SEED PREFERENCES AND DIGESTIVE EFFICIENCY OF CARDINALS AND SONG SPARROWS

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Laboratory experiments on seed preferences of several species of North American finches have indicated that a major determinant of seed preferences is ease of handling, and that the number of calories per seed, and the potential caloric intake per unit time from each seed type, are less important in determining seed preferences (Willson 1971). In the present study, we used seed gathered from wild plants rather than commercial seed. Metabolic tests permitted the estimate of actual rather than potential caloric intake from each seed type.

METHODS

Cardinals (*Richmondena cardinalis*) and Song Sparrows (*Melospiza melodia*) were caught during the fall in the vicinity of Champaign-Urbana, and kept in the laboratory for over a week before testing. They were fed on a commercial mixture of seeds, with nutrient supplements and some wild seed.

Preference tests and metabolic efficiency tests were conducted during the winter on birds held individually in large cages at room temperature (about 26°C), with a day length usually about an hour longer than natural and at 0°C in smaller cages in a walk-in cold cabinet with a 9-hr day length. Preference trials lasted 3 hr each, one trial per day, for 6 days. Seeds were presented to the birds in circular dishes divided into four wedge-shaped compartments, in sufficient abundance that the birds never emptied any compartment. For Cardinals, metabolic tests, conducted separately on each seed type, lasted 6 hr at room temperature and 5 hr at freezing temperatures, the reduction in time necessitated by the shorter day length in the cold cabinet (see below). For Song Sparrows, room temperature metabolic tests lasted 6 hr. At 0°, however, three birds died on standard rations with ad-lib feeding. In addition, four birds nearly or actually died during trials on pigweed and smartweed at room temperature. Therefore, the trial periods were shortened to 3 hr in order to allow the birds to feed on suitable seeds at the beginning and end of the day. When this was done, only one Song Sparrow died during metabolic tests (a bird fed on pigweed). Each species of seed was run twice, and all trials were run in randomized order. For metabolic tests at room temperature, birds were left without food for about 2 hr at the beginning and end of the trial in order to clear their guts of previously eaten

food (Stevenson 1933; Wallgren 1954). At 0°, tests were begun at 09:00 when the lights came on and the digestive tract was empty (Kontogiannis 1967), and again the birds were left without food for about 2 hr at the end of the trial. At the end of each test, the weight of seed eaten was calculated. For metabolic tests, the feces were collected, dried, and burned in a micro-bomb calorimeter. Surviving birds were weighed and released at the end of the experiments; mean weight of both species was near normal for that of wild-caught birds (Cardinal, 44 g, Song Sparrow, 25 g). The constant-weight criterion for condition of the birds could not be used because restricted diets are known to produce changes in fat accumulation and weight.

Seeds used in the preference tests were foxtail (mainly *Setaria faberi*), hemp (*Cannabis sativa*), smartweed (*Polygonum pensylvanicum*) for both bird species, plus giant ragweed (*Ambrosia trifida*) for cardinals and pigweed (*Amaranthus* prob. *retroflexus*) for Song Sparrows. All seeds were collected locally in habitats commonly frequented by the birds. The same seed species were used in metabolic tests, with the addition of trials with commercial sunflower (*Helianthus annuus*) for Cardinals.

Caloric content of kernels was determined by oxygen bomb calorimetry; protein and fat content of kernels were determined by Kjeldahl and nuclear magnetic resonance spectroscopy techniques. The energy content of seeds is generally correlated with lipid content (Grodzinski and Sawicka-Kapusta 1970). Water content was estimated by measuring water loss after a minimum drying period of 24 hr at 65°C. Seed-handling (husking and eating) was timed with a stop watch to the nearest tenth of a second; pigweed was generally swallowed whole, so all figures for that species are based on whole seeds. Seed characteristics are summarized in table 1, but care must be used in applying these values to other studies due to the known variation in seed calories, nutrients, and other qualities of the kernels with maturity, growth conditions, etc. (Smith and Follmer 1972; Johnson and Robel 1968; F. I. Collins, pers. comm.).

Digestive efficiency was computed as the ratios of calories ingested −calories excreted:calories ingested.

