

ENERGETIC RESPONSES OF AVIAN GRANIVORES TO WINTER
IN NORTHEAST KANSAS

by

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OVERALL INTRODUCTION

Energy is the essential currency for maintenance of all levels of biological organization (King 1974). At the individual level, energy is allocated for maintenance, growth, and reproduction. The energy an organism must obtain per unit body weight and time for these basic activities depends upon a complex suite of biotic and abiotic factors including temperature, solar radiation, wind, relative humidity ("climate space" of Porter and Gates 1969), body size, metabolic efficiency, competition, and predation. The latter two variables influence individual energy requirements by affecting foraging efficiency, food handling time, food preference, and/or affect the time available for energy intake as opposed to other energy-demanding activities.

At the population and community levels, the importance of estimating energy flow through trophic levels lies in gaining an understanding of the roles of respective trophic levels in ecosystem functioning. Because numbers overestimate the importance of small organisms (e.g., bacteria) and biomass overestimates the importance of large organisms, neither is a reliable criterion for comparing ecosystem populations that differ greatly in size-weight relationships (Smalley 1960, Odum 1968). Although Chew (1974) and Boyd and Goodyear (1971) both suggest that energy flow per se is an oversimplification of the relationship between organisms and their food supply, estimating rates of energy flow allows for general comparisons of the relative importance of ecosystem components (Odum 1968).

During the last decade, sophisticated models have been developed to estimate energy flow through avian communities, most notably those models of Wiens and Innis (1974), Wiens and Nussbaum (1975), and Wiens and Scott (1975). Several basic energetic assumptions in these models have been general of necessity either because refined data are not available or have not been applied to

these energy flow theories. See Furness (1978) for a review of avian energetics models.

The underlying assumptions of current energy flow models form the basis for many active areas of avian research, including bird foraging efficiencies (e.g., Burtt and Hailman 1978, Bryant and Westerterp 1982, Elgar and Catterall 1982, Schluter 1982), overlap of food use and comparative feeding ecologies (e.g., Allaire and Fisher 1975, Abbott et al. 1977, Alatalo 1982, Sherry and McDade 1982), general avian community structure (e.g., Pulliam 1975, Landres and MacMahon 1980, Hanski 1981, Grzybowski 1982), assessing the impact of granivorous birds on agriculture (e.g., Wiens and Dyer 1977, Weatherhead et al. 1982), and bird time-energy budget studies (e.g., Ashkenazie and Safriel 1979, Ettinger and King 1980, Mugaas and King 1981, Barnard et al. 1982, Biedenweg 1983). An extensive literature has developed in the area of avian bioenergetics and the reader is referred to Gessaman (1973), Paynter (1974), Grodzinski et al. (1975), and Pinowski and Kendeigh (1977) for an historical perspective and thorough treatment of the subject.

Emphasis on population dynamics, community structure, and the role of birds as consumers in grassland and other ecosystems has focused on the breeding season (e.g., Brenner 1968, Wiens 1973, 1974a, 1974b, 1977, 1983, Holmes et al. 1979). Although breeding season energetics are critical (Walsberg 1983), concepts of annual community dynamics in temperate grassland ecosystems are difficult to develop due to the relative lack of studies conducted during or including the non-breeding season (Emlen 1972, Pulliam 1975, 1983, Rotenberry et al. 1979, Smith and MacMahon 1981, Grzybowski 1982). Yet the ideas of Lack (1966), Pulliam and Enders (1971), Fretwell (1972), Raitt and Pimm (1976), and of Grzybowski (1982) suggest that breeding season community structure is strongly influenced by the interaction of winter resources and climatic factors, especially for temperate-zone wintering birds.

The primary objective of this research was to enhance the precision of avian energy flow models by testing 2 general assumptions of those models. The main portion of the research addresses several energetic and behavioral aspects of 4 granivorous sparrow species wintering in northeast Kansas. These aspects are: (1) a test of the model assumption of 70% metabolization of food energy ingested, (2) a test of the model assumption of a 40% requirement over existence energy for free-living conditions [where existence energy is that amount required by a bird maintaining weight in the absence of major activity (Kendeigh 1949)], (3) the influence of food energy content on confined cardinal time budgets, (4) sparrow seed preferences based on energy content and handling time, and (5) analysis of 4 seed diets for trypsin inhibitor content as related to metabolic efficiency.

Metabolic efficiencies were determined in the laboratory under simulated winter conditions for the Emberizid species, northern cardinal (Cardinalis cardinalis), slate-colored junco [dark-eyed race (Junco hyemalis)], American tree sparrow (Spizella arborea), and Harris' sparrow (Zonotrichia querula) on each of 4 seed diets, white proso millet (Panicum miliaceum), cracked sorghum (Sorghum vulgare), Maximilian sunflower (Helianthus maximiliani), and oil-type sunflower (Helianthus spp.).

Percent energy required over existence was calculated for male and female cardinals in outdoor flight pens on Konza Prairie Research Natural Area (KPRNA), 25 km south of Manhattan, Kansas. Existence energies for all 4 species were determined in the laboratory under simulated winter conditions.

Male and female cardinals in outdoor flight pens on KPRNA were again used as test species to assess the influence of food energy content on wintering sparrow time budgets.

Seed preferences based on seed energy content and handling time were assessed in the laboratory under simulated winter conditions for each of the 4 sparrow species.

To gain insight into observed diet differences in metabolic efficiencies within a bird species, each of the 4 diets was assayed for trypsin inhibitor content. Spectrophotometric methods (Erlanger et al. 1961) were used to assess the "decrease (inhibition) of enzyme hydrolysis of synthetic substrate caused by the inhibitor" (Richardson 1977).

Also reported are several energetic characteristics of an occasionally wintering avian granivore, the mourning dove (Columbidae: Zenaidura macroura). Dove energetics aspects addressed are: (1) determination of metabolic efficiencies on 8 seed diets, timothy (Phleum pratense), canary grass (Phalaris arundinacea), thistle (Niger spp.), cracked sorghum (Sorghum vulgare), Maximilian sunflower (Helianthus maximiliani), white proso millet (Panicum miliaceum), corn (Zea mays), wheat (Triticale spp.), (2) determination of existence energies on the 8 test diets, and (3) trial dove consumption of Illinois bundleflower (Delmanthus illinoensis), wild senna (Cassia marilandica), sandvine (Gonolobus laevis), and buckwheat (Fagopyrum esculentum).

GENERAL LABORATORY METHODS

Sparrows used in the metabolic efficiency, existence energy, and seed preference determinations were captured in 1.9-cm² mesh mist nets within 10 km of Manhattan, Kansas, in October 1980, and individually confined to 33 x 21 x 24-cm cages. Mourning doves were similarly captured in 2.1-cm² mesh mist nets within 200 km of Manhattan, Kansas in September 1982, and similarly confined. A walk-in environmental chamber housing the cages exposed the birds to constant simulated winter conditions for northeast Kansas [5°C, 50% RH, 10L:14D photoperiod (Flora 1948)]. Birds were acclimated for at least 10 days prior to testing. Harris' sparrows suffered a high initial mortality when placed directly into the chamber in individual cages, while the other 3 sparrow species and mourning doves adapted better to captivity. Harris' sparrow mortality decreased dramatically when birds were retained in individual cages outdoors for 3 days and then placed in the chamber.

Harris' sparrows, tree sparrows, and slate-colored juncos are all winter residents of northeast Kansas, while cardinals are year-round residents of the area. The 4 species are winter sympatric members of the Emberizidae, a family of granivorous birds characterized by strong beaks adapted for cracking seeds (Bent 1968). These species were selected because of potential niche overlap, availability of individuals, ease of handling, and the potential for making laboratory-field comparisons. Mourning doves were selected for experimentation to gain insight into the energetics of an avian granivore which does not husk seeds prior to ingestion and is not as frequent a winter resident of northeast Kansas.

The test diets of white proso millet, cracked sorghum, and oil-type sunflower were selected based on known consumption by the birds, while additionally, Maximilian sunflower was selected based on its similarity to native

annual sunflower which grows throughout Kansas (Barkley 1973). The latter diet was obtained from the U.S.D.A. Soil Conservation Service Plant Materials Center in Manhattan, Kansas. Dove test diets were selected based on previous food habits studies (Leopold 1943, Korschgen 1958, Chambers 1963, Davison and Sullivan 1963, Hennessy and Van Camp 1963, Carpenter 1971, Keeler 1977, Armstrong and Noakes 1981).

Between tests, nutritionally balanced maintenance mashes were included in the diet (See Appendix A. and A.1 for formulations). All diets were stored at or below 5°C to inhibit respiration and deterioration (Kendeigh and West 1965). Birds were provided water ad libitum during all test and non-test periods.

To document weight maintenance to within 5% of individual body weight, birds were weighed every other day to 0.1 g. Weights were consistently monitored 15 min after onset of the light period to standardize the effects of diurnal weight change (West 1960, Kontogiannis 1967).

Trypsin inhibitor assays for the 4 sparrow seed diets were performed in the laboratory of Dr. Gerald R. Reeck at Kansas State University.

Metabolic efficiency and further energetic data were analyzed via analysis of variance and Duncan's New Multiple Range Test based on a Latin Square design blocking bird and trial (order). This design guaranteed that each bird received each diet completely randomly (Figure 1). A 0.05 level of significance was used except where noted. The experimental design for the dove laboratory experiments consisted of 2 5 x 5 Latin Squares with 2 diets common to each and 3 unique to each (Figure 2). Other data were analyzed via analysis of variance and simple linear regressions were performed to obtain further information. Levene's test for homogeneity of variances was used to assess variances between sparrow species on energetic variables. The arcsine transformation was used to adjust the interpretation of percentage data (metabolic efficiencies and behavioral time allocations). All statistical procedures followed the guidelines of Snedecor and Cochran (1980).

	1	2	3	4
1	D	A	B	C
2	B	C	D	A
3	A	B	C	D
4	C	D	A	B

	5	6	7	8
1	C	B	A	D
2	D	C	B	A
3	A	D	C	B
4	B	A	D	C

Figure 1. Example replicated Latin Square design used to determine energetics experimental procedure for each sparrow species on 4 diets (treatments: A,B,C,D) blocking bird and trial (order). Diets tested were white proso millet, cracked sorghum, Maximilian sunflower, and oil-type sunflower, and sparrow species tested were cardinal, junco, tree sparrow, and Harris' sparrow.

BIRD

	1	2	3	4	5		6	7	8	9	10
1	C	A	D	E	B	1	B	H	G	A	F
2	A	D	B	C	E	2	F	A	H	B	G
3	E	C	A	B	D	3	H	F	B	G	A
4	D	B	E	A	C	4	G	B	A	F	H
5	B	E	C	D	A	5	A	G	F	H	B

TRIAL

Figure 2. Latin Square design for 10 mourning doves on 8 seed diets (treatments: A,B,C,D,E,F,G,H); 2 of the 8 diets (sorghum and Maximilian sunflower) are present in both Latin Squares. Diets tested were cracked sorghum, Maximilian sunflower, timothy, corn, wheat, canary, thistle, and white proso millet.

STUDY I. INTRODUCTION AND LITERATURE REVIEW

The Assumption of 70% Metabolization of Ingested Food Energy

The ability which a bird possesses in evolutionary, behavioral, and physiological senses, to utilize the food it ingests is one facet of the complexity of "achieving" maximum fitness. Prior to deriving metabolic gain from food items, an individual must find, capture, and successfully ingest the food. All of these activities involve constant tradeoffs.

Mautz (1978) defines digestible energy as that energy in ingested food which is absorbed from the gastrointestinal tract. Since most bird species have no urinary bladder and urine thus drains directly into the cloaca (Welty 1975), urine and feces are ultimately excreted in the same packet. As a result, there is little information on the loss of nutrients during digestion (Fisher 1972). The term metabolizable energy was introduced by Armsby (1922) as "the maximum quantity of energy a feed could contribute to the chemical transformation within the organism". More recent definitions are those of Fisher (1972), King (1974), and Mautz (1978) who state that metabolizable energy is that energy left after urinary, fecal, and methane losses. Blem (1968) found insignificant energy loss as gas voided in birds; methane production is usually associated with rumen activity in herbivores. Thus, since urine and feces are inseparable in birds, metabolizable energy or metabolic efficiency (in a different context) rather than digestible energy, is the appropriate description of the process.

Kleiber and Dougherty (1934) introduced the measurement of avian metabolic efficiency based on food consumption which Kendeigh (1949) later applied to wild granivorous passerines in an ecological context.

Wiens and Innis (1974) state the objectives of their breeding season energy flow model as (1) to make detailed estimations of energy demands and impacts of avian consumers in ecosystems, and (2) to assess effects of

environmental and ecological changes through model simulations on these demands and impacts. They admit that "the output estimates may be most sensitive to variations in [metabolic] efficiency" (among other variables) but believe the model is essentially robust. Although Wiens and Innis (1974) suggest that ideally, [metabolic] efficiency be an input variable, they assume a 70% metabolization of ingested food based on Kale's (1965) classic work on the energetics of the long-billed marsh wren (Telmatodytes palustris). Kale (1965) found a range of metabolic efficiencies (73.5% - 78.3%) for breeding wrens on mealworm-wren mixture, but assumed 70% since the wrens are usually within their thermal neutral zone (TNZ) during the breeding season. Where Wiens and Innis (1974) use equation constants, Furness (1978) considers all inputs to be variables, with an 80% base value for metabolic efficiency.

Kendeigh (1949), Seibert (1949), Davis (1955), West (1960), Zimmerman (1965), and Willson and Harneson (1973), all experimenting with birds, found that metabolic efficiency increases with increasing temperature below the TNZ. Birds adapted to migrating to remain within their TNZ do not experience temperature extremes and the model assumptions of Wiens and Innis (1974) may be valid in those cases. But Kale (1965) also observed that adult wrens are generally more metabolically efficient than juveniles within the same area and season. Willson and Harneson (1973) found that cardinal metabolic efficiencies varied significantly between diets at room temperature while metabolic efficiencies for all seed diets were the same at freezing temperatures. In the same study, song sparrow (Melospiza melodia) metabolic efficiencies on different diets which were significantly different at room temperature did not vary at freezing temperatures and vice versa. Their estimate of metabolic efficiencies for cardinals ranges from 60% - 90%, with most values falling between 65% - 80%. Taylor (1977) suggests that the wide variation in Willson and Harneson's (1973) results was failure to account for bird trial weight loss.

Photoperiod also influences metabolic efficiency, a longer photoperiod generally resulting in greater efficiency (West 1960, Cox 1961, Zimmerman 1965, Kendeigh 1969b). These authors suggest slower food passage and thus more efficient food utilization as the mechanism for this phenomenon.

Literature values of avian metabolic efficiencies range from 41% for wintering bobwhites (Colinus virginianus) on native grass (Robel et al. 1974), 45% for willow ptarmigan (Lagopus lagopus) on willow (West 1968), 54% for wintering cardinals on roundhead lespedeza (Browning and Robel 1981), 62% for desert house finches (Carpodacus mexicanus) on mistletoe berries (Walsberg 1975), 85% for wintering bald eagles (Haliaeetus leucocephalus) on mallard ducks (Anas platyrhynchos) (Stalmaster and Gessaman 1982), and 100% for hummingbirds (Trochilidae) on nectar (Hainsworth et al. 1981).

Data from this section of the present study will be used to determine the metabolic efficiencies of 4 wintering sparrow species on 4 seed diets and of wintering mourning doves on 8 seed diets.

STUDY I. METHODS

Sparrow and Dove Metabolic Efficiencies and Existence Energies

Gross energy intake, excretory energy, metabolizable energy, metabolic efficiency, and existence energy were calculated for each of 8 randomly-selected individuals of each sparrow species and 10 randomly-selected mourning doves for 4-day and 2-day continuous trials, respectively. Values for excreta weight, total excreta energy content, daily energy intake, daily diet intake by weight, and energy metabolized were also calculated for each bird. All data were collected using the direct calorimetry feeding method as described by Kendeigh (1949) and Case and Robel (1974).

Trials were initiated at the onset of the light period subsequent to cleaning cages and weighing birds. Food was removed immediately following the end of the previous day's light period to allow for gut clearance. During trials each bird was provided a known amount of test seed diet in excess of potential ingestion capacities, accessible through glass feeders affixed outside the cages. Each of the test diets was previously included in the maintenance diet to avoid an unfamiliarity bias during testing (Kear 1962, Willson 1971). To minimize seed spillage from the cages, fine mesh aluminum screen, side-supported with wooden dowels, was used for containment during trials (Figure 3).

Following each 4-day (2-day for doves) trial, birds were weighed and all feces and uneaten (and spilled) seed were collected, separated, and dried at 60°C for at least 48 hr to obtain dry weights to 0.1 g. The weight of uneaten seed was subtracted from the initial amount to calculate the amount ingested by each bird. Dried feces and spilled seed were stored at 25°C in labeled vials. Dried samples were ground in a Wiley micro-mill once through a 20-cm mesh screen and stored in a dessicator immediately prior to energy content determination.

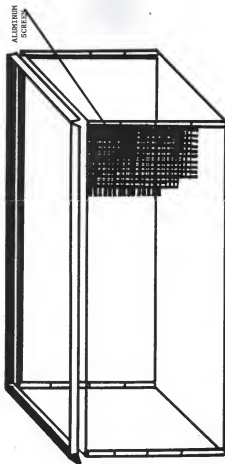


Figure 3. Covered aluminum screening containment device placed around individual bird cages to minimize seed spillage during energetic trials.

Energy content of each sample was determined using a Parr series 1200 adiabatic [occurring without heat loss or gain via a water jacket surrounding the calorimeter (Paine 1971)] oxygen bomb calorimeter with 2 Parr 1108 oxygen bombs used under 30 atm pressure. A separate water equivalent was calculated for each bomb and periodically rechecked. The Parr instruction manual No. 130 (1960) outlines specific instructions for bombing procedures and the subsequent correction factors and calculations which were used in this study. See Appendix B. for a sample calorimetry worksheet.

Two approximately 0.8-g subsamples from each fecal sample were used to obtain an average sample value. A third sample was analyzed for energy content if the first 2 differed by more than 5%. The same procedure was used for spilled seed samples until high operator proficiency justified analyzing 1 subsample per spilled sample. Average energy contents of the 9 test seed diets were determined from at least 10 approximately 0.8-g bombed samples of each diet using the methods described above.

