SELECTION RESPONSES OF AVIAN GRANIVORES TO VARIOUS MORPHOLOGICAL FOOD CHARACTERISTICS

by

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OVERALL INTRODUCTION AND REVIEW

Optimal foraging models are based on the tenet that natural selection ultimately favors those individuals which consume the foods that convey maximum net benefit to the individual. The benefit is usually assumed to be energy-based (Lacher et al. 1982). Numerous authors (see Charnov 1976) have considered the mechanisms for the food choice. Most of the models proposed have been concerned with the maximization of the rate of energy intake within the group of available food choices (Emlen 1966, 1968; Schoener 1971; Krebs 1978; Pulliam 1974).

Pyke et al. (1977) summarized the predictions concerning optimal foraging theory made by the various authors. Foraging animals should rank food items according to each item's value, with value based in some currency. As above, this currency is assumed to be the rate of energy intake. The diet selected to maximize this currency when multiple food types may be simultaneously searched for will have three properties. First, the decision to accept or reject a food item will depend only on the abundance of food types of higher rank. If foods of higher rank are available, lower valued foods should not be consumed (foods are ranked to maximize the ratio of calories:handling time). Second, as the amount of high-valued food increases in the diet, the number of lower ranked items in the diet should decrease.

Conversely, as high valued foods decrease in abundance, lower valued foods should increase in the optimal diet. The third property is that a food item should either always be accepted, or always be rejected; no partial preferences should exist. However, dietary constraints may allow, or even promote, partial preferences (Pulliam 1975).

Numerous studies have supported the first two properties of the theory. Charnov (1976) found that mantids (*Hierodula crassa*) reduced their number of attacks on prey as the prey was moved further from the mantid. Increasing the distance of the prey increased the handling time required by the mantid to capture and consume the prey. The extended handling time reduced the ratio of calories:handling time, decreasing the value of distant prey items. As predicted, lower valued food items were not consumed as readily as higher valued items. Goss-Custard (1976) found that redshank (*Tringa totanus*) preferred to consume that prey size which provided the highest reward per unit handling time, i.e., the highest valued prey. Werner and Hall (1974) working with bluegill sunfish (*Lepomis macrochirus*), Krebs et al. (1977) working with great tits (*Parus major*) and Lacher et al. (1982) working with rodents (*Kerodon rupestris*) all found that only the abundance of more favorable prey affected the selection of less valued items. Regardless of the quantity of low-valued items, these were usually selected only when the higher valued items were of low abundance. Further, all found that the consumptions of high ranked and low ranked items were inversely related. Krebs et al. (1977) and Lacher et al. (1982) uncovered partial preferences, as did Belovsky (1981).

The advantage accrued by an organism foraging optimally is an increase in fitness due to maximizing some critical factor (Schoener 1971), the factor usually considered to be net rate of energy intake (Pyke et al. 1977). As outlined by Pyke et al. (1977), natural selection will favor those individuals which genetically contribute the most to subsequent generations (genetic contributions are offspring which live long enough to successfully reproduce themselves). Assuming all other factors equal, and that foraging behavior is not linked to another factor, those organisms which maximize net energy intake will produce the most offspring and genetically contribute the most to future generations. Because foraging behaviors are heritable (Pyke et al. 1977), natural selection should advance that behavior which conveys maximum fitness, i.e., foraging optimally.

As outlined above, natural selecton should favor those organisms which choose to consume foods maximizing net energy / sec intake. Choosing food types presupposes the ability to recognize and rank items (Pyke et al. 1977). In birds, the ability to recognize items is both inherited and learned. The young of many avian species initially consume a wide range of food items and respond to general stimulatory patterns which are common to many objects (Hinde 1959). The birds then learn which of these objects to eat. Rabinowitch (1969) found that restricting zebra finch nestlings (*Taeniopygia castanotis*) to a normally non-preferred seed during the first 5-weeks of their life resulted in a learned preference for that seed. This preference gradually declined over the following 2-4 months as the birds received seeds normally preferred.

Assuming the abilities of innately recognizing food types and learning to discriminate food types to be heritable, then the recognition and selection of optimal diets should spread, as the number of optimal foraging birds increases. The birds should be able to identify, within the range of general stimulatory patterns, those characteristics which are common to most high valued foods, or unique to one or a few valuable items. Once identified, these patterns should be selectively sought and preferred.

Various authors have attempted to identify the food characteristics important in bird seed selection. However, most of these studies could not control all characteristics of the food being tested. Problems encountered due to this lack of control include confounding of food selection factors and limited flexibility in experimental design. Davison (1962), Willson (1972), and Willson and Harmeson (1973) tested seed preferences by offering different seeds to birds. Because seeds may vary in size, shape, color, flavor, texture, nutrient content, energy content, etc., difficulties arose when attempting to pinpoint the importance of any one factor in food selection. Goldstein and Baker (1984) eliminated much of the seed variation by pelleting the seeds prior to testing; however, pelleting does not allow for any method to test the effect that different seed shapes have on bird seed selection.

Extrusion processing is another method that eliminates the confounding of food selection parameters. This process allows a finely ground mixture of feedstuff to be agglomerated, with the addition of steam and heat, into larger morsels (McEllhiney 1985). Extrusion processing permits the variation of one or more desired food characteristics while keeping other characteristics constant. Thus, the effect of the most pertinent factors may be independently assessed. Size, shape, color, flavor, energy content, nutrient content, and other food characteristics may be methodically tested until the most important variables are determined.

Another benefit of extrusion processing is the increased palatability of the food products formed (McEllhiney 1985). Items normally excluded from an animal's diet may be reprocessed and made acceptable. Geis (1980) and Grey (1979) report that most wild songbirds will not consume cereal grains at backyard feeding stations. Extrusion processing may be a method allowing cereal grains to be made more acceptable to songbirds. The acceptance of grain-based morsels may enable cereal grains to be competitive with other bird foods at feeding stations.

The goals of this research include: 1) The development of an extruded food morsel from cereal grains that will be accepted by granivorous songbirds; 2) The determination of seed characteristics important for granivorous Passerines' food selection; 3) The discovery of the sparrow's ability to discern color, shape, size, and flavor; 4) The acquisition of sufficient knowledge to recommend which morsel appearances will maximize granivorous passerine morsel consumption at feeding stations; and 5) The testing of Optimal Foraging Theory's ability to predict morsel selection.

Harris' sparrows (*Zonotrichia querula*) and American tree sparrows (*Spizella arborea*) were the songbirds used in this study. These two species were selected because of their granivorous tendencies, difference in body size, overlap of food selection (Bent 1968), ease of capture, amiability, and quick adjustment to captivity.

GENERAL METHODS

Test feeds were formulated and processed in the Kansas State University Feed Technology Mill. Corn, grain sorghum, wheat flour, and soybean oil meal comprised the bulk of the final formula, which was supplemented with calcium, phosphorus, and lysine, plus vitamin and mineral premixes (Appendix A1). The least-cost formulation procedure of the software computer package MIXIT-II was used to prepare the diet. Nutritional constraints were set to insure adequate levels of methionine, cysteine, lysine, arginine, and tryptophan (Austic and Scott 1984, Holsheimer 1981), and to limit the amount of protein, fat, and metabolizable energy (See Appendix A2 for nutrient formulation). Dietary protein levels and amino acid amounts were based on Martin (1968) and Parrish and Martin (1977). Amino acid levels used by Martin (1968) and Parrish and Martin (1977) were calculated from amino acid analyses of the ingredients [corn (Bressani and Mertz 1958), soybean oil meal (Smith et al. 1964), and soft red wheat (Waggle et al. 1967)] used in those diets (Appendix A3). The calculated levels were placed into this study's formula (Appendix A3). Total energy was set over 4000 cal / g to meet the winter energy requirements of sparrows (Kendeigh 1949, Martin 1968). The metabolizable energy (ME) of 3425 cal / g approximated the values used by Martin (1968). Carbohydrates served as the main energy source, as in

Holsheimer (1981) and Thomas et al. (1975). Oil was added to provide for an easily extruded product. Vitamin, mineral, and salt levels (Appendix A1) were adequate to meet the requirements of songbirds in an over-wintering, maintenance condition (Ullrey pers. comm.).

Prior to combining the ingredients to be used in the base mix, all grains in the diet were ground once through a 3.18-mm hammer mill screen. The diet was prepared in 90.72-kg batches. Each dry ingredient was hand-weighed (ingredients > 4% of total diet weighed to 0.0454 kg, ingredients < 4% weighed to 0.00454 kg), batched, and mixed for 3 min in a double ribbon mixer. The batch was then reground once through a 1.59-mm hammer mill screen, weighed, and again placed in the mixer. Soybean oil was measured to 3% by weight of the finished product, and poured into the batch while the mixer was operating. This procedure produced the base mix used in processing food morsels.

A Wenger X-20LBM extrusion cooker was used to form the base mix into a number of different morsel types (See Appendix B for extruder settings). Once formed, the morsels were cooled and dried at room temperature. To decrease the variability in size within one morsel type, morsels smaller and larger than the desired size were removed by sifting each morsel type on a Model 4-18-24 Forsberg Screener. The size of the mesh used in the screener varied as the size of the different choices varied. Specific bulk density was determined for feed types using a Model 930 Beckman Air Comparison Pyconometer. Apparant bulk density was determined by weighing the volume of morsels required to fill a Winchester bushel (0.03482 m3) level full, following the procedure outlined in USDA Circular No. 921. The feed was stored at room temperature.

Sparrows used in the food preference experiments were caught in a 36-mm mesh nylon mist net, 8 km north of Manhattan, Kansas (see Barnes 1987, Appendix A, site 2), during November 1987. All tree sparrows were captured in vegetation dominated by pigweed (*Amaranthus ssp*) and ragweed (*Ambrosia ssp*), with scattered sunflower (*Helianthus* annus) plants. Harris'sparrows were captured in vegetation dominated by pigweed and ragweed, with intermittent Johnson grass (*Sorghum halepense*) and velvetleaf (*Abutilon theophrasti*) plants. Harris' sparrows were observed at the tree sparrow capture site; however, not when tree sparrows were present. Individual tree sparrows were captured at the Harris' sparrow capture site.

All birds were initially confined 2-3 per cage, each cage 39 x 22 x 27 cm. Cages were placed in a walk-in environmental chamber maintained at 5 C, 75% relative humidity, under a 10-hour light:14-hour dark photoperiod. Birds were acclimated to chamber conditions for 10 days, being provided white proso millet, sunflower, and native grass seeds on days 1 and 2. Chick starter mash was introduced with the other seeds on day 3. After day 3, the amount of chick starter mash was proportionately increased every other day, and the amount of the other seeds decreased until birds received only chick starter mash on days 9 and 10 of the acclimation period. Food and water were provided *ad libitum*.

Experimental birds were individually caged following the acclimation period. Cages were randomly assigned to locations in the chamber. Birds were maintained in the same location for the remainder of the project. All experiments were performed on the same group of birds, with one exception. One tree sparrow that experienced a loss of breast feathers following the third experiment was replaced by a tree sparrow which had fed upon all test feeds used up to that point.

Feeding trial experiments were conducted to determine sparrow preferences for four classes of food characteristics; shape, size, color and flavor. Within each class, different types of morsels were extruded (e.g., the class "color" contained the types yellow, orange, brown, and blue) to test preferences within that class. The studies determined the utility of each class in food selection, and which type(s) of each class was(were) selected. In-between experiments all birds were provided an equal mix of the morsel types upon which they had just been tested. Food and water were provided *ad libitum* throughout.

Feeding trials were conducted in an environmental chamber. Trials consisted of pair-wise presentations of only two morsel types, because three or more choices overwhelms the bird's discriminatory ability (Miller and Clifton 1964, Sturkie 1986). Each cage contained two feeders, with each feeder presenting only one morsel type. Feeders were on opposite ends of the same side of the cage, 22.5-cm apart, equidistant from the waterer (Fig. 1). A perch was placed an equal distance from both feeders to reduce the influence of perch position on consumption.

The pair-wise morsel presentations were designed into either a 6 x 6 or a 3 x 3 Latin Square, blocking bird and day. Twelve birds of each species were used for all experiments, allowing for either two or four replications of each square. Birds were randomly assigned to squares. The daily consumption (g / day) of each morsel type was the response variable. Pair-wise presentations were assigned so that all morsel types were in successive presentations an equal number of times, and so that all types were novel to a presentation an equal number of times (Figs. 2, 3), minimizing the bias of a carryover effect due to the presence or absence of one morsel type in successive treatments. Pair-wise presentations were replicated once.

Test morsels were included in the rations 8 days prior to testing to reduce unfamiliarity/novelty biases (Coppinger 1970, Denslow et al. 1987). Equal amounts of novel test morsels were added to familiar food and proportionately increased every other day until the test morsels constituted 100% of the ration on days 7 and 8. Foods were presented at

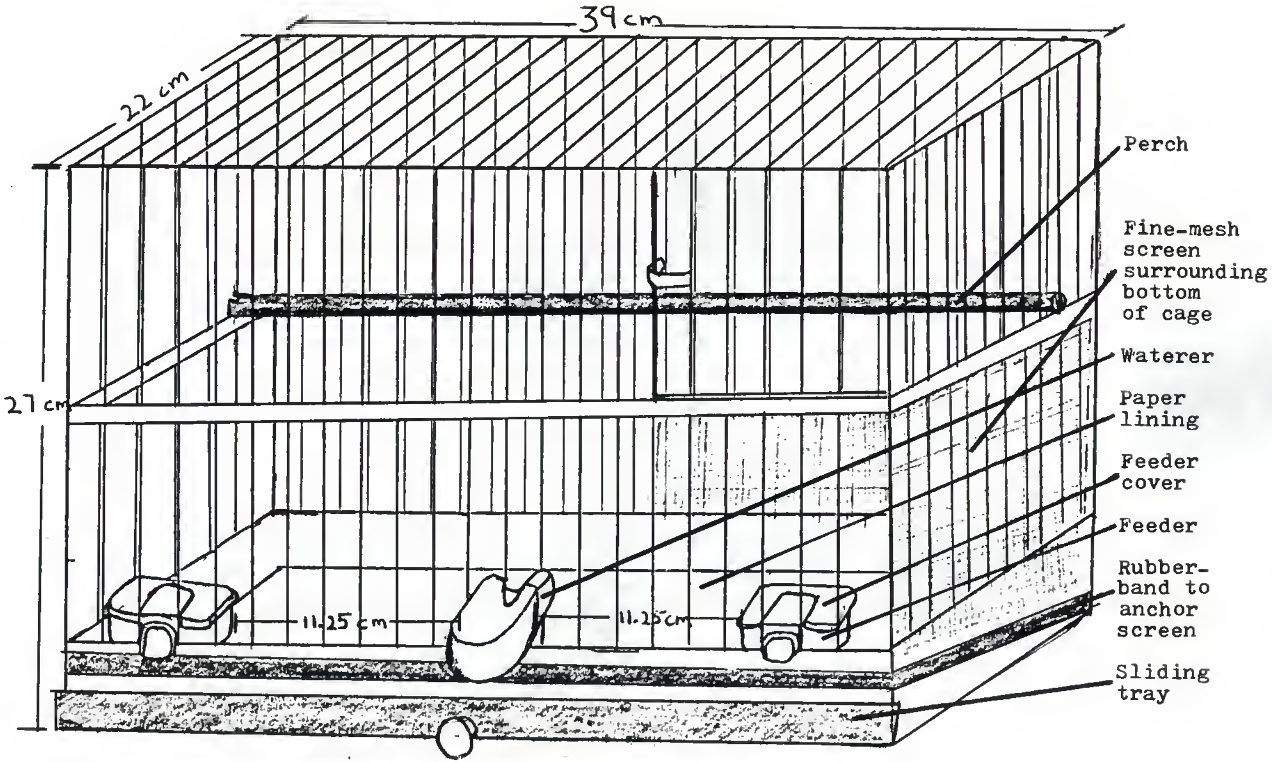


Figure 1. Diagram of cage used in pair-wise presentations.

Figure 2. The 6 x 6 Latin Square Block Design which placed morsel types so that all were in successive presentations an equal number of times, and all were novel to a presentation an equal number of times. Days and birds are the blocking factors. Treatments are represented by two numbers, each number designating one of the two morsel types in that treatment, e. g., Treatment 1 2 consists of testing morsel type 1 against morsel type 2. Both squares are required to balance the treatments.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Bird 1	1 2	3 4	1 4	2 3	2 4	1 3
Bird 2	1 3	2 4	1 2	3 4	2 3	1 4
Bird 3	1 4	2 3	1 3	2 4	3 4	1 2
Bird 4	2 3	1 4	3 4	1 2	1 3	2 4
Bird 5	2 4	1 3	2 3	1 4	1 2	3 4
Bird 6	3 4	1 2	2 4	1 3	1 4	2 3
Bird 7	1 3	2 4	1 4	2 3	3 4	1 2
Bird 8	1 4	2 3	1 2	3 4	2 4	1 3
Bird 9	1 2	3 4	1 3	2 4	2 3	1 4
Bird 10	2 4	1 3	3 4	1 2	1 4	2 3
Bird 11	3 4	1 2	2 3	1 4	1 3	2 4
Bird 12	2 3	1 4	2 4	1 3	1 2	3 4

Each morsel type is novel in 24 presentations, and was in successive presentations 12 times. All morsels are considered to have been in successive presentations on day 1. This is because a mixture of all food types was fed on the day prior to day 1 of the experiments.

Figure 3. The 3 x 3 Latin Square Block Design which placed morsel types so that all were in successive presentations an equal number of times and all were novel to a presentation an equal number of times. Also, each treatment follows the other treatments an equal number of times, and is followed by the other treatments an equal number of times. Days and birds are the blocking factors. Treatments are represented by two numbers, each number designating one of the two morsel types in that treatment, e. g., Treatment 1 2 consists of testing morsel type 1 against morsel type 2. Each block must be performed to balance the design.

	Day 1	Day 2	Day 3
Bird 1	1 2	1 3	2 3
Bird 2	1 3	2 3	1 2
Bird 3	2 3	1 2	1 3
Bird 4	1 2	2 3	1 3
Bird 5	1 3	1 2	2 3
Bird 6	2 3	1 3	1 2

Each morsel type is novel in a presentation 4 times. Each type is presented in successive treatments 8 times. All types are considered to be a successive treatment on day 1. This is because the day prior to testing, an equal mix of all types was presented to the birds.

the beginning of the photoperiod, and removed at the end.

Food to be offered to each bird for each pair-wise presentation was weighed to 0.1 g the night before testing and left uncovered overnight at room temperature. At the start of the photoperiod the following day each feeder was filled with the preweighed food. Twice each day all feed containers were refilled so that no feeder ever became half-depleted. Feeder positions were exchanged four times a day, every two hours, negating any bias due to innately preferred feeding positions, and precluding birds from learning where to expect preferred food (Pick and Kare 1962). To prevent a position x time bias from developing, all trials were replicated. During the same time slot, replications presented morsel types in the opposite positions from the previous day, insuring that each choice was in each position for all time periods. For example, if Day 1 presented yellow/red at 10:00 AM, Day 2 presented red/yellow at 10:00 AM. At the end of the photoperiod all food was removed from the chamber and set out at room temperature. The food removed was weighed 18-22 hr after it's removal from the chamber. Food that was spilled by each bird during the pair-wise presentation was collected, sorted, and weighed. Total consumption of each food type by each bird was determined as follows: total consumption = preweighed total - food removed + spilled food.

Aluminum covers fastened to the top of the feeders reduced food spilled and fine mesh aluminum screen attached to the lower half of each cage prevented the loss of spilled food (Fig. 1).

Birds were weighed to 0.1 g on the first day of each experiment and on the day immediately following the completion of each experiment. Weights were recorded within 30 min of the onset of the photoperiod, minimizing biases due to nighttime stress and diurnal weight change (West 1967, Kendeigh et al. 1969). Prior to the onset of the first experiment, bird weights were stable (varied less than 5% of total body weight for each bird, Browning et al. 1981) for 10 days while consuming the nutritionally-balanced test morsels (Appendix C).

Six birds of each species were randomly selected for necropsy at the completion of the study. Birds selected were killed by carbon monoxide gas and immediately examined. External examination consisted of breaking leg bones, inspection of the eyes, keel, and general body condition, and looking for morphological abnormalities. Internal examination inspected fat deposition, the condition of internal organs, and breast muscle condition.

Preferences for the different morsel types were analyzed by subjecting daily morsel consumptions to analysis of variance procedures. Analysis of variance methods were used to determine carryover effects, spilled food biases, and time effects.

