SEED SELECTION IN SOME NORTH AMERICAN FINCHES

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Food selection and feeding "strategies" have recently received considerable theoretical attention. The models of MacArthur and Pianka (1966), Emlen (1966, 1968) and Schoener (1969a, b) focus on the evolution of dietary specialists and generalists, and highlight the importance of the relationship between food preferences and harvest yield. One important measure (but not the only one, Rozin and Mayer 1961) of harvest yield is caloric intake: do "predators" (seed-eating birds in this case) prefer "prey" (seeds) of high caloric content, those providing the most calories per unit time, or does preferred "prey" have other characteristics? How does food selectivity change in response to food density, hunger levels, and metabolic stresses?

Food preferences and degree of selectivity might also be expected to vary with the ability of an animal to handle different sizes of prey. In birds, it has frequently been shown, and is generally assumed, that larger-billed birds tend to take larger food items than their smaller-billed relatives. (Lack 1947; Morris 1955; Cade 1960; Hespenheide 1966; Myton and Ficken 1967; Newton 1967; and Holyoak 1970) and may also take a wider range of food sizes (Snodgrass 1902; but see Bowman 1961; Newton, op. cit.).

The present study deals with seed selection of several species of finches in relation to bill size, seed-husking speed, seed size, caloric content, and rate of caloric intake under two temperature regimes in the laboratory. The data provide evidence relevant to the theoretical models and additional evidence regarding the closeness of the correlation between bill size and food-size preference.

METHODS

Birds utilized in experiments were captured near Champaign-Urbana in mist nets, mainly in the fall, and were brought into the laboratory for a week or more before testing. During this time, as well as between tests, the birds fed on a seed mixture containing the seed types used later in preference tests. This procedure allowed them to become at least somewhat familiar with the test seeds, so that they would not have to learn how to handle the various seed types during the tests. The rationale for this approach is the reasonable assumption that birds become familiar with many of the seed types they encounter in the wild, and become accustomed to handling them. If choices in the wild are based at least in part on various characteristics of seed shape and size, it is likely that the birds will carry their ability to discriminate by these characteristics into the lab with them, but the exercise of the ability surely depends on some familiarity with the new seed types. Preferences were quite stable during the tests; only rarely did a bird show a trend in its preference while the experiments were in progress (see also Brown 1969).

Tests were run on birds caged individually, to avoid interference between birds at the feeding dish. Cage size varied from slightly less than ½ m to almost 1 m in all dimensions. There was no evidence of any effect of cage size on discrimination in the manner shown by Neumann and Klopfer (1969), for birds in smaller cages were as consistent in preference as those in large cages. A pilot study on a few individuals indicated that visual isolation of each bird from its neighbor had a negligible effect on individual seed preferences. Visually isolated birds brought into sight of each other did not change their preferences any more than birds remaining isolated or birds in continual visual contact.

Eight kinds of commercial seeds (chosen for availability, low price, and variability in size and shape) were presented to each bird in a ring-shaped compartmented dish 15 cm. in diameter. The orientation of the dish with respect to the perches and water dish and the order of seeds in the dish were changed for each trial. It may be argued that this method of presentation meant that successive choices were not independent; however, the same may well apply in the wild, even if "searching images" (Tinbergen 1960) and feeding "bouts" are not involved, and experience may affect choice in any case (Holling 1955, Murdoch 1969; Rabinowitch 1969). I did not deal with the behavioral mechanisms of choice-making, nor with the possible effects of the presence of certain seed types on preferences (Beukema 1968; Dawkins 1969; Dawkins and Impekoven 1969; Holling 1959; Newton 1968), nor with effects of food distribution (Ivlev 1961).

A few species of the test seeds (hemp, *Cannabis sativa*; oats, *Avena sativa*; sunflower, *Helianthus annuus*) may have been sometimes available to free-living birds; but wild hemp and sunflower, and perhaps some strains of oats, are very different from the cultivated varieties used here. The remainder (flax, *Linum usitatissimum*; rape, *Brassica* sp.; millet, *Panicum miliaceum*; canary, *Phalaris canariensis*; niger thistle, probably *Guizotia abyssinica*) were probably seldom encountered. Each compartment of the seed dish was filled to the same level, low enough to prevent the birds from scattering the seeds about, and high enough that the birds never came close to emptying any compartment. A test series consisted of 10 presentations of the dish to each bird for a period of two to three hours on different days.

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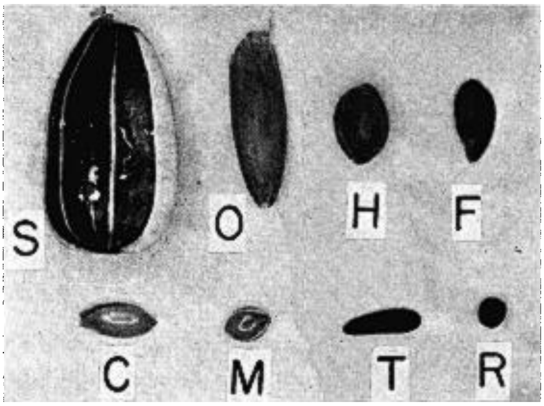

FIGURE 1. Seed types used in preference tests. S) sunflower; O) oats; H) hemp; F) flax; C) canary; M) millet; T) thistle, R) rape. Scale: hemp seeds average about 4 mm long.

Ideally, both duration and time of day should have been held constant; however, individuals with consistent preferences maintained those preferences regardless of the time, and individuals with fluctuating choices were found both among birds for which trials occurred at about the same time and among birds with variable trial times. Seeds were weighed before and after each presentation and the weights converted into an estimate of the number of seeds eaten and of the calories ingested. The birds were not observed during the tests.

The widely differing shapes of the test seeds render difficult any ranking of seed size by linear dimensions; therefore an index of seed size was obtained using seed weights. These averages were obtained for large seeds by making at least 10 one-gram weighings of each seed type. The weights of smaller seeds (of which it takes many to make a gram) were estimated by counting, again 10 times, the number needed to achieve a certain fraction ($\frac{1}{10}$–$\frac{1}{2}$) of a gram. While this index of size may not be totally satisfactory, it may be noted here that an index of size based on an average of the ranks of three linear dimensions for each seed yields a virtually identical ranking.

Caloric content of seed kernels was determined by combination in a bomb calorimeter. Protein and fat contents of whole seeds were determined by Kjeldahl and nuclear magnetic resonance spectroscopic techniques, respectively. Since these values may vary tremendously depending on the variety, growing conditions, etc. of the seeds, they should not be used in other studies using these seed types (F. I. Collins, pers. comm.). Water content was estimated by drying for 48 hr at 65°C. Seed weights and caloric contents and other characteristics are presented in table 1; seeds are shown in figure 1.