RESULTS

SEED PREFERENCES

The term "preference" is used here to indicate that certain seeds were eaten more frequently than others, that is, it refers to the relative numbers of seeds eaten. Seed preferences of

TABLE 1. Characteristics of seeds used in preference and metabolic tests.

	No. seeds/g	Calories/kernel	Cal/g kernel	% protein in kernel	% lipid in kernel
Foxtail (F)	824	7.6	4784	16	3
Smartweed (S)	208	10.7	4805	14	7
Hemp (H)	142	37.4	5906	33	21
Pigweed (whole) (P)	3070	1.3	4557	16	8
Ragweed (R)	28	141.8	7355	34	42
Sunflower (Sun)	8+	368.0	5256	15	24

individuals are given in appendix A for Cardinals and appendix B for Song Sparrows.

Cardinal. No consistent differences in preference were found between males and females, so they will be discussed together. At room temperature, seven of ten birds chose mostly foxtail seeds (F), and three preferred hemp (H). For six birds hemp was second choice, for three, foxtail, and for one, ragweed (R). At freezing temperatures, six of seven birds preferred hemp, the other preferred foxtail; second choices were foxtail (3 birds), smartweed (S) (3), and ragweed (1). See appendix A for a summary of these data. Although preferences existed, many birds showed tendencies to sample all kinds of seeds so that none was eaten with less than 10% frequency on the average.

At room temperature, the bulk of the diet (weight of kernel eaten) was composed of ragweed and/or hemp (9 of 10 birds) and one consumed mostly foxtail; ragweed and hemp were also second in bulk for most birds. At 0°C, the major portion of the diet was composed of either hemp (6 birds) or smartweed (1). At both temperatures, most birds showed consistent preferences from trial to trial.

When the test seeds are ranked by weight of kernel, the order is R > H > S > F. Since Cardinals preferred (by number) foxtail and hemp, clearly preference is not based on kernel weight. However, the major part of the diet in terms of weight of seed eaten is, in fact, composed of the larger seeds.

When seeds are ranked in decreasing order of calories per gram of dry kernel, the order is R > H > S ⩾ F. The preferred seeds are intermediate or low in caloric content per gram, and the bulk of the diet is not composed of seeds high in caloric content.

When seeds are ranked by caloric content per kernel, the order is R > H > S > F. Again, seeds of intermediate or low value are preferred. The largest portion of the diet is made up of seeds containing many calories, i.e., the larger seeds.

Seed-handling times (table 2) can be used in combination with the caloric content of each type of kernel to estimate the potential rate of caloric intake from each seed type: in rank order, H > R > S > F. No close association of preference with potential caloric intake per unit time is apparent. The potential intake rate and the seed weight in the diet are correlated, especially at colder temperatures.

Actual caloric intake per unit time can be estimated by adjusting the potential rate, using metabolic efficiency (see below) as the correction factor. When this is done, the rank order of the estimated actual rate of caloric intake is the same as the potential rate at both temperatures.

Seed-handling times (table 2) are ranked in the following order: F < H < S < R; differences between seed-handling times for each seed type are significantly different (Mann-Whitney U, $a = 0.05$) except that females crack foxtail and hemp at similar rates. Two birds actually chose seeds in order of their speed of handling. At room temperature, seven preferred foxtail and three preferred hemp; 9 of 10 had foxtail and hemp as both first and second choices. At the cold temperatures, preference for speed of handling was less noticeable; hemp was preferred and the second choice was variable with ragweed predominant. However, since some Cardinals (females) husked foxtail and hemp at similar rates, the shift in favor of hemp does not entirely oppose the tendency to choose easy-to-handle seeds.

Preference was not correlated with protein

TABLE 2. Seed handling times (seconds/seed). Values are based on observations of several birds.

		Cardinal	Song Sparrow[b]
Foxtail		3.0 sec	2.0
Smartweed		11.7	10.1
Hemp		5.5	11.4
Pigweed		—	2.2
Ragweed	Male	80.7[a]	—
	Female	43.6[a]	—

[a] Significantly ($a = 0.05$) different, t-test; see text.
[b] S = H > F = P, t-test between pairs of seed types, $a = 0.05$.