For birds losing more than 5% of body weight (17/32 tree sparrows, 26/32 juncos, 18/32 cardinals, 11/32 Harris' sparrows), a correction factor (after Clement 1970) was multiplied by body weight loss and subtracted from the excretory energy value to adjust the final energetic calculations. See Appendix, Table 1 for calculations. Data collected from 2 individuals of each sparrow species (starved until losing at least 15% of body weight) provided this information. The dove weight loss correction factor used was that of Clement (1970) for bobwhites. Excreta samples from sparrows were pooled by species to obtain a large enough sample to bomb. Weight gains were not adjusted similarly since the physiological processes involved may not be the same. Metabolic efficiencies and metabolized energies were calculated using the equations shown in Appendix C. A glossary of bioenergetic terms appears in Appendix D. For birds maintaining weight (and those with weight loss adjustments), metabolized energy equalled existence energy (Kendeigh 1949).

STUDY I. RESULTS

Sparrow and Dove Metabolic Efficiencies and Existence EnergiesSPARROWS

The gross energy content of sorghum, millet, Maximilian sunflower, and oil-type sunflower was 4.4 kcal/g, 4.4 kcal/g, 5.9 kcal/g, and 6.4 kcal/g, respectively. Daily energy intake and resultant energetic calculations formed 2 general diet-based categories, millet/sorghum and oil sunflower/Maximilian sunflower. Diets of millet and sorghum produced energetic results which never differed significantly while the sunflower diets varied from each other significantly in 2 of 7 variables measured per bird species.

Cardinals - Bird pre-trial mean body weights ranged from 39.8 g (trial 1) to 42.7 g (trial 3) with a mean of 41.1 g (Table 1). Metabolic efficiency (%), daily energy consumption (kcal), and metabolizable energy (kcal/g) all varied significantly among individual cardinals but only the former varied with diet (Table 2). Individual birds varied from 75% to 84% in metabolic efficiency. Metabolic efficiency by diet ranged from 75% on Maximilian sunflower to 85% on millet (Table 2). Metabolic efficiency was not dependent upon bird pre-trial weight.

Daily energy excretion (kcal), daily excreta production (g), and excreta energy contents all varied significantly among individual cardinals as well as with trial (Appendix, Table 2) and diet (Table 2). Cardinal excreta energy production ranged from 3.6 kcal/day on a diet of millet to 6.6 kcal/day on a diet of oil-type sunflower (Table 2). Birds on a diet of sorghum produced an average of 0.88 g/day excreta while those on a diet of Maximilian sunflower produced an average of 1.45 g/day (Table 2). A diet of millet produced a low excreta energetic value of 4.1 kcal/g while a diet of oil-type sunflower produced a high of 4.5 kcal/g (Table 2). Daily excreta weight (g) and energy

Table 1. Overall mean ($n = 32$ for each species) energetic values and standard errors for the 4 test sparrow species on all diets combined. Values with a common superscript read across a row do not differ ($P < 0.05$).

ENERGETIC VARIABLE	BIRD SPECIES			
	Cardinal	Harris' Sparrow	Junco	Tree Sparrow
Species Mean Body Weight (g)	41.1 ^c	34.1 ^b	21.4 ^a	21.1 ^a
Gross Energy Consumed (kcal/day)	25.7 ^b	31.6 ^c	17.6 ^a	20.0 ^a
Weight Diet Consumed (g/day)	7.9 ^b	8.8 ^c	5.0 ^a	5.8 ^a
Weight Diet Consumed Per g Body Weight	0.13 ^a	0.17 ^a	0.15 ^a	0.18 ^a
Excreta Energy Content (kcal/g)	4.3 ^a	4.3 ^a	4.3 ^a	4.2 ^a
Energy Excreted* (kcal/day)	5.0 ^c	3.9 ^b	3.0 ^a	2.9 ^a
Weight Excreta Produced (g/day)	1.17 ^c	0.91 ^b	0.71 ^a	0.70 ^a
Metabolic Efficiency* (%)	80 ^a	88 ^d	83 ^b	85 ^c
Existence Energy* (kcal/day)	20.7 ^b	27.7 ^c	14.6 ^a	17.0 ^a

* Corrected for weight loss

Table 2. Mean energy content and dry weight of excreta produced, energy consumption, and derived energetic calculations and standard errors for 8 each cardinals, Harris' sparrows, tree sparrows, and juncos on 4 seed diets. Values with a common superscript read across a row do not differ ($P \leq 0.05$).

BIRD SPECIES	DIET				STANDARD ERROR
	Sorghum	Millet	Maximilian Sunflower	Oil-type Sunflower	
Diet Energy Content ¹ (kcal/g)	4.4 ^a ±0.06	4.4 ^a ±0.11	5.9 ^b ±0.06	6.4 ^b ±0.16	
CARDINAL					
Energy Consumed (kcal/day)	20.8 ^a	23.7 ^{a,b}	27.2 ^{a,b}	31.0 ^b	+ 2.50
Wgt. Diet Consumed (g/day)	6.2 ^b	6.3 ^b	4.9 ^a	4.6 ^a	+ 0.33
Wgt. Diet Consumed/g Bird Wgt.	0.13 ^a	0.13 ^a	0.12 ^a	0.11 ^a	+ 0.01
Excreta Energy Content (kcal/g)	4.2 ^{a,b}	4.1 ^a	4.3 ^b	4.6 ^c	+ 0.05
Energy Excreted (kcal/day)*	3.6 ^a	3.6 ^a	6.2 ^b	6.6 ^b	+ 0.31
Wgt. Excreta Produced (g/day)	0.88 ^a	0.90 ^a	1.40 ^b	1.40 ^b	+ 0.06
Metabolic Efficiency (%)	82 ^{b,c}	85 ^b	75 ^a	79 ^{a,c}	+ 1.31
Metabolizable Energy (kcal/g)*	3.6 ^a	3.7 ^a	4.2 ^b	5.1 ^c	+ 0.07
Existence Energy (kcal/day)*	17.2 ^a	20.1 ^{a,b}	21.0 ^{a,b}	24.3 ^b	+ 2.30
HARRIS' SPARROW					
Energy Consumed (kcal/day)	29.3 ^{a,c}	25.4 ^a	36.0 ^{b,c}	35.7 ^{b,c}	+ 2.30
Wgt. Diet Consumed (g/day)	6.7 ^b	6.1 ^b	6.1 ^b	4.9 ^a	+ 0.31
Wgt. Diet Consumed/g Bird Wgt.	0.19 ^a	0.17 ^a	0.18 ^a	0.15 ^a	+ 0.01
Excreta Energy Content (kcal/g)	4.1 ^{a,b}	3.9 ^a	4.4 ^b	4.8 ^c	+ 0.09
Energy Excreted (kcal/day)*	3.4 ^b	2.0 ^a	4.9 ^c	5.4 ^c	+ 0.41
Wgt. Excreta Produced (g/day)	0.84 ^b	0.54 ^a	1.13 ^c	1.13 ^c	+ 0.09
Metabolic Efficiency (%)	89 ^b	92 ^c	86 ^{a,b}	85 ^a	+ 1.07
Metabolizable Energy (kcal/g)*	3.8 ^a	4.0 ^b	4.8 ^c	5.4 ^d	+ 0.06
Existence Energy (kcal/day)*	25.8 ^{a,b}	23.4 ^a	31.0 ^b	30.3 ^b	+ 2.10
JUNCO					
Energy Consumed (kcal/day)	14.7 ^a	15.4 ^a	19.5 ^b	20.2 ^b	+ 1.00
Wgt. Diet Consumed (g/day)	3.4 ^b	3.6 ^b	3.2 ^{a,b}	2.7 ^a	+ 0.14
Wgt. Diet Consumed/g Bird Wgt.	0.16 ^a	0.17 ^a	0.15 ^a	0.13 ^a	+ 0.01
Excreta Energy Content (kcal/g)	4.1 ^a	3.9 ^a	4.3 ^b	4.8 ^c	+ 0.05
Energy Excreted (kcal/day)*	2.3 ^a	2.0 ^a	3.8 ^b	4.0 ^b	+ 0.27
Wgt. Excreta Produced (g/day)	0.58 ^a	0.53 ^a	0.89 ^b	0.84 ^b	+ 0.06
Metabolic Efficiency (%)	85 ^b	87 ^b	80 ^a	81 ^a	+ 0.95
Metabolizable Energy (kcal/g)*	3.7 ^a	3.8 ^a	4.5 ^b	5.2 ^c	+ 0.05
Existence Energy (kcal/day)*	12.4 ^a	13.4 ^a	15.7 ^b	16.7 ^b	+ 0.79
TREE SPARROW					
Energy Consumed (kcal/day)	19.4 ^a	18.6 ^a	20.7 ^a	21.2 ^a	+ 1.10
Wgt. Diet Consumed (g/day)	4.5 ^b	4.3 ^b	3.4 ^a	3.0 ^a	+ 0.14
Wgt. Diet Consumed/g Bird Wgt.	0.21 ^b	0.20 ^b	0.17 ^b	0.14 ^a	+ 0.01
Excreta Energy Content (kcal/g)	4.1 ^b	3.8 ^a	4.3 ^c	4.7 ^d	+ 0.05
Energy Excreted (kcal/day)*	2.7 ^b	2.0 ^a	3.3 ^c	3.7 ^d	+ 0.15
Wgt. Excreta Produced (g/day)	0.67 ^a	0.54 ^a	0.78 ^b	0.80 ^c	+ 0.03
Metabolic Efficiency (%)	86 ^b	89 ^c	84 ^a	82 ^a	+ 0.61
Metabolizable Energy (kcal/g)*	3.7 ^a	3.9 ^b	4.7 ^c	5.3 ^d	+ 0.03
Existence Energy (kcal/day)*	16.7 ^a	16.5 ^a	17.5 ^a	17.5 ^a	+ 0.98

¹ Values represent means of at least 10 determinations ± standard deviation

* Corrected for weight loss

(kcal) productions were not dependent upon bird pre-trial weight. Diet energy content significantly positively influenced excreta energy content and excreta weight production (Table 2). Excreta unit energy content was significantly positively influenced by total excreta weight production (g) (Figure 4).

Existence energy in cardinals varied significantly only among individual birds, ranging from 14.2 kcal/day to 32.8 kcal/day. Bird existence energy did not depend upon bird pre-trial weight.

Cardinals on a 4-day diet of Maximilian sunflower lost a maximum body weight of 4.3 g while birds on a diet of oil-type sunflower lost the minimum of 1.0 g over 4 days (Table 3). Weight loss varied significantly with trial also, ranging from a 5.0-g 4-day loss (trial 2) to a 0.90-g loss (trial 4) (Table 3). Metabolic efficiency was not significantly influenced by bird trial weight loss.

Average energy content of spilled seed (husks and uneaten mixture) in the cage bottom ranged from 4.3 kcal/g for sorghum to 5.0 kcal/g for oil-type sunflower. Only spilled oil-type sunflower energy content was significantly different from energy values for purely uneaten samples.

Daily food consumption (g) varied significantly among individual cardinals as well as with trial (Appendix, Table 2), but not with diet (Table 2). Individual birds varied in daily food consumption from 6.4 g to 11.9 g. Daily food consumption by weight was not dependent upon bird pretrial weight.

Of the calculations affected by the weight loss correction factor (metabolic efficiency, metabolizable energy, existence energy, and excretory values), 2 individual cardinal metabolic efficiencies and metabolizable energies changed from not significant to significant. Male and female cardinals did not vary significantly in any measured laboratory energetic variables.

Harris' Sparrows - Bird pretrial mean body weights ranged from 33.6 g (trial 3) to 34.8 g (trial 4) with a mean of 34.1 g (Table 1). Metabolic

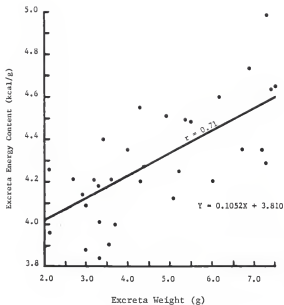


Figure 4. Regression of individual excreta unit energy contents (kcal/g) of 8 cardinals over 4 days on corresponding excreta productions by weight (g). The slope is significantly different from zero at $P \leq 0.05$.

Table 3. Sparrow mean 4-day weight changes (g) and standard errors as influenced by diet (averaged over all trials) and trial (averaged over all diets). Values with a common superscript read across a row within diet or trial do not differ ($P < 0.05$). Means are each derived from 8 values.

BIRD SPECIES	DIET				TRIAL				STANDARD ERROR
	Sorghum	Millet	Maximilian Oat-type Sunflower	STANDARD ERROR	1	2	3	4	
Tree Sparrow	-1.2 ^a	-1.3 ^a	-1.3 ^a	+ 0.32	-1.3 ^a	-1.4 ^a	-1.1 ^a	-1.2 ^a	+ 0.33
Junco	-2.8 ^b	-2.6 ^b	-2.1 ^b	+ 0.39	-2.0 ^a	-2.1 ^a	-2.4 ^{a,b}	-2.5 ^b	+ 0.43
Cardinal,	-2.6 ^b	-1.9 ^a	-4.9 ^c	+ 0.86	-3.3 ^b	-5.0 ^b	-1.3 ^a	-0.9 ^a	+ 0.84
Harria's Sparrow	-1.6 ^b	-2.4 ^b	-1.1 ^b	+ 0.43	-1.5 ^a	-1.9 ^a	-0.5 ^a	-1.1 ^a	+ 0.58

efficiency (%), daily energy consumption (kcal), metabolizable energy (kcal/g), daily energy excretion (kcal), daily excreta production (g), excreta energy content (kcal/g), and existence energy (kcal/day) all varied significantly with diet (Table 2), but not among individual birds or with trial (Appendix, Table 2). Metabolic efficiency by diet ranged from 85% on a diet of oil sunflower to 92% on millet (Table 2). Metabolic efficiency was not statistically dependent upon bird pretrial weight.

Harris' sparrow excreta energy production ranged from 2.0 kcal/day on a diet of millet to 5.4 kcal/day on oil sunflower (Table 2). Birds on a diet of millet produced an average of 0.54 g/day excreta while those on Maximilian sunflower and oil sunflower produced an average of 1.13 g/day excreta. A diet of millet produced a low excreta energy content of 3.9 kcal/g while a diet of oil sunflower produced a high of 4.8 kcal/g (Table 2). Daily excreta weight (g) and fecal energy (kcal) production were not dependent upon bird pretrial weight. Diet energy content significantly influenced excreta energy content and excreta weight production (Table 2). Excreta unit energy content (kcal/g) was significantly positively influenced by total excreta weight (g) (Figure 5).

Existence energy in Harris' sparrows ranged from 23.4 kcal/day on millet to 31.0 kcal/day on Maximilian sunflower (Table 2). Bird existence energy did not depend upon bird pretrial weight.

Daily food consumption (g) by Harris' sparrows varied significantly among individual birds as well as with trial (Appendix, Table 2). Individual birds varied from 7.1 g to 12.6 g in daily food consumption. Daily food consumption by birds was not dependent upon bird pretrial weight.

Harris' sparrows on a 4-day diet of millet lost 2.4 g while birds on a 4-day diet of oil sunflower gained 0.1 g (Table 3). Weight loss varied significantly with trial, ranging from a 1.9-g 4-day loss (trial 2) to a 0.5-g loss (trial 3) (Table 3). Metabolic efficiency was negatively influenced by bird trial weight loss (Figure 6).

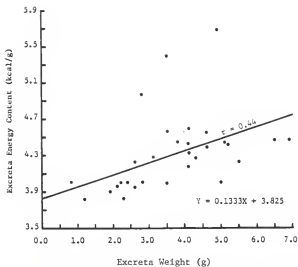


Figure 5. Regression of individual excreta unit energy (kcal/g) of 8 Harris' sparrows over 4 days on corresponding excreta productions by weight (g). The slope is significantly different from zero at $P < 0.05$.

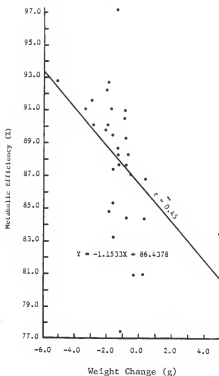


Figure 6. Regression of individual metabolic efficiencies (%) of 8 Harris' sparrows over 4 days on corresponding weight changes (g). The slope is significantly different from zero at $P < 0.05$.

Average energy content of spilled seed (husked and uneaten mixture) in the cage bottom ranged from 4.2 kcal/g for sorghum to 5.4 kcal/g for oil sunflower. Only spilled oil sunflower energy values were significantly different from those for purely uneaten samples.

The weight loss correction factor did not affect the statistical significance of Harris' sparrow energetic results.

Juncos - Bird pretrial mean body weights ranged from 20.5 g (trial 2) to 21.9 g (trial 4) with an overall mean of 21.4 g (Table 1).

Metabolic efficiency (%), daily energy consumption (kcal), metabolizable energy (kcal/g), daily energy excretion (kcal), daily excreta weight production (g), and excreta energy (kcal/g) all varied significantly with diet (Table 2) but not among individual birds or with trial (Appendix, Table 2). Metabolic efficiency by diet ranged from 80% on a diet of Maximilian sunflower to 87% on millet (Table 2). Metabolic efficiency was not dependent upon bird pretrial weight.

Junco excreta energy production ranged from 2.0 kcal/day on millet to 4.0 kcal/day on oil sunflower (Table 2). Birds on a diet of millet produced an average of 0.53 g/day excreta while those on oil sunflower produced an average of 0.84 g/day excreta (Table 2). Daily excreta weight (g) and fecal energy (kcal) productions were not dependent upon bird pretrial weight. Diet energy content significantly influenced excreta energy content and excreta weight production (Table 2). Excreta unit energy content (kcal/g) was positively influenced by total excreta weight production (g) (Figure 7).

Junco existence energy varied significantly with diet, ranging from 12.4 kcal/day on sorghum to 16.7 kcal/day on oil sunflower (Table 2), and with trial ranging from 13.6 kcal/day (trial 1) to 16.6 kcal/day (trial 3) (Appendix, Table 2). Bird existence energy did not depend upon bird pretrial weight.

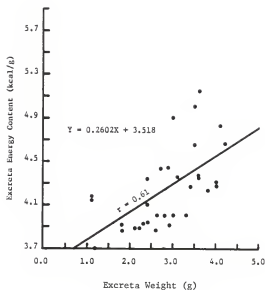


Figure 7. Regression of individual excreta unit energy (kcal/g) of 8 juncos over 4 days on corresponding excreta productions by weight (g). The slope is significantly different from zero at $P \leq 0.05$.

