a factor modifying the sex ratio of survivors, a skewed ratio should have been evident at younger as well as older adult ages given in Table 1.

Summers-Smith (Bird Study 3:265–278, 1956) attributed higher male House Sparrow overwinter mortality to predation due to a lack of vigilance on the part of the males, a trait presumably lacking in females. At a high latitude site like Calgary, winter conditions should be a greater source of mortality than would be observed in more moderate climates such as in England or throughout much of the continental U.S. (Beimborn, M.Sc. thesis, Univ. Wisconsin, Milwaukee, 1967; Cink, Ph.D. diss., Univ. Kansas, Lawrence, Kansas, 1977). Cink's (1977) autumn and winter observations at Jamestown, North Dakota indicate that males are dominant over females and should obtain better positions at feeding sites. Bumpus (Biol. Lectures, Marine Biol. Lab., Woods Hole, 1899:209–226) reported that 72 individuals in a sample of 136 House Sparrows survived a severe winter storm in Providence, Rhode Island. Fifty-one of 87 males (59%) but only 21 of 49 females (43%) survived. Mortality was not independent of sex ($\chi^2 = 3.14$, df = 1, $0.05 < P < 0.1$), suggesting that harsh winter conditions disproportionately reduce the survivorship of females.

Our observations of House Sparrows in Calgary are atypical for sexually dimorphic species and coincide with those for monomorphic species wherein males usually survive better than females, presumably because of higher reproductive costs for females (Lack, The Natural Regulation of Animal Populations, Oxford Univ. Press, London, England, 1954). The differences between our observations and those of Summers-Smith (1956, 1963) indicate that higher susceptibility of males to predation is overriden in harsh winter climates by higher vulnerability of females to severe winter conditions.

Acknowledgments.—We would like to thank G. Erickson, R. C. Fleischer, E. James, P. E. Lowther, M. Luchanski, S. C. McGillivray, J. T. Paul, Jr., and G. Pittman for assistance in the field. S. C. McGillivray, and P. H. R. Stepney read and improved the manuscript with their constructive comments. R. F. Johnston provided the initial impetus for our studies and constant encouragement throughout. Financial support was supplied by National Science Foundation grants DEB-02374 and DBS-7912412 to R. F. Johnston.—W. BRUCE MCGILLIVRAY, *Dept. Ornithology, Alberta Provincial Museum, Edmonton, Alberta T5N 0M6 Canada* AND EDWARD C. MURPHY, *Instit. Arctic Biology and Div. Life Sciences, Univ. Alaska, Fairbanks, Alaska 99701.* *Accepted 30 Mar. 1984.*

Wilson Bull., 96(3), 1984, pp. 458–463

Seed selection by juncos.—Evidence suggests that avian predators may respond to food characteristics other than, or in addition to, energy content of the items (Pulliam, Ardea 68:75–82, 1980), yet little is known of the exact determinants of diet selection (Willson, Condor 73:415–429, 1979). Investigations of food variables that influence dietary choices should be valuable in understanding foraging behavior. In the present study, we asked whether Dark-eyed Juncos (*Junco hyemalis*) select seeds on the basis of physical characteristics of the seeds, such as size, shape, and color, or on the basis of nutrient content.

Materials and methods.—Thirty juncos were captured near Fort Collins, Colorado, color banded, and maintained on 12L:12D photoperiod at room temperature in cages (25 × 25 × 25 cm) individually so that they could hear but not see each other. Age and sex were unknown. Subjects were fed a mixed diet consisting of niger thistle (*Guizotia abyssinica*) (hereafter "thistle"), canary grass (*Phalaris canariensis*) (hereafter "canary"), millet (*Panicum milliaceum*), and flax (*Linum usitatissium*). Seed and water were freely available.

