7.250
			Male	1.861 ± 0.575	0.281, 3.440
	Rural	Adult	Female	2.520 ± 0.556	0.750, 4.290
			Male	2.520 ± 0.556	1.000, 4.040
		Juvenile	Female	2.512 ± 0.849	0.182, 4.840
			Male	4.673 ± 1.421	0.783, 8.560

[a] Within a food category, a higher log-odds indicates increased likelihood of consumption of the food by that group of birds; no comparisons were made across food categories.

[b] Simultaneous confidence intervals are shown for each habitat-age-sex category of birds; categories may have been combined in certain comparisons.

TABLE 4
FREQUENCIES OF OCCURRENCE OF FOOD CATEGORIES IN REGURGITATED AND STOMACH SAMPLES FROM HOUSE SPARROWS (N = 322) IN CENTRE COUNTY, PENNSYLVANIA, 29 MAY–28 JUL. 1981[a]

Food category	Regurgitated	Stomach[b]
Commercial cereal grains	246	274
Commercial birdseed	77	91
Other seeds	189	220
Plant fragments	148	185
Insects and arachnids	286	310

[a] Frequencies of food categories in regurgitated and stomach samples were not different ($\chi^2 = 2.29$, df = 4, $P > 0.05$).
[b] Includes stomach and regurgitated samples combined for each bird.

Although use of tartar emetic causes food categories present in individual birds to be missed, the technique still gives a reliable indication of the diet of a population as long as certain foods are not consistently overlooked. For the 322 sacrificed House Sparrows, the frequencies of food categories in regurgitated samples were not different from those present in the birds ($P > 0.05$) (Table 4).

Discussion.—Food items were tabulated by frequency of occurrence, and statistical analysis was based on presence or absence of a food category in a bird. Problems exist with all methods of food analysis (Hartley, Ibis 90:361–381, 1948). Frequencies have the disadvantage that food items may receive the same rating whether a small fragment or a full crop is present. A combination of frequencies and volumes of items may be most useful (Korschgen, pp. 233–251 *in* Wildlife Management Techniques, R. H. Giles, Jr., ed., The Wildlife Society, Washington, D.C., 1971), but volumes were too small to measure in House Sparrows. Instead, major items were ranked visually by volume in each sample.

Urban and rural House Sparrows differed significantly in their use of food categories, probably reflecting differences in food availability to these opportunistic feeders (Kalmbach 1940). Urban sparrows relied on more food sources than did rural sparrows. Rural birds consumed primarily cereal grains and insects, mostly coleopterans. In urban sparrows, on the other hand, grains, birdseed, other seeds (primarily mast), and insects (primarily coleopterans) were all important foods. Urban sparrows may not have a single food source as abundant and consistently available as grains are for rural sparrows.

Corn was the most important cereal grain in the diet of rural House Sparrows. In our study area, feed corn was grown and stored on most farms. Sparrows presumably obtained corn from fields, waste feed, and animal dung.

Corn was present in fewer than half of the urban birds. Here, corn and other grains probably were derived from commercial birdseed mixtures. Bird feeding is common in State College, even during summer. Geis (U.S. Fish and Wildl. Serv., Spec. Sci. Rep. Wildl. 233, 1980) found that coarsely cracked corn in feeders was eaten by several species of birds, including House Sparrows, but he considered wheat and oats to be relatively unattractive.

The commercial birdseed category included only sunflower, millet, and milo; it was consumed by 61.9% of urban birds and was most often ranked number 1 in regurgitated samples. If we had grouped corn, wheat, and oats with commercial birdseed for urban House Sparrows, birdseed would have been recorded in 82.6% (180/218) of urban samples. Insects and arachnids were more frequent (93.1%), but birdseed was much more important volumetrically.

Birdseed in urban birds and commercial cereal grains in rural birds were consumed more frequently by adult sparrows than by juveniles. Juveniles and nestlings are known to consume more animal matter and fewer seeds than adults (Kalmbach 1940). No age differences, however, were noted in the use of other seeds, which were often smaller and softer than birdseed or grains. Age differences in the use of some food items may have been blurred as older juveniles acquired adult food habits.

Coleopterans were the most important insect foods of both urban and rural House Sparrows. Resistance of the tough exoskeleton to digestion may bias results in favor of beetles over softer bodied insects. House Sparrows, however, are likely to encounter many beetles as they forage along the ground.

The significant difference between habitats in consumption of other seeds was largely due to the preponderance of elm seeds in urban birds. The Borough of State College has many elms as street trees, and sparrows exploited elm mast as a food source.