TABLE 3. Summary of seed preferences, caloric content, seed weights, and speed of handling, in rank orders.

	Room temperature	Freezing temperature
Cardinal		
Preferences (number eaten)	F > H > R = S[a]	H > F > S = R
Wt. in diet	H > R > F > S	H > R > S > F
Wt./kernel	R > H > S > F	R > H > S > F
Cal/g/dry kernel	R > H > S > F	R > H > S > F
Cal/kernel	R > H > S > F	R > H > S > F
Potential rate of caloric intake	H > R > S > F	H > R > S > F
"Actual" rate of caloric intake	H > R > S > F	H > R > S > F
Speed of handling	F < H < S < R	F < H < S < R
Protein content of kernel	R = H > F = S	R = H > F = S
Lipid content of kernel	R > H > S > F	R > H > S > F
Digestive efficiency	R = H = F ⩾ S	F = S = H = R
Song Sparrow		
Preferences (number eaten)	F = P > H > S	F > P > H > S
Wt. in diet	F > H > P > S	F > H > S > P
Wt./kernel	H > S > F > P	H > S > F > P
Cal./g/dry kernel	H > S > F > P	H > S > F > P
Cal/kernel	H > S > F > P	H > S > F > P
Potential rate of caloric intake	F > H > S > P	F > H > S > P
"Actual" rate of caloric intake	F > H > S > P	F > H > S > P
Speed of handling	F = P < S = H	F = P < S = H
Protein content of kernel	H > P = F ≃ S	H > P = F ≃ S
Lipid content of kernel	H > P = S > F	H > P = S > F
Digestive efficiency	F > H = P	F = H > P = S

[a] F = foxtail, H = hemp, R = ragweed, S = smartweed, P = pigweed.

or lipid content of the seeds. At both temperatures, the bulk of the diet was composed of the two seed types highest in protein and fat, but the rank orders did not correspond well and the high-protein and fat seeds were also the largest ones. These results are summarized in table 3.

Song Sparrow. At room temperature, 4 of 10 birds preferred pigweed, 5 preferred foxtail, and one chose both most frequently. Second choices were variable. At 0°C, five of six birds preferred foxtail, one chose pigweed; these were also the second choices (see appendix B). In general, Song Sparrows strongly preferred the small seeds, pigweed and foxtail.

The major portion of the diet (by weight of kernel ingested) was foxtail (7 birds), hemp (2), or both (1). Hemp (7), foxtail (1), and smartweed (1) were second in importance. At freezing temperatures, four birds ate mostly foxtail, one ate mainly hemp, and one ate both in equal amounts; foxtail (1) or hemp (3) were usually second in order of amount consumed.

Preference by number was not closely associated with kernel weight, calories per gram of dry kernel, calories per kernel, potential or actual rate of caloric intake, protein or lipid content of the kernel. Foxtail and pigweed were preferred seeds at both temperatures and were the two most easily handled seeds; however, hemp was chosen more often than smartweed although they were husked at the same rate. Therefore, the best correlation of seed preferences is seed-handling time, although again the correlation is not perfect (table 2).

The bulk of the diet in weight, however, was not composed primarily of large seeds, since foxtail (small) was first-ranked in weight consumed. Rates of caloric intake and digestive efficiency (see below) corresponded fairly well with ranks of importance in diet, especially at the lower temperatures.

DISCUSSION OF SEED PREFERENCES AND DIET

For both species tested, seed preferences (by number) were associated more closely with seed-handling time than with any other measured characteristics of the food, at least at room temperature. Cardinals in the cold, however, showed a tendency to prefer seeds yielding calories at high rates. Song Sparrows did not, nor did birds tested in earlier experiments (Willson 1971). The bulk of the diet was composed primarily of high-yield seeds for both species.

In most cases, then, food-selection behavior as reflected in the preferences did not maximize rate of food intake, although Cardinals

did respond to cold temperatures in a theoretically appropriate way. For both species, proportion of the diet by weight was associated, especially in the cold, with rates at which the seeds yielded calories to the birds.