STUDY 1. INTRODUCTION AND LITERATURE REVIEW

Optimality theory is the use of evolutionary theory to predict what solution to an ecological problem would most increase an individual's fitness (Pulliam 1981). Considering the problem of food consumption, the optimal solution predicts that an individual should select foods which maximize energy gained per unit of foraging time, i.e., maximize feeding efficiency. Selection is an arbitrary term not intended to imply conscious thought, instead meaning animals follow certain rules (Krebs 1978). Various studies have tested the ability of animals to follow these rules. Emlen and Emlen (1975) tested the ability of mice (Swiss-Webster mice) to determine the energy content of seeds, and to select those seeds that maximized feeding efficiency. The results were consistent with theory after corrections for imperfect decision making were performed. Browning and Robel (1981) concluded that cardinals (*Cardinalis cardinalis*) selected foods high in total energy and metabolizable energy, although the study was not designed to measure feeding preferences. Conversely, Robel et al. (1974) found that bobwhites (*Colinus virginianus*) indicated no selection for food with high energy content, high metabolizable energy, or high efficiency of utilization. Willson (1971) and West (1967) detected no tendency of songbirds to select seeds high in energy content.

The failure of Robel et al. (1974), Willson (1971), and West (1967) to detect preferences for high-energy food suggests that organisms may not select for energy per se, but select for other characteristics. McNamara and Houston (1987) emphasize the importance of basing the criterion for optimal foraging selections on the attributes that the animal uses to make selections. Handling time may be as critical as energy to forager's selection of food. Willson (1971) found that all bird species tested could handle those seeds most consumed faster than those less consumed seeds. Search time, a component of handling time, has been found to be inversely proportional to preference in heteromyid rodents (*Dipodomys merriami* and Perognathus *pericillatus*, Smigel and Rosenzweig 1974) and in great tits (Royama 1970). Similarly, Rosenzweig and Sterner (1970) found a negative correlation between husking speed and caloric gain for heteromyid rodents. Squirrels (*Scirus carolinensis* and *S.* niger) base preferences in part on husking speed, another component of handling time (Smith and Follmer 1972). Willson and Harmeson (1973) found that songbird preference was related to speed or ease of handling.

Livdahl (1979) concludes that the forager attributes of handling time are search, capture, and ingestion efficiency. Sherry and McDale (1982) acknowledge that handling time is not a simple function of any one variable, but is influenced by food width and depth (shape and size), mass, hardness, and distastefulness. They conclude that handling behavior plays an important role in food selection. Goldstein and Baker (1984) report that when size, shape, and handling characteristics were eliminated from thistle and canary seeds through pelleting, while other parameters such as taste and color remained unaltered, juncos (*Junco hyemalis*) preference changed from niger thistle (*Guizotia abyssinica*) to canary grass seeds (*Phalaris canariensis*). Fantz (1957) found that newly-hatched chicks (*Gallus gallus*) had an innate preference for pecking at rounded objects, particularly ellipses and spheres, and that the chicks would not peck at angular objects. Similarly, white Vantress crossbreed chicks demonstrated innate shape preferences for serrated circles, ovals, and normal circles; small sizes of these shapes (3-mm dia.) were preferred over larger sizes (6-mm dia., Goodwin and Hess 1969). Studies on the attractiveness of different foods at wild bird feeders show that most wild birds prefer millet seeds (spherical shape), whole peanut kernels (ellipse shape), and sunflower seeds (ovate shape) more than they prefer any other seed (Grey 1979, Geis 1980).

Optimal foraging theory also predicts that when food resources are in short supply, those factors which influence food selection will also influence competition among, and evolutionary divergence of foragers eating that food (Sherry and McDade 1982). The divergence of foragers may occur due to small changes in the morphology of the foragers.

In many groups of organisms, small morphological differences of the foragers are associated with considerable differences in foods selected (Pulliam 1985). Larger species of tiger beetles (*Coleoptera Cicindelidae*, Pearson and Sternberger 1980), sunfish (Keast 1970), *Anolis ssp* lizards (Schoener and Gorman 1968), flycatchers (*Tyrannidae*, Hespenheide 1971), and heteromyid rodents (Brown and Lieberman 1973) all eat larger prey than smaller, closely related species. It is often assumed that these differences in diet reflect differences in preference (Pulliam 1985).

The relationships between bill size, seed preference size, and handling ability remain unclear in birds. In some seed-eating finches (*Fringillidae* and *Carduelidae*), larger-bodied birds have larger bills and tend to eat larger seeds than their smaller-bodied relatives (Newton 1967; Pulliam and Enders 1971; Abbott et al. 1977). Other studies are not so conclusive. Myton and Ficken (1967) found that tufted titmice (*Parus bicolor*, larger birds) preferred larger seeds than chickadees (*Parus carolinensis*, smaller birds), but at low temperatures the chickadees increased the proportion of large seeds in thier diet. Willson (1971, 1972) and Hespenheide (1966) state that both large and small billed birds chose small seeds. Hespenheide (1966) detected no differences in the handling efficiency of small seeds between large and small birds. Willson (1971) demonstrated that large-billed finches generally husked larger seeds faster than did small-billed finches, but that birds of both bill sizes husked small seeds at the same rate. Willson (1972) determined that cardinals husked small, thin seeds faster than the smaller sparrows, although the cardinals were no quicker husking large seeds than small seeds. Conversely, Abbott et al. (1975) found that small beaked finches cracked and ate all seed sizes faster than large beaked finches. Further, no seed size preferences were uncovered within any bird size class (Abbott et al. 1975). Pulliam (1985) detected few differences in handling times between small and large sparrows eating small seeds. However, the handling times for large sparrows eating large seeds were significantly lower than those times of the smaller sparrows.

Handling time and handling characteristics (features of the food which influence the rate at which food can be consumed) appear to be important factors governing the food choice made by an optimal forager. The size and shape of food items are pivotal features determining handling time and handling characteristics, and are thus important in determining food selections. The objectives of this phase of the research are to determine the ability of Harris' sparrows and tree sparrows to discern food morsel shape and food morsel size, to determine the effect of morsel size and morsel shape on food selection by Harris' and tree sparrows, and to determine if morsel preferences differ with species size.

EXPERIMENT I. METHODS

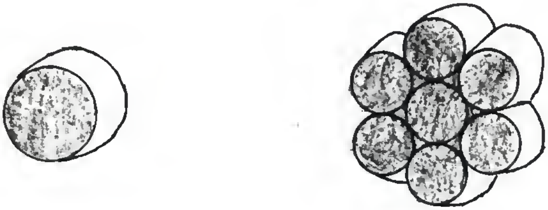
Preparing Different-shaped Morsels

Four shapes of food morsels were developed for this experiment; circular (to resemble a millet seed), ovate (to resemble a sunflower seed), elliptical (to resemble a whole peanut kernel), and rosette (to resemble a serrated circle). The four shapes were not of similar sizes (Fig. 4). Different shapes were attained by placing different holes into the 19-mm die inserts used in the extruder. One test shape was cut into each insert, with only one hole per insert (see Appendices D1-D4 for details). Circular-shaped openings had a diameter of 1.59 mm, producing morsels the size of millet seeds. Ovate-shaped openings were 3 x 6 mm, producing morsels resembling sunflower seeds in the small seed size category of Willson (1971), Hespenheide (1966), and Abbott et al. (1975). Elliptical-shaped openings were designed to produce peanut-kernel-shaped morsels corresponding to the width and length of the ovate shapes. Rosette-shaped openings produced circular morsels with an irregular perimeter. The rosette openings were made as small as possible without compromising the integrity of the shape. Four inserts of each shape were made and placed into a four-insert die plate (Appendix E1). The die plate was attached to the Wenger Extruder.

Food morsels were formed by the extrusion process, as

Elliptical-shaped morsel

Ovate-shaped morsel



Circular-shaped morsel

Rosette-shaped morsel

Figure 4. Diagram of the four morsel shape types. All morsels are pictured eight times larger than actual.

the heated base mix was forced through the die inserts of the extruder. All shapes were cut to similar depths (Fig. 4) by a four-blade variable-speed knife. Because the dies with circular openings prevented the flow of desirable product, one die insert (31.5-mm dia) was drilled with twenty-three 1.59-mm circular holes (Appendix F1). This die was placed into a one-insert die plate (Appendix E2), and the plate attached to the extruder. Morsels of a desirable size were formed through this insert.

After morsels had dried, a pellet durability tester (see McEllhiney 1985, pp. 359, 564, 565 for description) was utilized to round the square edges of the circular-shaped morsels. Into each compartment of the tester was placed 2.25 kg of circular-shaped morsels and ten 0.64 x 25.4-mm round-head-slotted-machine screws. After rotating for 35 minutes, the screws and bird food were removed from the tester. Screws were separated from the food by hand.

Each shape type was sifted through a Forsberg screener to reduce the variability in size within a shape. Morsels larger or smaller than the desired size were removed. Those circular morsels that would fall through a Tyler # HM43478, 8 mesh 0.025 screen, but remain over a Tyler # HM74304, 12 mesh 0.018 screen were retained for the experiment. Those sunflower pieces that would fall through a Tyler # HM45478, 6 mesh 0.028 screen, but remain over an 8 mesh 0.025 screen were retained. Those rosette morsels that remained over a 6 mesh 0.028 screen were retained. Those elliptical morsels that would fall through a 6 mesh 0.028 screen, but remain over an 8 mesh 0.025 screen were retained for the experiment.

Morsel shapes were presented to 12 Harris' sparrows and 12 tree sparrows in pair-wise presentations. The pre-weighed morsel samples were placed into two feeders in each cage at the beginning of the photoperiod, and removed from each cage at the end of the photoperiod. While the feeders were in the cage, food and water were provided ad *libitum*, and feeder positions were switched every two hrs. Food spilled by each bird during the day was collected, sorted into shape types, and added to the unconsumed food. The weight of each morsel shape consumed by each bird was then determined.

The four morsel shapes presented in every pair-wise combination gave six treatments. The experimental design followed the treatment sequence for the 6 x 6 Latin Square Block Design (Fig. 2). Birds were randomly assigned to treatment sequences. In order to detect changing preferences over time, each bird's treatment sequence was repeated. Preferences for the different morsel types were analyzed by subjecting daily morsel consumptions to analysis of variance procedures and by applying Dayton and Morrill's model to estimate palatability (Dayton and Morrill 1974) to the data.

Volume Measurements

Eight morsels from each shape class were measured to

0.254 mm (.001") using a model no. 8001 Mitutoyo dial caliper. The width, length, and depth of elliptical- and ovate-shaped morsels were recorded. Diameter and depth were the measured variables of rosette- and circular-shaped morsels. Values were converted into volumes for each morsel (Appendix G). Volumes within each shape class were averaged to determine the mean morsel volume of each shape.

Tree sparrow bill measurements were taken from those measurements reported by Willson (1971) for tree sparrows. Harris' sparrow bills were measured according to the procedure of Willson (1971) using a Mitutoyo dial caliper.

Determining Handling Time

Feeding bouts were measured to determine the time each species required to handle and consume each food type. A feeding bout was defined as a period of time when a bird would feed continuously, taking one food item immediately after another. The bout ended when the bird would swallow the food in it's bill and not immediately select another food item. A swallow was assumed when the bird ceased massaging the food with it's bill. If during a bout a morsel was selected, and then dropped and ignored by the bird, that bout was not recorded. However, if a morsel was dropped, then immediately picked up and ingested, the bout was recorded. The number of food items taken in each bout, and the overall time of the bout were recorded. Bouts were timed to 0.1 sec using a hand stopwatch. Birds were deprived of food for 20 hrs prior to timing to ensure seed consumption in the presence of an observer. Bird reaction to the observer varied by individual, but not by species.

Feeding bout measurements were performed one bird at a time. One feeder filled with one food type was placed in a cage. The observer stood unobtrusively 1 m directly in front of the feeder. Data collection began as the bird consumed the first food item. When the bird would no longer approach the feeder, measurements ended on that bird, and the feeder was removed from the cage. The next bird was then similarly timed. All birds were tested in this step-by-step fashion. Shapes were randomly assigned to birds. No birds were tested for all shapes. For two days prior to the food deprivation period, each bird was provided only with the shape to be used in a particular bird's subsequent test.

Determining Feeding Efficiency

Feeding efficiencies (cal / sec) of both bird species for each morsel shape were determined. Metabolizable energy ingested was substituted for net energy acquired in calculating feeding efficiencies (Pulliam 1985). To determine the mean calories in one morsel of each shape, three 5.0 ± 0.1 g morsel samples were taken from all shapes. The number of morsels in each sample was counted by hand. All samples of each shape were averaged to determine the number of morsels / five grams, or morsels / g. The inverse of this number provided the weight of one food item. The weight of one food item was multiplied by the calculated metabolizable energy value of 1 mg of food to determine the calories in one food morsel. [The metabolizable energy of 1 mg of food was taken from the poultry ME value calculated by MIXIT-II. Fisher (1972) reports that the average % of gross energy metabolized by poultry for ground corn is 83%, for ground sorghum is 82%, for wheat flour is 76%, for soybean oil meal is 54%, and for oil is 94%.] The calories of each morsel shape divided by the respective handling time of each shape by each species allowed for the feeding efficiency of each species consuming each shape to be calculated (Appendix H for example).

Analysis of Feeding Efficiency and Handling Time

To separate the effects of handling time and feeding efficiency on the consumption of different shapes, analysis of variance procedures were performed on the weighted mean handling times and feeding efficiencies of the various shapes for each species. Multivariate and covariance analyses allow for the comparison of the effects of handling time, feeding efficiency, and shape on each other, and the relative importance of each on consumption. Significance level was taken to be ‘ = 0.05.

The multivariate analysis model included morsel consumption, morsel ingestion time, and morsel feeding efficiency as dependent variables and morsel shape as the factor of interest. The analysis determined which of the three dependent variables was most strongly related to morsel shape when each was adjusted for the effects of the other two. Separate analyses were performed for Harris' and tree sparrows.

Three different covariance analysis models were set up for each bird species. These models placed consumption of each morsel type as the dependent variable and either morsel shape and morsel feeding efficiency, morsel shape and morsel ingestion time, or morsel feeding efficiency and morsel ingestion as pairs of independent variables. Analysis determined which variable of each pair of independent variables explained more of the consumption of each morsel shape type.

EXPERIMENT I. RESULTS

Shape Preferences

Preference rankings of morsel shapes' mean consumptions showed no significant differences from day 1 to day 2 of a test replication for either species, (Appendix I1), so data from both days were pooled.

Analyzing consumption means using ANOVA procedures, Harris' sparrows consumed 6.9 g / day of circular-shaped food morsels, significantly more than their daily consumption of elliptical-, ovate-, or rosette-shaped morsels (Table 1). Likewise, tree sparrows consumed 5.1 g / day of circular-shaped food morsels, significantly more than their daily consumption of the other shapes (Table 1). Both the Harris' sparrows' and tree sparrows' daily consumption of rosette-shaped morsels was significantly less than their respective daily consumption of the other shapes.

Whenever circular-shaped morsels were placed with another shape in a pair-wise presentation, a larger quantity of circular morsels was consumed by both bird species (Table 2). Conversely, whenever rosette-shaped morsels appeared in a presentation, a smaller quantity of these morsels was consumed by both bird species (Table 2). Regardless of the other choice, birds tended to consume circular morsels, and to not consume rosette morsels.

The effect of replicating a treatment sequence for

Table 1. Ranked means from Analysis of Variance (ANOVA) for the mass (g) of morsel shapes consumed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

Morsel Shape	$\bar{x}$ consumption [1,2] Harris' sparrow N = 12	 Tree sparrow N = 12
Circular	6.92 i	5.08 o
Elliptical	4.91 d	3.21 x
Ovate	4.70 d	2.71 x
Rosette	3.78 c	1.64 u
	S.E. = 0.27	= 0.23

[1] test day replications and treatment sequence replications were combined

[2] values with a common letter do not differ, $p > 0.05$

Table 2. Mean (+SE) mass (g) of morsel shapes consumed by captive Harris' and tree sparrows kept at Kansas winter conditions when the four morsel shapes were presented in every pair-wise combination.

Pair-wise presentation	$\bar{x}$ consumptions Harris' sparrow	 Tree sparrow
Circular	6.81 ± 0.30	4.88 ± 0.21
Elliptical	3.14 ± 0.27	1.45 ± 0.19
Circular	6.66 ± 0.25	4.87 ± 0.20
Ovate	3.35 ± 0.29	1.43 ± 0.20
Circular	7.29 ± 0.29	5.48 ± 0.16
Rosette	2.48 ± 0.26	0.85 ± 0.11
Elliptical	5.25 ± 0.32	3.72 ± 0.18
Ovate	4.94 ± 0.26	2.57 ± 0.16
Elliptical	6.11 ± 0.37	4.52 ± 0.24
Rosette	4.26 ± 0.25	1.74 ± 0.19
Ovate	5.80 ± 0.36	3.93 ± 0.27
Rosette	4.60 ± 0.32	2.39 ± 0.21

Harris' and tree sparrows (Table 3) was to decrease consumption, not to alter preferences. For both bird species the order and significance of preferences remained stable between treatment sequences (Appendix J1). No carryover effect due to the presence of a food type in the preceding trial developed in either species (Table 3). No significant alterations occurred to morsel shape consumption rankings when the amount of each shape spilled by each bird was added to the consumption data prior to analysis (Appendix K1).

When analysis of consumption data was performed using the Dayton and Morrill (DM) model to estimate palatability, no significant differences existed between the estimated tree sparrow consumptions of the four morsel shapes (Table 4). The DM model estimated Harris' sparrows to consume 9.72 g / day of rosette-shaped morsels, significantly less than the estimated consumptions of ovate-, elliptical-, and circular-shaped morsels (Table 4). No differences existed in the estimated consumptions of the latter three shapes. The ANOVA table for treatments, treatment means, and estimates of shape effects on consumption used to derive the DM model's estimated consumptions are in Appendix L.

Handling Times and Efficiency

Harris' sparrows handled one circular-shaped morsel in 1.68 sec, significantly faster than the time required to consume the other morsel shapes (Table 5). Tree sparrows

Table 3. ANOVA model of factors related to daily mean morsel shape consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	Source of variation	df	sum of squares	F	P
Harris' sparrows	Square	1	8.7850	2.05	0.1532
	Day (Sq)	10	11.4862	0.27	0.9874
	Bird (Sq)	10	23.1095	0.54	0.8610
	Shape	1	363.7419	28.32	0.0001
	TSR*	1	6.1996	1.45	0.2299
	Carryover	1	1.1676	0.27	0.6019
Tree sparrows	Square	1	0.0461	0.02	0.8812
	Day (Sq)	10	7.3886	0.36	0.9631
	Bird (Sq)	10	12.0515	0.58	0.8260
	Shape	3	452.5023	73.19	0.0001
	TSR*	1	8.2528	4.00	0.0464
	Carryover	1	3.6906	1.79	0.1820

* TSR signifies treatment sequence replication

Table 4. Ranked estimates from the Dayton-Morrill palatability model for the mass (g) of morsel shapes consumed daily, had each shape been fed alone to captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources. Compare estimates to the mean consumptions in Table 1.

Morsel shape	Consumption estimates *	
	Harris' sparrow	Tree sparrow
Circular	10.292 b	6.311 r
Elliptical	10.216 b	6.327 r
Rosette	9.792 o	6.333 r
Ovate	10.320 b	6.307 r

* numbers with a common letter do not differ, p > 0.05

Table 5. Mean (+ SE) handling times (sec) and feeding efficiencies (cal/sec) of morsel shapes consumed by captive Harris' and tree sparrows kept at Kansas winter conditions following a 20-hr food deprivation period.

Morsel shape	Sparrow species	Birds tested	Morsels consumed	Handling time *	Feeding efficiency *
Circular	Harris'	8	234	1.68 ± 0.33 b	14.70 ± 1.7 xl
	Tree	10	259	1.98 ± 0.21 b	12.18 ± 1.0 l
Elliptical	Harris'	3	38	3.47 ± 0.81 c	21.01 ± 4.1 xm
	Tree	5	32	5.02 ± 0.54 c	14.93 ± 2.7 lx
Ovate	Harris'	4	43	3.66 ± 0.78 c	24.29 ± 3.9 m
	Tree	1	8	6.21 ± 1.16 cr	14.61 ± 5.8 lxm
Rosette	Harris'	3	37	5.19 ± 0.94 cr	19.04 ± 4.7 xm
	Tree	3	26	7.24 ± 0.62 r	13.13 ± 3.1 lx

* values with a common superscript letter do not differ, p > 0.05

were also faster when consuming circular-shaped morsels (1.98 sec). The circular-shaped morsels had less volume (0.010 cm3) than the other morsel shapes (Table 6). Thus, both bird species consumed the smallest morsels fastest.

