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ROLE OF HANDLING TIME IN SELECTION OF EXTRUDED FOOD MORSELS BY TWO GRANIVOROUS BIRD SPECIES

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ABSTRACT.—After producing food morsels resembling seeds of different shapes and sizes, we determined the effect of these variables on food morsel selection by Harris' Sparrows (*Zonotrichia querula*) and American Tree Sparrows (*Spizella arborea*). Harris' Sparrows have larger bodies and bills than American Tree Sparrows. During pairwise feeding trials, where consumption (mass) was the measure of selection, both species of sparrows selected food items that required the least handling time, not those that maximized energy gain per unit of time. Extruder-processed food morsels may provide a new means to distinguish predictions of various foraging theories and hypotheses. *Received 15 August 1991, accepted 8 March 1992.*

SMALL MORPHOLOGICAL differences of mouth parts are often associated with considerable differences in size of foods selected by foragers (Pulliam 1985). Relationships between bill morphology and seed selection are well demonstrated in granivorous finches (Newton 1967, Lack 1971, Abbott et al. 1977). Larger-billed finches tend to eat larger seeds than do smaller-billed finches. It is often assumed that these differences in seed selection result from birds maximizing the energy gained per unit of handling time (e.g. Emlen 1966, Schoener 1971, Lacher et al. 1982). Yet, the relationships of bill size, preferred seed size, and handling ability remain unclear (Hespenheide 1966, Abbott et al. 1975). For example, Hespenheide (1966), Royama (1970), and Willson (1971, 1972) found that both large- and small-billed birds preferred small seeds.

Characteristics that influence handling time include width, depth, shape, and mass of food items (Sherry and McDade 1982). Various investigators have attempted to identify which of these characteristics is most important in seed selection by birds. Because seeds vary in size, color, shape, hardness, and energy and nutrient contents, it is difficult to isolate any one factor in experimental designs using natural seeds. Goldstein and Baker (1984) attempted to eliminate some variation in seed selection trials by grinding and then pelletizing seeds prior to testing; however, their end product did not resemble natural seeds.

Extrusion processing is a technique that allows an investigator to agglomerate a finely ground mixture of feedstuff into morsels of different sizes, shapes, and densities and to vary each characteristic independently. We used the extrusion process to form seedlike morsels of various sizes and shapes to determine the effect of size and shape on handling time and seed selection of Harris' Sparrows (*Zonotrichia querula*) and American Tree Sparrows (*Spizella arborea*).

METHODS

Food morsels were formulated and processed through an extrusion cooker in the Kansas State University Feed Processing Center. Corn (*Zea mays*), sorghum grain (*Sorghum vulgare*), wheat (*Triticum aestivum*), and soybean (*Glycine max*) oil meal comprised the bulk (96%) of the morsel formula, which was supplemented with calcium, phosphorus, and lysine plus vitamin and mineral premixes. Prior to combining the ingredients, the grains were ground once through a 3.18-mm hammer-mill screen, then batched, mixed in a double ribbon mixer, and reground once through a 1.59-mm hammer-mill screen. A Wenger X-20 LBM extrusion cooker was used to form the base mix into different morsel shapes and sizes by processing through specially designed die inserts and operating the extruder at various speeds. Procedural details are presented in Keating (1989) and summarized in Keating et al. (1991).

Food morsels were spherical-, ovate-, elliptical-, and rosette-shaped (Fig. 1), and the spherical morsels were subsequently produced in three sizes. Food morsels