In terms of an ideal time and energy budget for foraging, the diet should be composed primarily of high-nutrient-yield foods, items of lesser value to be included when the good items are scarce (MacArthur and Pianka 1966), or when they are particularly abundant (Emlen 1966). However, "nutrient" probably involves more than simple caloric or protein intake, etc. Some animals are known to select foods for particular ingredients, at least in some circumstances (see e.g., Pulliainen 1965; Pendergast and Boag 1971; Arnold 1964; Hughes et al. 1964). Further, wild birds often do not choose food in proportion to its abundance, size, or apparent availability (West 1967; Bookhout 1958; Dillery 1961). Individuals may vary in their ability to be selective of appropriate food (Dove 1935).

The various models of food selection (e.g., Rapport 1971; Schoener 1969) and a number of considerations (e.g., Willson 1971) suggest the importance of relative "profitability" (Royama 1970) of various food items, searching time, food distribution, total time and energy budgets, etc.

Search time, which was not tested with our birds, may well be an important factor. Experiments now in progress on the effect of search time on seed preference in the white-footed mouse (*Peromyscus leucopus*) indicate that changes in search time do, in fact, affect seed choice (D. Moriarty, pers. comm.), although this effect may be mitigated by learning or habit (see e.g., Croze 1970; but also Royama 1970). However, care is necessary in extrapolating from mammals to birds. Admitting some differences in method, we note that Rosenzweig and Sterner (1970) found a correlation of husking speed with body size for heteromyids, and an inverse correlation of the relative rate of caloric gain with relative body size; neither holds true for finches (data of Willson 1971).

If a tendency to approach an ideal foraging time-and-energy budget is to occur in the field, it may frequently be a function of the birds' ability to choose and utilize certain appropriate environmental patches (MacArthur and Pianka 1966; Cody 1971), taking more or less whatever suitable food items occur there; species might then show habitat preferences for areas where the seeds easiest for them to handle are commonly found (see also

Pulliam and Enders 1971) if these are sufficiently predictable.

Food-choosing behavior seems insufficient, at present, to result in a putatively ideal foraging budget. Perhaps in conjunction with habitat selection the approach to a theoretical ideal may be closer, although even in appropriate habitats, there are good reasons for arguing that it is often efficient for a bird to gather most of the suitable items it passes (MacArthur 1961; Willson 1971), rather than being highly selective.

Several questions for field study emerge from such suggestions. If birds in natural habitats are exposed to seeds or food pellets, what preferences are shown? During the course of the winter, as seed resources are gradually depleted, do the finch species become more restricted in habitats used for foraging? [The data presented by Eber (1956, fig. 1) suggest they may not, but more specific information is needed.] As the resource supply deteriorates, is there an increased tendency to flock (Cody 1971; Morse 1970), and does flocking increase the patchiness (and hence the predictability of food-finding) for all the flockers as Cody suggests? How do feeding rates change with habitat and the seeds found there?

METABOLIC EFFICIENCY

Cardinal. No consistent differences were found between males and females in caloric content of the feces or in efficiency of digestion, so the data were pooled. Considerable variability was found between individuals, however, and sometimes the same individual had different efficiencies of digestion of the same seed type on different trials.

The variability is difficult to account for:

1. There was no correlation (Spearman rank correlation, $a = 0.05$) of the fecal weight per bird with calories/gram of feces for any seed type, or of the average weight of feces produced from eating each seed type with the average caloric content of that fecal matter.

2. For each bird there was no correlation of the amount of seed ingested with the caloric content of the guano, nor of the amount ingested with the weight of excrement produced. Likewise, no correlation was apparent between the mean amount of each seed ingested by all the birds with the mean fecal weight from each seed type or with the mean caloric content of the guano.

3. At room temperature, for each type of seed except hemp, efficiency of each bird was

TABLE 4. Average efficiency of digestion at two temperatures.