Rosette-shaped morsels had a significantly greater volume (0.037 cm3) than the other morsel shapes (Table 6). Ovate and elliptical morsel volumes were similar to each other. The time required by Harris' sparrows to consume these three morsel types did not vary with morsel volume, as no differences in the consumption times of ovate-, elliptical-, or rosette-shaped morsels occurred (Table 5). Tree sparrow consumption of rosette-shaped morsels (7.24 sec) was slower than that for ellipses, but not slower than that for ovate-shaped morsels. Within these three larger morsel shapes, tree sparrows tended to consume bigger morsels slower, while Harris' sparrow consumption was not affected as much by size.

Averaging across all morsel shapes, the Harris' sparrows did not handle food faster (3.75 ± 0.26 sec) than tree sparrows (3.57 ± 0.28 sec), even though Harris' sparrow bills were greater in length (12.0 ± 0.35 mm), width (6.01 ± 0.27 mm), and depth (7.44 ± 0.36 mm) than tree sparrow bills (9.2 ± 0.32 mm, 4.4 ± 0.18 mm, and 5.6 ± 0.27 mm). Further, no differences in the amount of time required to consume any food shape type existed between species (Table 5).

Harris' sparrows foraged most efficiently when eating

Table 6. Ranked means from ANOVA for the volumes (cm3) of the morsel shapes used in Experiment I and of the morsel sizes used in Experiment II.

	Type	Volume *
SHAPES:	Circular	0.01033 b
	Ellipse	0.02685 r
	Ovate	0.02724 r
	Rosette	0.03705 m
SIZES:	Small	0.00946 b
	Medium	0.01986 c
	Large	0.03305 i
	S.E.	0.00128

* volumes with a common letter do not differ, $p > 0.05$

the ovate-shaped items, acquiring an average of 24.29 cal / sec (Table 5). However, this value was only significantly higher than the value for circular-shaped morsels. Tree sparrows displayed no significant differences in the cal / sec obtained when feeding on any of the morsel shapes, although the value for circular shaped morsels was lowest (12.18 cal / sec, Table 5).

Multivariate and Covariance Analyses

In a multivariate analysis, the dependent variable with the highest F-value is the variable most strongly related to the independent variable. (In this analysis, the independent variable was morsel shape). When mean consumption, feeding efficiency, and time to consume feed were analyzed as dependent variables, the higher F-values of handling time for tree sparrows (F = 69, Table 7) and Harris' sparrows (F = 17, Table 7) reveals that morsel shape explains more of the handling time variation than it does for either of the other two dependent variables.

In the covariance analysis with two independent variables or factors, the one with the higher F-value is more important in explaining the variation of the dependent factor. (For these covariance analyses the dependent variable was the consumption of different shapes). Comparing the independent variables feeding efficiency and time required to ingest morsels for tree sparrows (Table 8), ingestion time's

Table 7. Multivariate analysis of variance models of factors affected by morsel shape.

	Dependent variable	Source of variation	Sum of squares	Mean square	F *	p
Harris' sparrow	Consumption	shape	101.64	33.88	14.78	.0001
		error	73.36	2.29		
	Handling time	shape	60.93	20.31	16.56	.0001
		error	39.25	1.23		
	Efficiency	shape	329.15	109.72	3.84	.0186
		error	913.57	28.55		
Tree sparrow	Consumption	shape	84.99	28.33	24.19	.0001
		error	40.99	1.17		
	Handling time	shape	206.80	68.93	68.68	.0001
		error	35.13	1.00		
	Efficiency	shape	88.30	29.43	2.87	.0504
		error	359.34	10.27		

* The dependent variable with the highest F-value is associated closest to morsel shape.

Table 8. Covariance ANOVA models of factors related to mean morsel shape consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions.

	Source of variation	Sum of squares	F *	p
Harris' sparrow	Handling time	62.32	21.67	.0001
	Efficiency	27.07	9.41	.0043
	Morsel shape	17.16	5.40	.0264
	Handling time	5.22	1.64	.2089
	Morsel shape	84.26	11.94	.0001
	Efficiency	0.41	0.17	.6809
Tree sparrow	Handling time	71.04	56.18	.0001
	Efficiency	0.14	0.12	.7346
	Handling time	4.51	3.95	.0550
	Morsel shape	4.27	3.73	.0618
	Morsel shape	78.96	24.01	.0001
	Efficiency	2.06	1.88	.1801

* The higher F-value in a pair is associated closest to morsel consumption.

greater F-value (F = 56.18) demonstrates that the variation in the amount of each morsel shape consumed was more closely related to the variation in each morsel shape's time of consumption than to the feeding efficiency of the morsel. The lack of significance of feeding efficiency (F = 0.12, pr > 0.74) illustrates the ineffectiveness of efficiency in explaining morsel shape consumption. A comparison of the same factors for Harris' sparrows (Table 8) showed similar results. The time required to consume the different morsel shapes (F = 21.67) better explained morsel shape consumption than did feeding efficiency (F = 9.41), although efficiency was more effective in explaining Harris' sparrow's consumption than it was for tree sparrows. The fact that handling time was related closer to mean morsel shape consumption than was feeding efficiency suggests that the birds were selecting which morsels to consume based on time of consumption, and not on feeding efficiently.

Testing a covariance model using handling time and shape of morsels as independent variables for both sparrow species found that there were still unidentified shape effects that influenced morsel selection (Table 8). Handling time was not able to account for a significant amount of the variation in consumption after the effect of shape had been removed.

EXPERIMENT II. METHODS

Morsel Size Preparation

Food size pair-wise comparison trials were conducted after the food shape preference trials. The sizes tested were small (1.59-mm dia.), medium (3.18-mm dia.), and large (3.96-mm dia.) circular-shaped morsels, the preferred shape determined in Experiment I. Sizes were attained by drilling different-sized circular holes into 31.5-mm die inserts. Only one test size was drilled into each insert. The insert for small-sized morsels contained twenty-three 1.59-mm holes. The insert for medium-sized morsels contained thirteen 3.18-mm holes, while the insert for large-sized morsels contained eight 3.96-mm holes. The number of die insert holes was designed so that all inserts had a relatively equal open surface area, reducing the variability in morsel density (see Appendices F1-F3 for die designs). Each insert was placed into a one-insert die plate (Appendix E2) and attached to the Wenger extruder.

Food morsels were formed by the extrusion process, as the heated base mix was forced through the die insert of the extruder. Morsel sizes were made one at a time. All sizes were cut by a four-blade variable-speed knife, the depth of each size corresponding with that size's diameter, i.e., large items were thicker, small items were thinner (Fig. 5).

Each size type was sifted through a Forsberg screener to

SMALL SIZE MORSEL

MEDIUM SIZE MORSEL

LARGE SIZE MORSEL

Figure 5. Diagram of the shapes of the three size types. All morsels are pictured three times larger than actual size.

reduce the variability in size within each class. Morsels larger or smaller than the desired size were removed. Those small morsels that would fall through a Tyler #HM43478, 8 mesh 0.025 screen, but remain over a Tyler #HM74304, 12 mesh 0.018 screen were retained. Those medium morsels that would fall through a Tyler #HM45478, 6 mesh 0.028 screen, but remain over the 8 mesh 0.025 screen were retained. Those large morsels that would fall through a Tyler #HM27568, 5 mesh 0.032 screen, but remain over the 6 mesh 0.028 screen were retained.

Morsel sizes were presnted to 12 Harris' sparrows and 12 tree sparrows in pair-wise presentations. The preweighed morsel samples were placed into two feeders in each cage at the beginning of the photoperiod, and removed from each cage at the end of the photoperiod. While the feeders were in the cage, food and water were provided *ad libitum*, and feeder positions were switched every two hours. Food spilled by each bird during the day was collected, sorted into size types, and added to the unconsumed food. The weight of each morsel size consumed by each bird was then determined (see General Methods).

The three morsel sizes presented in every pair-wise combination gave three treatments. The experimental design followed the treatment sequences for the 3 x 3 Latin Square Block Design (Fig. 3). Birds were randomly assigned to treatment sequences. Each treatment sequence was presented to two birds of each species. No bird repeated it's treatment sequence.

Handling Time and Efficiency Determinations

Eight morsels from each size were measured using a Mitutoyo dial caliper. Measurements and calculations of each size were performed following the procedures outlined for the circular-shaped morsels in the Volume Measurements section of Experiment I Methods. Feeding bouts were measured to determine the time each species required to handle and consume each food morsel size. Feeding efficiencies (cal / sec) obtained by both bird species for each morsel size were determined following the procedures detailed in the Handling Times and Feeding Efficiency sections of Experiment I Methods.

EXPERIMENT II. RESULTS

Size Preferences

Preference rankings of morsel size mean consumptions showed no significant differences from day 1 to day 2 of a test replication for either species (Appendix I2), so data from both days were pooled.

Harris' sparrows consumed 5.7 g / day of small size food morsels, significantly more than their consumption of medium and large morsels (Table 9). Likewise, tree sparrows consumed 5.3 g / day of small food morsels, significantly more than the daily consumption of the other sizes (Table 9). The tree sparrows' daily consumption of large size morsels was significantly less than the daily consumption of the other sizes. Harris' sparrow's consumption of medium and large morsels did not differ.

Whenever small size morsels were placed with another size in a pair-wise presentation, a larger quantity of small morsels was consumed by both bird species (Table 10). Conversely, whenever large-sized morsels appeared in a presentation, a smaller amount of these morsels was consumed by both species. Regardless of the other choice, birds tended to consume small sizes, and to not consume large sizes (Table 10).

No carryover effect due to the presence of a food type in the preceding trial developed in either species (Table 11).

Table 9. Ranked means from ANOVA for the mass (g) of morsel sizes consumed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ consumption *,+	
Morsel size	Harris' sparrow N = 12	Tree sparrow N = 12
Small	5.77 f	5.39 f
Medium	4.50 c	2.74 x
Large	3.79 c	1.17 r
S.E. =	0.43	= 0.30

* test day replications were combined

\+ values with a common letter do not differ, $p > 0.05$

Table 10. Mean (± SE) mass (g) of morsel sizes consumed by captive Harris' and tree sparrows kept at Kansas winter conditions when the three morsel sizes were presented in every pair-wise combination.

	$\bar{x}$ consumptions	
Pair-wise presentation	Harris' sparrow	Tree sparrow
small	5.72 ± 0.50	5.15 ± 0.11
medium	4.02 ± 0.57	1.04 ± 0.15
small	6.24 ± 0.52	5.42 ± 0.12
large	3.21 ± 0.62	0.65 ± 0.11
medium	5.40 ± 0.41	4.43 ± 0.24
large	4.40 ± 0.32	1.70 ± 0.18

Table 11. ANOVA model of factors related to daily mean morsel size consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	Source of variation	df	Sum of squares	F	P
Harris' sparrows	Square	3	7.593	0.51	0.6775
	Day (Sq)	8	10.488	0.26	0.9745
	Bird (Sq)	8	16.639	0.37	0.9427
	Size	2	61.385	6.18	0.0041
	Carryover	1	9.526	1.92	0.1724
Tree sparrows	Square	3	0.136	0.02	0.9959
	Day (Sq)	8	0.600	0.03	1.0000
	Bird (Sq)	8	2.043	0.12	0.9984
	Size	2	189.752	43.28	0.0001
	Carryover	1	0.061	0.03	0.7429

No significant alterations occurred to tree sparrow morsel size rankings when the amount of each size spilled was added to the consumption data prior to analysis (Appendix K2). However, for Harris' sparrows, the consumption of medium and small morsels was not found to differ significantly when spilled food was added to the consumption data prior to analysis.

Handling Times and Feeding Efficiency

Harris' sparrows consumed one small size morsel in 1.68 sec, significantly faster than the time required to consume medium and large size morsels (Table 12). Tree sparrows were also faster when consuming small size morsels (1.96 sec). Small size morsels had less volume than the other morsel sizes (Table 6). Thus, both bird species consumed the smallest morsels fastest.

The times required by Harris' sparrows to consume large and medium size morsels did not differ with morsel volume. Even though large size morsels had a significantly greater volume, 0.033 cm3 to 0.020 cm3 (Table 6), no differences in the consumption times of large and medium size morsels occurred (Table 12) in Harris' sparrows. Tree sparrows' consumption of large size morsels (11.18 sec) was significantly slower than the consumption of the other sizes. Within the two larger-sized morsel types, tree sparrows tended to consume bigger morsels slower, while Harris'

Table 12. Mean (+ SE) handling times (sec) and feeding efficiencies (cal/sec) of morsel sizes consumed by captive Harris' and tree sparrows kept at Kansas winter conditions following a 20-hr food deprivation period.

Morsel size	Sparrow species	Birds tested	Morsels consumed	Handling * time	Feeding * efficiency
Small	Harris'	8	234	1.68 ± 0.28 b	15.28 ± 1.7 b
	Tree	11	259	1.96 ± 0.26 b	12.06 ± 1.2 b
Medium	Harris'	2	37	3.82 ± 0.70 c	15.49 ± 3.2 bc
	Tree	6	56	5.75 ± 0.56 x	10.44 ± 2.6 b
Large	Harris'	3	19	3.74 ± 0.97 cx	25.65 ± 4.4 c
	Tree	3	18	11.18 ± 0.95 r	7.28 ± 4.3 b

* values with a common letter do not differ, $p > 0.05$

sparrows' consumption times were not greatly affected by size.

Averaging across all morsel sizes, Harris' sparrows handled food items significantly faster (3.08 ± 0.41 sec) than tree sparrows (6.30 ± 0.38 sec). Harris' sparrows were significantly faster than tree sparrows in consuming medium and large morsels (Table 12). However, there were no differences between the species in handling the small-size morsels.

Harris' sparrows foraged most efficiently when eating the large size morsels, acquiring an average of 24.29 cal / sec (Table 12). However, this value was only significantly higher than the value for small size morsels. Tree sparrows displayed no significant differences in the cal / sec obtained when feeding on any of the morsel sizes, although the value of feeding on small-size morsels was highest.

Multivariate and Covariance Analyses

As explained on p. 37, in a multivariate analysis the dependent variable with the highest F-value is the variable most strongly related to the independent variable. The independent variable was morsel size consumption. When mean consumption, feeding efficiency, and time to consume food were analyzed as variables dependent upon morsel size, the higher F-value of handling time for tree sparrows (F = 122.0, Table 13) reveals that morsel size explains more of the

Table 13. Multivariate analysis of variance models of factors affected by morsel size.

	Dependent variable	Source of variation	Sum of squares	Mean square	F *	P
Harris' sparrow	Consumption	Size	22.53	11.27	4.37	.0585
		Error	18.03	2.58		
	Handling time	Size	20.36	10.18	33.54	.0003
		Error	2.12	0.30		
	Feeding efficiency	Size	41.13	20.56	183.56	.0001
		Error	0.78	0.11		
Tree sparrow	Consumption	Size	98.42	49.21	26.48	.0001
		Error	35.31	1.86		
	Handling time	Size	459.66	229.83	122.03	.0001
		Error	35.78	1.88		
	Feeding efficiency	Size	100.68	50.34	5.67	.0017
		Error	168.60	8.87		

* The dependent variable with the highest F-value is associated closest to morsel size.

handling time variation than it does for either of the other two dependent variables. Contrarily in Harris' sparrows, the higher F-value of feeding efficiency ($F = 183.4$, Table 13) reveals that morsel size explains more of the feeding efficiency variation than it does for either of the other two dependent variables.

As explained on p. 37, in a covariance analysis with two independent variables or factors, the one with the higher F-value is more important in explaining the variation of the dependent factor. The dependent variable was the consumption of different morsel sizes. Comparing the independent factors feeding efficiency and time required to ingest morsels for tree sparrows, handling time's greater F-value ($F = 21.45$) suggests that the variation in the amount of each morsel size consumed was more closely related to the variation in each morsel's time of consumption than to the feeding efficiency of each morsel (Table 14). The lack of significance of feeding efficiency ($F = 2.43$, $pr > 0.14$) illustrates the ineffectiveness of efficiency in explaining morsel size consumption.

A comparison of the same factors for Harris' sparrows (Table 14) proved inconclusive. Neither handling time nor feeding efficiency accounted for a significant amount of the variation in morsel size consumption after the effect of the other variable was removed.

Table 14. Covariance ANOVA models of factors related to mean morsel size consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions.

	Source of variation	Sum of squares	F *	P
Harris' sparrow	Efficiency	3.06	0.77	.4095
	Handling time	0.04	0.01	.9217
	Size	0.18	0.04	.8385
	Efficiency	0.82	0.21	.6626
	Size	2.74	0.68	.4371
	Handling time	0.36	0.09	.7745
Tree sparrow	Efficiency	6.66	2.43	.1358
	Handling time	58.90	21.45	.0002
	Size	70.99	33.65	.0001
	Efficiency	1.44	0.68	.4188
	Size	19.83	9.66	.0058
	Handling time	2.52	1.23	.2822

* The higher F-value in a pair of variation sources represents the variable of the pair most closely associated with morsel consumption

EXPERIMENT I. DISCUSSION

Discerning Food Shape and Size

Because the rankings of morsel shape consumptions coincided with ranking the morsel shapes by size, the ability of birds to discern food shape was not definitively demonstrated. However, Fantz (1957) demonstrated the ability of newly-hatched chicks to discriminate between shapes of objects, as chicks would peck at rounded objects, but not at angular objects.

Both Harris' and tree sparrows demonstrated the ability to discern food morsel sizes. Both bird species distinguished small morsels from medium and large morsels, consuming a significantly greater quantity of small size morsels. The ability of Harris' and tree sparrows to discern food sizes agreed with the results of Goodwin and Hess (1969), who found that chickens preferred small sizes of circles and ovals over large circles and ovals. Willson (1971, 1972), Abbott et al. (1977) and Myton and Ficken (1967) also found that birds discriminated between seed sizes.

Selection of Food Morsels Based on Maximizing Feeding Efficiency

If sparrow morsel shape selections were based on choosing those shapes that maximized energy gained / sec feeding, both Harris' sparrows and tree sparrows should have selected, in descending order, ovate- and elliptical-shaped morsels, then rosette-shaped morsels, and lastly circular morsels, the order of decreasing efficiencies. However, a significantly greater quantity of circular-shaped morsels was consumed by both tree and Harris' sparrows whenever these millet-like items were offered with another choice. Therefore, these birds were not selecting to consume the morsel shapes that maximized energy / unit handling time.

If Harris' sparrow morsel size selections were based on choosing those sizes that maximized energy / sec feeding, then large size morsels should have been the most consumed. Medium and small size morsel consumptions should have occurred in approximately equal amounts. These predictions were not substantiated, as Harris' sparrows consumed a significantly greater quantity of small morsels whenever small morsels were paired with either medium or large morsels. Further, there was no significant difference in the mean amount of large and medium morsels consumed per trial. Therefore, Harris' sparrows were not consuming those morsel sizes that maximized energy / sec handling time.

If tree sparrow morsel size selections were based on choosing those sizes that maximized energy gained / sec feeding, then small size morsels should have been the most consumed by tree sparrows. Medium and large size morsel consumption should have followed in descending order. However, because morsel size selection based on least handling time predicted the same rankings of food sizes for tree sparrows, size consumption rankings will not reveal whether feeding efficiency or handling time was more important for food selection. Multivariate and covariance analyses, though, do provide a measure of relative importance. These analyses suggest that feeding efficiently is not the more important variable for tree sparrow morsel size selection.

Robel et al. (1974) reported similar results, finding that bobwhites showed no selection for food with high efficiency of utilization. Neither could Emlen and Emlen (1975) support the hypothesis that animals select those foods which optimize feeding efficiency. However, Emlen and Emlen (1975) did find that the seed selection of mice optimized feeding efficiently after corrections for imperfect decision making were performed.

The present research results are opposed to the results of Warner and Hall (1974), Goss-Custard (1977), and Krebs et al. (1977), who found that their study animals (bluegills, redshank, and great tits, respectively) selected the food items that optimized energy intake.