TABLE 1

INDIVIDUAL PREFERENCES[a] FOR CANARY (C) AND THISTLE (T) PELLETS, DYED SEEDS, AND UNALTERED SEEDS[b]

Grams pellets				No. dyed seeds			No. unaltered seeds			
Bird	C	T	Pref.	C	T	Pref.	Bird	C	T	Pref.
Group A							Group C			
1	0.24	0.07	NP	1	83	T	1	78	99	NP
2	0.57	0.07	C	37	93	T	2	37	140	T
3	0.01	0.17	T	7	179	T	3	58	82	NP
4	0.02	0.19	T	12	76	T	4	112	71	C
5	0.01	0.19	T	1	83	T	5	86	58	NP
6	0.48	0.05	C	11	102	T	6	107	31	C
7	0.55	0.13	C	59	32	NP	7	61	104	T
8	0.52	0.05	C	61	75	NP	8	67	40	C
9	0.51	0.08	C	64	107	T	9	84	94	NP
							10	80	68	NP
Group B										
1	0.45	0.06	C	41	65	NP	1	23	66	T
2	0.41	0.03	C	52	10	C	2	56	59	NP
3	0.54	0.01	C	0	117	T	3	40	81	T
4	0.32	0.10	NP	19	165	T	4	6	155	T
5	0.48	0.01	C	78	8	C	5	34	110	T
6	0.45	0.03	C	55	22	NP	6	50	84	NP
7	0.42	0.01	C	45	68	NP	7	18	104	T
8	0.54	0.01	C	44	49	NP	8	25	97	T

[a] Preference judged by significant difference in consumption of alternative food types according to a 2-tailed t-test on 10 preference trials for each individual with $P < 0.05$; NP = no statistically significant preference.
[b] Tabled values for each bird are means of 10 trials.

Only canary and thistle were used in preference experiments. Ground seeds reconstituted as pellets, dyed seeds, and unaltered seeds were used in that sequence in tests. The rationale for these manipulations was that if the same preference for a food type (canary or thistle) was maintained in both seed and pellet tests, one could conclude that some nutritional component or taste was being detected by the birds and that shape, size, and handling characteristics were less important. If the birds differed in their preference for canary or thistle, depending upon the condition of the seed (e.g., pellets, dyed, unaltered), then handling characteristics or other physical properties could be considered more important.

During feeding, a junco obtained an individual seed by a pecking action then hulled the seed by rapid mandibulation while in an upright posture. While upright between pecks the individual would move its head as in scanning or shift its position slightly during the hulling activity. We interpret each peck taken during such feeding as a separate and independent action and the number of these actions as a measurement of preference when the bird was presented with alternative food types. To evaluate the possible significance of handling times for the two different seeds, we examined consumption on the basis of numbers of seeds. Therefore, we have analyzed numbers of seeds consumed, whenever possible, as a measure

TABLE 2

MEAN HANDLING TIMES (SEC) AND PREFERENCES[a] FOR CANARY (C) AND THISTLE (T) SEEDS IN DYED AND UNALTERED CONDITIONS

	Dyed seeds							Unaltered seeds		
Bird	C	T	Pref.	Bird	C	T	Pref.	C	T	Pref.
Group A				Group B						
1	10.4	6.4*	T	1	6.1	6.2	NP	9.4	5.4*	T
2	4.3	3.8	T	2	4.5	3.6	C	3.6	4.2	NP
3	5.4	3.8*	T	3	7.8	4.3*	T	7.8	4.3*	T
4	6.4	4.8*	T	4	9.0	3.7*	T	5.9	4.4*	T
5	6.4	4.5*	T	5	5.0	6.3*	C	4.0	4.8	T
6	5.1	4.9	T	6	5.9	3.7	NP	3.9	4.7	NP
7	9.3	3.2*	NP	7	4.9	5.5	NP	8.8	3.7*	T
8	3.6	3.4	NP	8	4.4	4.7	NP	3.9	4.4	T
9	4.3	4.8	T							

[a] Preference judged by significant difference in consumption of alternative food types according to 2-tailed *t*-test on 10 preference trials for each individual with $P < 0.05$ (see Table 1).