Daily food consumption (g) by juncos varied significantly with diet, ranging from 4.4 g on sorghum to 5.7 g on Maximilian sunflower (Table 2), and trial, ranging from 4.5 g (trial 2) to 5.8 g (trial 3) (Appendix, Table 2).

Juncos on a 4-day diet of sorghum lost 2.8 g while birds on a 4-day diet of oil sunflower lost only 1.5 g (Table 3). Metabolic efficiency was negatively influenced by bird trial weight loss (Figure 8).

Average energy content of spilled seed (husked and uneaten mixture) in the cage bottom ranged from 4.2 kcal/g for sorghum to 5.6 kcal/g for oil sunflower. Only spilled oil sunflower energy content was significantly different from that of purely uneaten samples.

The weight loss correction factor did not affect the statistical significance of junco energetic results.

Tree Sparrow - Bird pretrial mean body weights ranged from 20.9 g (trial 2) to 21.4 g (trials 1 and 3) with an overall mean of 21.1 g (Table 1).

Daily energy consumption (kcal) did not vary significantly among individual birds or with trial (Appendix, Table 2) or diet (Table 2).

Metabolic efficiency (%) and metabolizable energy (kcal/g) varied significantly among individual birds as well as with diet (Table 2). Individual metabolic efficiencies ranged from 83% to 87% and metabolic efficiencies by diet ranged from 82% on oil sunflower to 89% on millet (Table 2). Metabolic efficiency was not dependent upon bird pretrial weight.

Daily energy excretion (kcal) and daily excreta production (g) both varied significantly among individual birds but only daily excreta production varied with trial (Appendix, Table 2) and diet (Table 2). Birds on a diet of millet excreted an average of 2.0 kcal/day while those on oil sunflower excreted an average of 3.7 kcal/day (Table 2). Tree sparrows produced 0.5 g/day of excreta on a diet of millet compared with 0.8 g/day on a diet of oil sunflower (Table 2). Daily excreta weight (g) and fecal energy (kcal) productions were not

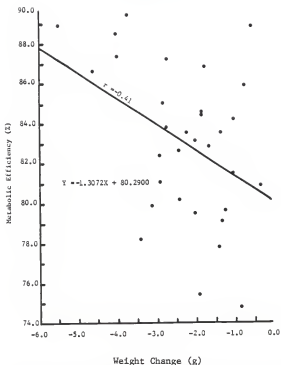


Figure 8. Regression of individual metabolic efficiencies (%) of 8 juncos over 4 days on corresponding weight changes (g). The slope is significantly different from zero at $P < 0.05$.

dependent upon bird pretrial weight. Diet energy content positively ($p \leq 0.05$) influenced excreta energy content and excreta weight production (Table 2). Excreta unit energy content (kcal/g) was positively influenced by total excreta weight production (g) (Figure 9).

Existence energy in tree sparrows did not vary significantly among individuals or with diet or trial.

Daily food consumption (g) by tree sparrows varied significantly among individual birds and with trial (Appendix, Table 2). Daily food consumption by birds was not dependent upon bird pretrial weight.

Tree sparrow 4-day weight loss did not vary significantly with diet or trial, averaging an overall loss of 1.2 g/4 days (Table 3).

Average energy content of spilled seed (husked and uneaten mixture) in the cage bottom ranged from 4.2 kcal/g for millet to 5.8 kcal/g for oil flower. Only spilled oil sunflower energy values were significantly different from those for purely uneaten samples.

The weight loss correction factor did not affect the statistical significance of tree sparrow energetic results.

Overall Sparrow Comparisons - Cardinal mean body weight was 41.1 g, significantly heavier than Harris' sparrows at 34.1 g, which were significantly heavier than juncos at 21.4 g and tree sparrows at 21.1 g (Table 1).

For all diets combined, each species varied from the others in metabolic efficiency with mean values of 80%, 83%, 85% and 88% for cardinals, juncos, tree sparrows, and Harris' sparrows, respectively (Table 1). This trend was paralleled with metabolic efficiency results on Maximilian sunflower (Table 4). On the other 3 single diets, the 4 sparrow species' comparative metabolic efficiencies exhibited significant differences in some cases but not in others (Table 4).

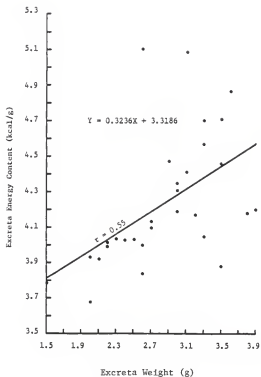


Figure 9. Regression of individual excreta unit energy (kcal/g) of 8 tree sparrows over 4 days on corresponding excreta productions by weight (g). The slope is significantly different from zero at $P < 0.05$.

Table 4. Interspecific sparrow comparisons of mean energy content and dry weight of excreta produced, energy consumption, and derived energetic calculations with standard errors. Values with a common superscript read across a row do not differ ($P < 0.05$).

DIET	BIRD SPECIES				STANDARD ERROR
	Cardinal	Harris' Sparrow	Junco	Tree Sparrow	
Species Mean Body Wgt. ¹	41.1 ^c	34.1 ^b	21.4 ^a	21.1 ^a	± 0.50
SORGHUM					
Energy Consumed (kcal/day)	20.8 ^b	29.3 ^c	14.7 ^a	19.4 ^{a,b}	± 2.10
Wgt. Diet Consumed (g/day)	6.2 ^c	6.7 ^c	3.4 ^a	4.5 ^b	± 0.64
Excrete Energy Content (kcal/g)	4.2 ^a	4.1 ^a	4.1 ^a	4.1 ^a	± 0.07
Energy Excreted (kcal/day)*	3.6 ^b	3.4 ^b	2.3 ^a	2.7 ^{a,b}	± 0.38
Wgt. Excreta Produced (g/day)	0.88 ^b	0.84 ^b	0.58 ^a	0.67 ^{a,b}	± 0.08
Metabolic Efficiency (%)	82 ^a	89 ^b	85 ^{a,b}	86 ^b	± 1.10
Existence Energy (kcal/day)*	17.2 ^a	25.8 ^b	12.4 ^a	16.7 ^a	± 1.80
MILLET					
Energy Consumed (kcal/day)	23.7 ^{b,c}	25.4 ^c	15.4 ^a	18.6 ^{a,b}	± 2.10
Wgt. Diet Consumed (g/day)	6.3 ^b	6.1 ^b	3.6 ^a	4.3 ^a	± 0.64
Excrete Energy Content (kcal/g)	4.1 ^b	3.9 ^a	3.9 ^a	3.8 ^a	± 0.07
Energy Excreted (kcal/day)*	3.6 ^b	2.0 ^a	2.0 ^a	2.0 ^a	± 0.38
Wgt. Excreta Produced (g/day)	0.90 ^b	0.54 ^a	0.53 ^a	0.54 ^a	± 0.08
Metabolic Efficiency (%)	85 ^a	92 ^c	87 ^{a,b}	89 ^b	± 1.10
Existence Energy (kcal/day)*	20.1 ^{b,c}	23.4 ^c	13.4 ^a	16.5 ^{a,b}	± 1.80
OIL SUNFLOWER					
Energy Consumed (kcal/day)	31.0 ^b	35.7 ^b	20.7 ^a	21.2 ^a	± 2.10
Wgt. Diet Consumed (g/day)	4.6 ^{a,b}	4.9 ^b	2.7 ^a	3.0 ^a	± 0.64
Excrete Energy Content (kcal/g)	4.6 ^a	4.8 ^b	4.8 ^b	4.7 ^{a,b}	± 0.07
Energy Excreted (kcal/day)*	6.6 ^c	5.4 ^b	4.0 ^a	3.7 ^a	± 0.38
Wgt. Excreta Produced (g/day)	1.40 ^c	1.13 ^b	0.84 ^a	0.80 ^a	± 0.08
Metabolic Efficiency (%)	79 ^a	85 ^b	81 ^a	82 ^{a,b}	± 1.10
Existence Energy (kcal/day)*	24.5 ^b	30.3 ^c	16.7 ^a	17.5 ^a	± 1.80
MAXIMILIAN SUNFLOWER					
Energy Consumed (kcal/day)	27.2 ^b	36.0 ^c	19.5 ^a	20.7 ^a	± 2.10
Wgt. Diet Consumed (g/day)	4.9 ^b	6.1 ^c	3.2 ^a	3.4 ^a	± 0.64
Excrete Energy Content (kcal/g)	4.3 ^a	4.4 ^a	4.3 ^a	4.3 ^a	± 0.07
Energy Excreted (kcal/day)*	6.2 ^c	4.9 ^b	3.8 ^a	3.3 ^a	± 0.38
Wgt. Excreta Produced (g/day)	1.40 ^c	1.13 ^b	0.89 ^a	0.78 ^a	± 0.08
Metabolic Efficiency (%)	75 ^a	86 ^c	80 ^b	84 ^c	± 1.10
Existence Energy (kcal/day)*	21.0 ^b	31.0 ^c	15.7 ^a	17.5 ^{a,b}	± 1.80

¹ Mean represents weights from 10 individuals of each finch species ± standard deviation

* Corrected for weight loss

The energy content of excreta per gram was not significantly different between species overall although cardinals excreted 3.6 kcal/day on millet, significantly more energy than all other species, and significantly less energy on oil-type sunflower (Table 4). Combining data from all diets, cardinals excreted the maximum (5.0 kcal/day) energy of the 4 sparrow species (Table 1), with Harris' sparrow energy excretion (3.9 kcal/day) exceeding that of the 2 smaller species (Table 1). Excreta energy results for all 4 species on each diet examined singly were significantly different in some cases but not others (Table 4). Bird species mean body weight did not influence the amount of energy excreted per day.

Harris' sparrows exhibited a significantly greater combined mean existence energy (27.7 kcal/day) on all diets than the other 3 bird species, with cardinals requiring more energy for existence than the 2 smaller species (Table 1). These results were paralleled on diets of sorghum and oil-type sunflower (Table 4). Junco mean existence energy was always less than that for Harris' sparrows and cardinals, while tree sparrow mean existence energy was not significantly different from those of cardinals on millet and Maximilian sunflower diets (Table 4). Existence energies determined for only birds which maintained weight (no correction factor necessary) were not significantly different from those means determined using the correction factor.

Combining all diets, Harris' sparrows ingested a mean of 31.6 kcal/day gross energy, significantly more than the 25.7 kcal/day ingested by cardinals, the 20.0 kcal/day by tree sparrows, and the 17.5 kcal/day by juncos (Table 1). Harris' sparrows ingested more gross energy per day than juncos and tree sparrows on all diets examined singly (Table 4).

Harris' sparrows always consumed more diet by weight than either of the 2 smaller species, while cardinals consumed amounts similar to tree sparrows on the sunflower diets (Table 4).

Levene's test for homogeneity of variances demonstrated that cardinals exhibited a wider range in metabolic efficiency than juncos and tree sparrows, while Harris' sparrows and juncos varied more in metabolic efficiency (not significantly) than only tree sparrows (Figure 10). Sparrow respective variances for selected variables appear in Table 5.

MOURNING DOVE

The gross energy content of test seed diets in increasing order was corn (4.4 kcal/g), wheat (4.4 kcal/g), millet (4.5 kcal/g), sorghum (4.6 kcal/g), canary (4.7 kcal/g), timothy (4.7 kcal/g), Maximilian sunflower (5.6 kcal/g), and thistle (6.2 kcal/g) (Table 6). Dove mean pre-trial body weights ranged from 120.5 g (trial 3) to 128.4 g (trial 1), with a mean of 124.8 g.

All energetic variables measured varied significantly with diet and most varied by trial (Appendix, Table 3).

Dove energy consumption ranged from 37.9 kcal/day on a diet of timothy to 80.8 kcal/day on a diet of millet. Excreta production ranged from 1.6 g/day on a diet of corn to 6.3 g/day on millet, while excreta energy content ranged from 4.2 kcal/g on sorghum to 4.5 kcal/g on timothy. Mourning doves excreted from 2.3 kcal/day on a diet of corn compared to 13.2 kcal/day on a diet of thistle. Heavier doves did not ingest more diet energy or produce more excreta by weight than lighter doves. There was also no significant relationship between excreta energy content and excreta production by weight. However, both excreta energy content and excreta production by weight increased significantly with diet energy content.

Metabolic efficiencies ranged from 69% on a diet of Maximilian sunflower to 97% on a diet of corn. Metabolizable energies ranged from 3.7 kcal/g on canary to 4.5 kcal/g on a diet of thistle. Dove body weight did not significantly influence metabolic efficiency.

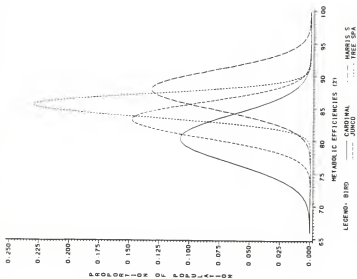


Figure 10. Respective variances in metabolic efficiency for cardinals, Harris' sparrows, juncos, and tree sparrows, combining data from all diets.

Table 5. Actual variances for energetic variables for 8 each cardinals, Harris' sparrows, tree sparrows, and juncos. Superscripts relate to results from Levene's Test for homogeneity of variances. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE TESTED	BIRD SPECIES			
	Cardinal	Harris' Sparrow	Junco	Tree Sparrow
Species Pretrial Wgt.	3.06 ^c	2.05 ^{b,c}	0.44 ^a	0.60 ^{a,b}
Species Posttrial Wgt.	6.40 ^b	1.20 ^{a,b}	1.07 ^a	0.49 ^a
Energy Consumed	805,822,624 ^b	664,149,310 ^b	127,697,509 ^a	147,699,476 ^a
Wgt. Excreta Produced	0.47 ^a	1.11 ^b	0.47 ^a	0.11 ^a
Energy Excreted	12,343,330 ^b	21,228,623 ^b	9,066,357 ^a	2,696,329 ^a
Wgt. Diet Consumed	37.32 ^c	53.67 ^{b,c}	6.82 ^a	20.81 ^{a,b}
Metabolic Efficiency	13.76 ^b	9.14 ^a	7.27 ^a	3.01 ^a
Existence Energy	43,456,974 ^b	41,509,332 ^b	7,981,094 ^a	9,231,217 ^a

Table 6. Hurling dove (mean body weight 124.8 g) laboratory mean values and standard errors of energetic variables on 8 diets. Values with common superscripts read across a row do not differ ($p \leq 0.05$). Means for Maximilian sunflower and sorghum were derived from 10 values while means for all other diets were derived from 5 values. Diet energy content (kcal/g) appears in parentheses beneath diet titles.

ENERGETIC VARIABLE	DIET							
	Canary (4.7)	Corn (4.4)	Maximilian Sunflower (5.6)	Millet (4.5)	Sorghum (4.6)	Thistle (6.2)	Timothy (4.7)	Wheat (4.4)
Gross Energy Consumed (kcal/day)	51.1 ^a ±5.0	38.3 ^{a,b} ±5.0	40.1 ^{a,b} ±3.2	80.8 ^d ±5.0	64.8 ^c ±3.2	46.6 ^{a,b} ±5.0	37.9 ^b ±5.0	44.3 ^{a,b} ±5.0
Weight Diet Consumed (g/day)	11.5 ^c ±1.4	8.2 ^{a,b} ±1.4	7.3 ^a ±0.90	17.4 ^d ±1.4	15.1 ^d ±0.90	8.0 ^{a,b} ±1.4	8.4 ^{a,b} ±1.4	9.3 ^{b,c} ±1.4
Excreta Energy Content (kcal/g)	4.2 ^a ±0.03	4.3 ^{a,b} ±0.03	4.3 ^{b,c} ±0.02	4.2 ^a ±0.03	4.2 ^a ±0.02	4.4 ^{c,d} ±0.03	4.5 ^e ±0.03	4.3 ^{b,d} ±0.03
Energy Excreted* (kcal/day)	11.1 ^c ±1.4	2.3 ^a ±1.4	12.8 ^c ±0.87	13.2 ^c ±1.4	6.1 ^b ±0.87	13.2 ^c ±1.4	7.5 ^b ±1.4	6.3 ^c ±1.4
Hgt. Excreta Produced (g/day)	2.66 ^a ±0.29	0.81 ^b ±0.29	3.02 ^a ±0.18	3.13 ^a ±0.29	1.48 ^{b,c} ±0.18	3.05 ^a ±0.29	1.85 ^{c,d} ±0.29	1.51 ^{b,d} ±0.29
Metabolic Efficiency* (%)	79 ^{a,c} ±2.5	97 ^b ±2.5	69 ^{c,e} ±1.6	84 ^{a,d} ±2.5	90 ^d ±1.6	73 ^e ±2.5	85 ^{a,d} ±2.5	85 ^{a,d} ±2.5
Existence Energy* (kcal/day)	40.0 ^a ±4.4	36.1 ^{a,b} ±4.4	27.3 ^{b,c} ±2.8	67.6 ^d ±4.4	58.7 ^d ±2.8	33.5 ^{a,c} ±4.4	30.6 ^{a,c} ±4.4	38.0 ^a ±4.4
Metabolizable Energy* (kcal/g)	3.7 ^a ±0.12	4.3 ^{b,d} ±0.12	3.9 ^a ±0.07	3.8 ^a ±0.12	4.1 ^{b,c} ±0.07	4.5 ^d ±0.12	3.9 ^{a,c} ±0.12	3.8 ^a ±0.12
Trial Weight Change (g)	+0.4 ^a ±1.6	-6.8 ^c ±1.6	-0.9 ^a ±1.5	+3.4 ^b ±1.6	+1.3 ^a ±1.5	+1.5 ^a ±1.6	-4.7 ^c ±1.6	-1.2 ^a ±1.6

* Corrected for weight loss

Dove existence energy ranged from 27.3 kcal/day on Maximilian sunflower to 67.7 kcal/day on millet. Heavier birds did not consume more diet by weight than lighter doves.

Doves on diets of corn, Maximilian sunflower, timothy, and wheat sustained weight losses of 3.4, 0.5, 2.4 and 0.6 g/day, respectively (Table 6).

Trial dove consumption of Illinois bundleflower, wild senna, sandvine, and buckwheat resulted in respective weight losses of 17.5, 14.5, 13.2 and 14.7 g/day (Table 7). Diet consumption by doves ranged from 0.9 g/day on sandvine to 3.5 g/day on wild senna, and excreta production from those diets was 0.4, 0.5, 0.1 and 0.2 g/day, respectively (Table 7). Fecal pellets never formed and excreta was liquid green.