Because optimal foraging theory hypothesizes the maximization of net energy intake, and the present research measured total energy intake (following Pulliam 1985), a direct comparison between the present work and optimal foraging theory may not be appropriate. Had net energy been used as the measure of feeding efficiency, the results of the present research may also have supported foraging theory. In the present research, only the time required to ingest a morsel was important in determining handling time, as the time required to find and capture a morsel was negligible. Therefore, net energy would be defined as the energy gained from a food morsel minus the energy expended while ingesting the morsel. If ingesting large morsels was energetically more costly than ingesting small morsels, the birds would have expended more energy / sec handling time eating large morsels. An efficient sparrow might then have maximized net energy gained / unit handling time by selecting small morsels, and optimal foraging theory would predict the selection of small morsels. The observed consumption of small morsels would then have been predicted by optimal foraging theory. The logistics to determine net energy gain of the different morsels were not performed. Therefore, total energy was substituted as the index.

Selection of Food Morsels Based on Least Handling Time

If sparrow morsel shape selections were based on choosing those shapes that minimized handling time, both Harris' sparrows and tree sparrows should have selected circular-shaped morsels first, followed in descending order by elliptical-, ovate-, and rosette-shaped morsels. Circular morsels, the items consumed fastest, were always selected in significantly greater amounts by both sparrow species when offered against any other shaped morsel, substantiating the above prediction. Rosette morsels, the items consumed slowest, were never selected over other morsel shapes. On preference pairings of ovate and elliptical morsels, both bird species selected the elliptical shape, the morsel with the lower handling time. Thus, these birds appeared to select shapes they could ingest the fastest.

If Harris' sparrow's morsel size selections were based on choosing those sizes which minimized handling time, then small size morsels should have been the most consumed. Medium and large size morsel consumptions should have occurred in approximately equal amounts. These predictions were substantiated, as Harris' sparrows consumed a greater quantity of small morsels whenever small morsels were paired with either medium or large morsels. Further, there was no significant difference in the mean amount of large and medium morsels consumed per trial. Harris' sparrows appeared to select the morsel sizes they could ingest the fastest.

As above, because morsel size selection based on feeding efficiency or handling time predicted the same rankings of food sizes for tree sparrows, size consumption rankings did not reveal which of the two factors was more important for food selection. However, multivariate and covariance analyses suggest that the selection of morsel size depended more upon the time required to consume the morsel than upon feeding efficiently. The faster morsels were consumed, the more important they became to tree sparrow diets.

The preference for foods handled quickly has been well-documented. Willson and Harmeson (1973) found that songbirds preferred those seeds ingested fastest. Similarly, squirrel preference for nuts was based on selecting those nuts husked quickest (Smith and Fullmer 1972). And Willson (1971) determined that all of the bird species she tested could handle their more favored seeds faster than their less favored seeds.

Of the handling time components, i. e., search time, capture time, and ingestion efficiency (Livdahl 1979), only ingestion efficiency affected morsel selection in the present research.

Search and capture time were negligible (though equal) for all food morsels. Sherry and McDade (1982) concluded that the shape of food items was an important variable of ingestion efficiency, and that width of food better predicted handling time than length for insectivorous birds. The present research supports these conclusions in granivorous birds. Circular-shaped morsels (thinnest) were handled fastest, while rosette-shaped morsels (widest) were handled slowest. However, ovate- and elliptical-shaped morsels (longest) were handled faster than the shorter rosettes, but slower than the shorter circular morsels. Because morsel width correlated with handling time better than morsel length did, morsel width would have been the more accurate predictor of morsel handling time in the present study.

Apparantly birds were selecting food morsels which could be consumed the fastest when all food characteristics except morphology were held constant, and selection was not governed by feeding efficiently (as defined by Pulliam 1985). The preference of both bird species for circular-shaped and small-sized morsels supports this conclusion, as these morsel types were the fastest consumed, within the shape and size categories. However, circular-shaped and small-sized morsels did not provide the most cal / sec. The covariance and multivariate analyses of both Harris' and tree sparrows also support this conclusion. The analyses reveal that morsel handling time was related closer to morsel consumption than was feeding efficiently. However, the anlyses also suggest that other effects of morsel shape and size beyond handlng time effect morsel selection. Morsel width may have been one of these factors.

Confounding of Size and Shape

In Experiment I, morsel shape was confounded with size. Preferences for morsel shapes corresponded with sizes of morsels, smaller sizes being preferred. Circular morsels, the preferred shape for each species, were statistically smaller than the other shapes. Rosette morsels, the least preferred shape, were statistically larger than the other morsel shapes. Elliptical and ovate morsels, similar in preference, were also similar in size. Size and shape effects were not separable in this study.

Species Comparison of Food Size Selection

If a relationship between bill size and food preference size existed, as optimal foraging theory assumes, tree sparrows would select to consume smaller morsels than Harris' sparrows and Harris' sparrows would select larger morsels. This study did not substantiate the assumed relation between bill size and food size. In Experiment I, both bird species preferred to consume the smaller circular-shaped food morsels. Tree sparrows as well as Harris' sparrows consumed lesser amounts of the larger morsel shapes. Further, no differences in preference were demonstrated by either sparrow species, as morsel shape consumptions were ranked in the same order, with identical significant groupings, by both. In Experiment 2, both bird species preferred to consume the small size food morsels. Tree sparrows as well as Harris' sparrows consumed lesser amounts of the larger morsel sizes. This study did not find that Harris' sparrows preferred to consume large morsels and that tree sparrows preferred to consume small. Rather, both sparrow species preferred to consume the smallest morsel available.

Willson (1971, 1972) reported similar results. She found that both large-billed and small-billed finches chose to consume small seeds over large seeds. Hespenheide (1966) also found that large and small billed birds consumed greater quantities of small seed sizes.

Contrary to the above studies, larger species of flycatchers (Hespenheide 1971) were found to eat larger prey items than smaller, closely-related species. Newton (1967), Pulliam and Enders (1971) and Abbott et al. (1977) reported that some larger-billed finches tended to eat larger seeds than their smaller-billed relatives. Tufted titmice also preferred larger seeds than did smaller chickadees (Myton and Ficken 1967). Bowman (1961) suggests that the ability of large birds to handle large seeds faster is a function of their larger bill. Greater bill width and depth facilitate handling larger seeds by providing a broader base for holding seeds and by permitting greater forces to be applied to the seed (Bowman 1961, 1963).

Optimal foraging theory also assumes that large sparrows are more efficient in energy intake than small sparrows when both consume larger seeds, and smaller sparrows more efficient when both consume small seeds (Pulliam 1985). The larger Harris' sparrows supported this assumption, consuming larger morsels quicker than tree sparrows consumed these sizes. By definition, faster consumption of the same morsel type provides shorter handling times, increasing the efficiency (cal / handling time) of that morsel type. Therefore Harris' sparrows were more efficient than tree sparrows in consuming the larger morsels (elliptical-, ovate-, and rosette-shapes, large and medium sizes).

Contrary to the assumption, tree sparrows were not more efficient than Harris' sparrows eating small morsels. However, morsel sizes may not have been small enough to be within the tree sparrow's most efficiently utilized size range. Pulliam (1985) estimated that chipping sparrows (*Spizella passerina*) and juncos, birds similar in size to tree sparrows, obtained the greatest cal / sec when consuming seeds weighing 0.4-0.6 mg. In the present research the small seeds weighed approximately 6 mg. Still, Pulliam (1985) found little difference between the handling times of small seed species for small and large sparrows, even on the 0.4 mg seeds, a trend repeated for the small morsels in the present study.

The present research results agreed with Willson (1971), who demonstrated that large-billed finches husked larger seeds faster than did small-billed finches, but that birds of both bill sizes husk small seeds at the same rate. Hespenheide (1966) determined that large-billed birds were more efficient consuming small seeds (length 9-11 mm) than were small-billed birds. Willson (1972) also found that large-billed birds husked small, thin seeds (width $\leq$ 4.7 mm, length $\leq$ 12 mm) faster than the smaller-billed birds could. However, the small seeds of Willson (1972), and of Hespenheide (1966) were larger than the morsel shape types used in the present research, and would have been classed as large seeds in the present research. Therefore, in perspective of the present research, Willson (1972) and Hespenheide (1966) found that large birds husked large seeds faster than smaller species could, in agreement with the present research.

Dayton-Morrill Palatability Model

Discrepancies occurred between the morsel shape consumption estimates obtained by the Dayton-Morrill (DM) Palatability model and the daily consumption means. Both methods assume that the preferred (or more palatable) item will be that item most consumed. The DM model uncovered no tree sparrow preference for morsel shapes, estimating that all morsel shapes would be equally consumed. Similarly for Harris' sparrows, the DM model estimated that circular-, elliptical-, and ovate-shaped morsels would be equally consumed. These results were in obvious conflict with the experimental results, as the consumption of circular-shaped morsels was 3.5 x greater than the consumption of any other morsel shape when both were offered in the same trial.

The discrepancies between the experimental results and the estimates of the DM model may be explained by assumptions made in deriving the model. The DM model estimates consumption of each morsel shape by estimating the consumption had that shape been fed alone. It is assumed that the food item which maximizes total consumption is the preferred food. Anthropomorphically this seems valid, but it may not be true when nutritionally identical food items are fed to organisms which eat only enough to survive, as in this research.

Bird food intake during a winter day is dependent upon the amount of energy metabolized during the night (Kendeigh 1969), as birds eat only enough to replace the lost energy. Birds could thus be called time-minimizers (Schoener 1971), animals whose fitness is maximized when time spent feeding to gather a given energy requirement is minimized. Assuming large seed consumption energetically more costly than small seed consumption, (e. g., if more force is needed to crush larger seeds, more energy is spent generating the force), birds may expend more energy per unit handling time eating large seeds. Five seconds of large seed consumption requires more force, and thus more energy, than five seconds of small seed consumption. The extra energy required to consume large seeds must be repaid by eating a greater amount of the larger seeds. So the increased ingestion of larger seeds may be a function of an increased energy demand, and unrelated to any preference for these seeds. A greater weight of large seeds must be ingested to obtain the same net energy derived from a lesser amount of smaller seeds (see Fig. 6 for hypothetical example). Even though fewer seeds need be consumed, more time must be spent to ingest them.

Figure 6. Hypothetical example of increased energy demand resulting from large seed consumption causing an increase in the weight of seeds required to meet energetic needs.

	Seed energy (cal)	Energy to ingest seed (cal)	Net energy received (cal)	Seed wt (mg)	Time to consume seed (sec)
Seed A	3	1.0	2.0	2	2
Seed B	5	2.5	2.5	3	3

ORGANISM REQUIRES 10 CALORIES

		Energy (cal)				
	Seeds needed	Total ingested	Required to eat seed	Net gain	Seed weight eaten	Ingestion time (sec)
SEED A	5	15	5	10	10 mg	10
SEED B	4	20	10	10	12 mg	12

Another assumption of the DM model is that the different trials will produce variable amounts of total consumption. When total intake is constant between trials, the model cannot determine preferences of the food types. Birds in this study maintained a relatively constant food intake, independent of the trials. The constant food intake of the test subjects further compromised the DM model's utility in determining food preference.

When pair-wise comparison tests are performed using food items with variable nutritional quality, and when total intake of each trial is not constant, the DM model will provide food preference estimates that correspond with the experimental results. Browning et al. (1981) successfully determined that field sparrows (*Spizella pusila*) and cardinals selected Maximilian sunflower (*Helianthus maximilianii*) and sawtooth sunflower (*H. grosseserratus*) seeds over roundhead lespedeza (*Lespedeza capitata*) and thickspike gayfeather (*Liatrus pycnostachya*) seeds. The sunflower seeds were nutritionally superior to lespedeza and gayfeather seeds, having a higher energy content. Also, total consumption in four of the six pair-wise treatment combinations were significantly different. Because the total intake of each trial varied in Browning's study, the DM model was able to successfully separate preferred seeds from non-preferred seeds.

Use of the DM model was discontinued due to the apparant discrepancies between the model and the data. Daily consumption means were used in analysis of variance models for the remainder of the research.

STUDY 2. INTRODUCTION AND LITERATURE REVIEW

The Effect of Color and Flavor on Morsel Selection

Optimal foraging theory has been used to predict food preferences of vertebrate and invertebrate predators. Werner and Hall (1974) successfully predicted which size classes of invertebrate prey bluegill sunfish would select by using optimality theory. Elmer and Hughes (1978) found that shore crabs (*Carcinus maenas*) accepted or rejected food according to the food's energetic value. Redshank feeding in the field selected the worm size class combinations predicted by Optimal Foraging Theory that maximized the rate of energy return (Goss-Custard 1977).

Most of the theoretical work predicting that foragers feed efficiently has assumed that food types are instantly recognizable, and that food appearance corresponds directly to profitability (profitability = net energy / handling time, Erichson et al. 1980). If, for instance, there are good-green and bad-blue types, we can refer to the good ones or green ones interchangeably. It is food's appearance, however, not food's profitability, that is apparant to the forager (Getty 1980). Foragers would thus be expected to base food selections directly on appearance, not profitability, if food selection were made according to Optimal Foraging Theory. Appearance would serve as an index for profitability. Foragers' sensory apparati would then allow for the selection of profitable food, and would influence which characteristics of a food item's appearance will be detected (Hinde 1959), and the distances at which food will appear and be identifiable (Orians 1981).

Many organisms use visual cues to detect and evaluate food. Eyes can detect the direction, distance, size, shape, color, depth, and motion of an object (Welty 1982). Heinrich and Collins (1983) demonstrated the ability of black-capped chickadees (*Parus atricapillus*) to correlate leaf appearance with the liklihood of prey's presence. The chickadees determined the presence of prey concealed in a leaf by seeing the amount of leaf damaged by the prey. Marden (1985) found that bumblebees (*Bombus* edwardsii) could find nectar in artificial flowers by visually detecting the presence of finger prints on the flowers.

Other organisms are receptive to tactile or chemical cues. Shore crabs foraging in the ocean detect mussels at a distance by chemoreceptors on the antennae, while the tips of the crabs legs respond to touch, allowing the crab to grasp the mussel when encountered (Elmer and Hughes 1978). The sensitivity of wood ibis (*Mycteria americana*) beaks to tactile stimulation allows the ibis to capture fish by touch alone (Kahl and Peacock 1963).

Evidence of Visual Abilities in Birds

The importance of the sense of vision to birds is suggested by the large size of the eye, which may be 1.5% of total body weight (Welty 1982). The avian eye differs little from the eye of other vertebrates (Sillman 1973), including the occurence of at least four visual pigments in chicken and pigeon (*Columba livia*) cone cells. These pigments are thought to be involved, as in other vertebrates, in color vision (Govardovskii and Zueva 1977). Electrophysiological studies have discovered that pigeons possess 2-3 color sensitivity curves (Donner 1953; Ikeda 1965), indicating that pigeons, at least, have color vision.

Birds in general are probably capable of color vision (Sillman 1973). Common grackles (*Quiscalus quiscalus*) (Ridsdale and Granett 1969), white leghorn pullets (Hurnik and Schulze 1977), California quail (*Lophortyx californicus*), varied thrushes (*Ixoreus naevius*), and juncos (Pank 1976) all responded to colored food, eating more food items colored yellow or blue than items dyed red or green. In contrast, straight run Broad-breasted white turkey poults preferentially selected green feed (Cooper 1971). Slaby and Slaby (1977) noted a definite preference for red-dyed peanuts by Stellar's jays, while Pauperova (1962) reported a marked rejection of red foods by several sparrow species, titmice, and siskins (*Carduelis spinus*). The selection or avoidance of certain colored foods in these studies indicate that birds can detect color, and can discriminate between different colors when selecting food.

Evidence of Chemo-receptive Capabilities in Birds

The presence of taste buds in the chicken (Lindenmaier and Kare 1959), European bullfinch (*Pyrrhula pyrrhula*) (Duncan 1960), and Japanese quail (Warner et al. 1967), coupled with the neural activity of the taste bud to physiological stimuli (Landolt 1970) provides evidence for the sense of taste in birds. Further evidence of avian taste perception comes from preference testing experiments. Kare et al. (1959) and Deyoe et al. (1962) found that Hy-line cockerels preferred butter solutions over water, but rejected other flavored solutions. Bobwhites and Japanese quail rejected bitter and salt solutions, and preferred sweet and acid solutions when each was paired with water (Brindley 1965). Great tits consumed sweet solutions more readily than water, but not acid, salt, or bitter solutions (Warren and Vince 1963). Domestic chickens, herring gulls, starlings (*Sturnus vulgaris*), and robins (*Turdus migratorius*) did not select sugar solutions over water (Kare and Maller 1967). However, when the chickens were on a caloric deficient diet, their preference switched to the sugar solution. Kare and Ficken (1963) found chickens tolerant to acidic solutions. Kare et al. (1957) and Kare and Ficken (1963) state that the tastes classed by man do not appear to be applicable to fowl. Sturkie (1986) found that frugivorous birds were likely to positively respond to sugar solutions, but that granivorous and insectivorous birds were not.

Sizemore and Lillie (1956) and Romoser et al. (1958) detected no significant increase in chicken's feed intake when the feed was flavored with various fruits and spices. Conversely, Davison (1962) concluded that songbirds select food chiefly on taste. Grieg-Smith (1985) determined that bullfinches select against pear buds with high phenolic contents, as these buds taste bitter. Hill (1972) found that house sparrows (*Passer domesticus*) detected toxic chemicals in food and reduced their consumption of toxic-laden food. Likewise ring-necked pheasants (*Phasiaus colchicus*, Bennett and Prince 1981) and grackles (Ridsdale and Granett 1969) demonstrated the ability to avoid toxin-treated foods.

Birds possess olfaction receptor cells comparable to those in other vertebrates. The size of the olfaction lobes of the brain varies widely among bird species (Wenzel 1973). Electrical activity in response to odorous stimuli has been recorded in 14 different avian species, including the blue jay (*Cyanocitta cristata*), domestic goose (*Anser anser*), and turkey vulture (*Cathartes aura*, Tucker 1965). Avian reliance on foraging by olfaction may be of direct use to species well-equipped with olfactory lobes, such as turkey vultures (Stager 1964) and kiwis (*Apteryx spp*, Wenzel 1968), but ignored by other birds that have minimal, though functional, olfaction receptor cells, olfactory nerves, and olfactory lobes, such as Passerines (Wenzel 1973).

Evidence of Tactile Capabilities in Birds

Herbst corpuscles are highly developed in birds, and similar to the Pacinian (touch) corpuscles in mammals (Welty 1982). The Herbst corpuscles occur in great numbers in the beaks of most birds (Schwartzkopff 1973). Engleman (1940, 1943) found evidence that tactile stimulation will predominate over a strong taste stimulation, and concluded that taste is not important for pigeons, as hungry birds will eat. Moran (1982) agrees, citing evidence that indicates feed texture is perceived prior to any cognizance of taste, and that tactile detection is meaningful in food selection. Pank (1976) found that varied thrushes, juncos, and California quail selected against Douglas fir (*Pseudotsuga menziesii*) seedlings colored with agents that added texture to the seedlings. Conversely, Davison (1962) reported that songbirds were not selecting by texture, but by taste.

In general, evidence suggests that Passerines respond to visual, tactile, and chemical characteristics of food while foraging, utilizing the senses of taste, touch, and sight to identify preferred food items. Optimal foraging theorists have given little consideration to the relationship between food appearance and diet selection. The objectives of this phase of the research are to determine the ability of Harris' sparrows and tree sparrows to discern colored food and flavored food, and to determine the effect of different colors and flavors on food selection by Harris' and tree sparrows.