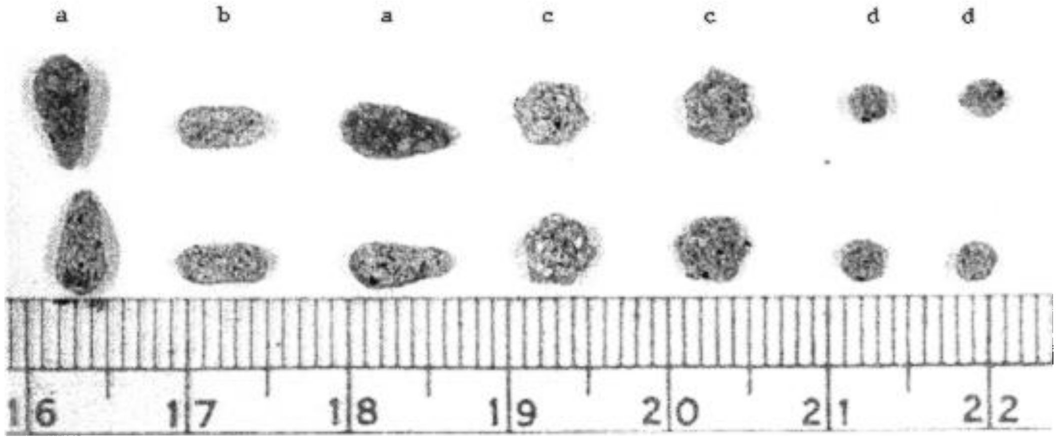

Fig. 1. Extruded food morsels used in this study. Shapes: (a) ovate, (b) elliptical, (c) rosette, and (d) spherical. Millimeter rule provides scale.

contained 13.8 kJ/g of calculated metabolizable energy. All morsels were of the same density, texture, color, and consistency (i.e. they differed only in shape and size).

Harris' Sparrows and American Tree Sparrows were caught locally in mist nets during November 1987, and confined individually in cages (39 × 22 × 27 cm) in an environmental chamber maintained at 5°C and 75% relative humidity under a 10L:14D-h photoperiod. All birds were acclimated to cage conditions for at least 10 days prior to experimental trials, with chick starter mash and water provided *ad libitum.*

Bills of Harris' Sparrows were greater in length (12.0 ± SE of 0.4 mm), width (6.0 ± 0.3 mm) and depth (7.4 ± 0.4 mm) than those of American Tree Sparrows (9.2 ± 0.3, 4.4 ± 0.2, and 5.6 ± 0.3 mm, respectively). The Harris' Sparrows weighed an average of 37.3 g, whereas the American Tree Sparrows weighed an average of 20.3 g.

Handling time for each food morsel shape and size was determined by timing birds feeding continuously on each food. During periods of continuous feeding (feeding bouts), the number of food items consumed was recorded. Food handling time was the inverse of the number of items consumed per unit of time. Birds were deprived of food 20 h prior to determining handling times to ensure feeding activity. Two days prior to the deprivation period, birds were provided only the type of food to be used in the subsequent test. Handling times for shape of foods were determined for 1 to 11 individuals of each species, and those for morsel size for 2 to 11 individuals of each species. During the feeding bouts, some birds ate more than others, with some not eating at all. We felt that the best estimate of handling time could be obtained by using a weighted analysis using the number of morsels consumed during a bout as the weighting factor. Thus, if one bird ate two morsels while another ate five morsels during a particular bout, the handling time estimates based on each bird's data were weighted by two and five, respectively. The weighted analysis was performed using SAS GLM with a two-way factorial treatment structure (Neter and Wasserman 1974).

Two feeding experiments were conducted, the first using different shapes of morsels and the second using different sizes of one morsel shape. Birds were exposed to all sizes and shapes of food morsels prior to feeding trials.

Morsel-selection experiments consisted of singly replicated day-long feeding trials in the home cages of the birds in the environmental chamber. A trial involved pairwise presentations of two food morsel types (shapes or sizes), each offered in a separate feeder on opposite ends of the same side of the cage, equidistant from a waterer and a perch. A preweighed quantity of food in excess of daily requirements was provided in each feeder at the onset of the light period. Feeder positions were exchanged every 2 h. Replications presented food types in opposite positions from the previous day. Unconsumed food was collected at the end of the light period and reweighed. Selection was determined from amount (mass) of a certain type of food (size or shape) consumed (i.e. the greatest amount reflected positive selection by the birds).