Table 7. Daily diet consumption (g), weight loss (g), and excreta production (g) of mourning doves on 4 diets. An extremely small sample size precluded making conclusive comparisons between diets for the measured variables.

VARIABLE	DIET			
	Illinois Bundletreeflower (n=1)	Wild Senna (n=2)	Sandvine (n=2)	Buckwheat (n=1)
Diet Energy Content (kcal/g)	4.8	4.5	6.3	4.6
Wgt. Diet Consumed (g/day)	1.4	3.5	0.9	0.8
Weight Loss (g/day)	17.5	14.5	13.2	14.7
Excreta Production (g/day)	0.4	0.5	0.1	0.2

STUDY I. DISCUSSION

The Assumption of 70% Metabolization of Ingested Food Energy and Energetically Based Winter DistributionsSPARROWS

The assumed model value of 70% metabolization of ingested food energy used by Wiens and Innis (1974) is not supported in this study. Cardinals, juncos, tree sparrows, and Harris' sparrows exhibited respective metabolic efficiencies of 80%, 83%, 85%, 88% on all diets combined. Only 1 cardinal on a diet of Maximilian sunflower (1 treatment out of 128) exhibited a metabolic efficiency equal to or below the assumed 70% value. (The value was 69%). Further, if metabolic efficiencies decrease or remain the same with decreasing temperature, as documented by Kendeigh [house sparrow (1949)], Davis [house sparrow (1955)], West [American tree sparrow (1960)], Zimmerman [dickcissel (1965)], Willson and Harmeson [northern cardinal (1973)], and Robel [Harris' sparrow and northern cardinal (pers. comm.)], breeding season metabolic efficiencies based on temperature are predicted to be higher than winter values.

Based on differential metabolic efficiencies found in this study, it is suggested that cardinals', Harris' sparrows', juncos', and tree sparrows' respective winter energetic adaptations vary. Wintering, breeding, and resident distributions for each species appear in Figure 11 (after Robbins et al. 1983). Harris' sparrows have restricted wintering and breeding ranges and are not considered year-round residents at any location. Tree sparrows also winter and breed in completely disjunct areas but have a broader east-west range expansion than Harris' sparrows. Juncos have still broader east-west and north-south wintering and breeding ranges than tree sparrows and are year-round residents in some areas. Cardinals are nonmigratory residents in approximately the eastern 2/3 of the United States.

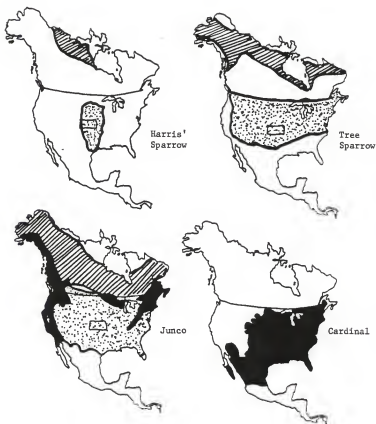


Figure 11. Respective winter, breeding, and/or resident ranges of Harris' sparrows, tree sparrows, juncos, and cardinals (Robbins et al. 1983). Cross-hatching represents breeding range, dotting represents wintering areas, and solid coloring represents resident status.

Harris' sparrows, the species most restricted in winter range, were consistently more metabolically efficient on all test diets while the resident cardinals were the least efficient on all diets. All 4 species exhibited the highest respective metabolic efficiency on a diet of millet and the lowest on 1 of the 2 sunflower diets, although the differences were not always significant. This efficiency difference trend may reflect the relative inability of the sparrow species to metabolize diets with high fat content (i.e., sunflowers). Millet also has a higher moisture content and lower fiber content than the sunflowers (Petrak 1969) which may further contribute to the bird species' higher metabolic efficiency on that diet. Study IV on trypsin inhibitor content in the 4 seed diets explores another possibility for decreased efficiency on the sunflower diets.

Reflective of lower metabolic efficiencies, the resident cardinals consumed less and excreted more energy than the distributionally restricted Harris' sparrows on all 4 diets. Harris' sparrows appear to have adapted extremely well in terms of metabolic efficiency to a specialized (narrow) winter range, while cardinals have adapted differently to temperate winter conditions. At the population level, year-round residency may be advantageous for cardinals in terms of early breeding territory establishment (Ketterson and Nolan 1983) and the lack of migratory stress. Warnock (1980) found evidence that cardinal pairs maintain winter territories in rural fencerows.

If Harris' sparrows with their high metabolic efficiency and restricted winter range are used as a gauge for the other 3 species' metabolic efficiency performances and distributional relationships, tree sparrows, juncos, and cardinals also exhibit a pattern. Tree sparrows inhabit a wider winter range than Harris' sparrows but a narrower one than juncos. Harris' and tree sparrows were the most similar in metabolic efficiency on all diets. Tree sparrows exhibited a higher absolute metabolic efficiency than juncos and

cardinals on all diets. Juncos, in turn, which are resident in only limited areas, still have a superior metabolic efficiency to cardinals on all diets. It is suggested that these 4 winter-sympatric emberizids are adapting to diffuse interspecific competition in part through differential metabolic efficiencies on different diets. Harris' and tree sparrows appear to be high metabolic efficiency specialists restricted in distribution while juncos and cardinals are more generalistic in metabolic efficiency but have more widespread and/or stationary distributions.

A successful sparrow must capture, process, and absorb enough energy to meet metabolic requirements (Fretwell 1972). Birds cannot survive on diets which fail to provide the daily energy requirement for existence. As predicted by body size requirements, energy consumption should reflect body size and when ranked by body weight, cardinals were heaviest, followed by Harris' sparrows, juncos, and tree sparrows. Results from this study show that Harris' sparrows and tree sparrows, which are lighter than cardinals and juncos, respectively, required more energy for caged weight maintenance than their counterparts on all diets. (A noticeably higher activity level in Harris' sparrows suggests a higher basal metabolic requirement for that species.) These results are reflective of increased daily energy intake and/or decreased energy excreted in Harris' and tree sparrows. On per gram body weight basis, Harris' and tree sparrows consumed 0.17 and 0.18 g diet, respectively, compared with values of 0.13 and 0.15 g diet for cardinals and juncos. Juncos did consume less energy than tree sparrows on all diets but excreted more energy on only the sunflower diets. However, lower metabolic efficiencies resulted when juncos consumed 4.7 kcal/day less on sorghum and 3.2 kcal/day less on millet than tree sparrows even while excreting similar amounts of energy.

Mainly reflecting the 2 sunflower diets, all 4 bird species produced increasing weights of excreta which contained correspondingly higher unit

energy contents. This suggests a more rapid and thus inefficient passage of food, reflected in the lower metabolic efficiencies. Harris' sparrows, juncos, and cardinals all lost the least amount of weight on a diet of oil sunflower even with its lower metabolic efficiency. This points out that a relatively low metabolic efficiency on a high energy diet can be a superior energy source to a diet low in energy with a high metabolic efficiency. Further evidence for this was demonstrated in juncos and Harris' sparrows where in general, high metabolic efficiencies corresponded with higher weight losses, reflecting high efficiency on a diet negatively coupled with inadequate existence energy requirements. Cardinals, however, lost the least amount of weight on oil sunflower and the most on Maximilian sunflower even though comparable amounts of energy were consumed on each diet. This may be reflective of increased gizzard and/or enzymatic activity necessary to break down the single smaller Maximilian sunflower seeds which yield much less energy per seed than oil sunflower. Tree sparrows lost comparable amounts of weight on all diets. The 5-12% body fat in tree sparrows compared with 12-17% in juncos as reported by Stuebe and Ketterson (1982) suggests that tree sparrows are not resistant to fasting (relative to juncos) and may have evolved a higher realized metabolic efficiency (i.e., no hidden internal digestive costs), while juncos can rely on fat reserves if necessary. As a note, during handling time trials, juncos were starved longer (some 48 hr more) than the other 3 species before they would consume food in the presence of an observer, and suffered no apparent ill-effects. Perhaps hunger overcame fear in the other 3 species which may not possess the fat storage capacity of juncos.

It seems counterintuitive from a fat storage argument why tree sparrows do not winter farther south than juncos. Examination of breeding ranges of the 2 species reveals that tree sparrows breed only in northern Canada while juncos breed additionally farther south. Spring travel distance to the breeding

grounds is likely energetically restricted (Ketterson and Nolan 1983). If tree sparrows have very specific breeding site requirements, they must winter within a distance to reach these areas the following spring (Ketterson and Nolan 1983). Juncos perhaps have less restricted (or their preferred breeding habitat is more expansive) breeding site requirements and are able to additionally breed farther south in Canada and thus energetically able to winter farther south in terms of reaching breeding areas (Figure 11). See Ketterson and Nolan (1983) for a review of migratory mechanisms. Smith (pers. comm.) suggests that if tree sparrows are energetically better-adapted to more northerly wintering areas (regardless of less resistance to fasting), they should also be similarly adapted to more northerly breeding areas.

The "distance to breeding site" and "specialized energetic adaptation" hypotheses coupled with the higher metabolic efficiency of tree sparrows (relative to juncos) and perhaps fewer internal digestive costs, suggest the strong adaptation of tree sparrows to northerly areas. Perhaps Harris' sparrows restricted winter range is also reflective of energetically limited migration distances and/or specialized energetic adaptation to restricted areas. Also, Harris' sparrows and tree sparrows may have more restricted ranges because they evolved higher non-size related basal metabolic requirements which had to be equalled or exceeded by energy intake in order to survive (Walsberg 1983).

It is puzzling why the Harris' sparrow, which has a superior metabolic efficiency on all tested diets, does not expand its winter range. As an intermediate-sized bird with an intermediate-sized beak, the Harris' sparrow conceivably might exploit a wider range of food items (Fretwell pers. comm.). However, according to Martin et al. (1951), Harris' sparrows, juncos, and tree sparrows maintain diets of which 70-75% consist of only 3 seed species (not necessarily the same 3). Alternatively, cardinals are more generalistic with

7 seed species comprising 60% of their winter diet. Although in reality Harris' sparrows may be of intermediate beak size, when relating sparrow beak size to the food resource, cardinals may better approximate the ideal intermediate beak size. Rather than viewing Harris' sparrows as a restricted species, perhaps a more appropriate description is that of a successful specialist.

Cardinals also varied more than the other species in metabolic efficiency. This suggests a strategic variation between migratory versus resident sparrow species. Initially, it seems that since cardinals are non-migratory and restricted in range that they should face selective pressures to be highly exploitative of constant resources. However, the generalist nature of the cardinals' diet reflects the selective pressure to exploit as broad a range of diets as possible. This capability may allow cardinals to be superior competitors, establish residency, and avoid migratory stress. Also, cardinals consume substantially more animal matter in winter, spring, and fall than do tree and Harris' sparrows and more animal matter than juncos in summer and fall (Martin et al. 1951). A more generalist diet approach implies low metabolic efficiency specialization.

Why the trend exists for a single bird species to require more energy to exist on 1 diet than another is not clear. All 4 sparrow species had the lowest relative metabolic efficiencies on the 2 sunflower diets while simultaneously exhibiting the highest maintenance requirements on those diets. This may reflect that those diets simply required more internal work to digest. If gizzard work, enzymatic activity, or intestinal movement varied based on diet, this might explain some of the observed differences. A bird which consumes sufficient energy (apparently) to maintain weight but burns more off internally may register a net weight loss. The stress of captivity may have also resulted in some weight loss unrelated to differential digestion of diets.

MOURNING DOVES

Dove metabolic efficiencies ranged from 69% on a diet of Maximilian sunflower to 97% on a diet of corn. All diets except Maximilian sunflower resulted in metabolic efficiencies greater than the 70% value used by Wiens and Innis (1974) in their model.

Similar to the sparrows, doves exhibited different metabolic efficiencies and existence energies on different diets which likely reflect both seed and bird digestive characteristics. Within the bird, an increased demand for digestive enzymes, gizzard work, or intestinal movement for different diets may result in differential efficiencies and bird energy requirements for weight maintenance. Looking at the seed diets, Maximilian sunflower and thistle, the diets with the lowest metabolic efficiency also contained the highest amount of fat and least amount of moisture (Petrak 1969). Doves' dependence on daily water intake may in part be due to the need for proper digestive functioning (Schmid 1965). The high fiber content in Maximilian sunflower and canary (Petrak 1969) may have also contributed to lower dove metabolic efficiencies on those diets.

Based on the amount of energy needed for existence, doves lost weight on diets of corn, Maximilian sunflower, timothy and wheat by consuming less than or near existence requirements on those diets (Table 8). The high dove metabolic efficiency on corn (97%) calculated for birds could have been a mathematical artifact resulting from extremely low excreta production on this diet. The liquid green excreta produced may have been normal on this diet but was difficult to collect. The high metabolic efficiency on corn (a diet low in gross energy content) which resulted in a high metabolizable energy (lower than only that of thistle) suggests a high internal cost associated with the digestion of corn. Corn presented to doves may not have been sufficiently cracked and the large pieces may have been retained at length in the gut. The

Table 8. Metabolic efficiencies, existence energies, diet unit energy contents, metabolizable energies, amount of diet (g) needed to meet daily requirements, and actual consumption by mourning doves on 8 seed diets.

VARIABLE	DIET							
	Canary	Corn	Maximilian Sunflower	Millet	Sorghum	Thistle	Timothy	Wheat
Metabolic Efficiency (%)	79	97	69	84	90	73	82	85
Existence Energy (kcal/day)	40.0	36.1	27.3	67.6	58.7	33.5	30.4	38.0
Diet Energy Content (kcal/g)	4.7	4.4	5.6	4.5	4.6	6.2	4.7	4.4
Metabolizable Energy (kcal/g)	3.7	4.3	3.9	3.8	4.1	4.5	3.9	3.8
Required Consumption (g)	10.8	8.4	7.0	17.8	14.3	7.4	7.8	10.0
Actual Consumption (g)	11.5	8.2	7.3	17.4	15.1	8.0	8.4	9.3
Weight Change (g)	+0.4	-6.8	-0.9	+3.4	+1.3	+1.5	-4.7	-1.2

resultant metabolic efficiency may have been high but the internal work necessary for digestion produced a net weight loss and low excreta production. Even with the high metabolic efficiency on corn, doves still lost more than 5% of their body weight daily. Diets of Maximilian sunflower and timothy, which also resulted in weight losses (less than 5% of body weight) but had low (both 3.9 kcal/g) metabolizable energies, may simply have been difficult for doves to handle. Sparrows were seen temporarily choking on Maximilian sunflower seeds which appeared to become lodged in the throat due to seed length; doves may have encountered similar pre-digestion difficulties. Once ingested, Maximilian sunflower was apparently digested normally by both sparrows and doves. Timothy is an extremely small seed and doves seemed only capable of ingesting that diet on the smooth cage floor if it was concentrated in piles or the feeding dish. (Dove activity usually resulted in dislocation of seed from dishes.) Again, pre-digestive handling difficulty and energy expenditure may have produced a net weight loss. A diet of wheat which resulted in an insignificant (1%) weight loss is a strongly 3-dimensional seed and ingestion appeared not to be a problem for doves. Doves consumed extremely low amounts of Illinois bundleflower, wild senna, sandvine, and buckwheat which resulted in substantial daily weight losses (Table 7). The low consumption rates by doves on these 4 natural diets suggest a low palatability of these seeds to doves. To the human senses, wild senna was acrid and distasteful. Additionally, the buckwheat used in this study had an extremely hard seed coat and may have been indigestible by doves. Illinois bundleflower and sandvine perhaps contained distasteful components, were difficult to handle or were simply too unfamiliar to the doves. Limited test quantities of these diets precluded prior inclusion of them in between-trial maintenance periods and the unfamiliarity bias may have played a role in decreased consumption. Individual confinement and thus lack

of social contact may have contributed additionally to dove weight loss in some cases.

Although doves gained weight on diets of sorghum and millet, the high required existence energies on these 2 diets could present winter energetic limitations for doves under unconfined conditions. Millet contains 158 seeds/g and thus a dove requiring 17.8 g millet/day for existence would be forced to consume 2812 seeds per 10 hours or about 5 seeds/minute. In addition to search time and other life-sustaining activities (predator scanning, drinking, microhabitat adjustments), doves would have to eat 1 millet seed every 12 sec for 10 hours simply to exist. Similarly, on a diet of sorghum which contains 260 seed pieces/g, doves requiring 14.3 g for existence would need to consume 3718 pieces per 10 hours or about 6 seed pieces/minute or 1 every 10 seconds. Time allocations to costly activities such as flight or running would substantially increase energy requirements. Perhaps the winter flocking behavior of doves facilitates this consumption rate through decreased predator scanning and decreased patch search time per individual as suggested by Moriarity (1976).

In a general comparison between doves and sparrows, all 4 sparrow species exhibited greater metabolic efficiencies than doves on diets of Maximilian sunflower and millet, while doves were superior on a sorghum diet. This result is not surprising since sparrows husked the 2 former diets and consumed only the endosperm whereas doves consumed the entire seed including the energy-poor husk. On a diet of cracked sorghum, however, the seed coat, which is thin when intact, was essentially removed and doves and sparrows consumed the same portions of quality seed. This suggests that doves on a diet of huskless seed might have superior metabolic efficiencies when compared with sparrows. It seems that natural patches of huskless seeds would rarely occur in nature, while cultivated fields after harvest would provide a mechanically-derived huskless seed source for doves.

Perhaps doves' lower relative metabolic efficiencies on diets with seed husks reflects partial maladaptation to temperate winter natural food resources and helps explain doves' concentration around unnatural (cultivated fields) food sources. This coupled with high existence energies (and subsequent necessary high energy intake amounts and rates) and only a 6% body fat component (Jenkins 1955) may explain the low winter numbers of mourning doves in north-eastern Kansas.

STUDY II. INTRODUCTION AND LITERATURE REVIEW

General Avian Bioenergetics and Requirement Over Existence for Free-Living

Natural selection is a process whereby individuals bearing genetically inferior traits are removed from the population through differential survival and reproduction. Thus the "success" of an individual is measured in terms of survival and successful reproduction, and these activities require energy. Differential apportionments of time and energy expenditure "are intimately associated with adaptation to a particular environment and thus the bioenergetics of a species is a basic determinant of its niche requirements" (Zimmerman 1965). Understanding avian bioenergetics is necessary before we can comprehend how birds use available resources (Owen 1970). Evolutionarily, energetics is important for understanding how energy availability and efficiency of use regulate the annual avian cycle and limit distribution (Cox 1961, Zimmerman 1965, Williams and Kendeigh 1982).