* Significantly different handling times for the two seed types shown by 2-tailed *t*-test with $P < 0.05$.

of preference. In our pellet tests we evaluated weight consumed of each food type; since the pellets, reconstituted from ground seed, were of similar size for canary and thistle, differences in weight of pellets consumed probably reflect differences in numbers of pellets consumed as well. In an independent evaluation of preferences of juncos for canary and thistle seed (Thompson et al., unpubl.), strong preference for thistle compared to canary in sequential choice tests was found; juncos selectively foraged for thistle even when seeds were presented in a ratio of four canary to one thistle and even though thistle seeds are about half the size of canary.

For simultaneous preference tests, two plastic cups approximately 3 cm diameter by 2 cm high were tacked side by side onto a small platform. Into these cups were placed paper cups approximately half full of seeds or pellets. Three groups of juncos (A = 9 birds, B = 8 birds, C = 10 birds) were studied from 16 January–4 May 1981. Three tests were conducted in the following order: (1) canary seed in pellet form vs thistle seed in pellet form; (2) dyed canary vs dyed thistle and (3) unaltered canary vs unaltered thistle. Ten separate trials of each bird were made for each type of preference test, usually on 10 consecutive days but at different times of the afternoon (most trials were made between 13:00 and 17:00). Groups A and B were used in preference tests 1 and 2, and groups B and C were used in preference test 3. An additional experiment was conducted in which birds in group C were placed either on a continuous diet of only unaltered canary or only unaltered thistle after one set of unaltered seed preference tests. Three weeks later these birds were given another set of preference tests.

For preference test 1, canary and thistle were ground separately, water was added to the powders, and the mixtures were allowed to air dry. The resulting cakes were broken into small pellets of irregular, but similar and edible, sizes. This treatment reduced handling time essentially to zero. For preference test 2, whole canary (light yellow) and whole thistle (dark grey to black) were soaked in black food dye created from a mixture of red, green, and blue, and then allowed to dry. Each experimental trial consisted of a 2-h deprivation period followed by a 1-h presentation of the two types of food. The location of a food type

TABLE 3

PERCENT OF EACH NUTRIENT COMPONENT IN CANARY AND THISTLE SEED, AND PERCENT ASSIMILATED (PARENTHESES) FOR BIRDS IN GROUP A, CALORIC VALUE OF EACH TYPE OF SEED (AND ASSIMILATED PERCENT) AND AVERAGE WEIGHTS (±1 SD) OF EACH TYPE OF SEED ARE ALSO GIVEN

	Canary	Thistle
Protein	19.53 (36.8)	19.22 (31.0)
Fat	4.51 (88.9)	20.89 (84.5)
Carbohydrates	61.61 (98.4)	15.18 (71.3)
Fiber	8.11 (82.5)	39.87 (86.7)
Ash	6.43	4.99
Calories/gm	1842 (84.3)	1124 (60.4)
Mg/seed	7.0 ± 0.02	3.1 ± 0.01

(right cup vs left cup) was alternated to control for positional effects. Similar superabundant amounts of each food type were available in the cups. The food was weighed before and after each trial with spillage poured back. Estimates of numbers of seeds eaten were derived from a regression equation for weight vs numbers of seeds. An individual's preference was judged by results of a 2-tailed *t*-test (Sokal and Rohlf, Biometry, W. H. Freeman and Co., San Francisco, 1969:330) on consumption data of the 10 trials in which the two alternative foods were presented simultaneously.

While observing each feeding bird through one-way glass, handling times for seeds were measured to the nearest 0.1 sec. Handling times were determined for groups A and B during the preference tests on dyed seed and again for group B during the preference tests on unaltered seeds. The number of measurements of handling time ranged from 10–60 ($\bar{x}$ = 25) for each bird for each kind of seed. The average number of days of experience with the seeds prior to measurements of handling time was 25 days for group A (dyed), 45 days for group B (dyed), and 55 days for group B (unaltered).