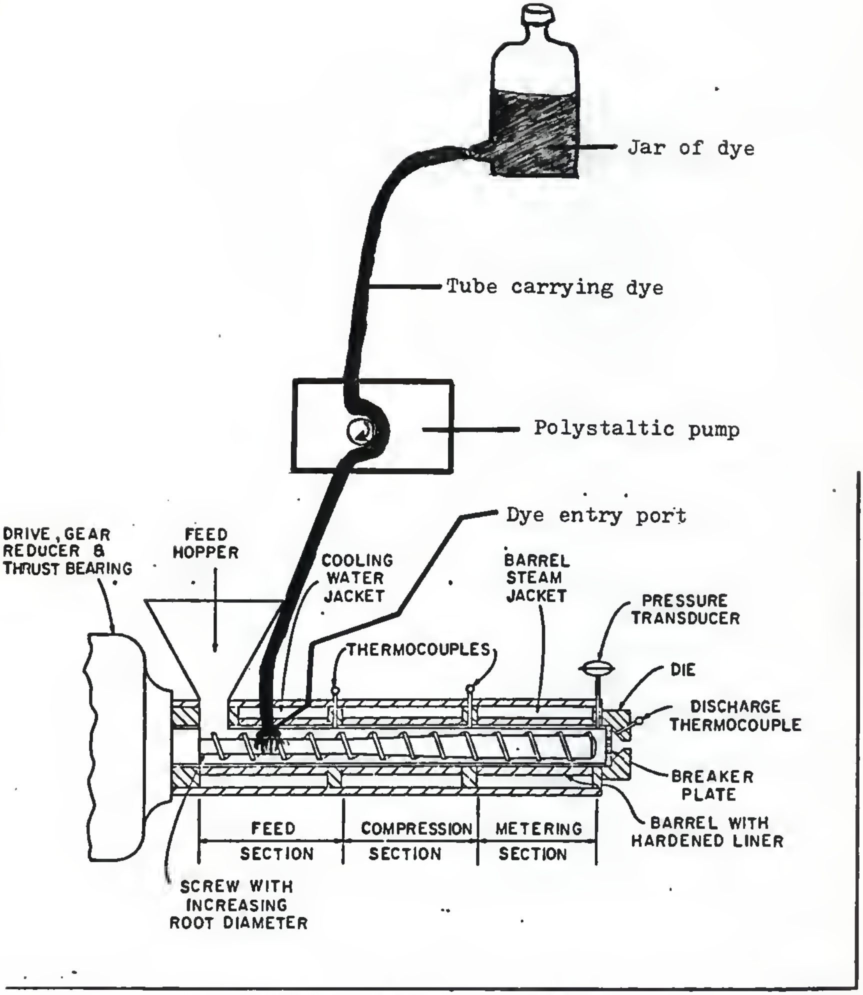
EXPERIMENT III. METHODS

Colored Morsel Preparation

Food color pair-wise comparison trials were conducted after the food shape preference trials. The colors tested were blue, brown, yellow, and orange. Preparation of the blue, brown, and yellow dyes entailed adding 25 g of organic, granular dye (either Warner-Jenkinson 05601 FDC-blue no. 1 lot A09210, Stange C01355 chocolate shade, or Warner-Jenkinson 08005 FDC-yellow no. 5 Lot AE0236) to 300 ml of tap water. To create the orange dye, 8 g of Warner-Jenkinson 07700 FDC-red no. 40 Lot AD9741 was blended with 17 g of Warner-Jenkinson 08006 FDC-yellow no. 6 Lot AD8248 and dissolved in 300 ml of tap water. The dye solutions were odorless and tasteless.

Food morsels were formed by the extrusion process, as the heated base mix was forced through the small-holed 31.5-mm die insert (Appendix F1) of the extruder. Small, circular-shaped food morsels were produced, the preferred morsel type determined in Study I. Morsels were cut to similar lengths by a four-blade variable-speed knife.

Food morsels were colored by adding the premixed solutions of food dye to the base mix in the extruder. Only one dye was added per run. Dye flow to the extruder was regulated by a Buchler Instruments polystaltic pump, serial no. 54537. The dye was pumped through an entry port into the feed section of the screw conveyor (Fig. 7). No rise in



-CROSS-SECTION OF A TYPICAL FOOD EXTRUDER

Figure 7. Diagram of apparatus used to send dye to the extruder.

temperature or pressure build-up occurred to the base mix prior to the insertion of the food color.

The extruder ran continuously during production. Upon attaining the required amount of one colored-morsel type, dye flow to the extruder was halted. After that dye color had passed through the extruder, and the extruded product returned to it's natural color, a new dye color was introduced. Color preparation proceeded from the lightest to the darkest, preventing previously run color trapped in the extruder from breaking loose and altering the color of the next product.

Morsels were dyed so that each color appeared equal in intensity to the human eye. The dial of the polystaltic pump was set at 3 when dying morsels yellow or orange, set at 1 to dye morsels brown, and set at 5.5 to dye morsels blue. Color shades of the morsels produced by these pump settings were identified in a Color Atlas (Kueppers 1982). Identification involved placing 3-4 morsels of the same color on the colored plates of the Atlas, and determining which colored square of which color series in the Atlas most closely resembled the morsels' color. Color comparisons were made on a sunny day in a room with fluorescent lighting that received direct sunlight, by an individual with no apparent color blindness. The color plates, partially shaded to eliminate glare, were viewed at 215.3 ± 32 lx, as measured by a Model C Gossen Trilux Footcandle Meter no. 01365. Brown morsel shade was identified to be Black40Yellow50Magenta-red30 (Kueppers 1982

p. 53). The numbers refer to the surface dot value coverage of the colors present in the offset films used to derive the color plates. E. g., B40Y50M30 means that black dots covered 40% of the surface, yellow dots covered 50%, and magenta-red dots covered 30%. Blue morsel shade was identified to be B10Cyan-blue70Y40, orange morsel shade was Y50M50C10, and yellow morsel shade was Y60M20C10 (Kueppers 1982, p. 71, 103, and 105, respectively).

After morsels had dried, a 190-l cement mixer was utilized to round the square edges of the colored, circular-shaped morsels. Forty 0.64 x 25.4-mm-round-head-slotted-machine screws and thirty 25.4-mm dia. ceramic balls were placed into the mixer with 18.25 kg of colored morsels. The mixer was rotated for 35 min. Screws and ceramic balls were separated from the food by hand. Each color type was then sieved on the Forsberg screener to reduce the variability of size within and between color types. Those morsels that would fall through an 8 mesh 0.025 screen, but remain over a 12 mesh 0.018 screen were retained for the experiment.

Colored morsels were presented to 12 Harris' sparrows and 12 tree sparrows in pair-wise presentations. The pre-weighed morsel samples were placed into two feeders in each bird's cage at the beginning of the photoperiod, and removed from each cage at the end of the photoperiod. Feeders were clear, uncolored. While the feeders were in the cage, food and water were provided *ad libitum*, and feeder positions were switched every two hours. Food spilled by each bird during the day was collected, sorted into color types, and added to the unconsumed food. The weight of each morsel color type consumed by each bird was then determined (see General Methods, p. 9, 10).

The four morsel colors presented in every pair-wise combination gave six treatments. The experimental design followed the treatment sequence for the 6 x 6 Latin Square Block Design (Fig. 2). Birds were randomly assigned to treatment sequences, and each bird repeated it's treatment sequence once.

Following the completion of the blue, orange, yellow, and brown morsel pair-wise presentations (Experiment 3a), a second set of colored morsel presentations occurred (Experiment 3b). In Experiment 3b, the natural base mix color (tan) was tested against the preferred colors of Experiment 3a. The circular-shaped morsels used to test shape in Experiment 1 served as the tan colored morsels (B20Y40M10, Kueppers 1982, p. 49) of Experiment 3b. Yellow, brown, and tan morsels were presented to Harris' and tree sparrows in pair-wise presentations as above. The three morsel colors presented in every pair-wise combination gave three treatments. The experimental design followed the treatment sequence for the 3 x 3 Latin Square Block Design (Fig. 3). Birds were randomly assigned to treatment sequences. Treatment sequence replications and test day replications were not performed.

EXPERIMENT III. RESULTS

Color Preferences - Experiment 3A

Preference rankings of colored-morsel mean consumptions showed no significant differences from day 1 to day 2 of a test replication for either species (Appendix I3), so data from both days were pooled.

Harris' sparrows consumed 5.6 g / day of brown food morsels and 5.4 g / day of yellow morsels, both significantly higher than the amount of blue and orange morsels eaten each day (Table 15). However, Harris' sparrows' consumption of brown morsels was not significantly different from their consumption of yellow morsels. Likewise, tree sparrows consumed 3.8 g / day of yellow food morsels and 3.6 g / day of brown morsels, both significantly higher than the daily amount of other colored morsels eaten (Table 15). Tree sparrows' consumption of brown morsels was not significantly different from their consumption of yellow morsels. Harris' sparrow's daily consumption of blue-colored morsels was significantly lower than their daily consumption of the other colors. No differences occurred in the daily amount of orange and blue morsels consumed by tree sparrows.

When brown morsels were paired with yellow morsels and presented to Harris' and tree sparrows, no differences in the consumptions of either color occurred (Table 16). However, when either color was paired with blue or orange, a

Table 15. Ranked means from Analysis of Variance (ANOVA) for the mass (g) of colored morsels consumed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ consumption *,+	
Morsel color	Harris' sparrow N = 12	Tree sparrow N = 12
Brown	5.56 d	3.60 x
Yellow	5.44 d	3.81 x
Orange	4.34 c	2.46 r
Blue	3.59 x	2.33 r
S.E. =	0.20	= 0.20

* test day replications and treatment sequence replications were combined

\+ values with a common letter do not differ, $p > 0.05$

Table 16. Mean (+SE) mass (g) of morsel colors consumed by captive Harris' and tree sparrows kept at Kansas winter conditions when the four morsel colors were presented in every pair-wise combination.

	$\bar{x}$ consumptions	
Pair-wise presentation	Harris' sparrow	Tree sparrow
Brown	6.15 ± 0.30	3.96 ± 0.29
Blue	3.44 ± 0.33	2.12 ± 0.30
Blue	4.17 ± 0.39	2.73 ± 0.42
Orange	5.23 ± 0.38	3.28 ± 0.40
Yellow	6.29 ± 0.31	4.05 ± 0.37
Blue	3.18 ± 0.33	2.10 ± 0.40
Brown	5.60 ± 0.29	4.01 ± 0.21
Orange	3.83 ± 0.35	2.12 ± 0.20
Brown	4.88 ± 0.24	2.86 ± 0.30
Yellow	4.45 ± 0.30	3.17 ± 0.26
Yellow	5.58 ± 0.32	4.17 ± 0.25
Orange	3.87 ± 0.30	1.99 ± 0.29

significantly larger quantity of yellow and brown morsels was consumed. In the present study, birds tended to select yellow and brown morsels, and to select against blue and orange morsels.

Replicating treatment sequences for tree sparrows decreased consumption, but did not alter preferences (Table 17). No effect from treatment sequence replication was observed in Harris' sparrows. For both species the order and significance of preferences remained stable between treatment sequences (Appendix J2). No carryover effect due to the presence of a food type in the preceding trial developed in either species (Table 17). No significant alterations occurred to tree sparrow colored morsel consumption rankings when the amount of each color spilled was added to the consumption data prior to analysis (Appendix K3). However, for Harris' sparrows, the consumption of blue and orange morsels consumed was not found to differ significantly when spilled food was added to the consumption data prior to analysis.

Color Preferences - Experiment 3B

Tree sparrows consumed 3.3 g / day of brown food morsels, and 3.1 g / day of yellow food morsels, both significantly higher than the daily amount of tan morsels consumed (Table 18). However, tree sparrows' consumption of brown food morsels was not significantly higher than their consumption of

Table 17. ANOVA model of factors related to daily mean colored morsel consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	Source of variation	df	Sum of squares	F	P
Harris' sparrow	Square	1	0.992	0.34	.5608
	Day (sq)	10	5.080	0.17	.9979
	Bird (sq)	10	23.049	0.79	.6401
	Color	3	189.000	21.55	.0001
	TSR *	1	0.006	0.00	.9648
	Carryover	1	3.760	1.29	.2579
Tree sparrow	Square	1	0.349	0.13	.7213
	Day (sq)	10	2.649	0.10	.9998
	Bird (sq)	10	7.021	0.26	.9895
	Color	3	124.706	15.17	.0001
	TSR *	1	0.246	0.09	.7648
	Carryover	1	5.573	2.03	.1550

* symbolizes treatment sequence replication

Table 18. Ranked means from ANOVA for the mass (g) of colored morsels consumed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ consumption *	
Morsel color	Harris' sparrow N = 12	Tree sparrow N = 12
Brown	5.00 o	3.34 r
Yellow	4.25 o	3.10 r
Tan	4.24 o	2.00 i
	S.E. = 0.27	= 0.33

* values with a common letter do not differ, $p > 0.05$

yellow morsels. Harris' sparrows did not have any significant differences in the daily amount of brown, yellow, or tan food morsels consumed (Table 18).

STUDY III. DISCUSSION

Selection of Color

Tree and Harris' sparrows demonstrated the ability to discern colors by repeatedly distinguishing and selecting greater quantities of yellow and brown food morsels, and by selecting fewer orange and blue morsels. These selections support Sillman (1973), who stated that birds in general are probably capable of color vision. Further evidence of color discriminatory ability in tree and Harris' sparrows was observed during pre-trial days, when the birds were fed a mix of blue, yellow, brown, orange, and tan morsels. The sparrows avoided eating blue morsels, or blue and orange morsels, while consuming the other colored morsels lying next to the blue and orange ones. A top layer of blue food, or blue and orange food, interspersed with the other colors, resulted. Avian color perception has been previously reported (Kalmbach 1943; Cullen 1963; Ligon and Martin 1974). However, it seems that color preferences may vary from species to species. Deucker and Schulze (1977) reported that Japanese quail distinguished and preferred green- and yellow-colored lights over blue and red lights. Slaby and Slaby (1977) discovered that Stellar's jays preferred yellow-colored peanuts to blue and green-colored peanuts, results similar to the present research. Conversely, starlings (Schwaab 1964) and chickens (Hurnik et al. 1977) selected food colored blue over food colored red or yellow, while doves (Davisson and Sullivan 1963) displayed no color discrimination when feeding on different-colored seeds.

The exact spectral characteristics of the colors used may be of importance in color discrimination and preference, as may the particular conditions of the test (Brunner 1983) or of the pre-test period. Pank (1976) has shown that coloring agents which add texture to food items are less preferred, and Goforth and Baskett (1971) suggested that the color of the food's background was important to selection. For reasons such as these, direct comparisons between different studies are not always meaningful.

The lack of consumption of blue- and orange-colored morsels may be explained by the avoidance of novel food items. Rabinowitch (1968) found that food to which individual birds had become familiar with in early life were selected preferentially. Further, he found that food color affected diet choice only when novel-colored items were presented. The effect of novel colors was to inhibit feeding behavior. Similarly, Coppinger (1970) found that birds would not attack butterflies if the butterflies were given a color pattern that the birds had not previously encountered. In all probability the experimental birds of this study had never encountered blue seeds, and had rarely, if ever, seen orange seeds, so orange and blue morsels were novel-colored food items to the birds.

Although it was impossible to know the exact foods eaten by the experimental birds prior to their capture, Bent (1968) reports that naturally occurring seeds commonly consumed by Harris' and tree sparrows include switchgrass (*Panicum virgatum*), old witchgrass (*Panicum capillare*) and other grass seeds, ragweed, lambquarters (*Chenopodium album*), and *Polygonums spp* (smartweed, knotweed, etc.). These seeds are either light yellow, whitish-yellow, tan, dark brown, light brown, or black (Montgomery 1977). Experimental birds were captured in vegetation dominated by ragweed and pigweed. In all liklihood, the experimental birds of the present study had previously consumed some or all of the seeds listed by Bent (1968) prior to capture, and entered the experiment familiar with yellow, tan, and brown seeds. Selection of similarly colored morsels in the experiment was likely influenced by the prior exposure to the natural seeds. Unfamiliar colored morsels were not well accepted when placed in the presence of familiar-colored morsels. These results support Kalbach's (1943) and Pank's (1976) conclusions that bird food consumption was deterred by unnaturally colored seeds. Ridsdale and Granett (1969) also found that undyed corn grains received the greatest consumption, and that dying grains unnatural colors reduced consumption.

Similar observations and interpretations have been made in experiments examining food presentations. Red-winged blackbirds (*Agelaius phoeniceus*) refused *Lespedeza* seed to the point of starvation (Neff and Meanly 1957). The authors believed that blackbirds lacked previous exposure to *Lespedeza*, and did not recognize these seeds as food. Tinbergen (1960) postulated that birds must acquire a 'search image' for a food item prior to acceptance of the item, and that this image is acquired through frequent chance encounters. Initial non-acceptance of food items is due to unfamiliarity with the item, not recognition then rejection. He believed that once a search image was formed, the food would be accepted readily.

Evidence of the acceptance of once-novel food items occurred in a separate experiment performed to study dominance hierarchies (unpubl. data). No color preference occurred when blue morsels were paired with brown morsels after the birds were fed only blue morsels for two days. Rather, a vigilant response to feeder position developed in which birds fed at the feeder allowing constant surveillance of the chamber door, regardless of the colored morsels within that feeder. Eating from this feeder allowed the birds to see the experimenter whenever he entered the chamber. In contrast, eating from the other feeder required that a bird turn it's back to the direction of entry. Deeming vigilance more important than food color, birds chose to select food based on feeder position, not morsel color, and consumed food from the feeder facing the chamber door over a two-day span. A similar response did not develop when size was used as the variable, as both sparrow species selected small morsels, regardless of feeder position.

Although birds were able to discriminate between colors, the importance of color did not seem to be absolute. Birds non-discriminately consumed yellow and brown morsels, displaying no preference for one over the other. Morsel color was important to selection when unfamiliar colored items were present. When only familiar colored items are present, other characteristics of the food will be more important in food selection (e. g., position, size of food).

EXPERIMENT IV. METHODS

Flavored-Morsel Preparation

Food flavor pair-wise comparison trials were conducted after the food color preference trials. The flavors tested were fruit (Fries & Fries artificial lime flavor #139121), butter (Fries & Fries artificial butter flavor #153979), and nut (an equal blend of Fries & Fries artificial pecan flavor #153972 and Fries & Fries artificial nut flavor #153973). All flavorings were liquid. The unconsumed yellow morsels of Experiment III were used for this experiment.

Liquid flavorings were sprayed onto the surface of the yellow morsels by a Crown aerosol sprayer, model 15-233 Spra-Tool Complete. Prior to flavor application, non-flavored morsels (2722 g) were placed in a 7000-g-capacity-unbaffled-tumbling-temperer. With the temperer turning, the experimenter's hand continuously flipped food to the center of the temperer. Flavoring was sprayed directly into the path of the flipped food, allowing the flavored-mist to coat all sides of the morsels. Flipping food from all areas of the temperer, and regularly stopping the temperer to remix the morsels provided all morsels an oppurtunity to be coated. Flavored morsels were placed directly into 13.25-l sealed plastic containers. The flavored morsel types were stored separately in three sealed plastic containers for the duration of the study.

The amount of flavoring applied to the morsels followed usage recommended by Fries & Fries Co. for each flavor. Undiluted lime flavoring was applied to be 0.75% by weight of the finished feed. Undiluted nut and butter flavorings were applied to be 1-2% by weight of the finished feed.

Flavored morsels were presented to 12 Harris' sparrows and 12 tree sparrows in pair-wise presentations. The pre-weighed morsel samples were placed into two feeders in each bird's cage at the beginning of the photoperiod, and removed from each cage at the end of the photoperiod. While the feeders were in the cage, food and water were provided *ad libitum*, and feeder positions were switched every two hours (see General Methods, p. 9, 10). Food spilled by each bird was not collected because flavor of morsels could not be determined, and thus separated, by visual inspection. The measured variable became the amount of food each bird removed daily from each feeder.

The three morsel flavors presented in every pair-wise combination gave three treatments. The experimental design followed the treatment sequences for the 3 x 3 Latin Square Block Design (Fig. 3). Birds were randomly assigned to treatment sequences. Each treatment sequence was presented to two birds of each species. No bird repeated it's treatment sequence. Preferences for flavor were determined by comparing the daily mean removal of each flavor from the feeders.

Following the completion of the fruit-, nut-, and butter-flavored morsel pair-wise presentations (Experiment 4a), a second experiment (Experiment 4b) was performed to test natural base mix (unflavored) morsels against the preferred flavor of Experiment 4a. Unflavored yellow morsels of Experiment 3 served as the natural morsels. These unflavored morsels appeared identical to flavored morsels. Unflavored and butter-flavored morsels were presented to the Harris' and tree sparrows in pair-wise presentations for four days.

Throughout this section, 'flavor' and 'taste' are used in a broad sense, to include any mechanism by which food chemicals are detected during feeding (Wenzel 1973). No distinctions between sensations arising from stimulation of taste buds and those due to other kinds of action, such as stimulation of trigeminal receptors or effects of gut physiology are made.

EXPERIMENT IV. RESULTS

Flavor Preferences - Experiment 4a

Rankings of tree sparrow's mean removal of flavored-morsels from feeders showed no significant differences from day 1 to day 2 of a test replication (Appendix I4), so data from both days were pooled. Tree sparrows removed 3.6 g / day of butter-flavored morsels, and 3.5 g / day of nut-flavored morsels, both significantly higher than the amount of lime-flavored morsels removed (Table 19). However, tree sparrow's removal of butter-flavored morsels was not significantly different from their removal of nut-flavored morsels. Whenever lime-flavored morsels were placed with another flavor, a smaller quantity of lime-flavored morsels was consumed (Table 20). When nut- and butter-flavored morsels were paired, a greater quantity of butter morsels was removed on day 1, and more nut-flavored morsels removed on day 2 of a test replication.