Techniques for measuring the energetic costs for free-living individuals to perform adaptive functions (e.g., flying, foraging, predator scanning, roosting, resting), though critically needed in energetics studies, have met with little success due to the difficulty in obtaining precise measurements.

Mullen (1973) reviews the procedures and history of estimating the cost of free existence using the doubly-labeled water technique first validated by Lifson et al. (1955) on laboratory rats (Rattus norvegicus). Utter and LeFebvre (1973) were the first to compare this method with estimates of energy expenditure based on the time-energy budget method. In general, they found marginal agreement, with the time-energy budget estimates being generally higher. Since Mullen's (1973) review, Hails (1979), Hails and Bryant (1979), and Bryant and Westerterp (1982), all working with the swallow family (Hirundinidae), have had some success with the method. Weathers and Nagy (1980), working with the phainopepla (Phainopepla nitens), simultaneously

assessed energy expenditure via doubly-labeled water and the time-energy approaches. They found that the latter comparatively underestimated daily energy expenditure, directly conflicting with the earlier results of Utter and LeFebvre (1973). Weathers and Nagy (1980) suggest that laboratory-estimated values for maintenance and other non-flight activities need reassessment and that all such estimates need confidence intervals. Cooper (1983) working with tenebrionid beetles cautions that studies using the doubly-labeled water method should be accompanied by laboratory validations prior to field application. Williams and Nagy (1984) examined several past time-energy budget studies and compared those to the doubly-labeled water techniques. They concluded that the time-energy budget is an inferior estimator (usually underestimates) of daily energy expenditure when compared with the doubly-labeled technique. Walsberg (1983) cites the expense and requirement of refined expertise as 2 current drawbacks to the latter method.

Other indirect calorimetry methods of estimating free-ranging energy expenditure are described briefly in this section. The heart rate measurement was first applied to a semi-free-ranging bird species by Owen (1969) and is reviewed in detail by Johnson and Gessaman (1973). They suggest that this index can be effective if used on resting or moderately active individuals. Respiratory rate as reviewed by Hargrove and Gessaman (1973) is not correlated with metabolism for most species studied to date, and they suggest it has little precision-increasing utility over laboratory estimates of energy expenditure. Sawby (1973) evaluates the radioisotope method and suggests that it deserves more investigation while currently not reflecting its initially considered high potential. The time-energy budget method is described in a later section.

The direct food consumption method which Kendeigh (1949) first applied to wild passerines (and which has been used extensively in laboratory estimates

of energy expenditure), has yet to be applied to even semi-free-ranging situations.

Literature estimates for daily energy expenditure (DEE) above existence energy, using various methods, bird species, and in different seasons, range from 0% (Weiner and Glowacinski 1975), 1% (Robel et al. 1974), 13% (West and DeWolfe 1974), 19% (Holmes and Sturges 1973), 30% (Clemans 1974), 33% (Robel et al. 1974), 30 - 50% (Uramoto 1961), 36% (Furness 1978), 40% (Schartz and Zimmerman 1971), 100% (Evans 1973), to 113% (Furness 1978). Thus, percent energy requirement above existence energy for free-living conditions remains uncertain in a generalized sense. The 40% general assumption Wiens and Innis (1974) use in their model as derived from Schartz and Zimmerman's (1971) dickcissel (Spiza americana) breeding season work, obviously does not apply to all situations.

Existence energy is the amount of food consumed by caged birds (less excretory energy) in the absence of sustained energetically costly activities and while maintaining constant weight (Kendeigh 1949, 1969b, 1970). It is critical to remember the energetic importance of body weight as it reflects an individual's prevailing energy balance (Williams and Kendeigh 1982). Weight is a summary of an individual's total biomass, an index of energy inputs and outputs, and of the general state of well-being of an individual. Seasonal body weight changes have been well documented (Baldwin and Kendeigh 1938, Bartelsson and Jensen 1955, Davis 1955, Helms 1963, Inozentsev 1964, Aschoff and Pohl 1970a, Ketterson and Nolan 1978) as has the relationship between energy metabolism and body weight (Brody 1945, Kleiber 1947, King and Farnar 1960, Lasiewski and Dawson 1967, Kendeigh 1970, Pimm 1976). See Clark (1979) for a review on the significance of body weight in birds.

This section of the present study estimates the cost over existence energy of semi-free-living conditions for cardinals, using direct calorimetry

procedures (food consumption method). Existence energies for all 4 sparrow species were previously determined in the laboratory under simulated winter conditions (See Study I.).

The Time-Energy Budget Method for Estimating Avian Daily Energy Expenditures

To survive and reproduce, i.e., to attain maximum fitness, an organism engages in various activities necessary for survival and reproduction, and these activities require time and energy. We assume that the evolutionary selective process has produced organisms which optimally allocate time and energy. These optimal allocations should be reflected in time-activity patterns. Verner (1965) emphasizes that optimal behavioral allocations vary by habitat, season, individual, and with a vast array of other environmental factors, and consequently, natural selection will favor an adaptable time-energy budget method that can (1) evaluate and quantify the complexity of an organism's energetic interactions with its environment and (2) provide insight into the evolution of the observed adaptive time-energy allocation patterns (King 1974, Ashkenazie and Safriel 1979, Biedenweg 1983). See King (1974) for an excellent review of the physical, morphological, physiological, and ecological processes which intertwine to influence avian time-energy allocations.

The time-energy budget method is one of several indirect techniques (see previous introduction sections) used to estimate the energetic cost of specific activities or to estimate the daily existence energy (DEE) of free-living birds. Such estimates seek to fill an important gap in avian bioenergetics studies. Conversion of a time budget (recording what proportion of time a bird spends engaged in various activities) into the corresponding energy budget involves multiplying the time spent in each activity by the estimated caloric cost equivalent of that activity. The DEE is the summation of all caloric cost equivalents for all activities. Orians (1961) first formalized the use of time-energy budget and the method has been used extensively since its

introduction (e.g., Verbeek 1964, Schartz and Zimmerman 1971, Utter and LeFebvre 1971, Wolf and Hainsworth 1971, Wolf 1975, Tarboton 1978, Askenazie and Safriel 1979, Biedenweg 1983). Criticism of the method (Gessaman 1973, King 1974) stems from the wide variation in laboratory-derived energetic cost equivalents and the use of inconsistent base values. For example, Tucker (1966) uses an estimated energetic cost for bird flight of $6.25 \times \text{BMR}$ (basal metabolic rate), while Schartz and Zimmerman (1971) use $6.0 \times \text{EE}$ (existence energy) for male dickcissels in flight, and Wakely (1978) uses $11.55 \times \text{SMR}$ (standard metabolic rate) for flight cost in raptors. Wakely (1978) also shows that female hawks do not follow the weight-based prediction of standard metabolic rate and he suggests that behavioral traits as well as weight be incorporated into calculations. Utter (1971), working with mockingbirds (Minus polyglottus), uses an estimated energetic cost for flight of $12.0 \times \text{BMR}$ while Biedenweg (1983), uses $9.4 \times \text{BMR}$ for the same species engaging in the same activity. Biedenweg (1983) attempts more critical estimates of variation in component contributions to DEE by inputting values 10 - 25% on either side of mean estimates.

The present study seeks to incorporate metabolic efficiency and daily energy intake under semi-free-living conditions into conventional time budget estimations of total DEE for wintering cardinals.

STUDY II. METHODS

Semi-Free-Living Energies and the Influence of Diet Energy on Time Budgets

To directly estimate the costs associated with free-living existence, a measure of food intake and weight dynamics over time must be determined. This segment of the research was designed to measure the average food consumption of 5 cardinals contained in an outdoor enclosure large enough to permit sustained metabolically costly activity, e.g., flight. Time budget data were concurrently collected on individual cardinals to assess the influence of diet metabolizable energy content on time budgets of cardinals.

Test birds were captured in 1.9-cm² mesh mist nets within 10 km of Manhattan, Kansas, in December 1981 and immediately housed randomly in 9.0 x 4.7 x 2.3-m flight pens on KPRNA constructed of hardware cloth and wood. Birds were acclimated for at least 10 days prior to testing. Five randomly-selected cardinals of known sex but unknown age were confined in each of 2 test flight pens. Birds were fitted with U.S. Fish and Wildlife Service aluminum bands as well as individual combinations of plastic color bands.

Metabolic efficiency and handling time data were used to design a flight pen test to assess the influence of diet on cardinal time budgets. Birds were provided a diet high in metabolizable energy with a low handling time in 1 pen and a diet low in metabolizable energy, also with a low handling time in the other pen. Diets of white proso millet and cracked, dehusked oil sunflower, respectively, met those qualifications.

Time budgets of individual birds in each of the 5-bird groups were constructed from data collected at 10-sec discrete intervals during 4 quarters of the day (early morning, late morning, early afternoon, late afternoon). Ten second intervals were signalled using the metronome method as described by Wiens et al. (1970). Observational categories were flying, perching (no

movement other than head turning and actively clutching perch), sitting (not actively clutching perch), feeding at the feeders, predator scanning, maintenance behavior (preening, scratching), interactions (movement toward or away from another bird based on aggression), nest-building behavior, and foraging away from the feeders. The experimental unit was actually the pen and consisted of 25 data points (5 birds x 5 trials). See Appendix E. for a sample time budget data sheet.

Food was provided in excess at each of 6 platform feeders fitted with collecting bins covered with hardware cloth (to prevent out-of-sight bird activity and loss of collected food) (Figure 12). Food was replenished as needed throughout the study. The excess of feeders was intended to minimize intraspecific interactions during trials. Water was provided ad libitum throughout the study in plastic bins equipped with sticks for perching and easy access by the birds. At temperatures below freezing, hot water was provided daily, unless snow was available for consumption. A dense red cedar (Juniperus virginiana) dome was placed centrally in each pen for general cover and roosting (Figure 12).

Time budget trial length varied based on the time required to complete a data set (observation of all birds during all 4 quarters of the day, not necessarily completed in 1 day). A total of 5 trials were completed during the period of 24 February - 21 March 1981. Before and after each trial, birds were captured, weighed to 1.0 g using a 100-g Pesola field scale, rerandomized, and assigned to each of the 2 pens. In the event of mortality of test birds, replacement birds were observed for a complete trial prior to initiating the next trial. Ambient temperature and relative humidity were both monitored continuously throughout the study via a Belfort hygrothermograph placed in a standard weather station at the site.

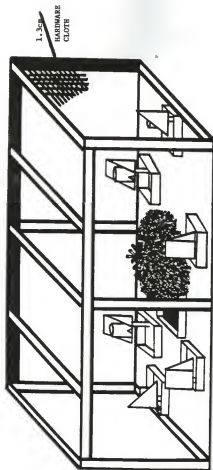


Figure 12. Outdoor flight pen (9.0 x 4.7 x 2.3 m) on Konza Prairie Research Natural Area, used to house cardinals during time budget trials. Six individual feeders, cedar dome, and water provision are also depicted.

Upon completion of all trials, uneaten and spilled seed were collected from each feeder (and from a radius of 1.5 m around each), dried, and weighed to 0.1 g. An average consumption per bird per day was determined from total seed consumed per pen during the entire experiment divided by the number of bird-days (number of birds multiplied by number of days pen was utilized). These data were combined with laboratory-estimated existence energies to estimate the energetic cost of semi-free-living conditions for cardinals.

STUDY II. RESULTS

Estimation of Cardinal Semi-Free-Living Energies

Laboratory determined existence energies were 24.5 and 20.1 kcal/day for cardinals on diets on oil-type sunflower and millet, respectively (Table 9). Cardinal metabolic efficiencies for those 2 diets were 79% and 83%, respectively (Table 9). The amount of gross energy consumed by cardinals in the field under semi-free-living experiments was 72.8 kcal/bird/day for sunflower and 49.9 kcal/bird/day for millet, with a resultant metabolized energy of 57.8 kcal/day on sunflower and 42.4 kcal/day on millet (Appendix, Table 4). Semi-free-living energy for cardinals was estimated at 136% over existence on sunflower and 111% over existence on millet.

Cardinal Time Budgets

Individual cardinals maintained weight (to within 5%) during all time budget trials, although mean weight varied significantly with diet. Millet-fed birds weighed 41.8 g, significantly lighter than sunflower-fed birds at 42.2 g (Table 10).

Cardinals spent 70% of their time perching, significantly more than in any other documented activity. Time spent feeding at feeding stations averaged 14% overall while time spent foraging away from the stations averaged 5%. Other relatively time-consuming activities included sitting (4%) and flying (4%). Maintenance, predator scanning, drinking, interspecific interactions, and pre-nesting behaviors together accounted for the remaining time spent (Figure 13).

The percent of time cardinals spent flying varied significantly with quarter of the day, ranging from 2% (quarter 4) to 6% (quarter 1) (Appendix, Table 5), but did not vary with diet or trial (Appendix, Table 6). Percent of

Table 9. Semi-free-living energies and related calculations as influenced by diet for cardinals in outdoor flight pens. Values are derived from 5-bird group means summed over 5 trials in each of the 2 test pens. Standard deviations or standard errors do not appear with some calculations due to lack of replication. Laboratory-determined values have corresponding standard errors. Values with a common superscript read across a row do not differ ($p < 0.05$).

VARIABLE	DIET	
	White Proso Millet	Dehusked/Cracked Oil-type Sunflower
Gross Energy (kcal/g)	$4.4^a \pm 0.11$	$6.4^b \pm 0.16$
Metabolic Efficiency (%)	$85.1^b \pm 1.31$	$79.4^a \pm 1.13$
Metabolizable Energy (kcal/g)	$3.7^a \pm 0.07$	$5.1^b \pm 0.07$
Metabolized Energy (kcal/bird/day)	42.4	57.8
Semi-Free-Living Energy (kcal/bird/day)	22.3	33.3
Existence Energy (kcal/day)	$20.1^a \pm 2.30$	$24.5^a \pm 2.30$
Percent Over Existence Energy (%)	111	136

Table 10. Cardinal mean body weights (g) and behavioral time allocations (percent of time) and standard errors as influenced by diet in outdoor flight pens. Values with a common superscript read across a row do not differ ($P \leq 0.05$). Means were derived from 5-bird groups over 5 trials.

VARIABLE	DIET	
	White Proso Millet	Dehusked/Cracked Oil-type Sunflower
Bird Pretrial Weight (g)	41.8 ^a \pm 0.38	42.4 ^a \pm 0.38
Bird Posttrial Weight (g)	41.6 ^a \pm 0.38	42.1 ^a \pm 0.38
Flying (%)	3.9 ^a \pm 0.45	4.0 ^a \pm 0.45
Perching (%)	67.0 ^a \pm 2.10	73.5 ^b \pm 2.10
Maintenance (%)	1.4 ^a \pm 0.63	1.5 ^a \pm 0.63
Sitting (%)	5.7 ^a \pm 0.97	2.6 ^a \pm 0.97
Predator Scanning (%)	1.0 ^a \pm 0.15	0.8 ^a \pm 0.15
Drinking (%)	0.7 ^a \pm 0.26	1.1 ^a \pm 0.26
Interspecific Interaction (%)	0.9 ^a \pm 0.14	0.5 ^a \pm 0.14
Nesting Behavior (%)	0.0 ^a \pm 0.06	0.1 ^a \pm 0.06
Foraging 1.5m From Feeder (%)	2.4 ^a \pm 0.82	7.5 ^b \pm 0.82
Feeding 1.5m From Feeder (%)	17.1 ^b \pm 1.20	10.8 ^a \pm 1.20

* Mean not different from zero ($P \leq 0.05$)

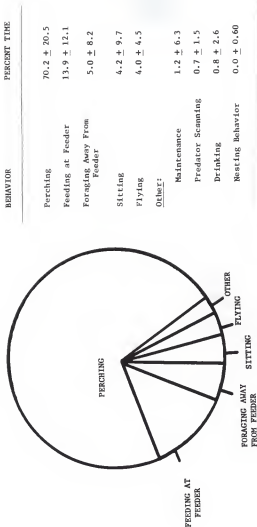


Figure 13. Mean percent time spent by cardinals in outdoor flight pens. Values and associated standard errors derived from 5-bird groups over 5 trials during 4 quarters of the day.

time spent scanning for predators varied significantly with trial, ranging from 0.13% (trial 5) to 2.3% (trial 1) and was not significantly different from zero for trial 5 (Appendix, Table 6). Predator scanning time did not vary with diet or quarter. Percent of time spent foraging away from the feeding stations varied significantly with diet, with values of 2.4% on millet and 7.5% on sunflower (Table 10), but not with trial or quarter. Percent of time spent perching varied significantly with quarter, trial (Appendix, Tables 5, 6), and diet (Table 10). During trial 1, cardinals perched 59% of the time compared to 79% of the time during trial 4. Cardinals perched 64% of the time during quarter 1, significantly less than the 79% of the time spent perching during quarter 3 (Appendix, Table 5). Cardinals on a diet of sunflower perched 73.5% of the time, more than the 67% of time spent perching by birds on a diet of millet.

Percent of time spent in intraspecific interaction varied significantly with both quarter and trial (Appendix, Tables 5, 6), but not with diet. Intraspecific interaction time was highest during trial 1 and was different from zero for trials 1, 2, and 3, and for all 4 quarters (Appendix, Tables 6, 5).

Percent of time spent feeding at the feeding stations did not vary by quarter but varied significantly with trial (Appendix, Table 6) and diet (Table 10), ranging from 10% (trial 5) to 21% (trial 1), and 11% on a diet of sunflower to 17% on a diet of millet (Table 10).

Percent time spent engaged in maintenance, sitting, drinking, and pre-nesting activities did not vary with trial, diet or quarter.

Male cardinals spent significantly more time scanning for predators than females, and both means were different from zero (Table 11). The sexes did not vary significantly in any other behavioral variables measured (Table 11).