In Experiment I, spherical- (1.6-mm diameter), ovate- (3.2 × 6.0 × 1.5 mm), elliptical- (2.4 × 6.0 × 1.6 mm), and rosette-shaped (4.8-mm diameter × 1.6 mm) food morsels were presented in all six pairwise combinations to 12 Harris' and 12 American Tree sparrows in four 6 × 6 Latin Square blocks. In Experiment II, three sizes (1.6-, 3.2-, and 4.0-mm diameter) of spherical-shaped food morsels were presented in all three pairwise combinations to 12 Harris' and 12 American Tree sparrows in eight 3 × 3 Latin Square blocks.

TABLE 1. Weighted mean handling times ($\bar{x} \pm$ SE) for food morsels of different shapes and sizes consumed by Harris' Sparrows and American Tree Sparrows. Means followed by the same letter within a column do not differ ($P < 0.05$).

	Harris' Sparrows		American Tree Sparrows	
Morsel	Individuals	Handling time (s)	Individuals	Handling time (s)
Elliptical	3	3.47 ± 0.73 ABEH	5	5.02 ± 0.80 BEF
Ovate	4	3.66 ± 0.69 EG	1	6.21 ± 1.71 DEF
Rosette	3	5.17 ± 0.83 AGF	4	7.23 ± 0.89 F
Spherical[a]				
Small	8	1.68 ± 0.30 I	11	1.96 ± 0.28 HI
Medium	2	3.82 ± 0.74 BCDG	4	5.75 ± 0.61 CF
Large	3	3.74 ± 1.04 BCDGI	3	11.18 ± 1.01

[a] Diameters: small, 1.6 mm; medium, 3.2 mm; large, 4.0 mm.

RESULTS

Handling time.—Less than 2 s were required for Harris' Sparrows and American Tree Sparrows to consume a small, spherical-shaped food morsel, significantly less than that required to consume other shapes of food morsels (Table 1). Harris' Sparrows took between 3.5 and 3.7 s to pick up, manipulate, and consume (handling time) elliptical- and ovate-shaped morsels, not significantly less ($P > 0.05$) than the 5.2 s handling time for rosette-shaped morsels. American Tree Sparrows required 5.0 s to handle elliptical-shaped morsels which was not significantly less than the 7.2 s needed to handle rosette-shaped morsels (Table 1).

Harris' Sparrows required significantly less time (1.7 s) to handle small, spherical-shaped morsels than the 3.8 s needed to handle medium and large spherical morsels. American Tree Sparrows required only 2.0 s to handle small, spherical morsels compared to 5.8 and 11.2 s to handle medium and large spherical morsels, respectively. The time required for American Tree Sparrows to handle large, spherical morsels (11.2 s) was significantly greater ($P < 0.05$) than any of the other handling times determined for either bird species in this study (Table 1).

Experiment I.—Harris' Sparrows consumed between 6.7 and 7.3 g per day of spherical-shaped food morsels when those were offered with any of the other morsels (Table 2). This was significantly greater ($P < 0.05$) than the consumption of elliptical-, ovate-, or rosette-shaped morsels. American Tree Sparrows consumed between 4.9 and 5.5 g per day of spherical-shaped food morsels, significantly more ($P < 0.05$) than any other food morsel shapes with which it was paired (Table 2). The consumption of rosette-shaped morsels was significantly less ($P < 0.03$) than the consumption of any other morsel shape for both sparrow species. The highest consumption of spherical morsels by Harris' Sparrows (7.3 g per day) occurred when spherical morsels were paired with rosette-shaped morsels. Likewise, the consumption of spherical morsels by American Tree Sparrows was greatest (5.5 g per day) when they were offered with rosette-shaped morsels. Consumption of rosette-shaped morsels was least when

TABLE 2. Mean (±SE; $n = 12$) mass of different-shaped food morsels consumed by Harris' Sparrows and American Tree Sparrows during pairwise feeding trials, Experiment I.