Timings of the husking and eating of seeds were made with a stop watch, approximately to the nearest 0.1 sec.

Bill meaurements were made to the nearest 0.1 mm with a vernier caliper. Bill length was measured from the posterior edge of the nostril to the tip, width and depth, at the anterior edge of the nostril. Bill dimensions are given in table 2. All three bill dimensions are significantly correlated (Spearman rank correlation, all $r_s > 0.90$, $n = 8$, $P < 0.05$) (see figure 2 for illustrations of bills).

Numbers of individuals tested at room temperature (approx. 25°C) and at freezing temperature ($\leqslant$ 0°C) are as follows: Cardinal (*Richmondena cardinalis*), 4 and 0; Fox Sparrow (*Passerella iliaca*), 3 and 0; Song Sparrow (*Melospiza melodia*), 9 and 3; Swamp Sparrow (*M. georgiana*), 4 and 2; White-throated Sparrow (*Zonotrichia albicollis*), 7 and 3; Slate-colored Junco (*Junco hyemalis*), 9 and 6; Tree Sparrow (*Spizella arborea*), 10 and 6; Field Sparrow (*S. pusilla*), 6 and 0. Some individuals were tested at both temperatures. Except for cardinals, individuals were not identified as to sex; all were released at the end of the trials. None of the species tested are obligate seed-eaters; all consume arthropods at some seasons and feed arthropods to their young.

SEED PREFERENCES IN THE LABORATORY

The number of seeds eaten and the caloric intake are both necessary measures of seed preferences. The importance of each seed type as an energy source is measured by caloric intake; the numbers of seeds of each type chosen are an indication of the birds' behavioral responses in adjusting their diets.

All species tested showed distinct seed preferences in terms of numbers of seeds eaten. Figure 3 shows also that four of the test seeds were preferred to the virtual exclusion of others by the experimental birds as a group: sunflower, oat, rape, and flax seeds were seldom eaten in any quantity. Field Sparrows,

TABLE 1. Characteristics of seeds used in tests.

	No. whole seeds/g		Approx cal.		Whole seed composition (%)		
Seeds	$\bar{x}$	$SE_{\bar{x}}$	per kernel	per g kernel	water	protein	fat
Sunflower	8.3	0.18	440	7325	3	15	24
Oats	33.8	0.68	90	4719	5½	13	4
Hemp	59.5	0.81	59	7195	3½	25	34
Canary	153.2	3.0	12	4387	6	12	7
Flax	182.9	5.8	21	7115	3	29	40
Rape	271.0	27.9	18	7457	2½	15	55
Millet	293.0	18.0	8	4494	6½	13	4
Thistle	343.5	11.0	10	6733	3	21	40

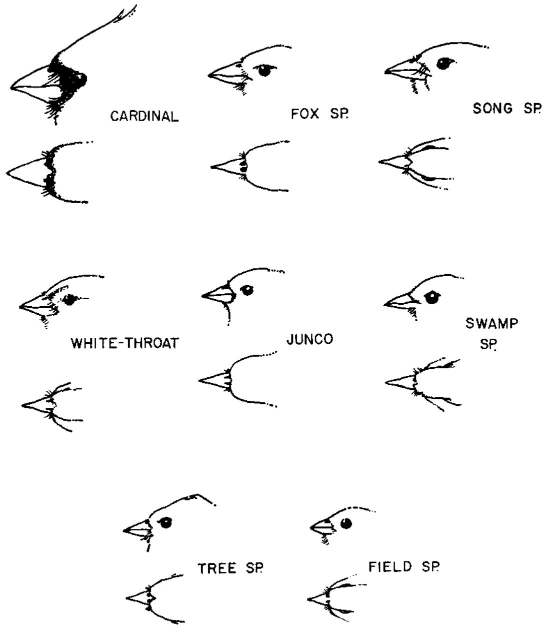

FIGURE 2. Bills of bird species tested, top and side views. To scale.

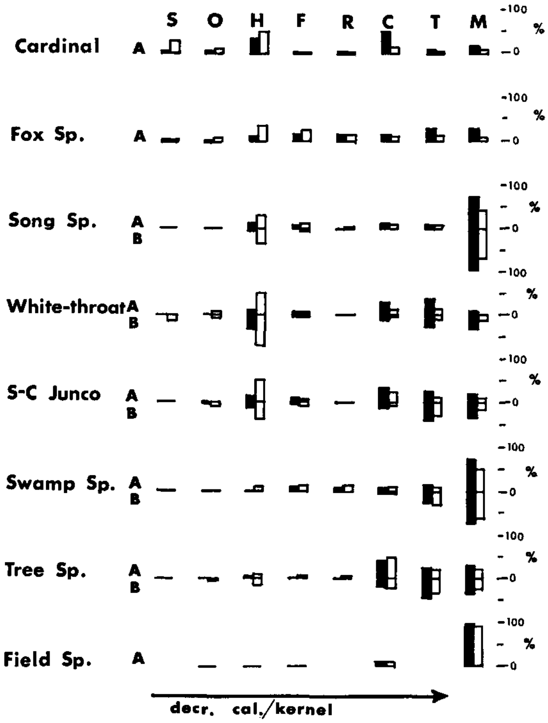

FIGURE 3. Seed choice vs. caloric content of kernel. Average per cent of diet comprised by different seeds A) at room temperature (~25°) and B) at freezing temperatures ($\leqslant 0°C$). Solid bars: per cent of seed numbers; open bars: per cent of calories. Birds are ranked in order of decreasing bill length; seeds are ranked in order of decreasing caloric content of the kernel.

Swamp and Song Sparrows preferred millet to any other type of seed (Wilcoxon matched-pairs signed-rank test, $P < .05$), white-throats ate mostly thistle and canary, Tree Sparrows ate mostly canary but also considerable millet and thistle. Fox Sparrows, juncos, and male Cardinals showed no statistically significant preference among the four general favorites. Using the averages in figure 3 as the best estimators presently available for degrees of preference, the choices of seeds by all species are significantly different from each other (χ^2 on numbers eaten, interspecific pairwise comparisons, df ranging from 2–6, $P < 0.05$).

Considering the *calories* contributed to the diet by each seed type (fig. 3), rather than numbers, Field, Swamp, and Song Sparrows still utilized millet most heavily, and for Tree Sparrows canary seeds were most important in calories as well as in numbers. For Fox and White-throated Sparrows, juncos, and male Cardinals, hemp was the main source of calories, but was not most prominent in numbers eaten.