Table 11. Cardinal mean body weights and behavioral time allocations (percent of the time) with standard errors as influenced by sex of bird in outdoor flight pens. Means are derived from 5-bird groups over 5 trials in 2 pens. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE	SEX OF BIRD	
	Female	Male
Bird Pretrial Weight (g)	39.7 ^a \pm 0.23	45.4 ^b \pm 0.27
Bird Posttrial Weight (g)	39.6 ^a \pm 0.22	45.3 ^b \pm 0.26
Flying (%)	4.2 ^a \pm 0.45	3.7 ^a \pm 0.53
Perching (%)	70.8 ^a \pm 2.22	69.4 ^a \pm 2.61
Maintenance (%)	1.4 ^a \pm 0.58	1.5 ^a \pm 0.68
Sitting (%)	3.5 ^a \pm 0.97	5.1 ^a \pm 1.14
Predator Scanning (%)	0.57 ^a \pm 0.16	1.39 ^b \pm 0.28
Drinking (%)	0.68 ^a \pm 0.24	1.29 ^a \pm 0.19
Interspecific Interaction (%)	0.65 ^a \pm 0.14	0.78 ^a \pm 0.17
Neating Behavior (%)	0.0 ^{a*} \pm 0.05	0.12 ^{a*} \pm 0.07
Foraging 1.5m From Feeder (%)	5.2 ^a \pm 0.95	4.6 ^a \pm 1.12
Feeding 1.5m From Feeder (%)	14.7 ^a \pm 1.37	12.9 ^a \pm 1.16

* Mean not different from zero ($P = 0.05$)

STUDY II. DISCUSSION

Cardinal Existence Energies, Semi-Free-Living Conditions and Time Budgets

The assumption of a 40% requirement over existence for free-living in the model of Wiens and Innis (1974) was not supported here. Cardinals in this study were provided with constant and over-abundant food and water and were thus not forced to forage for food or fly long distances to reach resources. The minimization of the extremely costly activity of flying in these pen studies suggests that the values of 111% and 136% over existence on millet and sunflower, respectively, are representatively low.

Although winter may not necessarily be energetically more demanding than the breeding season, as suggested by Mugaas and King (1981), the time available to acquire food decreases. Birds wintering in Kansas have approximately 10 hours during which they must intake enough energy to maintain themselves during the subsequent 14 dark hours. Small passerines typically have limited energy storage capacity and high existence energy requirements (Walsberg 1983). When food is scarce, of low relative net quality, or simply not preferred, bird efforts to acquire enough energy for existence should be reflected in time allocations. Survival is really the summation of an "optimal" behavioral repertoire of which energy acquisition is only a part. Thus, a foraging bird attempting to gather energy which fatally exposes itself to a predator, has not behaved "optimally". Willson and Harneson (1973) suggest that foraging bouts as opposed to foraging continuously may be safer in terms of predation yet act to further restrict valuable foraging time. Cardinals in this study did not substantiate that hypothesis, not because they continuously foraged, but because they were exposed visually to predators the entire day as they perched on pen side supports. However, an artificial "sense of security" may have developed in these penned cardinals based on predator scanning time which decreased from a high during trial 1 to a low during trial 5.

Sufficient energy acquisition for maintenance and other necessary activities can result from spending more time foraging or from indirectly spending less time foraging but having a higher metabolic efficiency on food ingested.

In this study it was predicted and substantiated that cardinals would be forced to increase their foraging time on the energetically inferior diet of white proso millet in order to consume enough energy to sustain normal activity (Cardinals had a higher metabolic efficiency on millet but millet had a lower metabolizable energy content). The differential feeding times on millet and sunflower (17.1% and 10.8%, respectively) apparently did not approach a theoretical threshold where predator scanning, maintenance, sitting, and drinking was replaced by foraging. Adaptively, perhaps, maintenance, sitting, and drinking are constants while a time allocation change in predator scanning occurs with varying flock sizes, not diet per se. Male cardinals did, however, scan for predators more than females perhaps because of males' bright coloration. Cardinals on a diet of sunflower spent significantly more time perching than those on millet, suggesting a diet-based change in time allocation of that behavior. Cardinals required more energy to exist on sunflower but based on its higher energy content, reached the necessary intake level more quickly than did those birds on millet. The "extra" feeding time was then channelled into perching (the most commonly observed activity) and foraging away from the feeders. This increased time spent foraging away from the feeders by sunflower-fed birds may reflect a nutrient deficiency of that diet.

Extreme differences in diet metabolizable energies (metabolic efficiency x diet unit energy content) might produce shifts in time allocations of additional behaviors under natural conditions, and allow further assessment of birds' behavioral similarity to theoretical prediction of "optimal" activity.

While birds on sunflower required more to exist than birds on millet (based perhaps on previously-mentioned seed and bird internal digestive characteristics), sunflower-fed birds used more energy over existence for semi-free-living conditions. This could be reflective of higher costs associated with consumption of sunflower or from increased net power available for more energy-demanding and supplemental activities.

STUDY III. INTRODUCTION AND REVIEW

The Mechanisms of Seed Selection in Sparrows

Natural selection should favor more efficient foragers as long as their survival or reproductive success, i.e., fitness, improves as a result of specific foraging behaviors. Thus, through evolutionary selective pressures, organisms tend to collect food efficiently (Emlen 1966, MacArthur and Pianka 1966, Krebs 1978).

Decision and selection are arbitrary human terms, not intended to imply conscious thought, saying that animals are designed to follow certain rules (Krebs 1978). Emlen (1966) and MacArthur and Pianka (1966) pioneered predicting animal foraging behavior using mathematical models. Schoener (1971) proposed the idea of measuring the efficiency of foraging using some currency, usually energy. Optimal foraging theory predicts that animals will forage in such a way as to maximize net energy gain per unit time. Although not all species typify foraging to maximize net energy gain (Goss-Custard 1977, Kushlan 1978), optimal foraging theory predicts what food items will be included in the diet in what order, and under what conditions. See Pyke et al. (1977) for a review of the subject.

Emlen and Emlen (1975) explored the ability of mice to accurately "judge" the energy content of individual seeds and subsequently make optimal selections as predicted by theory. They found theoretical predictions supported generally, but only with corrections made for imperfect selections made by the foragers (supported by Hughes 1979). Schluter (1981) cautions the application of simple foraging models to complex communities. Lacher et al. (1982) echo that caution, noting that empirical support for optimal foraging models is limited to simple situations. They additionally suggest that forager learning adds realism to current models (supported by Hughes 1979).

Livdahl (1979) assesses the assumption that forager handling time (a variable influencing preference) is constant. He concludes that handling time is dynamic, determined by forager attributes of search, capture, and ingestion efficiency, and prey attributes relating to evasion, etc. Waddington (1982) reinforces those ideas, maintaining that the modeling of any biological process is dynamic. He proposes a more realistic simultaneous encounter model in contrast to the standard sequential encounter model. The former model incorporates travel and handling times and caloric values, and results in the prediction of partial preferences as does Pulliam's (1975) nutrient constraints model. Rapport (1971) emphasizes that while the ideal forager minimizes time spent foraging while maximizing energy, in reality, one parameter may be more important than the other. Real et al. (1982) state that net energy gain may not completely characterize an organism's food choice. The empirical evidence of Real et al. (1982) suggests that foragers assess reward variance as well as reward absolute value. It may be as advantageous to minimize the uncertainty of the expected reward as it is to maximize the expected reward (Real et al. 1982).

Optimal foraging also predicts the expansion or contraction of the number of types of items included in the diet based upon overall food densities of only those food items that improve the feeding rate. Ivlev's (1961) work on fish shows that selectivity increases positively with overall food density. Emlen (1966) supports that idea and suggests that foragers will take any food encountered when food is scarce and become more selective when food is abundant. These results support formalized optimal foraging theory predictions. The recent work of Werner and Mittelbach (1981) shows that fish feed in richer habitats and switch habitats when the profitability of one drops below that of another.

Emlen (1966) suggests that when food is abundant, items are included in the diet in proportion to their relative abundances, regardless of energy content. These findings are supported by Willson (1971) and Willson and Harneson (1973), working with New World sparrows, Robel et al. (1974), working with bobwhites, and Gillespie (1982), working with greenfinches (Carduelis chloris). Schuster (1982) found that Darwin's finches (Geospizinae) did not generalize use of food patches despite a large decrease in food abundance; this evidence directly contradicts optimal foraging theory predictions.

Smigel and Rosenzweig (1974), working with heteromyid rodents, suggest that preference is inversely proportional to search time. Royama (1970) suggests the same mechanism for food selection in the great tit (Parus major). Smith and Follmer (1972) state that preference is in part based on husking time in squirrels. Rosenzweig and Sterner (1970) found a positive correlation between husking speed and body size for heteromyid rodents and an inverse correlation between the relative rate of caloric gain and relative body size. Neither of those relationships holds for [emberizid] sparrows (Willson 1971, Abbott et al. 1975). Hespenheide (1966) found a correlation between seed choice and husking time in sparrows. His data support the idea that beak size and shape correlate with size of food taken, as does that of Kear (1962) and Schluter [for small sparrow species (1982)]. Willson (1971) found a similar trend for small-billed sparrows, but found that cardinals (a larger-billed sparrow) showed no seed size preference. She suggests that not all seed types tested pushed the upper and lower limits of husking capabilities in her test species. Abbott et al. (1975) found no significant seed size preferences overall but suggest the critical seed characteristics limiting bird handling are seed breadth (supported by Schluter 1982) and hardness. Sherry and McDade (1982) emphasize that seed handling time is not a simple function of one variable such as width, mass, hardness, or taste. Davison (1962) suggests that

taste per se, but not color, attracts birds to potential food items. Goldsmith and Goldsmith (1982) document a sense of smell in hummingbirds but conclude that vision is a more important food selective sense. Bennett and Prince (1981), working with ring-necked pheasants (Phasianus colchicus), Mason and Reidinger (1982), working with red-winged blackbirds (Agelaius phoeniceus), and Rooke (1983), working with silvereyes (Zosterops spp.), found that previously preferred foods were avoided after treatment with chemicals, suggesting that taste and smell are important in food selection. Bennett and Prince (1981) note that reversion to former food preferences eventually occurred when untreated foods were offered.

Hughes (1979) proposes a model which incorporates prey recognition time, misidentification of prey, and learning into the selection process. Through learning to handle various prey more efficiently, the forager may slightly alter food selection and transpose previous preference rankings (Hughes 1979). The ideas of effects of learning or experience on food preference are supported by Croze (1970), working with crows (Corvus spp.), and Gillette and Thomas (1981), working with domestic chicks (Gallus gallus). Restriction to a non-preferred seed during the first 5 weeks of life results in a preference for that seed in zebra finches (Taeniopygia guttata) (Rabinowitch 1979). This learned preference may persist in some individuals for 2 - 4 mo but generally decreases gradually with exposure to naturally preferred seeds (Rabinowitch 1969). Kear (1962) found that juvenile sparrows preferred smaller seeds than adults and concluded that observational learning by juveniles may be important in early preference formation (supported by Gillespie 1982).

Food selection based on diet nutritional characteristics has been investigated frequently with differing results. Several authors (Pulliainen 1965, Moss 1968, Gardarsson and Moss 1968, Postler and Barrett 1982) found that some

organisms select food based on a specific nutrient or on energy content. Bookhout (1958), working with bobwhites and Dillery (1961) and West (1967), both working with sparrows, found that food selection was not based upon abundance, size or apparent availability of food.

A further complication is the intraspecific variability in morphology and/or foraging technique (Dove 1935, Herrera 1978, Ebersole and Wilson 1980) which may additionally reduce the predictability of food selection in birds.

Hogan-Warburg and Hogan (1981), studying domestic chicks, suggest that continued sampling behavior by inexperienced individuals is necessary for the development of appropriate selection of food items. This behavior helped explain why chicks repeatedly ate sand. Smith and Follmer (1972) suggest that digestibility of food eaten (along with husking time) are the bases for preference in 2 species of squirrels.

Ebersole and Wilson (1980) suggest a dynamicity of food preference relating to fulfillment of changing nutritional requirements. Myton and Ficken (1967) found that chickadees (Parus spp.) showed a strong preference for small seeds on warm days. In response to decreasing ambient temperature, chickadees switched preferences from small seeds to energetically more rewarding large seeds. Handling time for large seeds was twice that of small seeds as was the energetic gain; energetic savings was accrued by a decrease in trip numbers per food item for large seeds (Myton and Ficken 1967). Willson (1971) and Willson and Harmeson (1973) did not observe a similar preference shift in tested sparrows. Documenting an alternative strategy, Alatalo (1982) found that northern forest birds shifted to less energy-demanding foraging techniques and decreased niche breadth and overlap as temperatures decreased. Taylor (1977) proposes that preference for 1 seed type is directly influenced by prior consumption of other seed types.

Not surprisingly, food selection by birds is based upon an array of nutritional, psychological, physical, ecological, and ethological variables. In general, seed physical and distributional characteristics appear to be the most influential variables in avian food preferences.

This portion of the present research will assess the influence of seed energy content and handling time, not seed species per se, on sparrow seed preferences.

STUDY III. METHODS

Seed Preferences and Handling Times

The purpose of this experiment was not to examine all possible combinations of diets for preferences per se but rather to construct pairings to assess preference based on seed metabolizable energy content and/or seed handling time. The gross energy contents of Maximilian sunflower, dehusked and whole oil-type sunflower, cracked sorghum, and white proso millet were determined previously, as described in the metabolic efficiency methods section.

By multiplying the metabolic efficiencies for each sparrow species on each diet by the gross energy in each diet, metabolizable energy (energy available) for each diet was determined. The time required for a bird to husk and otherwise prepare a seed for consumption (handling time) was measured for 8 individuals of the 4 sparrow species on each of the 4 seed diets. Birds were timed to 0.1 sec using a hand stopwatch. The time taken for a bird to initially manipulate a single seed until the seed husk appeared at the side of the beak (Kear 1962) was recorded. Seeds which were repeatedly dropped were not used in handling time determinations. See Figure 14 for the mechanics of seed-husking by a typical sparrow. Cracked sorghum was used as an index for the minimum handling time as it required no husking.

Birds were starved for 12 hr prior to testing to ensure seed consumption in spite of observer presence. Some individuals, particularly juncos, required a longer starvation period (up to 36 hr) to obtain handling time data. This prolonged fasting period had no apparent detrimental effects on the birds, although test birds were not weighed during trials. Ten handling time observations were made for each individual bird on each diet (a Latin Square design). Only those observations during which seeds were continuously manipulated were recorded (Abbott et al. 1975). A mixture of all seed diets was

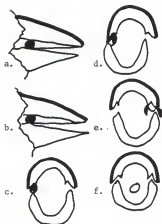


Figure 14. Diagram of the typical seed-husking process in sparrows. From Ziswiler and Farner (1972), In Farner and King (1972).

provided to all birds prior to testing to ensure equal familiarity with each (Kear 1962, Willson 1971). Trial length varied because of species' differential handling times and individual variability regarding fear of observer.

Mean metabolizable energy content and mean handling times on each diet for each sparrow species were subsequently used to develop 4 separate diet pairings to test the influence of those seed characteristics on seed preference. The first diet pair was sorghum and dehusked oil-type sunflower, seeds with similar handling times but different metabolizable energy contents. The second pair was Maximilian sunflower and dehusked oil-type sunflower, seeds with different handling times but similar metabolizable energies. The third diet pair was millet and cracked sorghum, seeds with similar handling times and similar metabolizable energies. The fourth diet pair was millet and whole oil-type sunflower, seeds with different handling times and different metabolizable energy contents.

Eight individuals of all 4 sparrow species received each of the 4 diet pairs once (a Latin Square design) in 3-hr trials initiated 1 hr after light period onset. Seed pairs were presented in equal volumes and known weights in 4.8 x 3.2 x 3.2-cm plastic seed dishes, and in excess supply of potential consumption. Seed dishes were placed equidistant from the water dispenser, approximately 5 cm apart. After each trial, cages were cleaned and all remaining seed collected. The weight of each seed diet eaten was the sum of the weights of uneaten seeds and those spilled and uneaten, subtracted from the initial weight of seeds presented. Weight of seed eaten was used as the preference index.

STUDY III. RESULTS

Handling Times

All sparrow species exhibited the lowest handling time on diets of cracked sorghum and the highest on diets of oil sunflower (Table 12). Cardinals, Harris' sparrows, and tree sparrows all handled millet more quickly than Maximilian sunflower, while juncos handled those 2 diets with equal speed.

Species comparisons on single diets showed that Maximilian sunflower, millet, and cracked sorghum were handled with the same speed by all bird species. Cardinals took an average of 11.8 sec to husk 1 oil sunflower seed, not significantly different from the 10.7 sec required by Harris' sparrows. Juncos took 15.8 sec to handle 1 oil sunflower seed, significantly less time than the 20.9 sec required by tree sparrows. These 2 smaller sparrow species were both less efficient at handling oil sunflower seeds than cardinals and Harris' sparrows.

Averaging over all diets, Harris' sparrows were more efficient than juncos and tree sparrows, cardinals more efficient than tree sparrows, and juncos more efficient than tree sparrows (Table 11).

None of the 4 sparrow species became more "experienced" over time at handling any diet.

Seed Preferences

Cardinals, Harris' sparrows, and juncos all displayed no significant preference between the seed pair of equal energy content and unequal handling time (Maximilian sunflower versus dehusked oil sunflower) (Table 13). Tree sparrows selected dehusked oil sunflower (the diet with the lower handling time) significantly over Maximilian sunflower. On a diet pairing of equal energy content and equal handling time (millet versus sorghum), Harris' sparrows and juncos displayed no significant preference while tree sparrows

Table 12. Mean handling times (sec) and associated standard errors for 8 individuals each of the 4 sparrow species on all diets (averaged over trials). Values with a common upper case letter to the left of each number read down a column do not differ ($P < 0.05$). Values with a common lower case letter to the right of each number read across a row do not differ ($P < 0.05$).

DIET	BIRD SPECIES			
	Cardinal	Harris' Sparrow	Junco	Tree Sparrow
Maximilian Sunflower	C _{4.6^a} ± 0.37	C _{3.9^a} ± 0.34	B _{4.4^a} ± 0.19	B _{5.0^a} ± 0.64
	B _{2.4^a} ± 0.37	B _{1.8^a} ± 0.34	B _{4.4^a} ± 0.19	A _{2.3^a} ± 0.64
Oat-type Sunflower	D _{11.8^a} ± 0.37	D _{10.7^a} ± 0.34	C _{15.8^b} ± 0.19	C _{20.9^c} ± 0.64
	A _{0.3^a} ± 0.37	A _{0.3^a} ± 0.34	A _{0.3^a} ± 0.19	A _{0.3^a} ± 0.64
Sorghum				

Table 13. Mean seed preferences of 8 individuals of each of the 4 sparrow species on each of 4 diet pairs based on diet energy content and handling time. Significant ($P \leq 0.05$) preference is indicated by an asterisk, with the preferred diet appearing in parentheses.