	Room temperature			0°C		
	$\bar{x}$	N (birds)	Range	$\bar{x}$	N (birds)	Range
Cardinals						
Foxtail	68%[b]	5	47–80%	78%	5	65–95%
Smartweed[a]	49*	5	12–81	77[b,c,*]	6	71–86
Hemp	73	6	54–84	73	6	61–78
Ragweed	77	6	68–86	69	6	60–87
Sunflower	80[h,*]	6	67–85	67[b,c,*]	6	48–81
Song Sparrows						
Foxtail	89%[h,i]	3	85–91%	88%[d,e]	2	85–90%
Smartweed	—	—	—	55[d,f]	2	35–67
Hemp	80[h,*]?	3	75–83	86[f,g,*]?	2	83–88
Pigweed (whole)	80[i,*]	4	71–86	57[g,e,*]	2	45–69

[a] For Cardinals with smartweed, the first set of trials was much lower in efficiency than the second; if the first ones are excluded, $\bar{x}$ = 65%, which is still significantly lower than the 77% at 0°C, and lower than most other seeds at room temperature.
[b-i] Significant difference between pairs of values at the stated temperature as matched by superscripts, Mann-Whitney U, a = 0.05 or no overlap.
* Significant difference between values for the given seed type at different temperatures, Mann-Whitney U, a = 0.05 or no overlap.

correlated (Spearman, a = 0.05) with the amount eaten. At 0°C, similar correlations were found for foxtail, ragweed, and sunflower (but not for smartweed and hemp).

Therefore, the variability in efficiency of digestion between trials and between birds could not be accounted for by the quality or quantity of the end products alone or by the relationship between either amount or caloric content of the end products and the amount ingested. Some variation in efficiency appeared to be a function of the amount of each seed type eaten, but this was true only for a few individuals. Between-bird variability of efficiency on each seed type (analyzed separately) was in most cases influenced by the amount eaten—the greater the quantity of a seed type eaten, the more efficiently it was digested. In many cases, condition of the bird probably affected efficiency but this was not assessed.

The amount eaten and the weight of the excreta both increased at the lower temperature. In addition, the caloric content (per gram) of the guano was significantly higher at low temperatures (Mann-Whitney U, a = 0.05) for sunflower, smartweed, hemp, and ragweed (not for foxtail). Furthermore, at 0°C, the differences in caloric content (per gram) of the excreta formed from different seeds were greater than at room temperature.

Efficiency of digestion also varied at different temperatures, and different seed types changed in different ways (table 4). Digestive efficiency of sunflower and ragweed decreased significantly (Mann-Whitney U, a = 0.05), while that of smartweed increased, and foxtail and hemp showed no significant change. As a result, different seeds were most efficiently utilized at each temperature. The general increases ($\bar{x}$ = 16% greater than at room temperature) in caloric value of the excreta at low temperatures imply that the digestive "machinery" was somehow processing food less effectively at cold temperatures, and to fairly similar degrees for all seeds (range 11–27%); this may be compensated by a rather large increase in the amount ingested (mean 233%, range 141–430%). The differential treatment of various seeds presumably was a function of differential seed composition, but we do not know enough about avian temperature responses of digestibility of various constituents to assess the matter. One perhaps needs to know how utilization of various fatty acids, amino acids, etc. and combinations of them (see e.g., Bayley and Lewis 1962) may vary with temperature. Another variable of possible importance is the length of time different seeds are held in the gut; our allowance of about 2 hr for gut clearance is quite minimal.

Song Sparrow. There was individual and trial variability in this species also (table 4), especially for smartweed and pigweed. The sample size, however, is very small and the data can only serve as indicators. As with Cardinals, no correlation was present between caloric value of the guano and its quantity, nor with the amount ingested and either the quality or quantity of the excreta. For Song Sparrows there was also no indication of a correlation between efficiency of digestion and the amount consumed. Since mortality of this species on restricted diets was higher than for Cardinals, possibly the physical condition of the experimental sparrows had a greater

influence on their metabolic efficiency than was the case for Cardinals.