House Sparrows probably ingested plant fragments inadvertently while feeding on seeds and insects. Plant fragments rarely were the most abundant food category in a sample. Approximately twice as many rural as urban birds consumed grass fragments. This was due to the inclusion of hay and straw among the grass fragments. Rural sparrows probably ingested such fragments while foraging for waste grain in manure and barnyards.

House sparrows often were observed feeding on discarded food and refuse, especially in the urban area. The extent of this feeding was difficult to determine, as much of this food may have been digested too quickly to be detected in food samples.

Examination of regurgitated and residual stomach samples from a large number of birds showed that tartar emetic gave a reliable representation of the frequency of occurrence of food categories in the sparrow population, even though food items in individual birds often were missed. The emetic was also relatively quick and easy to administer and took effect rapidly. This minimized the amount of time between catching a bird and obtaining a food sample, reducing the possibility that easily digested food items could not be identified. Sparrows were sacrificed or released approximately 15 min after treatment with the emetic. All birds appeared healthy when released, but subsequent mortality was not determined. Zach and Falls (Can. J. Zool. 54:1599–1603, 1976) used tartar emetic on captive Ovenbirds (*Seiurus aurocapillus*), and most birds regurgitated; however, 12.5–50.0% died within a week.

Conclusions.—The bulk of the food consumed by both urban and rural House Sparrows came directly or indirectly from man. Management of House Sparrows through control of these food sources should therefore be feasible, although difficult as sparrows will readily exploit alternate food sources. Furthermore, the major spring and summer food of urban sparrows in our study area, commercial birdseed, cannot be made less available without affecting other species that frequent bird feeders and reducing the enjoyment of many urban residents.

Diets of House Sparrows were affected by age and sex of the birds as well as by habitat. Probable reasons include maturation of juveniles and differences in foraging behavior or dominance in relation to the dispersion pattern of different food types. Among urban birds, higher use of birdseed by adults may have been due in part to their dominance over young birds at food patches (feeders). When they fed on other seeds, a similar but more widely dispersed food source, juveniles consumed as much or more than adults.

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Vegetation structure and Vesper Sparrow territory location.—Vegetation structure can affect avian habitat selection (e.g., Whitmore, Wilson Bull. 91:592–598, 1979; Meents et al., Auk 98:818–827). As it also affects reproductive success in some species (Wray and Whitmore, Auk 96:802–805, 1979; Redmond et al., Can. J. Zool. 60:670–675, 1982), it should therefore affect territory location. Wray and Whitmore (1979) found that Vesper Sparrow (*Pooecetes gramineus*) reproductive success was positively correlated with percent litter cover and vertical vegetation density, and negatively correlated with percent bare ground around the nest. I tested the hypothesis that vegetation structure also affects where Vesper Sparrows locate their territories.

The study site was located on an upland grassy ridge in central west Montana, 1.4 km north of Missoula, Missoula County (114°W, 47°48'N; elevation 980 m). The vegetation was mostly mixed grasses and forbs of variable height and density.

In the first three weeks of April 1983, I established four plots, each of which was a 175 ×

TABLE 1

MEAN VALUES (STANDARD DEVIATION) OF CONTINUOUS VARIABLES USED IN THE DISCRIMINATION OF GRID POINTS FROM USED AND UNUSED AREAS

Variable	Used (N = 52)	Unused (N = 88)
Vegetation height (cm)		
Mean at the grid point	20.23 (13.1)	22.67 (18.5)
Mean at 1 m	24.01 (10.9)	31.26 (18.5)
Mean at 5 m	28.97 (9.5)	34.47 (10.8)
% ground cover[a]	351.26 (29.1)	343.25 (36.7)
% grass cover[a]	144.96 (94.9)	125.82 (76.8)
% forb cover[a]	206.30 (95.6)	217.96 (76.7)
Vertical vegetation density[b]	3.54 (1.8)	3.49 (1.9)
Horizontal vegetation density[c]		
At 1 m	505.63 (275.7)	633.27 (333.7)
At 5 m	1710.45 (758.2)	2163.85 (984.5)
Height of nearest perch (cm)	90.00 (39.0)	93.7 (24.0)
Distance from grid point to nearest perch (m)	9.32 (6.4)	8.06 (5.5)

[a] Cumulative percent cover (max = 400).
[b] Mean number of contacts with vegetation.
[c] Cumulative percent cover (max = 4000).