BIRD SPECIES	DIET PAIR			
	=Energy/#Handling time ¹	=Energy/#Handling time ²	=Energy/#Handling time ³	=Energy/#Handling time ⁴
Cardinal	N.S.	* (Millet)	N.S.	* (Millet)
Harris' Sparrow	N.S.	N.S.	* (Dehusked-oil)	* (Millet)
Junco	N.S.	N.S.	N.S.	* (Millet)
Tree Sparrow	* (Dehusked-oil)	* (Millet)	* (Dehusked-oil)	* (Millet)

1 Maximilian sunflower and dehusked oil-type sunflower (latter has lower handling time)

2 Millet and sorghum

3 Sorghum and dehusked oil-type sunflower (latter has higher energy content)

4 Millet and oil-type sunflower (latter has higher energy content and handling time)

and cardinals both selected millet over sorghum. Cardinals and juncos displayed no significant preference between the diet pair of unequal energy content and equal handling time (sorghum versus dehusked oil sunflower), but Harris' sparrows and tree sparrows both preferred dehusked oil sunflower (the diet with the higher energy content) significantly over cracked sorghum.

All 4 sparrow species displayed a significant preference for millet (low energy content and low handling time) over oil sunflower (high energy content and high handling time).

Diets included in more than 1 pairing (millet, cracked sorghum, and dehusked oil sunflower) were consumed in equal amounts, regardless of diet pairing, by all 4 sparrow species.

STUDY III. DISCUSSION

Seed Preferences and Handling Times

A diet which has a low handling time, high metabolic efficiency, and resultant high metabolizable energy for a bird will provide no energetic benefit if that diet is not preferred (consumed) (Taylor 1977).

If handling time were the single most important determinant of seed preference, birds in this study would have selected sorghum, dehusked (and cracked) oil sunflower, millet, Maximilian sunflower, and oil-type sunflower (intact) in decreasing order. On the preference pairing of Maximilian sunflower and dehusked oil sunflower (latter should be preferred), only tree sparrows substantiated the prediction while the other 3 bird species displayed no preference (Table 13). On the diet pair of intact oil sunflower and millet, however, all 4 bird species preferred the predicted diet of millet. In the other 2 diet pairs (millet versus sorghum and sorghum versus dehusked oil sunflower) where handling time was the same, birds should have displayed no diet preference. This was substantiated in 4/8 (50%) of the cases. Over all diet pairs for all sparrow species, 9/16 (56%) were accurately predicted based on diet handling times. Juncos followed handling selection predictions 75% of the time and the other 3 species followed predictions 50% of the time.

Seed preference based on unit energy content predicted that birds would have selected dehusked oil sunflower, intact oil sunflower, Maximilian sunflower, sorghum, and millet in decreasing order. On the preference pairing of sorghum and dehusked oil sunflower (latter should be preferred), both Harris' sparrows and tree sparrows substantiated the prediction while cardinals and juncos displayed no preference. On the diet pair of millet and intact oil sunflower, all 4 bird species selected the unpredicted diet of millet. In the other 2 diet pairs (Maximilian sunflower versus dehusked oil sunflower and

millet versus sorghum), where energy content was the same, birds should have displayed no diet preference. This prediction was substantiated in 5/8 (62.5%) of the cases. Over all 4 diet pairs for all sparrows, 7/16 (44%) were accurately predicted based on diet energy content. Harris' sparrows followed energy content selection 75% of the time, while juncos did 50%, and cardinals and tree sparrows both did 25% of the time.

Obviously, diet handling times and energy contents examined independently are too simple to explain a dynamic behavioral process for even a single bird species.

Table 14 shows preference indices which combined the diet attributes of actual consumption, metabolizable energy, and handling time. An ideal index value of 3 ($1 + 1 + 1$) for top ranking of all 3 characteristics was the basis for predicting diet preferences. Each seed diet for each bird species, was assigned a value from 1 to 5 (1 = high) for each of the 3 diet attributes and subsequently compared with the ideal value of 3. Numbers in parentheses show the ranking of theoretically preferred diets (1 = most preferred). Based on the index, cardinals should have shown no preference between sorghum, dehusked oil sunflower, and millet followed by decreasing preferences of Maximilian sunflower and oil sunflower. These predictions were substantiated only 1/4 (25%) of the time when millet was preferred over oil sunflower in that pairing. Harris' sparrows should have preferred sorghum, dehusked oil sunflower, Maximilian sunflower and millet, and intact oil sunflower in that order. These predictions were substantiated only 25% of the time when millet was preferred over intact oil sunflower in that pairing. Juncos should have shown no preference between sorghum and dehusked oil sunflower followed by decreasing preferences of millet, Maximilian sunflower, and intact oil sunflower. These predictions were substantiated in 2/4 (50%) of the cases. Tree sparrows should have preferred sorghum, dehusked oil sunflower, millet, Maximilian sunflower,

Table 14. Preference index combining the diet characteristics of past consumption (C), metabolizable energy (M), and handling time (H) for cardinals, Harris' sparrows, juncos, and tree sparrows on 5 diets. A ranking of 1 is the most beneficial, a ranking of 5 the least. An ideal index value of 3 (1 + 1 + 1 for top ranking of all 3 characteristics) is the basis for predicting diet preferences. Predicted preferences by number appear in parentheses under each set of rankings.

DIET	Cardinal			Harris' Sparrow			Junco			Tree Sparrow		
	H	M	C	H	M	C	H	M	C	H	M	C
Maximilian Sunflower	4	3	3 (2)	4	3	2.5 (3)	3.5	3	3 (3)	4	3	3 (4)
Millet	3	4	1 (1)	3	4	2.5 (3)	3.5	4	1 (2)	3	4	2 (3)
Oil Sunflower	5	1.5 (3)	4.5	5	1.5 (4)	4.5	5	1.5 (4)	4.5	5	1.5 (5)	4.5
Sorghum	1	5 (1)	2	1	5 (1)	1	1	5 (1)	2	1	5 (1)	1
Dehusked Oil Sunflower	2	1.5 (1)	4.5	2	1.5 (2)	4.5	2	1.5 (1)	4.5	2	1.5 (2)	4.5

and intact oil sunflower in decreasing order. These predictions were substantiated 50% of the time. Overall, the consumption, metabolizable energy, and handling time attribute combinations accounted for only 7/16 (44%) of the actual preferences of the birds.

The incorporation of another potential mechanism (past consumption) for diet preferences in birds revealed no clear explanation for the observed preferences. The results do suggest that sparrows do not select food based directly on energy content, handling, or prior consumption amounts. A controlled field study where diets are not presented ad libitum might provide further preference information (Willson and Harmeson 1973).

Willson and Harmeson (1973) suggest that birds are likely selecting generalized habitats for an array of factors rather than specific diets or their characteristics. Nutritive components, susceptibility of seeds to insect or fungal infestation and actual taste of the seeds may be important variables which further influence seed selection in birds.

STUDY IV. INTRODUCTION AND LITERATURE REVIEW

Trypsin Inhibitors in Plant Seeds Related to Metabolic Efficiencies in Sparrows

Proteinase inhibitors are proteins or polypeptides that bind to peptide proteolytic (bond-splitting) enzymes, resulting in inhibition of the proteolytic activities of those enzymes (Ryan 1979). Natural proteinase inhibitors are found throughout the living world and serve either to regulate proteolytic enzymes or protect tissues and fluids from proteolytic attack (Ryan 1979). See Tsechesch (1974), and Richardson (1977) for reviews on the history and development of proteinase inhibitor discovery and characterization, and distribution in nature.

Trypsin inhibitors are a class of proteinase inhibitors that have been documented mainly in the plant families Fabaceae, Graminae, and Solanaceae (Ryan 1979, Tsechesch 1974, and Richardson 1977). This is primarily the result of the nutritional and economic importance of these groups which include peas, soybeans, beans, all grain grasses, and tomatoes and potatoes.

Inhibitors are generally concentrated in the reserve tissue in plants (e.g., seeds and fruits) but do occur in vegetative portions (Chang 1977). Absolute amounts of inhibitor may vary with germination and Halim et al. (1973) suggest that absolute amount is genetically and environmentally controlled.

Chang (1977) found that cereal inhibitors, in contrast to legume inhibitors, appear to be weak. He found that whole wheat flour and whole rye flour exhibited, respectively, 1% and 2 - 3% of the trypsin inhibitory activity found in soy flours. To date, no study has attempted to provide an ecological connection between biochemical digestive processes and adaptive variation in metabolic efficiencies in birds. The present study seeks to assay 4 diets (sorghum, millet, and 2 species of sunflower) of granivorous birds for trypsin inhibitor content to gain biological insight into differing metabolic efficiencies.

STUDY IV. METHODS

Analysis of Four Seed Diets for Trypsin Inhibitor Content

To gain biochemical insight into why proximate differences in metabolic efficiency occurred within bird species on the different seed diets, the relative amounts of trypsin inhibitor in oil sunflower, Maximilian sunflower, sorghum, and white proso millet were determined via spectrophotometric assay analyses.

Extraction Procedure - A 3.5-g sample of each seed diet was ground twice in a Wiley micro-mill (Filho 1974), once through a 20-mesh screen and a second time through a 30-mesh screen. The resultant fine flour was mixed with 15 ml distilled water (Filho 1974) and magnetically stirred at medium speed for 1 hr, then set aside and covered for 1 hr. The resultant slurry was filtered through cheesecloth and centrifuged at 10,000 rpm for 10 min. The supernatant was collected, recentrifuged at 10,000 rpm for another 10 min and then recentrifuged again. The final supernatant was then centrifuged at high speed in an Eppendorf 5412 centrifuge for 2 min and that supernatant collected and recentrifuged for another 2 min. This procedure produced a particle-free sample which is crucial for proper spectrophotometric analysis (Lei 1981).

Sample Analysis - Required reagents were prepared and stored according to the procedures described in Lei (1981). Calibration, reference, and sample assays were also prepared and analyzed spectrophotometrically according to Lei's (1981) procedures, except that the samples were not diluted beyond the initial 15 ml distilled water addition.

Final assays plotting absorbance over time for each seed extraction, were analyzed in triplicate and averaged.

STUDY IV. RESULTS

Trypsin Inhibitor Assays

Percent inhibition of the digestive enzyme trypsin was 4% for sorghum, 5% for millet, 12% for Maximilian sunflower, and 37% for oil-type sunflower. Sorghum and millet were not significantly different in percent inhibition but were significantly lower in amounts than Maximilian sunflower which was significantly lower in trypsin activity than oil-type sunflower (Figure 15).

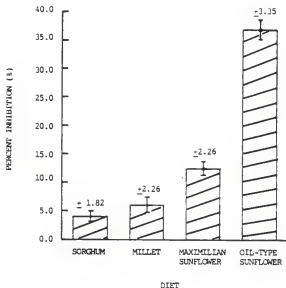


Figure 15. Histograms of mean percent trypsin inhibition with associated standard errors, documented for sorghum, millet, Maximilian sunflower, and oil-type sunflower. Each sample represents an average of an assay performed in triplicate (e.g., $n=11$ for millet actually = 33 tests for inhibitor).

STUDY IV. DISCUSSION

Trypsin Inhibitor Content in Seed Diets and Sparrow Metabolic Efficiencies and Existence Energies

Based solely on the relative activity of trypsin inhibitor in the 4 seed diets (37% oil sunflower, 12% Maximilian sunflower, 5% millet, 4% sorghum), sparrows should exhibit lower metabolic efficiencies and higher existence energies on the 2 sunflower diets relative to those on millet and sorghum. While millet and sorghum-based metabolic efficiencies should not be different from each other, a diet of oil sunflower should produce a relatively lower metabolic efficiency and higher existence energy than a diet of Maximilian sunflower. The predicted differential metabolic efficiencies and existence energies are based on the hypothesis that a higher proportion of trypsin inhibitor activity will result in an increased amount of indigestible (excreted) energy (and thus a lower metabolic efficiency) and increased internal work by the sparrows to extract energy from the seed (and thus a higher existence energy).

Tree sparrows exhibited the same existence energy on all 4 diets while in Harris' sparrows, the existence energy on millet was different from that of the 2 sunflowers while that of sorghum was not. In cardinals, the existence energy on sorghum was different from that of oil-type sunflower while that of millet was not. Neither millet nor sorghum existence energies were different from that of Maximilian sunflower. Even though junco existence energies followed some trypsin inhibitor activity predictions, contrary to predictions, Maximilian sunflower existence energy was not significantly different from that on oil-type sunflower. Metabolic efficiency findings relating to trypsin inhibitor activity were also at variance with the predicted responses. In tree sparrows, all diet metabolic efficiencies were significantly different

from each other while in juncos, sorghum and millet diets resulted in similar metabolic efficiencies which were significantly higher than those of the similar pair of Maximilian and oil-type sunflower. Harris' sparrows displayed metabolic efficiencies ranking in decreasing order from millet, sorghum and Maximilian sunflower, to Maximilian sunflower and oil-type sunflower. Cardinals on millet and sorghum diets produced the highest relative metabolic efficiencies while sorghum produced a similar efficiency to oil-type sunflower which was not significantly different from the efficiency on Maximilian sunflower.

Although diet metabolic efficiencies and existence energies did not parallel the predictions well from a significance-testing approach, the small sample size of trypsin inhibitor assays and lack of knowledge of sparrows' interspecific variations in internal digestive chemistry may serve to mask some valuable results. Also, bovine trypsin was used in the assay procedure.

Since oil-type sunflower had a much greater trypsin inhibitor activity than millet and sorghum, comparisons between respective bird metabolic efficiencies and existence energies on oil-type sunflower and millet or sorghum may be more revealing. Existence energy was significantly greater on a diet of oil-type sunflower than on one of sorghum for cardinals (30% greater) and for juncos (26% greater). Existence energy was significantly greater on a diet of oil-type sunflower than on one of millet for Harris' sparrows (23% greater). For tree sparrows, while the existence energy on diets of oil-type sunflower and millet/sorghum were not different at the 0.05 level, the oil-type sunflower existence energy was still 12% greater than that of millet.

Metabolic efficiency comparisons between oil-type sunflower and sorghum or millet also showed a stronger parallel with predictions. Metabolic efficiency was significantly greater on a sorghum diet for Harris' sparrows (8% greater),

juncos (5% greater), and tree sparrows (8% greater). Cardinals showed a 7% increase in metabolic efficiency on millet compared to that of oil-type sunflower.

While not a totally reliable predictor of sparrow metabolic efficiencies and existence energies at this stage, trypsin inhibitor activity in seeds is perhaps one of several interdependent variables (including gut length, food retention time, and other possible plant defenses within the seed) physiologically influencing sparrow energetics.

OVERALL DISCUSSION

Wintering birds are confronted with an array of selective pressures which influence their capacity to intake energy for maintenance and sustained normal activity necessary for survival. Selective pressures also act to limit or expand bird distributions. The combination of an individual birds' physiological capacities (metabolic efficiencies and existence energies), evolutionarily-determined behaviors (diet preferences, differential allocations of time to activities), morphology (reflecting diet handling times and size limitations, flight foraging distance), reaction to ecological pressures (competition and predation), and characteristics of the resources itself (shape and size, nutrient and energy contents, trypsin inhibitor activity) interact to produce a resultant species-specific approach to resource acquisition. Searching for a single variable to explain bird behavioral responses to selective pressures is obviously unrealistic.

Studies I, II, III, and IV explored physiological and digestive capabilities and the facultative behavioral responses of wintering sparrows to varying energy provisions. Junco, cardinal, tree sparrow, and Harris' sparrow differential metabolic efficiencies and existence energies on different diets expose possible partial mechanisms for wintering and breeding distributions. Ideally, each species' energetic characteristics should be investigated on at least an annual scale to gain an overall perspective of energy fate and allocation. It is clear that a high metabolic efficiency on a diet is certainly less important if the bird loses weight or becomes digestively impaired as a result of consuming that diet. In this study, all sparrow mean metabolic efficiencies for each of the 4 test diets were greater than the 70% value used by Wiens and Innis (1974) in their model and all species lost weight on all diets except for Harris' sparrows on a diet of oil-type sunflower. Taylor (1977) found that

some birds will actually starve rather than consume certain diets. Perhaps those birds were better off taking the chance of encountering beneficial food types rather than consuming a diet which could result in earlier death from starvation.

Table 15 summarizes metabolic efficiencies, necessary consumption for existence energy (weight maintenance), actual consumption, the rate of seed intake required to meet the energetic demand, and weight change for each sparrow species on each test diet. The daily consumption in grams necessary for existence was calculated by dividing existence energy on a particular diet by the metabolizable energy per gram on that diet. The required intake rate was calculated based on the gram intake necessary for existence multiplied by the number of seeds per gram. This number of required seeds for existence was converted to a rate by dividing by the 10 hours of winter foraging time available, divided by 60 minutes per hour. The maximum intake rate was calculated based on the mean handling time (in seconds) for each bird species on each diet, and converted to minutes. The data from this study indicate that even on diets where sparrows 1) were capable of handling and thus ingesting adequate amounts of a diet for existence and 2) did consume apparent amounts necessary to meet existence requirements, they still lost weight. This again points to the differential internal energetic costs associated with digestion of various seeds based on both seed characteristics and bird physiological capabilities. The final situation in which birds lost weight was the intuitive case where they simply did not consume enough to maintain themselves. This is puzzling since substantial albeit insufficient amounts were consumed with ad libitum provisions, and the opportunity for actual weight gain existed. Taylor (1977) found a similar situation when field sparrows (Spizella pusilla) and cardinals limited their consumption of ad libitum quantities of thickspike gayfeather (Liatrus pycnostachya) and roundhead lespedeza (Lespedeza capitata) to the point

Table 15. Metabolic efficiencies, existence energies, diet unit energy contents, metabolizable energies, amount of diet (g) needed to meet daily energy requirements, actual consumption, intake rate needed to meet daily energy requirements, and the maximum intake rate (continuous feeding) based on handling time for cardinals, Harris' sparrows, juncos, and tree sparrows.