Paired morsel shapes		Daily consumption (g)			
		Harris' Sparrows		American Tree Sparrows	
Choice 1	Choice 2	Choice 1	Choice 2	Choice 1	Choice 2
Spherical	Elliptical	6.81 ± 0.30	3.14 ± 0.27	4.88 ± 0.21	1.45 ± 0.19
Spherical	Ovate	6.66 ± 0.25	3.35 ± 0.29	4.87 ± 0.20	1.43 ± 0.20
Spherical	Rosette	7.29 ± 0.29	2.48 ± 0.26	5.48 ± 0.16	0.85 ± 0.11
Elliptical	Ovate	5.25 ± 0.32	4.94 ± 0.26	3.72 ± 0.18	2.57 ± 0.16
Elliptical	Rosette	6.11 ± 0.37	4.26 ± 0.25	4.52 ± 0.24	1.74 ± 0.19
Ovate	Rosette	5.80 ± 0.36	4.60 ± 0.32	3.93 ± 0.27	2.39 ± 0.21

TABLE 3. Mean ($\pm$SE; $n = 12$) mass of different sizes of spherical-shaped food morsels consumed by Harris' Sparrows and American Tree Sparrows during pairwise feeding trials, Experiment II.

Paired morsel sizes		Daily consumption (g)			
		Harris' Sparrows		American Tree Sparrows	
Choice 1	Choice 2	Choice 1	Choice 2	Choice 1	Choice 2
Small	Medium	5.72 ± 0.50	4.02 ± 0.57	5.15 ± 0.11	1.04 ± 0.15
Small	Large	6.24 ± 0.52	3.21 ± 0.62	5.42 ± 0.12	0.62 ± 0.11
Medium	Large	5.40 ± 0.41	4.40 ± 0.32	4.43 ± 0.24	1.70 ± 0.18

they were offered with spherical morsels (2.5 and 0.9 g per day for Harris' Sparrows and American Tree Sparrows, respectively). Consumption of elliptical- and ovate-shaped morsels was similar for both bird species (Table 2).

Experiment II.—Total consumption of morsels by Harris' Sparrows was remarkably similar (9.7 to 9.8 g per day) during feeding trials to determine morsel size preferences, but sizes of the spherical morsels were consumed disproportionally (Table 3). Harris' Sparrows selected the smaller morsels in all trials. They consumed 6.2 g per day of small, spherical morsels when they were offered with large morsels, and 5.7 g per day when they were offered with medium morsels. The consumption of large, spherical morsels by Harris' Sparrows was 3.2 g per day when they were paired with small morsels and 4.4 g per day when they were offered with medium morsels (Table 3).

The total consumption of morsels by American Tree Sparrows also was very similar (6.0 to 6.2 g per day) during feeding trials to determine morsel size preferences. American Tree Sparrows always selected the smaller-sized spherical morsels when they were offered with larger morsels (Table 3). The greatest consumption of small, spherical-shaped morsels by American Tree Sparrows (5.4 g per day) occurred when they were offered with large, spherical morsels. Large, spherical morsels were consumed least (0.62 g per day) when offered with small, spherical morsels.

The preference for small, spherical morsels was stronger in American Tree Sparrows than Harris' Sparrows. When large, spherical morsels were paired with small, spherical morsels, 34% of the Harris' Sparrows' diet consisted of large morsels versus only 10% for American Tree Sparrows. When large, spherical morsels were offered with medium, spherical morsels, 45% of the diet of Harris' Sparrows consisted of large morsels versus only 28% for American Tree Sparrows.