Harris' sparrows displayed significant differences in rankings of mean removal of flavored morsels from day 1 to day 2 of a test replication (Table 19). On day 1, no significant differences occurred in the amount of nut-, butter-, or lime-flavored morsels removed (5.2, 4.6, and 4.6 g / day, respectively) from feeders. On day 2 of the replication, the removal of butter-flavored morsels (5.4 g) was significantly greater than that of lime-flavored morsels

Table 19. Ranked means from Analysis of Variance for the mass (g) of flavored morsels removed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ removals *			
Morsel	Harris' sparrow N = 12			Tree sparrow N = 12
flavor	Day 1 +	Day 2 @	total #	total #
Butter	4.63 fo	5.43 f	5.03 f	3.62 r
Nut	5.15 fo	4.51 fo	4.83 f	3.46 r
Fruit	4.61 fo	3.91 o	4.26 o	2.26 m
S. E.	0.30	0.33	0.15	0.18

* Values with a common letter do not differ, $p > 0.05$

\+ Day 1 of a test day replication

@ Day 2 of a test day replication

\# Test day replications averaged

Table 20. Mean (+ SE) mass (g) of morsel flavors consumed by captive Harris' and tree sparrows kept at Kansas winter conditions when the three morsel flavors were presented in every pair-wise combination.

		$\bar{x}$ consumptions	
Pair-wise presentations		Harris' sparrow	Tree sparrow
Day 1	butter	4.67 ± 0.42	3.99 ± 0.38
Day 1	lime	4.81 ± 0.33	2.30 ± 0.29
Day 2	butter	5.57 ± 0.45	3.88 ± 0.38
Day 2	lime	3.50 ± 0.43	2.35 ± 0.23
Day 1	butter	4.59 ± 0.37	3.61 ± 0.32
Day 1	nut	5.08 ± 0.39	2.81 ± 0.33
Day 2	butter	5.30 ± 0.48	2.98 ± 0.29
Day 2	nut	4.10 ± 0.39	3.28 ± 0.22
Day 1	nut	5.22 ± 0.40	3.84 ± 0.25
Day 1	lime	4.42 ± 0.42	2.42 ± 0.36
Day 2	nut	4.92 ± 0.38	4.00 ± 0.30
Day 2	lime	4.32 ± 0.30	1.98 ± 0.28

(3.9 g). The removal of nut-flavored morsels did not differ from the removals of the other two flavors.

Combining the two test replication days, Harris' sparrows removed 4.3 g / day of lime-flavored morsels from feeders (Table 19), significantly less than the removal of the other flavors. No significant differences occurred in the daily amount of butter- and nut-flavored morsels removed.

No carryover effect due to the presence of a flavor type in the preceding trial developed in either species (Table 21). Morsel flavor had an effect on determining consumption in tree sparrows (Table 21), but ANOVA detected no effect of morsel flavor on consumption for Harris' sparrows.

Flavor Preferences - Experiment 4a

Tree sparrows' removed 3.17 ± 0.13 g / day of unflavored food, not significantly more than the 3.11 ± 0.13 g / day of butter-flavored morsels removed. Likewise, Harris' sparrows' removal of butter-flavored food, 5.01 ± 0.14 g / day, was not significantly different than the 4.73 ± 0.14 g / day of unflavored food removed.

Table 21. ANOVA model of factors related to daily mean flavored morsel consumptions (g) by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	Source of variation	df	Sum of squares	F	P
Harris' sparrow	Square	3	5.987	3.45	0.0235
	Day (square)	8	2.002	0.43	0.8955
	Bird (square)	8	4.568	0.99	0.0028
	Flavor	2	7.668	6.63	0.4572
	Carryover	1	0.071	0.12	0.7269
Tree sparrow	Square	3	4.294	1.81	0.1582
	Day (square)	8	1.269	0.20	0.9895
	Bird (square)	8	8.903	1.40	0.2183
	Flavor	2	26.524	16.74	0.0001
	Carryover	1	0.257	0.32	0.5716

EXPERIMENT IV. DISCUSSION

Collection of spilled food was impractical in this experiment. No visual morsel characteristic distinguished any morsel flavor type, so sorting of spilled food by sight was impossible. Thus, food removed from the feeder was the measured variable, not food consumption. Food removal has been found to be a reliable indicator of preference. When analysis was performed using food removal rather than food consumption as the measured variable for Experiments I-III, only slight differences, if any, occurred in the results (Appendices K1-K3). In no case did a food item that was significantly preferred over another item in the consumption analysis become less preferred in the removal analysis. However, in two cases a food item that was significantly preferred over another item in the consumption analysis became not significantly different than the same item in the removal analysis.

Apparantly tree sparrows were able to discern flavored-food morsels, removing significantly fewer lime-flavored morsels whenever these morsels were presented with another flavored-morsel type. Davison (1962) also determined that birds could discriminate flavors. He concluded that bird food selection was based chiefly on taste. Kare et al. (1957) reported the ability of chickens to detect costus flavor at 0.0002% concentration. Westbrook et al. (1980)

and Grieg-Smith (1985) also demonstrated the abilities of birds to discern flavors.

Harris' sparrows did not appear to strongly discriminate between flavored morsels. Overall, the mean daily removal of lime-flavored morsels was significantly below that of nut- and butter-flavored morsels. But on a day-to-day basis, the consumption of lime-flavored morsels was not consistently lower. The effect of spilled food on the variability of flavored-morsel consumption is not known. The inconsistent discrimination of flavors displayed by Harris' sparrows agreed with Engleman (1940, 1943), who concluded that taste had little effect in hen food preference. Romoser et al. (1958) also found flavoring ineffective in altering food consumption of chicks. Neither strawberry, anise, nor grape flavorings caused an increase or decrease in food intake (Romoser et al. 1958).

Of those flavors most consumed by tree sparrows, no individual flavor increased consumption above the consumption of the other flavors. Nut, butter, and unflavored morsels were equally consumed. The importance of tree sparrow taste abilities seemed to be in discovering distasteful morsels, and in allowing for a depressed consumption of the distasteful morsel types. Kare and Pick (1960) also found that chickens could discern distasteful foods, and that the offensive flavoring decreased chick food consumption of these items. Westbrook et al. (1980) found that LiCl-induced flavor aversions were more intense and longer retained than LiCl-induced color aversions by pigeons. Thus, food flavor was more associated with sickness than was food color in pigeons.

Recognizing distasteful food items may be useful, as distasteful items are often harmful or create unpleasant side effects to the forager. For example, certain polyphenols found in pear floral buds, which have a bitter taste to humans (Grieg-Smith 1985), interfere with protein digestion.

The importance of flavor in sparrow food selection apparantly is to prevent the ingestion of seeds which are distasteful, since many distasteful items may be harmful. Other food characteristics, such as shape and size, are better suited for ranking acceptable food items.

EXPERMENT V. METHODS

Pair-wise comparison trials testing extruded morsels against white proso millet seeds were conducted after the flavored-food preference trials. Extruded morsels were small-sized, circular-shaped, butter-flavored, and colored yellow, the preferred characteristics determined in Experiments I-IV.

Extruded morsels and white proso millet seeds were presented to 12 Harris' sparrows and 12 tree sparrows in pair-wise presentations. Each bird was tested for four days. The preweighed food samples were placed into two feeders in each cage at the beginning of the photoperiod, and removed from each cage at the end of the photoperiod. While the feeders were in the cage, food and water were provided *ad libitum*, and feeder positions were switched every two hours. Food spilled by each bird during the day was collected, sorted into food types, and added to the unconsumed food. Husks removed from the millet seeds by the birds were included in the weighings of unconsumed food. The weight of each food type consumed by each bird was then determined (see General Methods). Food type consumption values were obtained by combining the consumption data from all four test days.

Eight millet seeds were measured using a Mitutoyo dial caliper. Length, width, and depth were the measured variables for each seed. Volume of millet seeds was determined by assuming millet seeds to be a sphere. The diameter of the seed was approximated by: 1) averaging the width and depth of each seed; and 2) averaging this value with the length of the seed, using the mean of (2) as the diameter of the sphere.

Feeding bouts were measured to determine the time each sparrow species required to handle and consume each food type, following the procedure detailed in the Handling Times and Feeding Efficiency section of Experiment I Methods. Seed consumption was assumed when a bird's peck into a feeder was followed by a massaging of the seed by the bird's bill and the ejection of a seed hull from the bill.

EXPERIMENT V. RESULTS

Food Type Preference

Harris' sparrows consumed 5.8 g / day of extruded food morsels, significantly more than the 3.0 g of millet seeds consumed per day (Table 22). Conversely, tree sparrows consumed 4.3 g / day of millet seeds, significantly more than the 1.0 g of food morsels consumed per day (Table 22). Both sparrow species seemed capable of distinguishing millet seeds from extruded morsels.

Handling Times

Harris' sparrows consumed one food morsel in 1.68 sec, significantly faster than the time (3.1 sec) required to handle millet seeds (Table 23). The differences in Harris' sparrow's handling times of the two food types was not explained by the food type volumes, as no significant differences existed between the volume of morsels and millet seeds (Table 24). Tree sparrows were equally proficient in consuming both food types, eating one millet seed in 1.9 sec, and one morsel in 2.0 sec (Table 23).

Tree sparrows consumed millet seeds significantly faster than Harris' sparrows did (Table 23), but there were no differences between the two bird species in handling food morsels.

Table 22. Ranked means from Analysis of Variance (ANOVA) for the mass (g) of food consumed daily by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources when millet seeds and extruded food morsels were paired.

Food type	$\bar{x}$ consumption *,@ Harris' sparrow N = 12	 Tree sparrow N = 12
Millet seed	3.05 d	4.50 r
Extruded morsel	5.83 c	1.05 i
S.E.	= 0.44	= 0.29

* Consumptions from 4 days of testing were combined
@ Values with a common letter do not differ, $p > 0.05$

Table 23. Mean (+ SE) handling time (sec) of food types consumed by captive Harris' and tree sparrows kept at Kansas winter conditions following a 20-hr food deprivation period.

Food type	Sparrow species	Birds tested	Food items consumed	Handling * time
Millet seeds	Harris'	7	174	3.09 ± 0.38 o
	Tree	9	416	1.86 ± 0.15 b
Extruded morsels	Harris'	7	234	1.68 ± 0.33 r
	Tree	10	259	1.98 ± 0.21 r

* Values with a common letter do not differ, $p > 0.05$

Table 24. Means from ANOVA of the volume (mm3) of millet seeds and small-size morsels.

Food Type	Volume *
Millet seeds	8.94 r
Small morsels	10.33 r
S. E.	0.54

* Values with a common letter do not differ, $p > 0.05$

EXPERIMENT V. DISCUSSION

Selection of Food Types Based on Handling Time

If Harris' sparrow food type selections were to be based on choosing those foods handled fastest, then extruded morsels should have been most consumed. This prediction was substantiated, as Harris' sparrows consumed a significantly greater quantity of morsels. Harris' sparrows thus appeared to be selecting to consume that food type handled fastest.

If tree sparrow food type selection were to be based on choosing foods handled fastest, no preference between millet seeds and food morsels should have existed. This prediction was not substantiated, as tree sparrows consumed a significantly greater quantity of millet seeds. Tree sparrow food selection did not appear to be based on handling time. Neither was preference based on food size, as both food types were similar in size. Differences existed between the two food types in color, shape, appearance, texture, and possibly flavor. Millet seeds also required husking prior to being swallowed.

Although this experiment was not designed to determine the importance of color in seed selection, other studies have found that non-dyed seeds were preferred over dyed seeds (Kalbach 1943; Ridsdale and Grannett 1969; and Pank 1976). Tree sparrows also may have been selecting against the dyed morsels. Food flavor alone seems improbable in explaining consumption differences. Engelmann (1940, 1943) and Romoser et al. (1955) found flavorings ineffective in altering consumption. Kare and Pick (1960) and Grieg-Smith (1985) found that distasteful food items reduced consumption; however, because tree sparrows readily accepted similarly flavored morsels in Experiment IV, it is unlikely the same flavor would be offensive in Experiment V.

The presence of a seed coat would seem to add to the time required to consume a seed (as compared to dehusked seeds), as the coat must be removed before ingestion, increasing handling time. Willson (1971), Willson and Harmeson (1973), Smith and Follmer (1972), and Experiments I and II of this research found that birds selected those foods which were handled fastest. Thus, selection for seeds based solely on the presence of a seed coat seems unlikely.

Tree sparrow preference for millet seeds may have been influenced by millet's rounder shape. Millet seed shape differed from morsel shape in having tapered, rounder ends rather than the flat ends of the morsels. Fantz (1957) found that circular objects received more pecks by chicks than did angular objects.

Species Comparison of Food Type

The relationship between bill size and food preference assumed in optimal foraging theory is based on the premise that smaller-billed birds are more efficient eating small food items, and larger-billed birds more efficient eating large items (Pulliam 1985). The consumption of millet seeds supported this premise. Tree sparrows consumed millet seeds faster than Harris' sparrows. By definition, faster consumption of the same food type provides a shorter handling time for that food, increasing the feeding efficiency (cal / handling time). It appeared during handling time trials that tree sparrows were better able to manipulate and remove the millet seed coats, thus consuming the seeds faster than Harris' sparrows. Abbott et al. (1975) similarly suggested that larger birds may have had difficulty in positioning small seeds in their bills to crack, which caused them to be slower in cracking small seeds.

The implications of this experiment are that no relationship between bill size and innate food size preference exists. Rather, sparrows prefer those foods which they can eat fastest, regardless of size. Willson (1971, 1972), Willson and Harmeson (1973) and Hespenheide (1966) also found that birds ate more of those seeds consumed fastest, and that the fastest consumed seeds were not always the smallest. When seed coats or other seed characteristics reduce the speed with which an item can be consumed, that seed will likely not be preferred over more easily consumed items. When Hespenheide (1966) fed small-size seeds which contained no air spaces between the kernel and the seed coat to juncos, juncos' consumption of this seed decreased from what it had been in earlier trials when seeds of the same size, but with the air space, were fed. Apparantly the closeness of the shell to the kernel made the seeds more difficult to open, increasing the time required to consume the seeds. The increased effort required for the same size seeds resulted in a decreased consumption of that seed size. Willson (1971) suggests that pecularities of each seed type (tightness, hardness, slipperiness, etc. of the husk) must be relevant to husking time. If small birds can manipulate and remove seed coats faster from small seeds than from large seeds, the birds will be faster eating these small seeds, and prefer to eat small seeds. Likewise, if large birds can manipulate and remove seed coats faster from large seeds than from small seeds, the birds will be faster eating these large seeds, and prefer to eat large seeds. However, when large birds can consume small seeds as fast or faster than the larger seeds, than the bill size-food size relationship breaks down, and large-billed birds prefer small seeds.

Implications For Use as Wild Bird Feed

The consumption of extruded food morsels by Harris' sparrows when the morsels were paired with millet seeds supports the possibility of these morsels being accepted in an outdoor, wildlife situation. Although not proving that morsels will be consumed at wildlife feeding stations, this experiment does suggest that birds can learn to consume and prefer the morsels.

GENERAL RESULTS

The extruded food morsel created from the dietary formula developed for the present research (Appendix A1) was found to be readily accepted by tree and Harris' sparrows after an 8-day initiation period. During this period, morsels were mixed with familiar food and presented to the birds. The nutrient content of the formula proved to be adequate in meeting the winter maintenance needs of confined sparrows. No sparrow died during the period that birds were provided extruded morsels.

Energetically, the birds displayed a positive weight gain throughout the experiments (Appendix C). The positive weight gain provides evidence that the birds obtained abundant energy from the extruded morsels. This weight gain contrasted with the results of Shuman (1984) and Taylor (1977). Shuman (1984) found that the majority of sparrow species feeding on Maximillian sunflower, oil-type sunflower, cracked sorghum or white proso millet lost weight even when sufficient seeds were consumed to meet calculated requirements. Taylor (1977) found that field sparrows (*Spizella pusilla*) and cardinals lost weight when the sparrows consumed only undesirable grass seeds.

Nutritionally, birds remained healthy throughout the experiments, as no symptoms of nutrient-deficiency diseases were evident. No abnormal or aberrant bird behaviors developed while the birds were being tested. Abnormal behaviors are early warning signs of nutritional-deficiency diseases. One bird successfully molted and two birds successfully replaced entire sets of tail feathers during the period of morsel consumption.

Results of the external portion of the necropsy performed at the completion of the research showed that all birds were fully feathered and had a plump body. The bird legs snapped clean when broken, and the keel was solid. No birds were observed to have scaly feet, mouth lesions, or abnormal-appearing eyes. The internal portion of the necropsy revealed that all birds had good stores of body fat anterior and posterior to the pectorals, surrounding the trachea, and on the small intestine, proventriculus, heart, and aortas. All pectoral muscles were solid red, with no signs of muscle atrophy. No lesions were found on any internal organs. Bird livers were red with no fat deposits. All hearts, lungs, duodenums and other organs appeared normal.

Because no birds had any signs of nutrient deficiencies at the completion of the experiments (following 177 days of morsel consumption), and because no bird lost weight while feeding on the morsels, the nutrient blend of this formula is confidently recommended for use in any situation that requires the feeding of confined Passerine birds during a winter maintenance period.

Ligon and Martin (1974) found that pinon jays selected to consume the heaviest seeds. No morsel density-dependent bias influenced food selection in the present research. The density of each morsel type within each experiment was comparable to the densities of the other morsel types in that experiment (Appendix M1).

GENERAL DISCUSSION

This research has developed an extruded food morsel from cereal grains that was accepted by Harris' and tree sparrows. The acceptance of this morsel was enhanced by providing the morsel characteristics which allowed shorter handling times, or by providing characteristics similar to those of naturally eaten seeds

Preferences for morphological characteristics coincided with those shapes and sizes which most decreased handling times. Circular morsels were the preferred shape. Because this was also the smallest shape, the separation of shape and size effects was not possible. However, circular morsels intuitively seem to be the easier shape to consume because of their rounded edges. These morsels required little manipulation in the beak to correctly position the morsel for ingestion. Contrarily, elliptical and ovate morsel consumption required that the bird turn each morsel sideways in the beak, so that the morsel length was perpendicular to the beak length prior to ingestion. If circular morsels required less handling time prior to consumption, and decreased handling time is important to selection, circular morsels should be preferred because of their shape.

The smallest morsels tested were the preferred size. In all liklihood, morsels smaller than 1.59-mm dia. (the small class of this experiment) would be more preferred. However, smaller-sized die holes will develop production problems regarding base mix particle size and morsel expansion, creating difficulties in decreasing morsel size below that of these experiments.

The importance of handling time in food selection did not support Optimal Foraging Theory, which predicted that feeding efficiency should have been the important factor. When morsels with different morphological characteristics were paired, handling times correctly predicted the preferred morsel in 17 of 18 (94%) trials. Feeding efficiency correctly predicted the outcome in only 8 of 18 (44%) trials. The ability to base selection on efficiency requires that a bird discriminate the energy content of each seed and the time needed to consume each seed. Numerous studies (Robel et al. 1974, Willson 1971, West 1967) have shown that birds were not able to detect the seeds with highest energy values. If birds lack the ability to determine energy content of seeds, then seed selection based on handling time may be the best mechanism for birds to use to maximize energy intake.

One word of caution before rejecting the importance of efficiency in this study. Efficiency was measured using the definition of Pulliam (1985), with feeding efficiency being "the ratio of prey energy content (in joules) or mass (in milligrams) to handling time (in seconds)." This definition utilizes total energy received, not net energy obtained. Defining and analyzing efficiency using net energy may predict the same food preferences as handling times do. If this were true, then basing food selection on handling times would be a direct, easy, and practical substitute to basing selection on efficiency.

The relationship between bill size and food size assumed in foraging theory was not supported in these studies. Birds preferred to consume those morsels which were handled fastest, regardless of size. These studies also failed to find the all-or-nothing response to food selection predicted by foraging theory. Even when one kind of morsel was strongly preferred, birds usually consumed some of the less preferred morsels. Partial preferences have been observed frequently in other studies (see McNamara and Houston 1987 for review), and are usually interpreted in terms of a forager sampling strategy.

Physical seed characteristics, such as color and flavor, seem important to the initial selection of food, i. e., whether a morsel is accepted or not. Birds did not appear to discriminate between morsels that had acceptable physical traits. For example, when brown morsels were paired with yellow morsels, neither color became more favored. Both colors were deemed acceptable by the birds, and both remained equally consumed. Selection of a single, preferred trait within the accepted range of that physical trait (color, flavor), did not occur.