TABLE 2. Bill dimensions (mm) of test species in order of decreasing bill length.[a]

		Length		Depth		Width	
Species	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Cardinal	21	14.2	.586	12.0	.425	8.6	.411
Fox Sparrow	40	11.3	.488	7.4	.475	5.7*	.356
Song Sparrow	50	10.5	.436	6.7*	.364	5.4*	.195
White-throated Sparrow	50	10.1*	.386	6.6*	.315	4.9	.272
Slate-colored Junco	50	10.0*	.374	5.7†	.250	4.5†	.234
Swamp Sparrow	50	9.6	.418	5.3	.258	4.2‡	.229
Tree Sparrow	50	9.2	.319	5.6†	.271	4.4†	.185
Field Sparrow	40	7.8	.476	5.0	.254	4.2‡	.293

[a] All specimens were collected in midwestern states and obtained from the Chicago Museum of Natural History; only male Cardinals were tested; other species not sexed.

Species pairs marked * or † or ‡ do *not* differ at the 0.05 level (t-test) in the indicated dimension; all others do.

TABLE 3. The average percentage of the number of seeds eaten by finches in three bill-size categories: long and deep (Cardinal and Fox Sparrow), medium (Song Sparrow, whitethroat, junco, plus Tree Sparrow for depth), and short (Swamp, Field, and Tree Sparrow for length).[a]

Bill category	Hemp	Canary	Millet
A. At room temperature (approx. 25°C):			
Long bill (deep)	20 (20)*	(32)	22 (18)
Medium bill (medium)	13* (10)*	(27)*	33* (35)*
Short bill (thin)	1* (1)	(7)*	65* (83)*
B. Outdoors ($\leqslant 0$°C):			
Medium bill	16*		
Short bill	2*		

[a] Data are presented *only* for seeds showing some significant differences between bill-size categories by the Mann-Whitney *U* test, $P < 0.05$. Percentages for bill-length categories are shown without parentheses, for bill-depth categories with parentheses. Asterisks indicate pairs of significantly different percentages.

BILL SIZE AND SEED PREFERENCES

Bill size and size of seeds eaten in large numbers. If large-billed forms select larger seeds than small-billed species, one would expect Cardinals and Fox Sparrows to choose larger seeds than Tree, Swamp, and Field Sparrows. However, all species tested chose mostly small seeds, although the small-billed forms tended to eat *only* small seeds.

The data of Kear (1962) were recalculated to express preferences in terms of numbers of seeds rather than weights. An average of the size ranks of preferred seeds vs. the ranks of bill length and depth show no correlation between bill size and preferred seed size (Spearman $r_s < 0.10$, $n = 6$, $P > 0.05$). The relatively thick-billed Bullfinch (*Pyrrhula pyrrhula*) and Greenfinch (*Carduelis chloris*) ate more of the large hemp seeds than did other species, but small rape seeds were the first choice by both medium- and thin-billed species.

Although there is no evidence of an increase in preferred seed size with each increase in bill size, a looser association is suggested by table 3A. Here the eight North American species are divided into three bill-length and bill-depth categories. The average percentage of numbers of seeds eaten by each species is presented for the bill-length and bill-depth categories that include some significant differences (Mann-Whitney *U*, $P < 0.05$). Short-billed species averaged significantly less consumption of hemp (a large seed), and significantly more of millet (a small seed) than longer-billed species. Thin-billed species ate significantly less canary (a middle-sized seed), and more millet than deep-billed birds; species with very deep bills also ate significantly more hemp than the others. A crude association thus exists, in that shorter- and thinner-billed species choose hemp less often, and millet more often than species with larger bills. That no such patterns appear for other seed types, both large and small, may indicate an interaction of seed size with other seed characteristics.

Another means of showing the effects of bill size on seed choice deals with the magnitude of *differences* in the sizes of the beaks. Character difference in jaw sizes of related sympatric species has been an important consideration in discussion of the regulation of the number of coexisting species in any area (see e.g., Hutchinson 1959; Schoener 1965). One wonders just how much difference in food might be associated with differences in bill size.

For the species used in these experiments, ratios of bills sizes were constructed among all possible species pairs of long:short and deep: thin. For ratios greater than 1.2:1.0, long- and deep-billed forms usually (in more than 90 per cent of the comparisons) consumed more hemp and canary seeds, and less millet, than smaller-billed forms. Species pairs with a ratio of less than 1.2 : 1.0 showed no trends: "large-billed" forms sometimes ate more, and sometimes less, of a given seed type. For ratios greater than at least 1.1:1.0, long- and deep-billed species generally ate more hemp seed, but consumption of other seeds was less predictable, as was true for species pairs which differed in size by less than 1.1 times.

Bill size and size of seeds providing many calories. Long-billed forms (specifically Cardinals) took major portions of their caloric intake from the large sunflower seeds; other species rarely ate them (table 4A). Short-billed forms used significantly fewer hemp calories than longer-billed species. When classified by bill-depth, the same patterns appear for sunflower and hemp seeds, and, in addition, thin-billed species consumed significantly more calories from millet than did deeper-billed forms. In general, then, the association between bill size and size of seed forming a major fraction of the diet is again a crude one; not all seeds show a trend (with bill size) predictable on the basis of seed size, and bird species must be *grouped* before any significant trends appear at all. A general (but again rather crude) trend of increase of seed size with increased bill size was shown by Morris (1955) and Kear (1962)

TABLE 4. Average percentage of calories ingested from various seeds by birds in different bill-size categories.[a]

Bill category	Sunflower	Hemp		Millet	Thistle
A. At room temperature (approx. 25°C):					
Long bill (deep)	13*	42	(42)	(8)	
Medium bill (medium)	—*	43*	(37)*	(20)*	
Short bill (thin)	—	5*	(3)*	(72)*	
B. Outdoors ($\leqslant 0$°C):					
Medium bill		46*			12*
Short bill		8*			32*

[a] Data are presented only for seeds showing some significant differences between bill-size categories (Mann-Whitney U, $P < 0.05$). Asterisks indicate pairs of significantly different percentages. Percentages for bill-length categories are shown without parentheses, for bill-depth categories, with parentheses.

on the basis of seed preferences by *weight* (which in the present study at least is correlated with caloric content, see below).

Bill size and husking time. The basis for the oft-assumed preference of large-billed species for larger seeds is generally supposed to lie in an ability of large-billed forms to husk seeds, especially large ones, faster than small-billed species.