DISCUSSION

Both American Tree Sparrows and Harris' Sparrows selected the food morsels that could be picked up, manipulated, and consumed in the least amount of time. This relationship held for both morsel shape and morsel size. Rosette-shaped morsels (the largest morsel) had handling times of 5.2 and 7.2 s for Harris' Sparrows and American Tree Sparrows, respectively, and were consumed least in all pairwise feeding trials to determine shape preference. Likewise, small, spherical-shaped morsels had a handling time of 1.7 to 2.0 s for our sparrows and were consumed in the greatest amounts in all pairwise feeding trials to determine shape and size preference. Because small food morsels had the lowest handling time for both bird species, we were unable to separate the effects of size and handling time in this study.

Optimal-foraging theory generally predicts that food consumption should maximize energy gain per unit of handling time. Although our study was not specifically designed to test elements of optimal foraging theory, the data lend themselves to an assessment of maximization of energy gain per unit of foraging time (feeding efficiency). We estimated feeding efficiency by determining individual food morsel weights (mg), the metabolizable energy content of each (J/mg), and dividing that value by the handling time (s). For Harris' Sparrows in Experiment I where shape was the variable, the calculated feeding efficiency was highest (101.7 ± 16.3 J/s) for ovate-shaped morsels and lowest (61.5 ± 7 J/s) for small, spherical-shaped morsels. Consumption data did not support optimal-foraging-theory predictions. Likewise, in Experiment I, where the calculated feeding efficiency of American Tree Sparrows was highest (62.4 ± 11.3 J/s) for elliptical-shaped morsels and lowest (51.1 ± 4.2 J/s) for small, spherical-shaped morsels, the consumption data did not support the optimal-foraging-theory predictions. In Experiment II, where size was the factor, the calculated feeding efficiency for Harris' Sparrows was highest (107.6 ± 18.4 J/s) for large spherical-shaped morsels and lowest (64.1 ± 7.1 J/s) for the smallest morsels, but again, the consumption data did not lend support for those values. However, for American Tree Sparrows in Experiment II, the calculated feeding efficiency values did predict food consumption during the trials. Those feeding efficiency values were 50.7 ± 5.0, 43.5 ± 10.9, and 30.6 ± 18.0 J/s for small, medium, and large spherical-shaped morsels, respectively, corresponding well with morsel consumption. Overall, feeding efficiency values correctly predicted the outcome of food consumption in 8 of our 18 (44%) feeding trials. In comparison, when morsels with different morphological characteristics were paired, handling time correctly predicted the outcome of 17 of the 18 (94%) feeding trials.

Because birds did not need to husk the food morsels in our trials, our food-handling data cannot be compared directly with those reported by Willson (1971), who found that large-billed birds handled larger seeds faster than did smaller-billed birds. There was evidence that our larger-billed Harris' Sparrows were more adept at eating large, spherical-shaped food morsels than were our smaller-billed American Tree Sparrows. However, we did not observe that larger-billed birds handled small morsels faster than smaller-billed birds, as reported by Hespenheide (1966) and Willson (1972). Hespenheide (1966), Willson (1971, 1972), and Willson and Harmeson (1973) found that birds preferred eating those foods consumed the fastest. However, the fastest consumed seeds were not always the smallest. If smaller-billed birds can consume small foods faster than large foods, those birds will prefer small foods. Likewise, if larger-billed birds can consume large foods faster than small foods, the birds will prefer large foods. In our study, the smaller-billed American Tree Sparrows and the larger-billed Harris' Sparrows both consumed small food morsels faster than large food morsels, and therefore, both preferred small food items regardless of bill size.

As a result of our research, we believe extruder-processed food morsels offer an opportunity to conduct research on various foraging theories and hypotheses. This process allows one independently to vary energy content, size, shape, and color of food items. These food morsels can be made to resemble many natural seeds and are readily accepted by wild birds (Keating et al. 1991). Once techniques are developed to produce food morsels that are durable under various environmental conditions, we may see an expanded use of them in ecological research.

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