In general, flavoring did not enhance the acceptance of food morsels, as chemoreception in birds seemed most important in discovering unacceptable or distasteful items. Increased consumption did not result in this research when an already accepted morsel was flavored. Provided that the base mix of food has a taste acceptable to birds, which cereal grains seem to have, further flavoring is unlikely to enhance granivorous bird's food consumption. Further, if a flavor is unacceptable to the birds, flavoring food may reduce consumption. Thus, the only change likely to occur when an already acceptable morsel is flavored is to reduce consumption in granivorous birds, so flavoring is not recommended.

Throughout the first four experiments, both Harris' and tree sparrows made equivalent morsel selections. At backyard feeders, both species prefer white proso millet (Geis 1980) over other seeds. Because both sparrow species normally prefer white millet, and both made equivalent morsel selections, the results of this study may be true for all white-proso-millet-preferring species. Future research should use extruded morsels to determine characteristics important in food selection of species that normally prefer other seeds (sunflower, peanut kernels) or other food types (fruits, buds, insects, etc.).

This research has demonstrated that confined birds will readily consume extruded food morsels, and preferentially select small, circular morsels colored similarly to native seeds. The next goal in this line of research should be to determine the acceptance of these morsels by Passerines at backyard feeding stations. A further topic for study might be to assess the importance of texture, density, and other seed characteristics in food selection.

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APPENDICES

Appendix A1. Ingredients and composition of the diet fed to tree sparrows and Harris sparrows.

Ingredients	% of diet
Yellow corn	66.45 kg
Sorghum grain	16.00 kg
Hard red wheat flour	6.00 kg
Soybean oil meal (44%)	4.50 kg
Soy oil	3.00 kg
DiCal	2.00 kg
Calcium carbonate	0.75 kg
Vitamin Premix *	0.50 kg
Sodium chloride	0.40 kg
Vitamin E premix (44,100 IU/kg)	0.20 kg
Lysine	0.10 kg
Selenium 90	0.10 kg
Manganese sulfate	2.00 g
Trace mineral premix	0.1 g

* vitamins in premix

Minimum Vitamin Levels / kg

Vitamin A, USP Units	2,205,000
Vitamin D3, USP Units	220,500
Vitamin E, USP Units	8,820
Vitamin K (menadione)mg/kg	882
Riboflavin, mg/kg	2,205
Pantothenic Acid, mg/kg	5,512
Niacin, mg/kg	12,128
Choline, mg/kg	220,500
Vitamin B12, mg/kg	11

Appendix A2. Estimated nutrient content of base mix used for extruding food. Constraints set to insure adequate levels of critical nutrients are noted.

NUTRIENTS	UNITS	AMOUNTS		
		Minimum Constraint	Actual	Maximum Constraint
Arginine	%	0.50	0.50	0.62
Ash	%		4.76	
Biotin	mg/kg		0.07	
Calcium	%	1.00	0.78	2.00
Chloride	ppm		76.67	
Choline C	mg/kg		1503.70	
Cobalt	ppm		0.02	
Copper	ppm		16.51	
Cysteine	%	0.11	0.37	0.37
Digestible energy (chicken)	kcal/kg	3306.90	3597.68	4078.00
Fat	%	4.00	6.00	6.00
Fiber	%		2.44	
Folic acid	mg/kg		0.90	
Iodine	ppm		2.21	
Iron	ppm		66.02	
Lysine	%	0.43	0.43	0.55
Magnesium	ppm		868.92	
Manganese	ppm		30.00	
Metabolizable energy (chicken)	kcal/kg	3031.00	3299.86	3425.00
Methionine	%	0.13	0.19	0.14
Moisture	%		10.61	
Niacin	mg/kg		72.30	
Pantothenic acid	mg/kg		23.31	
Phosphorus	%	1.00	0.63	1.80
Potassium	%		0.35	
Protein	%	9.00	10.00	10.00
Pyridoxine	mg/kg		5.67	
Riboflavin	mg/kg		9.28	
Salt	%	0.50	0.50	0.50
Selenium	mg/kg		5733.00	
Sodium	ppm		1883.56	
Sulfur	ppm		1160.80	
Thiamine	mg/kg		3.70	
Zinc	ppm		123.31	
Total dry nutrients	%		80.14	
Tryptophan	%	0.07	0.12	0.10
Vit. A	KUSP		7.26	
Vit. B12	mg/kg		0.02	
Vit. D3	KICU/kg		3.03	
Vit. E	IU/kg		4100.00	
Vit. K	mg/kg		1.59	
Xanthophyll	mg/kg		14.80	

Appendix A3. A comparison of the amino acid levels used by Martin (1968), Parrish and Martin (1977), and the present research.

	Amino acid levels (% wt/dry wt of total food)		
Amino acids	Martin	Parrish and Martin	present research
Arginine	0.616	0.497	0.50
Lysine	0.553	0.432	0.43
Tryptophan	0.073		0.12
Cysteine	0.108	0.232	0.18
Methionine	0.133	0.140	0.19
Histidine	0.214	0.210	
Tyrosine	0.317	0.280	
Phenylalanine	0.473	0.412	
Serine	0.415	0.420	
Threonine	0.333	0.290	
Leucine	0.724	0.723	
Isoleucine	0.424	0.351	
Valine	0.456	0.399	
Glutamic acid	1.610	2.840	
Aspartic acid	0.984	0.432	
Glycine	0.374	0.352	
Alanine	0.416	0.320	
Proline	0.499	0.903	
% protein in total diet	8.720	9.220	10.00

Appendix B. Settings that the Wenger X-20LBM extruder was set to, and run at, in preparing the morsels used for the present research.

	Screw +	Run #1	Run #2	Run #3	Run #4
TEMP & CONTROL INLET	none				
TEMP & CONTROL HEAD #1	1B Flight flat	H_2O *	H_2O *	H_2O *	H_2O *
TEMP & CONTROL HEAD #2	1B Flight 364	H_2O *	H_2O *	H_2O *	H_2O *
TEMP & CONTROL HEAD #3	2B Flight 364	H_2O *	H_2O *	H_2O *	H_2O *
TEMP & CONTROL HEAD #4	2B Flight 324	H_2O *	H_2O *	H_2O *	H_2O *
TEMP & CONTROL HEAD #5	2B Flight 324	H_2O *	H_2O *	H_2O *	H_2O *
TEMP & CONTROL HEAD #6	2B Flight 324	--	1/2 H_2O*	H_2O*	1/2 H_2O*
TEMP & CONTROL HEAD #7	2B Flight 324	--	--	1/2H_2O*	H_2O *
		105 C	105 C	90 C	100 C
STEAM TO MIXING CYLINDER		--	--	--	--
STEAM TO EXTRUDER		--	--	--	--
WATER TO MIXING CYLINDER (lb)		35-40	35-40	35-40	35-40
WATER TO EXTRUDER (lb)		10	10-15	10-15	10-15
EXTRUDER RPM		325	325	310	300-310
EXTRUDER AMPS		14-15	14-15	14-15	14-15
FEEDER RPM		5	5	5	5
MIXING CYLINDER TEMP		20 C	20 C	20 C	20 C
PRESSURE / LOCATION		not measured			
KNIFE TYPE four blade		long	short	short	short
EXTRUDER STABILITY		good	good	good	good
PRODUCT STABILITY		good	OK	OK	good
PRODUCTION RATE (WET) (kg/hr)		48	50	50	50
PRODUCT DENSITY (WET) (g/ml)		0.513	0.545		
PRODUCT DENSITY (DRY) (g/ml)		0.578	0.510	0.528	0.526

* refers to H_2O sent to steam jackets
\+ refers to style of screw segment in each Head section

Comments: ambient air temperature 16 C

Run #1: H_2O to mix cylinder 0.16 kg/min
H_2O to extruder inlet 0.022 kg/min
die = center discharge, multi-hole circles, 1/4" spacer

Run #2: H_2O to mix cylinder 0.16 kg/min
H_2O to extruder inlet 0.04 kg/min
die = 4 ovate shapes, 1/4" spacer

Run #3: same as Run #2, die = 4 rosette shapes

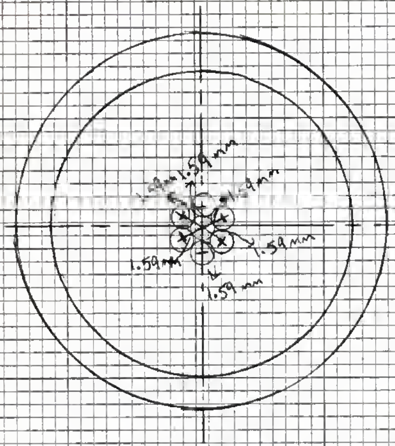
Run #4: same as Run #2, die = 4 elliptical shapes

Appendix C. Weights (g) of captive Harris anad tree sparrows undergoing pair-wise comparison trials kept at Kansas winter conditions. The first two weights recorded represent the 10-day period prior to the first study when birds maintained stable weights while eating experimental food. The last day of the 10-day period was the first day of the shape experiments. The birds starting and finishing weights for the first four experiments are listed.

	10-day	Shape		Color		Size		Flavor		
	stable	start	end	start	end	start	end	start	end	
Dates:	12/1	12/11	1/4	1/24	2/18	3/19	3/25	5/16	5/23	$\bar{x}$
Harris Sparrow Bird #:										
1	30.4	31.0	30.6	31.6	34.1	33.3	32.5	31.2	31.3	31.8
2	37.8	37.7	37.7	37.6	40.2	40.2	39.5	40.7	41.1	39.2
3	30.9	30.9	33.1	33.9	35.2	34.7	34.1	35.2	34.5	33.6
4	36.4	36.1	36.8	37.8	38.1	37.9	37.2	38.2	37.8	37.4
5	34.7	34.6	36.0	34.8	36.6	35.8	35.5	35.6	34.0	35.3
6	32.7	33.8	36.6	36.9	38.6	40.2	38.1	36.2	35.8	36.5
7	36.2	35.9	39.2	39.4	38.4	37.5	37.2	36.2	36.2	37.4
8	33.7	33.9	35.6	36.0	38.2	36.5	36.4	36.6	36.8	36.0
9	31.2	32.5	36.1	33.1	37.0	37.9	38.5	35.1	34.2	35.1
10	37.6	38.2	39.1	39.8	40.8	41.8	40.9	38.4	38.1	39.4
11	32.4	32.4	31.3	31.5	31.8	32.6	32.7	33.5	34.9	32.6
12	33.7	32.8	33.4	31.6	34.6	35.0	33.7	35.4	33.0	33.7
$\bar{x}$	34.0	34.2	35.5	35.3	37.0	37.0	36.4	36.0	35.6	35.7
Tree Sparrow Bird #:										
1	14.7	14.9	15.3	15.5	15.7	15.9	15.8	16.5	16.5	15.6
2	16.7	17.8	17.8	18.4	18.6	18.6	18.1	19.2	19.1	18.3
3	18.3	18.6	18.7	19.0	19.6	20.1	19.7	21.6	21.7	19.7
4	17.5	17.3	18.4	18.2	19.4	20.2	20.2	21.3	21.1	19.3
5	16.5	16.0	15.8	15.9	15.6	16.0	15.9	17.3	17.5	16.3
6	16.4	16.8	17.0	17.8	18.3	18.1	18.9	20.3	20.3	18.2
7	16.3	17.0	16.8	17.8	18.1	18.6	18.2	18.6	18.9	17.8
8*	15.1	15.3	15.9							
9	16.9	17.1	17.6	18.0	19.1	19.3	19.0	20.1	20.1	18.6
10	16.3	16.3	17.0	17.5	17.8	17.4	17.7	19.0	19.4	17.6
11	18.4	17.8	19.2	20.0	21.8	21.5	21.6	23.5	23.7	20.8
12	16.8	16.9	17.6	17.8	18.2	19.0	18.9	18.3	18.8	18.0
8	19.2	18.6	17.7	18.7	19.9	20.6	20.0	22.6	22.8	20.0
$\bar{x}$	17.0	17.1	17.4	17.9	18.5	18.8	18.7	19.8	20.0	18.4

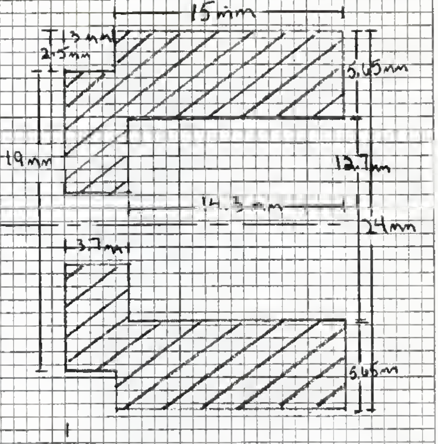
* Bird was removed from experiment due to loss of breast feathers

Appendix D1. Machinist directions to produce rosette-shaped opening in Die Insert.

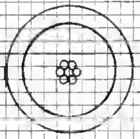


All holes are 1.59 mm dia. The center of the outer holes is 1.59 mm from the insert center. The center of each hole is also 1.59 mm from any adjacent hole's center.

3 x Actual Size



3 x Actual Size



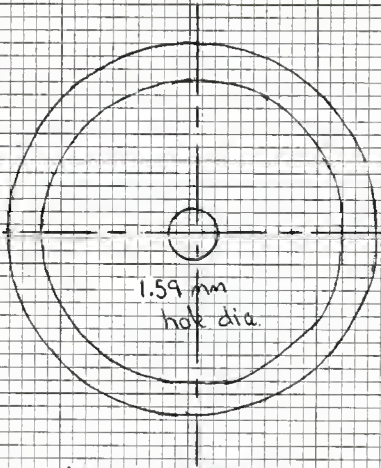
all 7 holes 1.59 mm

ACTUAL SIZE

FINAL DESIRED SHAPE

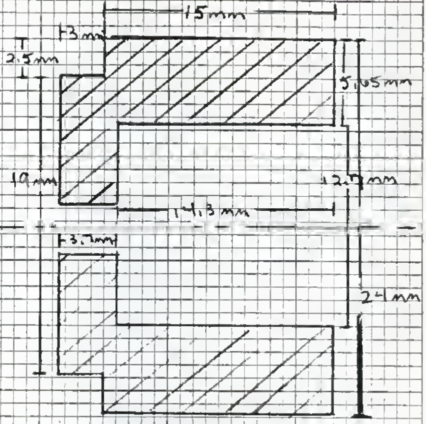
3 x Actual Size

Appendix D2. Machinist directions to produce circular-shaped opening in Die Insert.



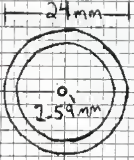
Die - 3 x Actual Size

Hole - 4 x Actual Size



Die - 3 x Actual Size

Hole - 4 x Actual Size

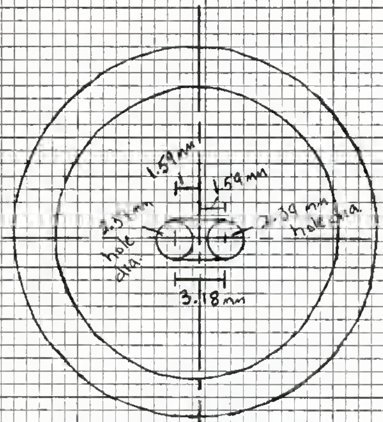


ACTUAL SIZE

FINAL DESIRED SHAPE

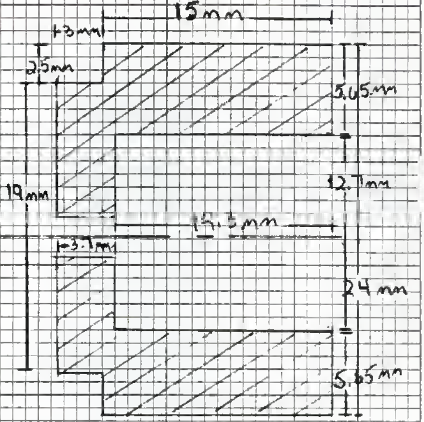
4 x Actual Size

Appendix D3. Machinist directions to produce elliptical-shaped opening in Die Insert.



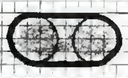
Drill two 2.39 mm holes adjacent to each other, each hole's center 1.59 mm from the center of the die insert.

3 x Actual Size



3 x Actual Size

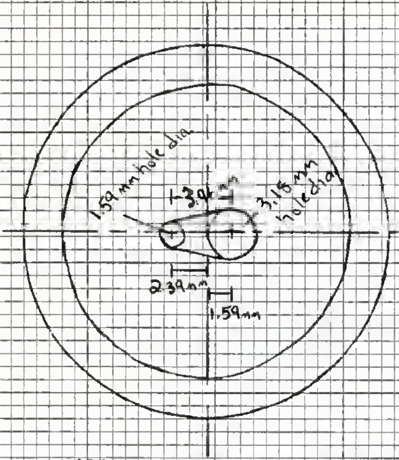
ACTUAL SIZE

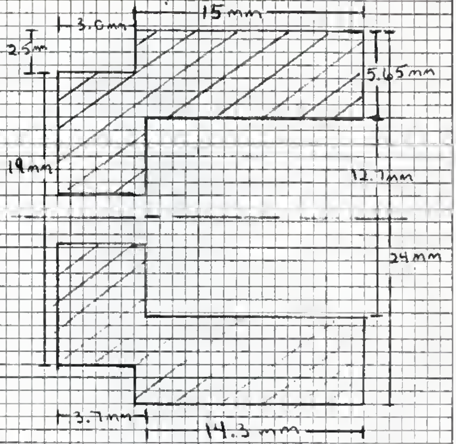


FINAL DESIRED SHAPE

4 x Actual Size

Appendix D4. Machinist directions to produce ovate-shaped opening in Die Insert.

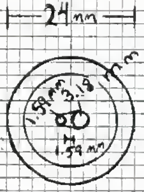




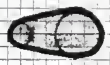
Drill a 1.59 mm hole 2.39 mm from insert center, and drill a 3.18 mm hole 1.59 mm from insert center. Gouge out the material left between the two holes.

3 x Actual Size

3 x Actual Size



ACTUAL SIZE



FINAL DESIRED SHAPE

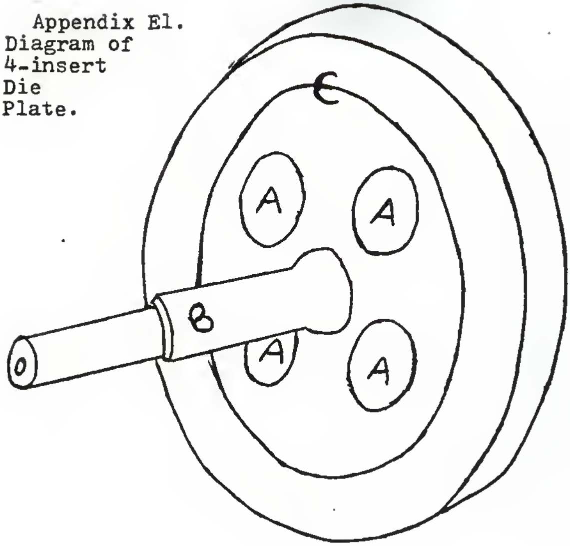
3 x Actual Size

Appendix E1. Diagram of 4-insert Die Plate.

A - Die insert hole

B - Knife blade attachment

C - Die plate

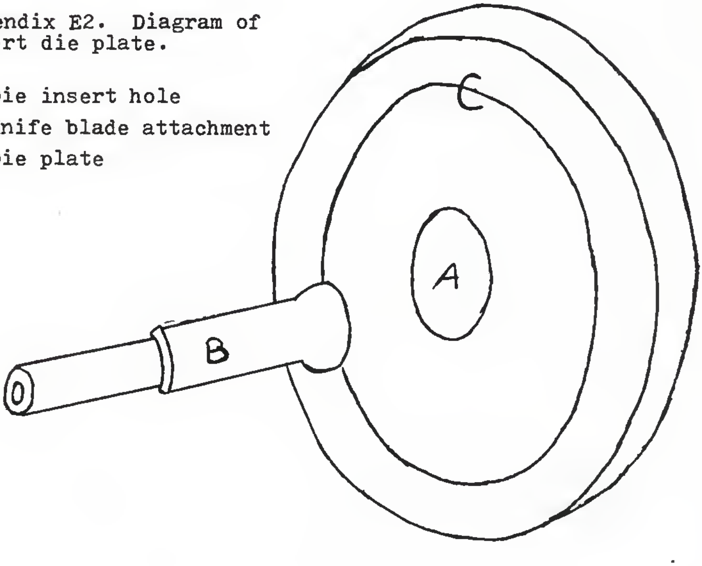


Appendix E2. Diagram of 1-insert die plate.