The results for Song Sparrows are more diverse than for Cardinals and changes are smaller. The weight of foxtail and smartweed consumed, and the weight of guano from fox-tail (smartweed values were lost), increased at lower temperatures (mean increase 139% and 58%, respectively). For pigweed, how-ever, both quantities decreased (about 25%) and for hemp they showed little change. The caloric value of the feces produced from smartweed and pigweed increased slightly at 0°C, but was somewhat lower for foxtail and hemp. This may indicate a possible increase in effectiveness of the digestive process for foxtail and hemp at lower temperatures.

Digestive efficiency of the seeds was similar at both temperatures for foxtail, but differed for pigweed and probably for hemp. Con-siderable numbers of pigweed seeds were passed through undigested, possibly more at low temperatures, but the data are not suffi-cient to test.

Discussion of digestive efficiencies. Several studies of avian energy requirements have produced data on digestive efficiency and its relation to temperature. The species studied include two kinds of redpolls (*Acanthis* spp.) (on short days), Field Sparrows (*Spizella pusilla*) (on long photoperiods), Tree Spar-rows (*S. arborea*), House Sparrows (*Passer domesticus*), Zebra Finches (*Taeniopygia castanotis*), Dickcissels (*Spiza americana*), and Blue-winged Teal (*Anas discors*). All of these showed significant changes of diges-tive efficiency with changes in temperature. The changes were seldom linear, and often showed a peak or two at certain temperatures (see Brooks 1968; Olson 1965; West 1960; Davis 1955; Siebert 1949; Kendeigh 1949; El-Wailly 1966; Zimmerman 1965a; Owen 1970 for details). On the other hand, little or no change in efficiency was reported for redpolls on long days (Brooks 1968), Field Sparrow on short days (Olson 1965), White-throated Sparrows (*Zonotrichia albicollis*) (Kontogiannis 1968), four species of tropical finches (Cox 1961), Red-winged Blackbirds (*Agelaius phoeniceus*) (Brenner 1966), and Canada Geese (*Branta canadensis*) (Williams 1964). This variability may possibly be due to seasonal changes in metabolism (Pohl 1971; Zimmerman 1965b) and habituation to diet (Pendergast and Boag 1971).

All of the above species, and a few others (Stevenson 1933), were tested in the labora-tory and fed on prepared, standard, laboratory "chow" in the form of duck meal, chick meal, or cracked corn. Estimates of digestive effi-ciency generally ranged from a little over 60% to slightly above 90%, the majority of them between 65 and 80%. Gessaman (1968) found slightly lower efficiency in a small number of meat-fed Snowy Owls (*Nyctea scandiaca*) caged indoors (70%) compared to those caged outdoors (74–80%). The values obtained in our study fall in the same range despite some differences in technique.

Digestive efficiency can be expected to vary with the food eaten. Robel (pers. comm.) has found such differences in game birds feeding on different seeds, and can show, for some seeds, changes in efficiency correlated with the temperature and light regime. Smith and Follmer (1972) have shown digestibility of nuts and acorns by squirrels to be correlated with lipid content, but this was not true in our study. The utilization coefficient for fats, proteins, and nitrogen-free extract in the diet of wild turkeys differed among various food items (Billingsley and Arner 1970).

COMMENTS AND SPECULATION

Many studies have been concerned with time and/or energy budgets of various species, and the approach has seemingly been a profitable one. In general, one might expect an ideal predator both to minimize the time spent foraging and to maximize the rate of energy yield, but in practice one factor may be more critical than the other so that various com-promises are reached (Schoener 1969; Rapport 1971).

Minimization of foraging time for small birds in winter may be difficult to achieve but could be critical to survival. Gibb (1960) has estimated that British titmice (*Parus* spp.) must find insects at an extraordinary rate throughout the winter day in order to main-tain themselves. Heppleston (1971) suggests that European Oystercatchers (*Haematopus ostralegus*) must sometimes feed at night dur-ing the winter as one means of obtaining suf-ficient food, but this course of action may be uncommon for seed-eaters. If foraging must be done during daylight hours, and if food often comes in small packages of variable abundance (e.g., seeds), both the difficulty and the importance of minimizing foraging time may be great. Seed-eating winter birds may have reduced foraging time as much as possible, given their food resource and its distribution.