Table 5 presents the husking times of commonly favored seeds for these eight finch species. Spearman rank correlations of any bill dimension for all species against husking times for millet, thistle, and canary are insignificant ($P > 0.05$). However, deep- and wide-billed species husked hemp significantly faster than more slender-billed forms, by the same test. The medium-sized flax seeds were eaten at the same rate by large-billed Fox Sparrows as by medium-billed juncos, but medium-billed white-throats husked the large oat seed faster than large-billed Cardinals. Thus the commonly assumed ability of large-bills to husk large seeds rapidly is only sometimes true; and on the other hand small-bills

TABLE 5. Average seed husking-and-eating times (sec).[a]

Cardinal	Sunflower 36.5 (40, 17.0)	>	Oats 28.9 (20, 18.6)	>	Hemp 13.5 (20, 7.6)	>	Canary 4.3 (20, 2.5)	≈	Millet 5.4* –	>	Thistle 2.7* –
Fox Sparrow	Hemp 8.1 (20, 2.3)	>	Flax 6.2 (20, 3.5)	>	Canary 2.8 (20, 0.6)	=	Millet 4.0 (20, 2.4)	>	Thistle 2.0 (20, 0.4)		
Song Sparrow	Hemp 12.8 (20, 5.9)	>	Thistle† 4.5 (45, 2.2)	=	Canary 3.5 (45, 2.1)	=	Millet† 2.9 (45, 1.3)				
White-throat	Oats 13.2 (20, 6.2)	=	Hemp 13.9 (20, 4.1)	>	Millet 4.9 (50, 2.4)	=	Thistle 4.8 (20, 2.0)	>	Canary 3.3 (20, 1.2)		
Junco	Hemp 30.3 (19, 13.1)	>	Flax 7.8 (20, 3.0)	>	Canary† 5.3 (50, 3.4)	=	Millet 3.9 (50, 1.8)	=	Thistle† 3.4 (50, 1.4)		
Swamp Sparrow	Thistle 3.1 (25, 1.3)	=	Millet 2.8 (25, 1.6)	=	Canary 3.5 (25, 2.1)						
Tree Sparrow	Hemp 19.0 (20, 10.9)	>	Thistle 4.6 (20, 1.5)	=	Canary 4.4 (20, 1.2)	>	Millet 1.6 (20, 0.6)				
Field Sparrow	Millet 3.2 (20, 1.2)										

[a] n and SD in parentheses; birds listed in order of decreasing bill length, seeds in order of decreasing husking times as indicated; equal signs indicate no significant difference (Mann-Whitney U, $P > 0.05$); * indicates overestimates, a result of certain birds sometimes eating more than one seed at a time; † denotes significant differences between the indicated nonadjacent seeds.

did not husk small seeds faster than large bills.

Even the small millet and thistle seeds are larger than many seeds available in the wild, so that the lower size limit, if any, for large-billed species may not have been reached under these experimental conditions. That husking speed often does not change significantly with an increase of bill size, as shown by the insignificance of most of the Spearman tests, suggests the existence of factors in addition to bill *size* which affect husking time. Special palatal structures, relative sizes of muscle masses, etc. are among the possibilities. Peculiarities of each seed type (tightness, hardness, slipperiness, etc. of the husk) must also be relevant. In this connection, an inspection of table 5 shows that canary, a medium-sized seed, can be husked at least as fast as smaller seeds by most species.

The desirability of testing all the experimental species with large seeds is evident, but there are a number of attendant difficulties. Juncos and some of the other smaller-billed forms would starve to death if given only this variety of sunflower seeds, even small ones. They would eat only a few seeds all day long, although they tried to crack many. Hespenheide (1966) must have used a different variety of sunflower seed or a different variety of junco for his experiments. Also, unpopular seeds are so slow to be eaten, even if they are the sole food offered all day, that the accumulation of timing data would be enormously protracted.

Bill size and seed diversity. Diversity of seeds eaten may be estimated in several ways. The simplest, perhaps, is the range of seed types offered that are actually eaten. However, so many birds sampled all types of seeds that using all types would forbid any discrimination of different ranges. Therefore, only seeds comprising at least 5 per cent of the test diet by number were included in the estimate of range. With this restriction, the data showed no correlation of range of seed types with bill size (Spearman, $P > 0.05$). The relatively large-billed Fox Sparrow and white-throat ate a wide range of seeds and the small-billed Field Sparrow ate a small range; all other species, including the very large-billed Cardinal, used an intermediate range.

Kear's (1962) data also show no evidence of correlation. Newton (1967) asserted that deep-billed species took more kinds of seeds in the wild than shallow-billed species, although the Spearman correlation calculated from his data is not statistically significant ($P > 0.05$). The large-billed Greenfinch did take more seed types and the small-billed Redpoll (*Acanthis flammea*) did eat fewer seed kinds than birds of intermediate bill size. But among these middle-sized birds, the Chaffinch (*Fringilla coelebs*), Linnet (*Carduelis cannabina*), and Goldfinch (*Carduelis carduelis*), there was no increase of variety of seeds eaten associated with an increase of either bill length or depth. Data for a larger number of species or for individual birds might permit a correlation to be shown.

TABLE 6. Diversities of seeds eaten (H′, see text), and their standard errors in parentheses, by captive finches offered a choice of eight seed types.

	At room temp.		Outdoors ($\leqslant$ 0°C)	
Cardinal[a]	.621	(.007)	–	
Fox Sparrow	.743	(.004)	–	
Song Sparrow	.448	(.009)	.123	(.006)
White-throat	.648	(.006)	.666	(.006)
Junco	.646	(.005)	.589	(.006)
Swamp Sparrow	.464	(.009)	.329	(.006)
Tree Sparrow	.553	(.005)	.533	(.005)
Field Sparrow	.187	(.008)	–	

[a] Birds listed in order of decreasing bill length.

Another means of indexing diversity is the use of the information theory formula $H' = -\Sigma\, p_i \log_{10} p_i$, in which p_i is the proportion of (in this case) seeds eaten that belong to the i$^{\text{th}}$ category. Although, under this sampling program, $H = (1/N) \log [(N!/N_1!\, N_2! \cdots N_8!)]$ theoretically may be a more appropriate index (Pielou 1966, 1967), the ranks of both H and H' are the same, which is all that is necessary for present purposes.

Diversities of seed eaten for the test species are presented in table 6. The Spearman coefficient indicates no correlation ($P > 0.05$) of diversity of seeds eaten by each species with bill size (any dimension), nor is there a correlation using the average H' of all conspecific individuals. Data from Kear's experiments, using either weights or numbers, and the field data of Newton also show no such correlation. Since the sample sizes are small, perhaps this is not surprising. The diversities of three kinds of seeds (by weight) eaten by Morris' (1955) birds are, however, significantly correlated with bill length.