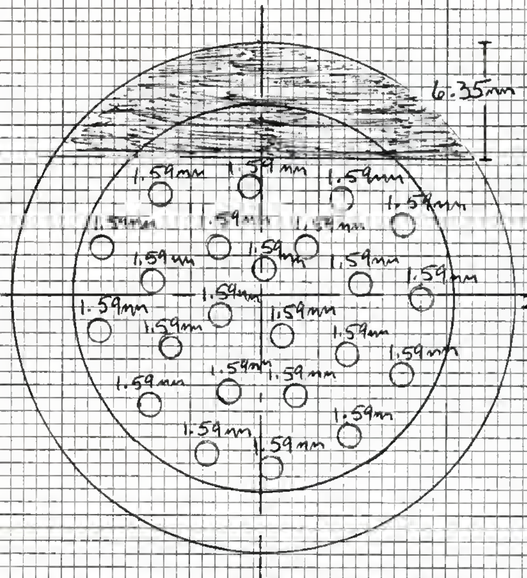
A - Die insert hole

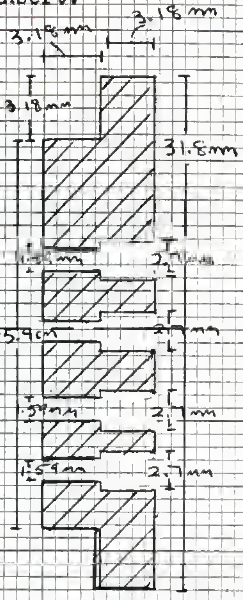
B - Knife blade attachment

C - Die plate



Appendix F1. Machinist directions to produce small-sized circular-shaped openings in a Die Insert.

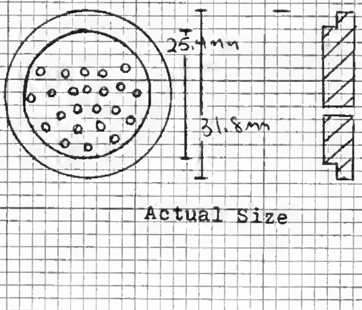




Drill 23 1.59 mm holes, actual pattern not being important. The shaded portion was devoid of holes because the knife would not reach this part of the die insert.

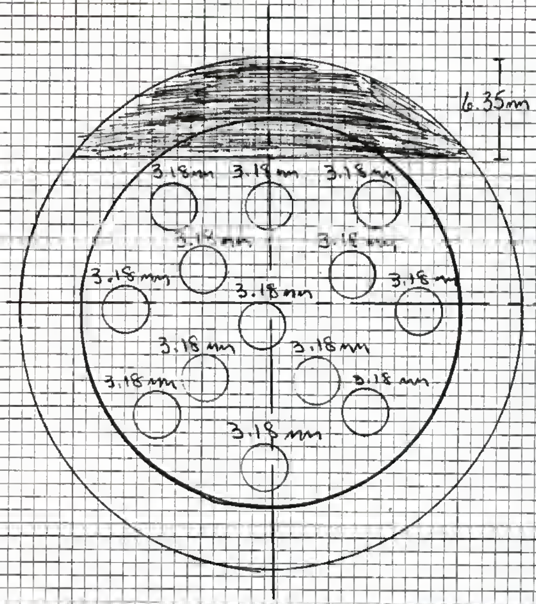
3 x Actual Size

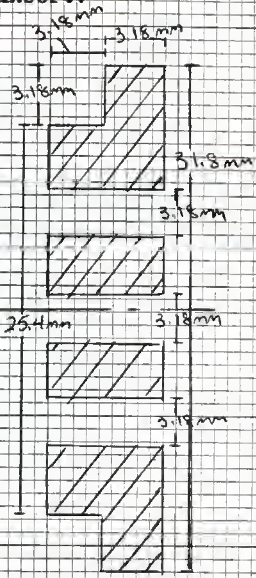
3 x Actual Size



Actual Size

Appendix F2. Machinist directions to produce medium-sized circular-shaped openings in a Die Insert.

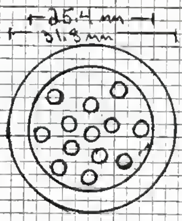




Drill 13 3.18 mm holes, actual pattern unimportant. The shaded region was devoid of holes because the knife would not reach this part of the die insert.

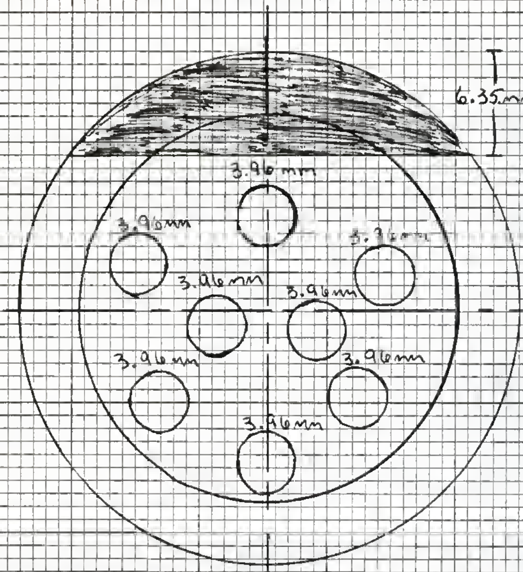
3 x Actual Size

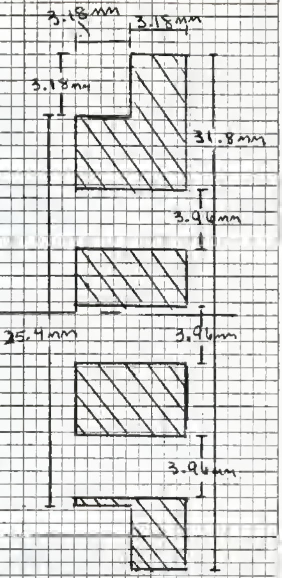
3 x Actual Size



Actual Size

Appendix F3. Machinist directions to produce large-sized circular-shaped openings in a Die Insert.

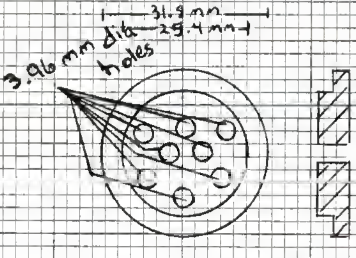




Drill 8 3.96 mm holes, actual pattern unimportant. The shaded region was devoid of holes because the knife would not reach this part of the die insert.

3 x Actual Size

3 x Actual Size



Actual Size

Appendix G. Procedure to estimate the volume of each shape.

1) Estimating circular shape volumes:

a) Measure the diameter of the morsel.
b) Calculate the area of a circle with the measured diameter.
   area = (3.14159) x (diameter/2)2
c) Measure the width of each morsel.
d) Multiply the area by the width to get spherical volume.
   volume = (3.14159) x (dia./2)2 x width

2) Estimating elliptical shape volumes:

a) Assume the two rounded ends, if sliced away from the morsel and put together, equals one sphere. Assume the width of the morsel equals the diameter of the sphere. Solve for standard volume of a sphere, = 4/3 x radius3 x 3.14159.
b) Assume remaining portion of morsel to be rectangular. The width and depth of the rectangle are equal to the measured width and depth of the morsel. The length to be used is equal to the length of the morsel minus the morsel's width.
c) Add the volume of the sphere to the volume of the rectangle.
   volume = (4/3) x (dia./2)3 + (L - W)(W)(D)

3) Estimating rosette shape volume

a) Follow steps a-d for estimating spherical shape volume.
b) Small triangular gaps around the periphery of the morsels disrupted the spherical shape. The volume of these gaps was assumed to be equal to the volume of a prism, and subtracted from the value of step a.
c) Assume the triangular gaps to be equilateral, and measure the length of one side of the gap. Refer to this as n.
d) The width of the morsel = the length of the prism.
e) Prism volume = (.433) x (n2) x (length)
f) Morsel volume = (volume of sphere) - (6) x (volume of prism)
   volume = [3.14 x (dia./2)2 x width] - [6 x .433 x n2 x L]

4) Estimating ovate shape volume

a) Measure width of morsel at widest area.
   Measure depth and length of morsel.
b) Assume ovate to be triangular, with height = length, and base = width/2.
c) Area of triangle = height x base
d) Volume of triangle = Area x width
   Ovate volume = L x W/2 x depth

Appendix H. Procedure to estimate feeding efficiency.

1) Count the number of morsels in a 5 g sample, taking 3 separate samples. Obtain # of morsels / 5 g.

2) Invert the value of #1, (morsels / 5 g), obtaining an estimate of the weight of one morsel (g / morsel). Convert to mg (mg / morsel).

3) Obtain the energy (cal) in each mg of food. This value was obtained from the energy value (kcal / kg) estimated by the MIXIT-II computer software package. The energy value used was 3.299 cal / mg.

4) Multiply the final value of step 2 (mg / morsel) by the value of step 3 (3.299 cal / mg). An estimate of the energy in each morsel is obtained (cal / morsel).

5) Divide the value obtained for the energy in each morsel (calculated in step 4, cal / morsel) by the time required to consume a morsel of that type (sec / seed). Feeding efficiency (cal/sec) is the outcome.

Example:

1) count 110 morsels in a 5 g sample - 110 morsels / 5 g

2) 5 g / 110 morsels = .045 g / morsel = 45 mg / morsel

3) 3.299 cal/mg

4) (45 mg / morsel) x (3.299 cal / mg) = 148 cal / morsel

5) $$\frac{148 \text{ cal / morsel}}{5 \text{ sec / morsel}} - 29.6 \text{ cal / sec}$$

Appendix I1. Ranked means from ANOVA for the mass (g) of morsel shapes consumed on day 1 and day 2 of a test replication by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

Morsel shape	$\bar{x}$ consumptions *			
	Harris' sparrow		Tree sparrow	
	Day 1 +	Day 2 +	Day 1 +	Day 2 +
Circular	6.80 d	7.04 d	5.08 c	5.09 c
Elliptical	5.01 c	4.79 c	3.40 x	3.04 xr
Ovate	4.86 c	4.54 c	2.55 i	2.79 ri
Rosette	3.66 o	3.91 o	1.69 v	1.60 v
S.E.	0.24	0.23	0.17	0.17

* Treatment sequence replications were combined

\+ Values with a common letter do not differ, $p > 0.05$

Appendix I2. Ranked means from ANOVA for the mass (g) of morsel sizes consumed on day 1 and day 2 of a test replication by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

Morsel size	$\bar{x}$ consumptions			
	Harris' sparrow		Tree sparrow	
	Day 1 *	Day 2 *	Day 1 *	Day 2 *
Small	5.91 b	5.69 b	5.40 b	5.18 b
Medium	4.43 c	4.63 c	2.74 x	2.73 x
Large	3.66 o	3.92 o	1.10 r	1.24 r
S.E.	0.48	0.48	0.30	0.30

* Values with a common letter do not differ, $p > 0.05$

Appendix I3. Ranked means from ANOVA for the mass (g) of morsel colors consumed on day 1 and day 2 of a test replication by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

Morsel color	$\bar{x}$ consumptions *			
	Harris' sparrow		Tree sparrow	
	Day 1 +	Day 2 +	Day 1 +	Day 2 +
Brown	5.50 d	5.73 d	3.65 x	3.69 x
Yellow	5.45 d	5.42 d	3.88 x	3.82 x
Orange	4.44 c	4.22 c	2.48 i	2.38 i
Blue	3.54 x	3.52 x	2.29 i	2.25 i
S.E.	0.22	0.23	0.20	0.18

* Treatment sequence replications were combined

\+ Values with a common letter do not differ, $p > 0.05$

Appendix I4. Ranked means from ANOVA for the mass (g) of flavored morsels consumed on day 1 and day 2 of a test replication by captive tree sparrows kept at Kansas winter conditions with abundant food resources.

Morsel flavor	$\bar{x}$ consumptions	
	Tree sparrow	
	Day 1 *	Day 2 *
Butter	3.80 b	3.44 b
Nut	3.32 b	3.59 b
Lime	2.36 c	2.15 c
S.E.	0.26	0.21

* Values with a common letter do not differ, $p > 0.05$

Appendix J1. Ranked means from ANOVA for the mass (g) of morsel shapes consumed in treatment sequence 1 and sequence replication 2 by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ consumptions *			
Morsel	Harris' sparrow		Tree sparrow	
shape	Sequence 1 +	Sequence 2 +	Sequence 1 +	Sequence 2 +
Circular	7.23 d	6.61 d	5.22 d	4.94 d
Ellipse	5.03 c	4.79 c	3.48 c	2.98 r
Ovate	4.64 cr	4.75 c	2.88 rx	2.49 x
Rosette	4.02 rx	3.55 x	1.86 l	1.42 m
S.E.	0.30	0.30	0.17	0.17

* Test day replications were combined
\+ Values with a common letter do not differ, $p > .05$

Appendix J2. Mean (+SE) mass (g) of morsel colors consumed in treatment sequence 1 and sequence replication 2 by captive Harris' and tree sparrows kept at Kansas winter conditions with abundant food resources.

	$\bar{x}$ consumptions *			
Morsel	Harris' sparrow		Tree sparrow	
color	Sequence 1	Sequence 2	Sequence 1	Sequence 2
Brown	5.53 ± 0.25	5.55 ± 0.23	3.65 ± 0.26	3.57 ± 0.21
Yellow	5.46 ± 0.32	5.43 ± 0.32	3.89 ± 0.28	3.68 ± 0.23
Orange	4.57 ± 0.32	4.04 ± 0.27	2.40 ± 0.29	2.54 ± 0.24
Blue	3.26 ± 0.31	3.95 ± 0.27	2.08 ± 0.33	2.59 ± 0.28

* Test day replications were combined

Appendix K1. Ranked means from ANOVA for the mass (g) of morsel shapes consumed by Harris' and tree sparrows when spilled food was added to consumption (removal analysis), compared to the morsel shape consumption when spilled food was not added to consumption (consumption analysis).

Morsel shape	Harris' sparrow Removal analysis *	Harris' sparrow Consumption analysis *	Tree sparrow Removal analysis *	Tree sparrow Consumption analysis *
Circular	7.73 b	6.92 k	5.60 i	5.08 d
Ellipse	5.93 c	4.91 w	3.94 o	3.21 m
Ovate	6.01 c	4.70 w	3.74 o	2.71 m
Rosette	4.88 r	3.78 e	2.36 s	1.64 y
S. E.	0.29	0.27	0.26	0.23

* values with a common letter do not differ, $p > 0.05$

Appendix K2. Ranked means from ANOVA for the mass (g) of morsel sizes consumed by Harris' and tree sparrows when spilled food was added to consumption (removal analysis), compared to the morsel size consumption when spilled food was not added to consumption (consumption analysis).

Morsel size	Harris' sparrow Removal analysis *	Harris' sparrow Consumption analysis *	Tree sparrow Removal analysis *	Tree sparrow Consumption analysis *
Small	7.25 o	5.77 b	6.12 x	5.39 i
Medium	6.49 o	4.50 c	3.77 n	2.74 x
Large	5.70 v	3.79 c	2.16 f	1.17 r
S. E.	0.56	0.43	0.32	0.30

* Values with a common letter do not differ, $p > 0.05$

Appendix K3. Ranked means from ANOVA for the mass (g) of colored morsels consumed by Harris' and tree sparrows when spilled food was added to consumption (removal analysis), compared to the colored morsel consumption when spilled food was not added to consumption (consumption analysis).

	Harris' sparrow		Tree sparrow	
Morsel color	Removal analysis *	Consumption analysis *	Removal analysis *	Consumption analysis *
Brown	7.00t	5.56b	4.54i	3.60o
Yellow	6.74t	5.44b	4.50i	3.81o
Orange	5.90f	4.34c	3.23w	2.46r
Blue	5.35f	3.59x	3.34w	2.33r
S. E.	0.30	0.20	0.23	0.20

* Values with a common letter do not differ, $p > 0.05$

Appendix L. 1) ANOVA model of factors related to mean treatment consumptions; 2) Means for the mass (g) of morsel shapes consumed daily for each treatment; and 3) Dayton-Morrill model's estimates of the effect of each shape on the daily consumption of captive Harris and tree sparrows kept at Kansas winter conditions.

1) Analysis of Variance

		Mean squares	
Source	df	Harris sparrow	Tree sparrow
Squares	1	19.4702	0.1689
Day (square)	10	1.9823	0.3730
Bird (square)	10	3.8726	1.0966
Treatment	5	1.8465	0.0119
Error	119	0.7129	0.2662

2) Treatment means, g

	$\bar{x}$ consumption	
Treatment	H. sparrow	T. sparrow
Circular / ellipse	9.95	6.35
Circular / rosette	9.77	6.31
Circular / ovate	10.02	6.33
Ellipse / rosette	10.38	6.29
Ellipse / ovate	10.41	6.30
Ovate / rosette	10.40	6.34
standard error	0.17	0.10

3) Dayton-Morrill estimates of shape effects on mean consumption

	H. sparrow	T. sparrow
Overall mean:	10.15	6.32
	Effects	Effects
Circular	+ 0.137	- 0.008
Ellipse	+ 0.061	+ 0.008
Rosette	- 0.363	+ 0.014
Ovate	+ 0.165	- 0.012
Circular / ellipse . . .	+ 0.059	- 0.014
Circular / rosette . . .	+ 0.023	+ 0.022
Circular / ovate	- 0.082	- 0.007
Ellipse / rosette	- 0.082	- 0.007
Ellipse / ovate	+ 0.023	+ 0.022
Rosette / ovate	+ 0.059	- 0.014

Appendix M. Apparant bulk density (kg/hl) and specific bulk density (g/ml) of two samples from each shape, size, and color morsel type.

Morsel type		Apparant density	Specific density
Circular	sample 1	57.75	1.46
	sample 2	57.75	1.45
Elliptical	sample 1	52.53	1.45
	sample 2	52.67	1.45
Ovate	sample 1	51.03	1.44
	sample 2	51.03	1.44
Rosette	sample 1	52.71	1.45
	sample 2	52.85	1.45
Small	sample 1	59.84	1.38
	sample 2	59.97	1.39
Medium	sample 1	59.57	1.37
	sample 2	59.39	1.37
Large	sample 1	55.30	1.40
	sample 2	55.53	1.40
Yellow	sample 1	64.43	1.41
	sample 2	64.25	1.42
Brown	sample 1	60.75	1.38
	sample 2	60.39	1.37
Orange	sample 1	63.29	1.44
	sample 2	63.57	1.44
Blue	sample 1	59.62	1.42
	sample 2	59.48	1.43

SELECTION RESPONSES OF AVIAN GRANIVORES TO VARIOUS MORPHOLOGICAL FOOD CHARACTERISTICS

by

JEFFREY FRANCIS KEATING

B.S., Benedictine College, 1985

AN ABSTRACT TO A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1989

Research was performed to develop nutritionally-sound extruded food morsels from cereal grains that would be accepted by Harris' sparrows (*Zonotrichia querula*) and American tree sparrows (*Spizella arborea*). Additional assessment of sparrow responses to extruded food morsels examined Harris' and tree sparrow's ability to discern the morsel characteristics of shape, size, color, and flavor, evaluated the importance of each characteristic in morsel selection, and tested the ability of Optimal Foraging Theory to correctly predict morsel selection.

Harris' and tree sparrows were mist-netted and individually confined in cages kept in an environmentally-controlled chamber maintained at winter conditions of northeast Kansas. Pair-wise feeding trial experiments displayed the morsels to the birds, the measured variable being the daily consumption of each morsel type. Morsel preferences were determined through ANOVA procedures.

The extruded food morsels created from the dietary formula of this study were readily accepted by Harris' and tree sparrows after an 8-day initiation period. The nutrient content of the formula proved to be adequate in meeting the winter maintenance needs of confined sparrows. Birds demonstrated the ability to discern and discriminate between morsel shapes, sizes, colors, and flavors.

Circular morsels and small morsels, the preferred morsel shape and morsel size of each bird species, were also the morsels ingested fastest. However, these morsel types did

not provide the greater feeding efficiency (cal / s feeding, measured as total energy, not net energy). Ingestion time predicted preferred morsels more consistently than did Optimal Foraging Theory. The importance of ingestion time in morsel selection did not support foraging theory. No relation between bird bill size and food size preference was observed. Rather, birds preferred eating those morsels ingested fastest, regardless of food size.

Both Harris' and tree sparrows preferred yellow- and brown-colored morsels, the color of seeds normally encountered in the wild. Both sparrow species also preferred nut- and butter-flavored morsels, although flavoring did not appear to enhance morsel acceptance.