The timing of foraging *bouts* may conceiv-ably have importance. If a small bird, while

TABLE 5. Estimated numbers of seeds per hour required at 0°C, for confined and for active birds, compared to the maximum number of seeds that *could* be handled in an hour.

	No. needed per hr		Potential no. handled per hr	Ratio of potential no. handled to no. needed	
	Confined	Active		Confined	Active
Cardinal (3100 cal/hr)					
Foxtail	525	630	1200	2.3	1.9
Smartweed	318	382	306	0.9+	0.8
Hemp	114	137	654	5.7	4.8
Ragweed	32	38	45(♂)	1.4(♂)	1.2(♂)
			84(♀)	2.6(♀)	2.2(♀)
Song Sparrows (2300 cal/hr)					
Foxtail	343	412	1800	5.2	4.4
Smartweed	390	468	354	0.9	0.8
Hemp	71	85	318	4.5	3.7
Pigweed	3286	3943	1638	0.5	0.4

foraging, is in some way more conspicuous to it predators (by moving about, rustling leaves, etc.), and/or is somehow less able to watch for predators (while it is looking at the ground, peering under dead grasses, etc.), then perhaps it would be advantageous to stop foraging for a while, possibly to allow a predator's attention to wander or to look about for potential predators. "Bouting" may have an additional advantage of temporal spacing of small meals, facilitating flight from predators. If true, this would restrict the total foraging time.

On the other hand, birds active in cold weather may have high energy demands and may be hard pressed to fulfill them. Gibb's (1960) estimate for British titmice in winter (about 24 insects, of average size for those woods, per minute) for maintenance implies not only a good deal of time spent foraging but also a high energy need.

Kendeigh (1970) relates "existence energy" of confined birds to body weight. Using data from his figure 1, we determined that a bird the size of a Song Sparrow might require roughly 23 Kcal/bird/day at 0°C, and a Cardinal, perhaps 31 Kcal. This amount of energy must be gained in a daylight period of 9–10 hr in winter. In each hour of daylight, therefore, a Song Sparrow must consume an average of roughly 2300 calories, and Cardinals must consume about 3100 calories. The equivalents in numbers of seeds needed are shown in table 5. Each of these species *could* handle only certain numbers of each seed type during an hour. Comparing values in the table, it is evident that Song Sparrows could maintain themselves only on foxtail and hemp, and Cardinals on all but smartweed.

"Existence energy" is not the same as en-

ergy required by a free-living bird, of course. Kontogiannis (1968, fig. 1) indicates that when caged birds are forced to be active at 0° their energy requirements may increase by about 21% over closely confined birds. A free existence may cost 10–20% more energy than confined existence (Kendeigh, unpubl. data; pers. comm.). Using the 20% figure, we would estimate again that Song Sparrows could maintain themselves on hemp or foxtail seeds alone, but not on smartweed or pigweed. Hemp, foxtail, or ragweed would also suffice as the sole energy source for Cardinals, but not smartweed (see table 5). If the birds do much flying, however, the cost of living may increase greatly (e.g., Lefebvre 1964; Wolf and Hainsworth 1971) with corresponding changes in the kinds of seeds capable of sustaining the birds.

In the field, no bird is likely to find any one kind of seed in sufficient numbers to feed on it exclusively. By the onset of winter most seed fall is finished (West 1967; J. Morris, pers. comm.), and is hence an unrenewed resource during winter and early spring. Removal of seeds by various seed-eaters may be great (e.g., Pulliam and Enders 1971), and weathering may also reduce the numbers of seed suitable for eating (West 1967). Perhaps, as winter wears on, intake of energy may pose a critical problem, although the increase in day length after December may mitigate this.

Maximization of energy intake may be solved in several ways:

1. Seeds might be selected in decreasing order of energy yield so that, toward the end of winter, the *relatively* unprofitable but still suitable seeds (and the virtually useless ones) would be almost the only ones left by the

birds of that habitat (minus any removed by mice and other animals). At the end of the season, then, all birds in the area would be forced either to use the poorer seeds, or to emigrate—perhaps only to find an area where the same thing had happened. Conceivably, this would be a fairly unsuccessful strategy in the long run. And one can argue that *any* suitable seed should be gleaned in passing in order of encounter rather than in order of energy yield (see above).