If the H′ values for individuals of large-, medium-, and small-billed species (grouped as before by both length and depth) are compared using Mann-Whitney U, all bill size

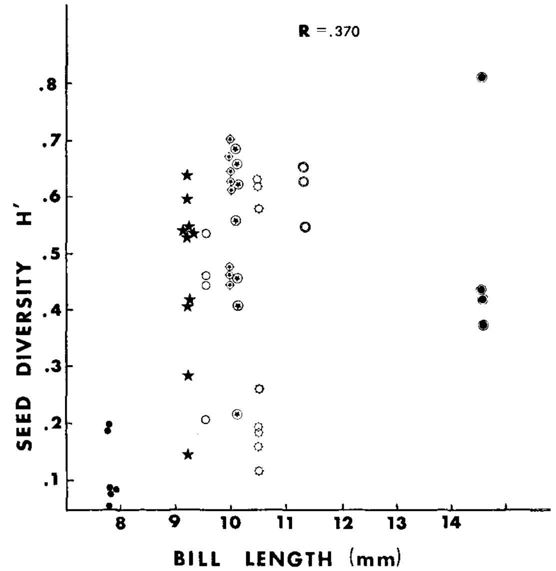

FIGURE 4. Seed diversity (H' based on number eaten) for each bird vs. bill length. $R = 0.370$, $F = 7.75$, $df = 1, 49$; $P < 0.05$.

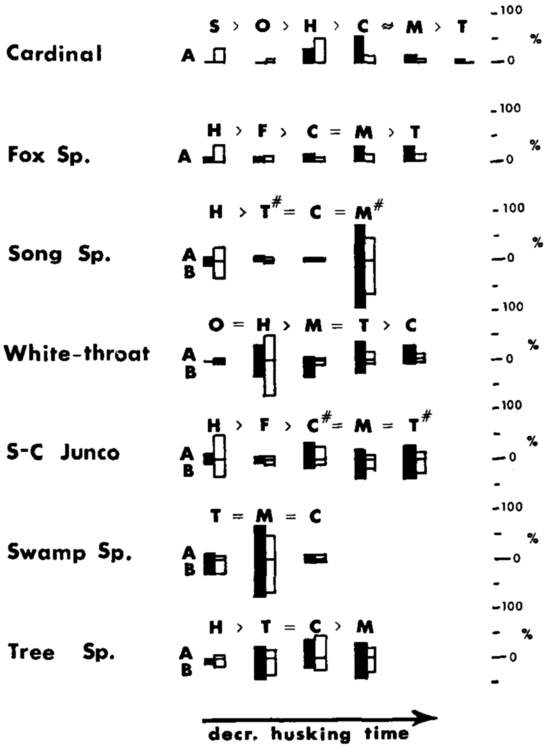

FIGURE 5. Seed choice vs. husking time for each seed type. Husking times from table 5. Legend as in figure 3; for Field Sparrow see table 5. Seeds ranked in order of decreasing husking time; # indicates a significant difference in husking times of non-adjacent seeds.

categories are significantly different from each other, larger-billed forms choosing a wider diversity of seeds than small-billed ones. The expected correlation appears when the sample sizes are thus increased and the data are combined in this way. Also, a correlation of H' for individual birds with bill size for each species yields a correlation coefficient significantly greater than 0 ($R = 0.370$, $F = 7.75$, $df = 1, 49$), although the scatter is considerable (fig. 4).

The low diversity for Song, Swamp, and Field Sparrows is reflected in the fact that all 6 Field Sparrows, all 4 Swamp Sparrows, and 8 of 9 Song Sparrows tested strongly preferred millet. Juncos, white-throats, and Fox Sparrows, in contrast, showed great individual differences in seeds preferred, and in degree of preference, which are reflected in the values in table 6 and shown in the appendix.

Ideally, one should know the relative contribution of intraspecific individual differences in preference and individual diversities of choice to the overall H' for the species. However, I have been unable to find a suitable statistical tool. The significant association of individual H' with bill size, as shown above, indicates the importance of the contribution of individual variability to the H' for the species, but I expect the "between-individual" differences to prove to be very important also, at least when large numbers of birds can be tested.

EFFICIENCY OF CALORIC INTAKE AND SEED PREFERENCE

Seed preference and caloric contents. Seed preference was decidedly not based on maximizing the number of calories ingested from each kernel. In table 1 it is seen that sunflower, oat, and hemp kernels (the largest ones) contain the most calories, but the usually preferred seeds (millet, thistle, canary) contain the fewest calories and are small- or medium-sized seeds (fig. 3). Most of the caloric intake of the three smaller-billed species came from seeds with the fewest calories, but larger-billed species (except the Song Sparrow) tended to consume most of their calories from larger seeds (fig. 3).

Field data for Tree Sparrows (West 1967) rated according to caloric value per *whole* seed (Kendeigh and West 1965), also yield no evidence of correlation between preferences and total calories per "package" (Spearman, $r_s < 0$, $P > 0.05$, $n = 23$).

Seed preference and husking speed. All species tested could husk their more popular seeds faster than less popular seeds (table 5, fig. 5).

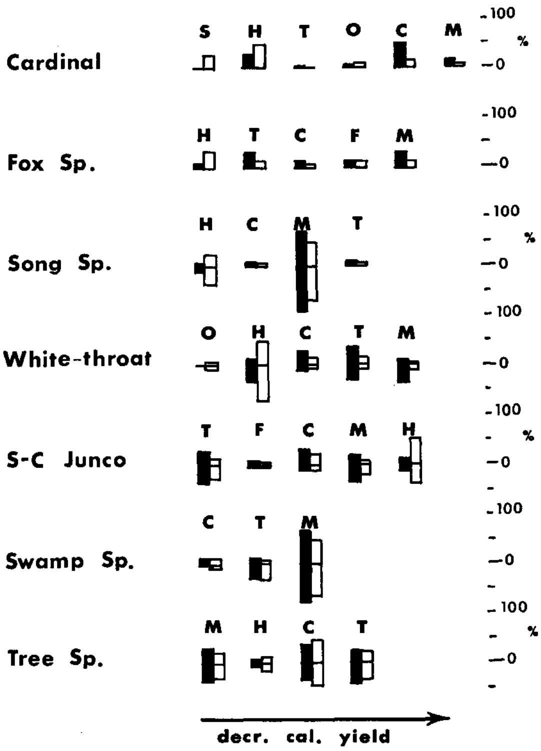

FIGURE 6. Seed choice vs. potential rate of caloric intake (from table 7). Legend as in figure 3; for field sparrow see table 7. Seeds ranked in order of decreasing rate of caloric yield.

At least for the smaller seeds, however, seed preference was clearly independent of husking speed for both large-billed and small-billed birds; for these seeds, husking speed varied little, although preferences varied greatly. Large-billed species, which ate some of the larger seeds, generally preferred the smaller seeds that could be hulled more quickly. Nonetheless, seeds that were husked slowly comprised a major portion of the caloric intake of the six larger-billed species (fig. 5).

Seed preference and total caloric intake. In natural habitats, birds may be as much concerned with maximizing their total caloric intake per unit time as with calories per capture. Assuming that the experimental birds ate only the kernels of the seeds (not always true; hemp, thistle, and flax hulls were occasionally eaten by a few species), and using the husking times, the potential number of calories to be gained per unit time can be estimated. For all birds tested, seeds eaten most frequently included those that yield the most calories per minute (table 7, fig. 6), but there was no correlation in rank orders: first choice of seed was about as likely to be third-ranked in caloric yield/min as it was to be first or second-ranked. Furthermore, commonly eaten seeds included types with a low caloric yield per minute.