Nutrients were analyzed by Triple S Laboratories, Loveland, Colorado. We conducted a study of the assimilation of nutrient components of canary and thistle seeds by collection and analysis of feces, and this information was used in comparing preferences with nutritional value of the food items. Assimilation data were obtained by placing two groups of birds on continuous diets of either canary or thistle seed for 3 days. Each day the birds were deprived of seed from 14:00–17:00 to allow the digestive tracts to empty (Stevenson, Wilson Bull. 45:155–167, 1933; Willson and Harmeson, Condor 75:225–234, 1973), then provided with seed for 1 h, and deprived again until 07:00 the next morning. The nutrient components were determined for an amount of seed equivalent to that consumed during the hour, as well as for the feces produced from the hour of feeding. The amount of each nutrient in the fecal sample was subtracted from that in the seed consumed to find the amount assimilated.

A possible problem for studies of this kind is in finding the appropriate length of time for the post-feeding period during which feces are collected. Too short a period may not allow the digestive tract to empty, and too long a period may result in body tissues being metabolized and excreted. Our assimilation data should be valid for comparisons between our experimental groups that ate the two different types of food because the groups were treated the same otherwise, but the data may not represent absolute assimilation values.

Results.—Eliminating shape and size characteristics of the two types of seeds by grinding

TABLE 4

PROFITABILITIES OF CANARY (C) AND THISTLE (T) SEED FOR BIRDS OF GROUP A[a]

	Protein		Fat		Carbohydrate		Fiber		Calories	
Bird	C	T	C	T	C	T	C	T	C	T
1	0.06	0.04	0.03	0.09	0.47	0.06	0.05	0.18	1.21	0.35
2	0.14	0.06	0.08	0.15	1.14	0.09	0.12	0.30	2.92	0.59
3	0.11	0.06	0.06	0.15	0.91	0.09	0.10	0.30	2.33	0.59
4	0.09	0.05	0.05	0.12	0.77	0.07	0.08	0.24	1.96	0.47
5	0.09	0.05	0.05	0.13	0.77	0.08	0.09	0.25	1.96	0.50
6	0.11	0.05	0.06	0.12	0.96	0.07	0.11	0.23	2.46	0.46
7	0.06	0.07	0.04	0.18	0.53	0.11	0.06	0.36	1.35	0.70
8	0.16	0.07	0.09	0.17	1.36	0.11	0.15	0.34	3.49	0.66
9	0.13	0.05	0.08	0.12	1.14	0.07	0.13	0.24	2.92	0.47

[a] Tabled values are milligrams of nutrient assimilated per second handling time for each major component analyzed.

and feeding reconstituted pellets showed that most of the birds significantly preferred canary pellets to thistle pellets (12 canary, 3 thistle, 2 no preference, $\chi^2 = 10.7$, df = 2, $P < 0.01$, Table 1). In contrast to the results on pellets, juncos usually preferred dyed thistle to dyed canary, although many did not have a significant preference (9 thistle, 2 canary, 6 no preference, $\chi^2 = 4.5$, df = 2, $P = 0.1$, Table 1). Compared to the clear preference for canary pellets, therefore, the birds had a different preference for intact dyed seeds (G-test for independence of seed type and condition of seed, i.e., pellet or dyed, $G = 13.2$, df = 2, $P < 0.005$). We obtained results similar to those on dyed seeds when tests were performed using unaltered seeds. Juncos usually preferred unaltered thistle to unaltered canary, although many did not have a significant preference (8 thistle, 3 canary, 7 no preference, $\chi^2 = 2.3$, df = 2, $P = 0.4$, Table 1). The results on unaltered seeds indicated a different preference for unaltered seeds in comparison to the preference for canary pellets found in the first experiment (G-test for independence of seed type and condition of seed, i.e., pellets or unaltered seed, $G = 11.1$, df = 2, $P < 0.005$).

The juncos also tended to change preference to thistle over time. Group C birds (fed only unaltered thistle and canary for 3 weeks) showed the following results: at the onset of the experiment, three birds preferred canary, two preferred thistle, and five had no preference; 3 weeks later, one bird preferred canary, eight preferred thistle, and one had no preference (G-test for independence of preference trial and seed preference, $G = 7.8$, df = 2, $P < 0.025$).