2. High-yield seeds might be selected particularly at times when the birds are temporarily hungry (early in the morning) or in preparation for a long fast (late in the afternoon); low-yield seeds would be eaten more frequently at other times. This is perhaps unlikely; hungry birds are expected to be less discriminating (both in theory according to some of the models mentioned earlier and by anthropomorphic logic), and birds that have been eating throughout the day seem unlikely to begin to pick particularly rich food packages.

3. "Good" seeds might be chosen especially when environmental stresses increase energy needs and/or make foraging difficult, i.e., cold weather or snow storms. However, when foraging is difficult, a premium may in fact be placed on grabbing every possible food item.

4. Increase of energy intake may be achieved not by choosing special items, but by more or less thorough gleaning along the path of foraging, as mentioned earlier. Energy maximization then depends on a relatively small effort in reaching for a seed encountered while moving along and the ability to choose a good place in which to search. The advantages of this strategy were discussed briefly above. This kind of strategy may be most common among species for which minimization of hunting time is particularly important.

These considerations are meant to apply to small birds such as the ones we studied: which spend a lot of time foraging, at least in winter; which forage by embarking on searching trips, during which searching is fairly continuous; and whose food takes relatively little time to capture, subdue, and swallow.

SUMMARY

Seed preferences and digestive efficiencies of two species were tested in the laboratory at two temperatures. Cardinals preferred mainly foxtail or hemp, but the bulk of the diet by weight was composed of large seeds, ragweed

and hemp. Song Sparrows chose foxtail and pigweed, but the diet was primarily foxtail and hemp, by weight. Preferences were associated with ease of handling in most cases; Cardinals in the cold chose seeds yielding calories at high rates. Major constituents of the diet, by weight, were associated with rates of caloric intake from each seed type, especially at cold temperature.

Metabolic efficiencies of the two species were often significantly different for different seeds and sometimes changed with temperature.

Discussions of efficient time and energy budgets for foraging consider aspects of habitat selection, food selection, and various ways of increasing foraging efficiency.

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APPENDIX A. Cardinal seed preferences (number eaten).

		Hemp	Ragweed	Foxtail	Smartweed	N
Room temperature						
Bird # 1	(♀)	26%	14%	49%	11%	1607
# 2	(♂)	37	15	42	6	2120
# 3	(♀)	6	2	88	4	4306
# 4	(♂)	28	16	46	10	1891
# 5	(♀)	42	3	37	18	2202
# 6	(♂)	24	12	52	12	2141
# 7	(♂)	32	16	37	15	1105
# 8	(♀)	45	19	19	17	2165
# 9	(♂)	47	12	32	9	2346
#10	(♂)	15	20	58	7	2389
x̄ =		30%	13%	46%	11%	2227
0°C						
Bird # 1	(♀)	43	11	34	12	3678
# 2	(♂)	8	4	7	8	2903
# 4	(♂)	58	16	18	8	2544
# 5	(♀)	15	4	48	33	6570
# 6	(♂)	59	11	29	1	2680
# 7	(♂)	62	16	14	8	2747
# 8	(♀)	47	9	20	24	3591
x̄ =		52	11	24	13	3530

APPENDIX B. Song sparrow seed preferences (number eaten).

	Hemp	Ragweed	Foxtail	Smartweed	N
Room temperature					
Bird # 1	20%	62%	18	<1%	8198
# 2	5	31	61	3	8676
# 3	9	47	42	2	10921
# 4	9	43	47	1	10126
# 5	7	45	44	4	9644
# 6	4	38	57	1	11958
# 7	10	36	52	2	6801
# 8	13	44	41	2	6063
# 9	7	56	35	2	9140
#10	5	41	52	2	10170
x̄ =	9%	44%	45%	2%	9170
0°C					
Bird # 1	15	40	36	9	8453
# 2	6	32	57	5	3971
# 5	8	24	64	4	11439
# 8	12	31	51	6	8020
# 9	7	29	57	7	12157
#10	3	36	53	6	11937
x̄ =	9%	32%	53%	6%	9330