Kear (1962), on the other hand, felt that there was a slight correlation between weight of kernels eaten per unit time and seed preferences in the Chaffinch. Seed weight is commonly taken as an index of caloric value. This assumption is valid at least for the seed types used in Kear's experiments (using my caloric

TABLE 7. Approximate number of calories/minute that *could* be obtained by husking and eating seeds.[a]

Cardinal	sunflower 744	>	hemp 262	>	thistle 218	>	oats 187	>	canary 173	>	millet 84*
Fox Sparrow	hemp 436	>	thistle 294	>	canary 266	>	flax 200	>	millet 111		
Song Sparrow	hemp 280	>	canary 213	>	millet 152	>	thistle 134				
White-throat	oats 410	>	hemp 254	>	canary 225	>	thistle 123	>	millet 93		
Junco	thistle 168	=	flax 166	>	canary 140	>	millet 117	>	hemp 85		
Swamp Sparrow	canary 213	>	thistle 190	>	millet 163						
Tree Sparrow	millet 285	>	hemp 186	>	canary 169	>	thistle 128				
Field Sparrow	millet 143										

[a] Data calculated from tables 1 and 5; birds listed in order of decreasing bill length, seeds in order of decreasing potential caloric yield; * indicates overestimates, as in table 5.

determinations) and in mine; kernel weight was significantly, although not perfectly, correlated with caloric content of the kernel (Spearman, $P < 0.05$; for Kear, $r_s = 0.90$, $n = 6$; for the present study, $r_s = 0.89$, $n = 8$).

Another means of indexing food preferences is by calculating the per cent of calories actually ingested from the various kinds of seeds. These figures may then be compared, by rank, with the ranks of the potential number of calories obtainable per minute (table 7). Many of the high-yield seeds are actually eaten in sufficient quantity that they provided a major fraction of the diet. However, some low-yield seeds also provide many calories, and there is no correlation of the ranks of preferences by calories ingested with the ranks of potential caloric yield (Spearman, all $r_s < 0.829$, $n \leqslant 6$, $P > 0.05$).

SEED PREFERENCES AT LOW TEMPERATURE

Several species were tested in small, individual outdoor cages at temperatures of 0°C or below. The vagaries of Illinois weather usually made impossible a continuous series of trials: a cold snap terminated by a warm spell of course necessitated interruptions of a series until cold weather returned. Zero degrees C was an arbitrary but convenient demarcation point. If seed preferences for finches do indeed shift markedly at low temperatures, as noted by Myton and Ficken (1967) for chickadees, it may well be that the turning point, if any, lies at another temperature and may differ among species.

All species kept outdoors shifted their preferences significantly (χ^2, intraspecific pairwise comparisons, df ranging from 5–7, χ^2 values all greater than 30, $P < 0.05$) from what they had been at room temperature (70–80°F). White-throats changed from thistle and canary to millet and hemp; juncos narrowed their sampling to emphasize millet and thistle. Tree Sparrows decreased their consumption of canary; Song and Swamp Sparrows preferred millet at both temperature ranges.

One might expect that, at cold temperatures, an increase of metabolic demands (e.g., Kontogiannis 1968; Kendeigh 1969a) would favor a shift in seed preferences toward larger seeds and/or seeds yielding calories at a higher rate. Kendeigh et al. (1969) have shown that amount of food intake varies with energy stresses, but Young (1945) and Young and Chapin (1945) have shown for rats that preferences are slow to change even under severe dietary deficiencies. However, only white-throats increased their consumption of large seeds; juncos and Tree Sparrows ate smaller numbers of large- and medium-sized seeds; Swamp and Song Sparrows maintained their preference for a small seed.

If these birds chose seeds by the potential rate of caloric intake (table 7, fig. 6), white-throats would choose hemp and canary rather than hemp and millet. Juncos would prefer thistle, flax, and canary instead of thistle and millet. Song Sparrows would choose hemp and canary, not millet; Swamp Sparrows canary and thistle, not millet; and Tree Sparrows hemp and millet rather than millet and thistle. Obviously, while there is a degree of overlap between preferences and potential caloric yield, even more noticeable is the difference between preferred types and those with the highest potential yield.

Diversities of seeds taken at freezing temperatures are shown in table 6, but because of the unknown contribution to diversity of individual variation and the difference in number of birds tested, the tabled values should not be compared critically with H' values at room temperature. Averages of the H' for individual birds did not shift with a change in temperature. High individual variability of seed preference of juncos and white-throats was maintained at cold temperatures as well as indoors, and both song and swamp sparrows again showed small individual variation. The correlation of H' for individuals with bill size of the species was not significant ($R = -0.296$, $F = 1.63$, $df = 1, 18$).

The proportions of some seeds taken by birds of different bill-size categories at low temperatures differed from the amounts taken at room temperature (tables 3B and 4B). The inverse relationship between bill size and amount of millet eaten at high temperatures disappeared in the cold. In terms of numbers of calories, the small-billed species ate more thistle calories in the cold. The avoidance of hemp by small-billed birds occurred at both temperature ranges. These shifts are the result of the above-mentioned preference for small, quickly-opened seeds by most species. They, and the lack of correlation of bill size with seed diversity at low temperatures but not at high, suggest the importance of exploring further the effect of temperature on the relation between bill size and seed selection.

SEED SELECTION IN RELATION TO PROTEIN AND LIPID CONTENT OF SEEDS

Seeds highest in protein are hemp, flax, and thistle. Only two species included any of these seed types among their first choices at room temperature, and only three species ate them most frequently at low temperatures. Under both temperature regimes, about half the seed types comprising at least 10 per cent of the test diet were seeds high in protein. Seed preferences based on calories compared with protein content showed that the greatest caloric intake is not primarily from seeds high in protein. It seems, therefore, that seed preferences were not determined by protein content (see also McFarland and George 1966; Field 1968; Gardarsson and Moss 1968; Martin 1968; Moss 1968; Bell 1970; and Lieff et al. 1970).

Fat content is greatest in flax, rape, and thistle, and intermediate in sunflower and hemp. Flax and rape were seldom eaten, and thistle was only rarely a first choice (in numbers or calories). Only about half the seeds comprising at least 10 per cent of the test diet were seeds high in fat. This does not argue for selection of seeds on the basis of fat content. Seeds of both high and low protein and fat content are available in both large and small sizes, so that seed sizes did not force birds to pick only those seeds low in protein or fat.