Considering the dyed seeds, we found that nine birds had similar handling times for canary and thistle, and seven had significantly longer times for canary (Table 2). In only one case did a bird have a significantly longer handling time for thistle than canary. We found that seven of eight birds preferred the seed with the shorter handling time when handling times differed significantly. Five of nine birds had no preference when handling times were not significantly different for the two types of seeds. In tests involving unaltered seeds, four of four birds preferred the seed with the significantly shorter handling time and two birds with similar handling times had no preference. Thus, of the 12 juncos that had significantly different handling times for the two seeds, 11 preferred the seed (10 thistle, 1 canary), with the shortest handling time (binomial test, $P = 0.006$, Table 2). Of the 13 juncos that did not have significantly different handling times for the two seeds, seven had no preference, five preferred thistle, and one preferred canary ($\chi^2 = 4.3$, df = 2, $P = 0.1$).

To take handling time into account when considering nutritional value of a seed, we calculated the number of milligrams of each nutrient assimilated per second handling time for each seed type for birds in group A. Weight per kernel of seed was multiplied by the percent of each nutrient in the seed (Table 3). This yielded the number of grams of nutrient ingested from one kernel, which was then multiplied by the fraction which was assimilated of the nutrient in question (Table 3) to give the amount of nutrient assimilated from one kernel. Finally, the number of milligrams assimilated was divided by handling time for each individual eating that seed to give the milligrams of nutrient assimilated per second handling time, the "profitability" of a seed type.

Examination of profitability values (Table 4) shows that handling time had little effect on the nutritional value of the seeds. Profitability of canary was usually higher with respect to carbohydrate, protein, and caloric content, while profitability of thistle was usually higher for fat and fiber.

Discussion.—Canary seed was preferred when offered in the pellet form. Since differences in size, shape, and handling time of the seeds were eliminated when the pellets were formed, these could not influence choices made. Color, taste and nutritional contents were possible cues for such choices. When dyed or unaltered seeds were presented, the general preference for canary disappeared and increasing numbers of individuals preferred thistle or expressed no preference for either seed. Thus, when shape, size, and handling characteristics were returned to the seeds, preference behavior changed. Because the seeds were dyed, color is unlikely to be the basis for this change. Therefore, we conclude that physical properties such as size, shape, or hardness, which determine handling characteristics of the seeds, are important in determining preferences. This conclusion is supported by the relationships between individual preference and handling time in the majority of birds tested. Most individuals preferred the seed with the shortest handling time or had no preference when the handling times were similar. It is worth emphasizing that in spite of variation in assimilation coefficients for nutrient components of the two seeds investigated here, the same general ranking of food items obtains, canary greater than thistle, whether nutrient content of the seeds is used (Table 3) or profitabilities (Table 4).

As a final point, we observed that the juncos on the whole did not exhibit absolute preferences for a particular seed type; even though one kind of seed was strongly preferred, some of the less preferred seed was usually consumed. This result has been observed frequently in other studies and usually interpreted in terms of a sampling strategy on the part of the forager. That is, a foraging animal consumes some of a "non-optimal" diet item perhaps because this keeps options open in a setting of changing resources. Some new food may be encountered which would increase the rate of energy intake, for example. An alternative to this view is the concept of balanced diet. It may be that a small subset of the resource array available to a forager is heavily used while a diversity of other items is consumed at low levels because these rare items in the diet provide some essential nutrients. Under this concept, all-or-none selection of seeds is not expected because it does not provide a balanced diet, rather than because of sampling.

Acknowledgments.—We thank D. F. Tomback, M. A. Cunningham, A. E. M. Baker, D. B. Thompson, P. R. Sutherland, and K. Bunch for their help and advice with the study. G. B. G. gives special thanks to G. Sherman for sharing the cold sunrises while trapping juncos, and to the members of her graduate committee for their guidance: G. C. Packard, R. E. Moreng, and P. N. Lehner. Helpful comments were provided by anonymous reviewers.—GAIL B. GOLDSTEIN AND MYRON CHARLES BAKER, *Dept. Zoology, Colorado State Univ., Fort Collins, Colorado, 80523.* (Present address GBG: *150–38 Road, Flushing, New York, 11376.*) *Accepted 1 May 1984.*