It is difficult to make any guesses as to the impact of carbohydrate content of seeds on seed selection. To do this, the amount of usable carbohydrate must be known, apart from the amount of unusable carbohydrate fiber (cellulose). We might guess that canary and millet (and perhaps oats, despite high per cent of fiber in the uneaten husk) are relatively high in carbohydrates, since they are low in protein and fat. Canary and millet are popular seeds, in terms of numbers eaten (¾ of the species made millet or canary first choice), but did not figure so prominently in providing calories. Still, it is difficult to conclude that seed preference is based on usable carbohydrate content, since canary and millet share another characteristic: speed of opening. They share this feature with thistle seeds, whose popularity was close to that of the others, but which is (probably) low in carbohydrates.

COMMENT

The interest in the numbers of seeds taken stems from the fact that the "capture" of each seed usually involves, in the wild at least, separate search and seizure effort, and each seed captured ideally should at least repay the efforts of the captor. Digestive efficiency is expected to vary among different food types (Gibb 1957) and under different conditions (Helms 1968; Kendeigh 1969b), and food handling efficiency with different body size (Rosenzweig and Sterner 1970). Until we know both the metabolizable energy per seed and the energy necessary to open and eat each kind of seed, we cannot determine the ratio of energy expended to that gained. An additional complication is that the efficiency of utilization of food energy may vary with the amount eaten (Beverton and Holt 1957:113). We can, however, ask if the birds maximized their caloric intake per capture; under laboratory conditions, there was little indication that they did so.

It may be that laboratory conditions did not permit (or force) the birds to exercise discrimination on energetic considerations. There was abundant food, and so no risk of starvation; the animals were not required to search for their food (beyond the initial discovery of particular compartments of the food dish).

Also, birds that have become cage-tame and have a continual abundance of food may cease discriminating in the way that they might in the field. Captive snakes may become "lazy" in striking prey when they learn that the prey cannot get away (T. H. Frazzetta, pers. comm.). However, increasing cage-tameness need not lead to decreased or apparently erratic discrimination. Re-analysis of Kear's (1962) data for British finches showed that the shift in preferences, by number, from the first two days of the trials to the last two days were usually in the direction of increased consumption of high-calorie seeds, as was reported by Kear for preferences based on weight. Eating of high-energy hemp seeds increased in all six native British species used. Consumption of low-energy seeds such as canary and millet frequently decreased. The Linnet, which ate very little hemp at all, increased its consumption of flax, a seed of intermediate caloric content, and decreased the intake of low-calorie seeds. Kear's birds were newly caught, and were presumably becoming cage-tame toward the end of the 12-day trials. At least partially cage-tame birds, then, may still select seeds on what biologists might call a "reasonable" basis.

Still, it is possible that laboratory-determined preferences reflect primarily choices made on the basis of flavor, for example, rather than energy considerations, particularly since time and energy spent searching were minimal in the lab. Another possibility is the selection of seeds on the basis of their trace element or vitamin content (e.g., Richter 1942; Albrecht 1945; Barnett 1953; Michael and Beckwith 1955; and Klein 1970), although the close relationship among several of these finches and their presumed metabolic similarities would suggest perhaps that food preferences should have been more similar than they actually were, if this were the basis of selection. Or it may be that in the wild, certain flavors or shapes are associated with high-energy foods not represented in the laboratory situation. In this case it would be too much to expect the birds somehow to know which of an artificial assemblage of seeds would do them the most good. A week or more of experience in the laboratory may be unlikely to simulate an association built perhaps by generations of natural selection or by weeks and months of experience, although quail apparently show little influence of "habit" on food preference (Michael and Beckwith 1955).

One might argue, however, that many small animals, when hunting, search virtually continually. Pursuit is confined simply to reaching out and grabbing an item; most of the food items are small and take little eating time. It may be disadvantageous for a continual searcher to pass by a potential food item, even a fairly small one, since the effort involved in reaching out and eating it is small and the risk of not finding a better and bigger one may be high. Failure to garner all or most possible food items en route may also increase searching time and perhaps increase the exposure to predation as well. Furthermore, these small birds may maintain best health and a greater ability to escape predators if they eat more or less continually instead of gorging themselves occasionally. (See also Beverton and Holt 1957:133 for references concerning the effect of the number of daily meals on growth rates of several animal species.) Under these conditions selection may not favor development of great discrimination, either built-in or learned, maximizing size and energy content of food items chosen. In this connection, Beverton and Holt (1957:125 ff.) note that amount of food consumption in some fish species is based on intake of bulk rather than of energy. Plainly, models of optimization of dietary strategy should be constructed in terms of the total time and energy budget of a "predator," as that of Schoener (1969b) begins to do, since forces of selection not concerned directly with food supply may reasonably be expected to have important influences on feeding strategy.

The apparent favoring of seeds that are easily handled, in this study and in continuing experiments using wild seeds, produces a tendency toward convergence in food habits of different species. Although there is an association of some differences in food choices with differences in bill size, the differences in foods taken under natural conditions may be primarily a result of different foraging sites and methods of the birds and variation in the spatial (Ivlev 1961; Murdoch 1969) and numerical (Emlen 1968) distributions of seed types in the birds' habitats.

SUMMARY

Seed preferences of eight species of North American finches of different bill sizes were tested in the laboratory on eight types of commercially available seeds. Bird species used in the tests were Cardinal, Fox Sparrow, White-throated Sparrow, Song Sparrow, Slate-colored Junco, Tree Sparrow, Swamp Sparrow, and Field Sparrow. All species expressed distinct preferences for different kinds of seeds, both in terms of numbers eaten and calories ingested. Long- (or deep-) and medium-billed species ate more hemp (large seeds) and ingested more calories from it than small-billed species, and chose significantly fewer millet seeds (small). The large sunflower seeds formed a noticeable portion of the caloric intake only of long- and deep-billed forms. Large-billed species generally husked larger seeds faster than small-billed forms, but birds of both bill sizes husked small seeds at the same rate. Species with large bills tended to eat a wider diversity of seed types in this study, but not in many other studies reported in the literature. Seed preference was not based on choosing seeds containing the highest number of calories, although birds with large bills frequently derived most of their calories from seeds with high caloric content that could be husked only slowly. Preferred seeds were often small or medium-sized types that could be husked more quickly, but among those three types, there was no correlation of preference with husking speed. Seeds eaten most frequently *included* those yielding the most calories per unit time, but also included those of low caloric yield. Preferences at low temperatures were somewhat different from those at room temperature, but did not shift toward larger seeds, those containing more calories, or seeds providing the highest rate of energy intake. Possible adaptive values of the selection of small seeds are discussed. Small birds perhaps cannot afford to pass by

suitable but small food items very frequently and thus increase the time spent hunting and the risk of not finding a more suitable food item. Small seeds generally are easier to handle and are more quickly swallowed than large ones, and so permit the birds to keep moving and reduce the risk of predation.

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APPENDIX

Seed preferences of individual birds; $\bar{x}$ for each group of conspecifics, and an estimated SD calculated by a short-cut method (Tate and Clelland 1957:12) on the arcsin transformed percentages of numbers eaten.

	S	O	C	R	H	F	M	T
Cardinal								
#1	4%	5%	13%	7%	26%	1%	18%	26%
#2	Tr	0	43	1	50	4	0	2
#3	1	2	71	0	20	Tr	6	0
#4	2	Tr	60	0	14	0	24	0
$\bar{x}$	2	2	47	2	28	1	17	4
SD	1.0%	1.2%	6.0%	1.6%	4.1%	1.0%	6.2%	6.9%
Fox Sparrow								
#1	Tr	1	13	19	18	8	23	18
#2	Tr	Tr	22	1	12	4	6	56
#3	Tr	2	18	3	2	14	51	11
SD	<1%	0.7%	0.5%	4.3%	3.0%	0.3%	10.1%	8.7%
Song Sparrow room temp.								
#1	Tr	1	29	3	2	4	21	40
#2	Tr	1	16	2	12	3	49	11
#3	Tr	Tr	19	6	8	6	43	17
#4	0	0	3	1	3	2	90	1
#5	Tr	Tr	Tr	1	1	Tr	94	3
#6	Tr	Tr	3	1	3	6	85	1
#7	0	0	0	0	2	11	87	0
#8	0	0	2	0	8	0	90	0
#9	Tr	Tr	2	0	7	0	89	2
$\bar{x}$	Tr	Tr	8	1	6	4	71	11
SD	<1%	0.1%	3.7%	0.7%	0.7%	1.3%	8.1%	5.3%
⩽0°C								
#1	0	0	0	0	10	0	90	0
#2	0	0	0	0	6	0	94	0
#3	0	0	1	0	2	3	94	0
$\bar{x}$	0	0	Tr	0	6	1	93	0
SD	0	0	0.4%	0	1.1%	1.1%	0.2%	0
White-throat room temp.								
#1	Tr	2	21	4	7	3	9	44
#2	0	2	45	7	1	4	12	30
#3	Tr	1	24	6	2	4	7	57
#4	Tr	Tr	33	5	21	7	7	48
#5	Tr	2	2	1	1	13	7	71
#6	Tr	1	67	1	1	6	7	17
#7	1	2	0	0	89	0	3	5
$\bar{x}$	Tr	1	27	3	17	5	9	39
SD	0.1%	0.3%	12.0%	1.0%	16.5%	0.5%	1.1%	7.9%
⩽0°C								
#1	Tr	Tr	20	Tr	18	3	20	38
#2	Tr	0	6	5	8	2	51	29
#3	Tr	0	0	0	70	0	30	0
$\bar{x}$	Tr	Tr	9	20	32	2	31	23
SD	<1%	<1%	7.3%	1.9%	16.3%	1.1%	3.8%	14.6%
S-C Junco room temp.								
#1	Tr	Tr	64	2	16	4	1	12
#2	1	Tr	10	3	33	7	17	30
#3	Tr	1	13	3	4	6	30	44
#4	Tr	2	25	1	25	4	26	19
#5	Tr	1	25	1	43	3	40	26
#6	Tr	2	13	3	11	5	6	29
#7	0	1	63	0	6	0	14	11

APPENDIX (Continued)

	S	O	C	R	H	F	M	T
#8	0	0	44	0	0	0	3	47
#9	0	0	38	0	0	0	45	17
$\bar{x}$	Tr	Tr	33	1	16	3	20	26
SD	0.1%	0.2%	4.2%	0.4%	5.8%	0.8%	6.0%	1.7%
≤ 0°C								
#1	Tr	Tr	8	3	13	3	51	22
#2	Tr	Tr	9	2	10	1	37	40
#3	Tr	1	16	0	5	0	23	55
#4	1	0	13	0	8	0	39	39
#5	Tr	Tr	20	0	13	11	14	41
#6	0	0	5	0	6	0	52	37
$\bar{x}$	Tr	Tr	12	1	9	3	36	39
SD	0.2%	0.2%	0.9%	0.5%	0.3%	1.8%	2.8%	1.9%
Swamp Sparrow room temp.								
#1	Tr	1	9	5	3	5	69	9
#2	Tr	Tr	10	3	Tr	4	63	18
#3	0	Tr	0	1	Tr	4	87	7
#4	Tr	Tr	4	10	2	3	52	28
$\bar{x}$	Tr	Tr	8	5	1	4	68	16
SD	<1%	<1%	2.5%	1.2%	0.7%	<0.1%	3.5%	2.0%
≤0°C								
#1	Tr	Tr	1	1	Tr	1	50	46
#2	Tr	Tr	3	1	Tr	1	91	4
$\bar{x}$	Tr	Tr	2	1	Tr	1	71	25
SD	<1%	<1%	4.4%	0	<1%	0	17.2%	21.6%
Tree Sparrow room temp.								
#1	Tr	1	26	5	3	2	34	30
#2	Tr	Tr	29	4	8	2	5	51
#3	Tr	Tr	48	4	5	3	14	27
#4	Tr	Tr	20	1	0	3	38	38
#5	Tr	Tr	3	0	Tr	5	56	36
#6	Tr	Tr	17	0	Tr	8	46	28
#7	Tr	1	64	0	0	0	20	15
#8	0	Tr	73	0	3	0	24	0
#9	0	Tr	26	0	0	0	72	2
#10	0	0	91	0	0	1	8	0
$\bar{x}$	Tr	Tr	40	1	2	2	32	23
SD	<1%	<1%	11.7%	0.5%	0.9%	0.9%	6.2%	6.4%
≤0°C								
#1	Tr	1	21	0	Tr	2	37	29
#2	0	0	9	0	3	0	47	41
#3	0	2	5	Tr	1	1	57	31
#4	Tr	Tr	Tr	Tr	Tr	2	66	31
#5	0	0	47	0	13	2	1	37
#6	0	0	30	0	Tr	1	3	66
$\bar{x}$	Tr	Tr	19	Tr	3	1	35	41
SD	<1%	0.3%	8.8%	<1%	2.2%	0.3%	11.0%	2.0%
Field Sparrow								
#1	0	0	4	0	Tr	0	96	0
#2	0	0	15	0	0	0	85	0
#3	0	0	1	0	0	0	99	0
#4	0	0	14	0	0	1	85	0
#5	0	Tr	3	0	0	0	97	0
#6	0	0	1	0	0	0	99	0
$\bar{x}$	0	Tr	6	0	Tr	Tr	94	0
SD	0	<1%	1.4%	0	1%	1%	1.4%	0