BIRD SPECIES	DIET			
	Sorghum	Millet	Maximilian Sunflower	Oil-type Sunflower
<u>Cardinal</u> (Mean Body Wgt. 41.1 g)				
Metabolic Efficiency (%)	82	85	75	79
Existence Energy (kcal/day)	17.2	20.1	21.0	24.5
Diet Energy Content (kcal/g)	4.4	4.4	5.9	6.4
Metabolizable Energy (kcal/g)	3.6	3.7	4.2	5.1
Daily Diet Requirement (g)	4.8	5.4	5.0	4.8
Actual Daily Consumption (g)	6.2	6.3	4.9	4.6
Number Seeds/g	260	158	416	23
Required Intake Rate (seed/min)	2	1.4	3.5	0.2
Maximum Intake Rate (seed/min)	200	25	13	5
Weight Change (g)	-0.65	-0.48	-1.23	-0.25
<u>Harris' Sparrow</u> (Mean Body Wgt. 34.1 g)				
Metabolic Efficiency (%)	89	92	86	85
Existence Energy (kcal/day)	25.8	23.4	31.1	30.3
Diet Energy Content (kcal/g)	4.4	4.4	5.9	6.4
Metabolizable Energy (kcal/g)	3.8	4.0	4.8	5.3
Daily Diet Requirement (g)	6.8	5.9	6.5	5.3
Actual Daily Consumption (g)	6.7	6.1	6.1	4.9
Number Seeds/g	260	158	416	23
Required Intake Rate (seed/min)	3	1.5	4.5	0.2
Maximum Intake Rate (seed/min)	200	33	15	6
Weight Change (g)	-0.4	-0.6	-0.28	+0.03
<u>Junco</u> (Mean Body Wgt. 21.4 g)				
Metabolic Efficiency (%)	85	87	80	81
Existence Energy (kcal/day)	12.4	13.4	15.7	16.7
Diet Energy Content (kcal/g)	4.4	4.4	5.9	6.4
Metabolizable Energy (kcal/g)	3.7	3.8	4.5	5.2
Daily Diet Requirement (g)	3.3	3.5	3.5	3.2
Actual Daily Consumption (g)	3.4	3.6	3.2	2.7
Number Seeds/g	260	158	416	23
Required Intake Rate (seed/min)	1.5	1	2.5	0.1
Maximum Intake Rate (seed/min)	200	14	14	4
Weight Change (g)	-0.7	-0.65	-0.53	-0.37
<u>Tree Sparrow</u> (Mean Body Wgt. 21.1 g)				
Metabolic Efficiency (%)	86	89	84	82
Existence Energy (kcal/day)	16.7	16.5	17.5	17.5
Diet Energy Content (kcal/g)	4.4	4.4	5.9	6.4
Metabolizable Energy (kcal/g)	3.7	3.9	4.7	5.3
Daily Diet Requirement (g)	4.5	4.2	3.7	3.3
Actual Daily Consumption (g)	4.5	4.3	3.4	3.0
Number Seeds/g	260	158	416	23
Required Intake Rate (seed/min)	2	1	3	0.1
Maximum Intake Rate (seed/min)	200	26	12	3
Weight Change (g)	-0.3	-0.33	-0.33	-0.28

of starvation. For a bird under winter conditions to receive evolutionary or physiological signals to cease consumption of the only food source available and simultaneously have no capability to forage for a better food source (due to confinement), seems maladaptive. However, under natural situations birds are presented with real choices and at least some capability to encounter further options.

From this study, consumption below requirements and the generally unsupported seed preference predictions based on a combination of diet energy content, handling time, and known consumptions are puzzling based on optimal foraging theory. Part of the difficulty is in accurately assessing what optimal behavior really implies (Krebs 1978), especially when the organism is faced with the complexity and fluctuating nature of the environment. For example, a sparrow limited by a particular nutrient necessary for maximum energy assimilation or normal body functioning may be evolutionarily programmed to pursue the nutrient and risk losing weight temporarily. With such extreme diversity and dynamicity of selective pressures, optimal could mean any number of completely different behaviors (Krebs 1978).

The next step in both avian energetics studies (Walsberg 1983) and optimal foraging assessments *per se* (Krebs 1978) is the integration of seasonal and point-in-time observations and measurements into the full context of organism life histories. Since birds must survive the winter in order to initiate breeding in the spring, studies considering only the breeding season present only a partial segment of an interdependent cycle.

The present study also evidences the need to explore sparrow internal digestive energy costs and the mechanism for differential existence energies on different diets and between different bird species.

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APPENDICES

Appendix A. Formulation of a balanced maintenance mash (P-17) obtained from the Kansas State University Poultry Science Department which was used between energetic trials for sparrows and doves.

Code No.	<u>P-17</u>	Type of Feed	<u>Chick Grower</u>
Formula data	<u>11/8/77</u>	Requested by	<u>Sanford</u> Dept. <u>Poultry Science</u>
Data Mixed	<u> </u>		

INGREDIENTS	AMOUNT/1000 lbs.	
	Individual	Cumulative

Bulk (pounds)		
Soybean oil meal (44%)	150	150
Ground yellow corn (8%)	250	400
Ground milo (9%)	240	640
Ground oats (13%)	100	740
Dehydrated alfalfa meal (19%)	50	790
Meat & bone meal (50%)	50	840
Fish meal (60%)	25	865
Wheat middlings (16%)	100	965

Premix A (pounds)		
Dicalcium phosphate	10	10
Limestone	10	20
Salt	5	25

Premix B (grams)		
Vitamin A (10,000 IU/g)	100	100
Vitamin D ₃ (15,000 IU/g)	20	120
Vitamin B ₁₂ (Profarm 20)	104	224
B-Complex (1233)	58	282
Amprol (25%)	227	509
Choline Chloride (50% mix)	400	909
Aurofac-10	208	1117
Trace minerals "CCC 2 S"	227	1344
Ground milo	3196	4540 (10 lbs.)

Services: Bulk	<u> </u>	Paper bags	<u>X</u>	Burlap bags	<u> </u>	Mix	<u>X</u>
Pellet	<u> </u>	Crumbline	<u>X</u>	Grind	<u> </u>	Other	<u> </u>
Extruda	<u> </u>	Compact	<u> </u>	Conditioning temperature	<u> </u>		

Appendix A.1. Formulation of a nutritionally balanced maintenance mash (layer ration-16) obtained from the Manhattan Coop Grain Elevator. Mash was used between energetic trials as diet component for sparrows and doves.

Net Weight Shown on Bag



LAYER RATION — 16

GUARANTEED ANALYSIS

Crude Protein (not less than)	18.0%
Crude Fat (not less than)	3.5%
Crude Fiber (not more than)	4.0%
Calcium (Ca) (not less than)	4.0%
Calcium (Ca) (not less than)	2.0%
Phosphorus (P) (not less than)	1.0%
Salt (NaCl) (not less than)	0.25%
Moisture (not less than)	0.00%

INGREDIENTS

Grain Products: Processed Grain By-Products, Plant Protein
 Product, Animal Protein Products, Dehydrated Alfalfa Meal,
 Animal Fat, Fat Sources, Bone, Ground Limestone, Dicalcium
 Phosphate, Salt, Vitamin A Supplement, D-Activated
 Animal Source, Source of Vitamin D₃, Riboflavin, Niacin,
 Calcium Chloride, Calcium Pantothene, Vitamin B₁₂ Sup-
 plement, Biotin, Folic Acid, Vitamin E Supplement,
 Menadione Sodium Bisulfite (Source of Vitamin K Activity),
 Manganese Oxide, Iron Carbonyl, Zinc Oxide, Copper
 Oxide and Manganese Oxide.

DIRECTIONS FOR USE

Feed to laying hens as the only feed.

GRAN 11771

Manufactured by
 FARMALAND INDUSTRIES, INC.
 General Office: Kansas City, Mo.

57-1500 (Series 27)

Appendix B. Sample completed bomb calorimetry data sheet used to record temperature change values used in determining the energy content of diet, fecal, and spilled seed samples of sparrows and doves.

CALORIMETRY WORKSHEET

Experimenter: Shuman Bomb: 182
 Sample I. D.: J #6 TR #1 Spilled
 Run No.: 1
 Date: 24 October 1982

	Before Bomb	After Bomb	
Sample + Capsule Wt. (gms)	<u>13.1923</u>	<u>12.4574</u>	
Capsule Wt. (gms)	<u>12.4300</u>	<u>12.4300</u>	
Sample Wt. (gms)	<u>.7623</u>	<u>.0274</u>	(Ash)
	<u>-.0274</u>		(Ash)
Amt. Bombed Wt. (gms)	<u>.7349</u>		(Adjusted Sample Wt.)
<u>90.900</u>	<u>+ -.010</u>	<u>= 90.89</u>	
<u>T_{final}</u>	<u>Correction</u>		
<u>87.750</u>	<u>+ -.0075</u>	<u>= 87.7425</u>	
<u>T_{initial}</u>	<u>Correction</u>		
	<u>Corrected T</u>	<u>= 3.1475</u>	
<u>3.1475</u>	<u>X 1330.15</u>	<u>= 4186.6671</u>	
<u>T</u>	<u>Water Equivalent</u>	<u>Cal. A</u>	

Acid Titration (1 cal/ml used)	Fuse Correction (2.3 cal/cm used)
Final (ml) <u>20.6</u>	Amt. Remaining (cm) <u> </u>
Initial (ml) <u>11.0</u>	Amt. Used (cm) <u>5.8</u>
Used (ml) <u>9.6</u>	Cal. C <u>13.34</u>
Cal. B <u>9.6</u>	

Correction Calories (B + C) 22.94

$A - (B + C) = \frac{4186.6671}{\text{Corrected Calories}} + \frac{.7349}{\text{Adj. Sample Wt.}} = 5665.6784 \text{ (cal/gm)}$

Run #1 5665.6784 (cal/gm) Titration #1 13.0630 (ml/gm)
 $\bar{X}_{n=4}$ 5665.635 (cal/gm) $\bar{X}_{n=4}$ 12.7393 (ml/gm)

Ash 3.59 %
 $\bar{X}_{n=4}$ 3.57 % (\bar{X} over 2 runs)

% Ash = Sample Wt. After \div Sample Wt. Before

Appendix C. Metabolic efficiency, metabolizable energy, and metabolized energy (existence energy with weight maintenance) formulas.

$$\text{METABOLIC EFFICIENCY (\%)} = \frac{\text{Gross Energy Ingested} - \text{Energy Excreted}}{\text{Gross Energy Ingested}} \times 100\%$$

$$\text{METABOLIZABLE ENERGY (KCAL/G)} = \text{Metabolic Efficiency} \times \text{Diet Unit Energy Content}$$

$$\text{METABOLIZED ENERGY (KCAL)} = \text{Gross Energy Ingested} - \text{Energy Excreted}$$

Appendix D. Glossary of energetic terms.

ACCLIMATION - Compensatory changes in organisms exposed to changes in one environmental factor over a short period of time.

BASAL (OR STANDARD) METABOLIC RATE (BMR) - Metabolic rate in a resting animal in a thermoneutral environment, while not digesting or absorbing food.

CRITICAL TEMPERATURES (high and low) - The upper and lower limits of the thermoneutral zone, beyond which energy must be used in thermoregulation.

EXISTENCE METABOLIC RATE (EMR) - An ecological, not physiological term describing the metabolic rate of caged birds maintaining constant weight and not undergoing reproduction, molt, migratory unrest, growth, fat deposition or weight loss. The integration of BMR, temperature regulation, cage locomotion, and assimilation energy over a 24 hr period. EXISTENCE ENERGY - The energy required by an organism to maintain its body weight in the absence of major activity.

FREE-LIVING ENERGY - That energy required by an organism to engage in necessary activities (i.e., flying, foraging, drinking, etc.) above the basal metabolic requirement.

METABOLIC EFFICIENCY - The degree of extraction of energy from a diet based on relative energy inputs and outputs resulting from consumption of a specific diet.

METABOLISM - All chemical reactions taking place in an organism, including constructive ones (anabolism) and destructive ones (catabolism).

METABOLIZABLE ENERGY - The net energy extracted from a diet based on the diet unit energy content multiplied by the organism's metabolic efficiency on that diet.

PRODUCTIVE ENERGY - The amount of energy a bird mobilizes beyond what it requires for existence as measured in caged birds (EMR).

THERMONEUTRAL ZONE - The range of environmental temperatures over which a small change in ambient temperature produces no change in metabolic rate.

Appendix E. Example completed data sheet used in time budget study in outdoor flight pens. Data recorded were date, pen number, bird identification code, seed diet (treatment), quarter of the day and time of initiation of quarter, day, cloud cover, wind velocity, and bird behavior.

TIME-ENERGY BUDGET DATA SHEET

<u>Date</u>	<u>Pen</u>	<u>Bird</u>	<u>Treatment</u>	<u>Quarter</u>	<u>Day</u>	<u>Weather</u>
2-23-82	3	CM SHORT	SUN	1(0705)	2	7-C O-W
<u>Interval</u>		<u>Activity</u>		<u>Interval</u>		<u>Activity</u>
1		F		1		F
2		F		2		F
3		F		3		F
4		F		4		F
5		F		5		F
6		F		6		F
7		F		7		F
8		F		8		F
9		F		9		F
10		F		10		Fnot
11		F		11		Fnot
12		F		12		Fnot
13		F		13		Fnot
14		F		14		Fnot
15		F		15		Fnot
16		F		16		Fnot
17		Fnot		17		S
18		Fnot		18		S
19		Fnot	KEY	19		PR
20		Fnot	F-perching (26.7%)	20		S
21		Fnot	Fnot-feeding > 1.5'	21		S
22		Fnot	from feeder (43.3%)	22		S
23		Fnot	F-feeding < 1.5' from	23		PR
24		Fnot	feeder (15%)	24		Fnot
25		Fnot	S-sitting (11.7%)	25		S
26		Fnot	PR-predator	26		S
27		Fnot	scanning (3.3%)	27		Fnot
28		Fnot		28		Fnot
29		Fnot		29		Fnot
30		Fnot		30		Fnot

Appendix, Table 1. Respective starvation correction factors* used to adjust energetic calculations when bird trial weight loss exceeded 5% of body weight. Values are derived from fecal collection from 3 each tree sparrows, cardinals, Harris' sparrows, and juncos. Values with a common superscript read across a row do not differ ($P \leq 0.05$).

VARIABLE	BIRD SPECIES				STANDARD ERROR
	Tree Sparrow	Cardinal	Harris' Sparrow	Junco	
Mean Weight Loss (g)	3.13 ^a	6.23 ^c	4.27 ^{a,b}	4.87 ^{b,c}	± 0.73
Mean Wgt. Excreta Produced (g) ¹	0.11 ^b	0.27 ^d	0.15 ^c	0.10 ^a	
Mean Excreta Energy Content (kcal/g) ¹	4.31 ^d	3.13 ^a	3.98 ^c	3.86 ^b	
Mean Energy Excreted (kcal) ¹	0.48 ^b	0.85 ^d	0.58 ^c	0.38 ^a	
Correction Factor*	0.1541 ^b	0.1362 ^b	0.1355 ^b	0.0777 ^a	± 0.0005

$$\text{* CORRECTION FACTOR} = \frac{\text{MEAN ENERGY EXCRETED (kcal)}}{\text{MEAN WEIGHT LOSS (g)}}$$

¹ Pooled values, no standard error calculated

Appendix, Table 2. Mean dry weight of excreta produced, energy consumption, and derived energetic calculations and standard errors for 8 each cardinals, Harris' sparrows, tree sparrows, and junco during 4 4-day trial periods. Values with a common superscript read across a row do not differ ($P < 0.05$).

BIRD SPECIES	TRIAL				STANDARD ERROR
	1	2	3	4	
<u>Cardinal</u>					
Energy Consumed (kcal/day)	24.5 ^a	22.6 ^a	28.3 ^a	27.5 ^a	+ 2.51
Wgt. Diet Consumed (g/day)	6.4 ^a	5.9 ^a	8.9 ^b	10.4 ^b	+ 0.54
Excreta Energy Content (kcal/g)	4.3 ^b	4.1 ^a	4.4 ^b	4.3 ^b	+ 0.49
Energy Excreted (kcal/day)*	5.3 ^b	3.8 ^a	5.7 ^b	5.2 ^b	+ 0.31
Wgt. Excreta Produced (g/day)	1.2 ^a	0.9 ^a	1.3 ^b	1.2 ^a	+ 0.60
Metabolic Efficiency (%)	78.8 ^a	81.6 ^a	79.9 ^a	81.0 ^a	+ 1.31
Existence Energy (kcal/day)*	19.2 ^a	18.8 ^a	22.6 ^a	22.3 ^a	+ 0.23
<u>Harris' Sparrow</u>					
Energy Consumed (kcal/day)	29.9 ^a	28.0 ^a	34.3 ^a	34.1 ^a	+ 2.28
Wgt. Diet Consumed (g/day)	7.4 ^a	7.8 ^a	9.8 ^b	10.4 ^b	+ 0.65
Excreta Energy Content (kcal/g)	4.3 ^{a,b}	4.2 ^a	4.4 ^{a,b}	4.3 ^b	+ 0.09
Energy Excreted (kcal/g)*	3.8 ^{a,b}	3.3 ^a	4.1 ^{a,b}	4.6 ^b	+ 0.41
Wgt. Excreta Produced (g/day)	0.9 ^{a,b}	0.8 ^a	0.9 ^{a,b}	1.1 ^a	+ 0.09
Metabolic Efficiency (%)	87.1 ^a	88.8 ^a	88.8 ^a	86.7 ^a	+ 1.07
Existence Energy (kcal/day)*	26.2 ^a	24.7 ^a	30.2 ^a	29.6 ^a	+ 2.07
<u>Junco</u>					
Energy Consumed (kcal/day)	16.8 ^a	17.3 ^{a,b}	19.9 ^b	16.4 ^a	+ 1.00
Wgt. Diet Consumed (g/day)	4.3 ^a	4.5 ^a	5.8 ^b	5.4 ^b	+ 0.23
Excreta Energy Content (kcal/g)	4.3 ^a	4.3 ^a	4.3 ^a	4.2 ^a	+ 0.05
Energy Excreted (kcal/g)*	3.1 ^a	3.0 ^a	3.3 ^a	2.7 ^a	+ 0.27
Wgt. Excreta Produced (g/day)	0.7 ^a	0.7 ^a	0.8 ^a	0.7 ^a	+ 0.06
Metabolic Efficiency (%)	81.6 ^a	83.7 ^a	83.8 ^a	83.8 ^a	+ 0.95
Existence Energy (kcal/day)*	13.6 ^a	14.3 ^{a,b}	16.6 ^b	13.7 ^a	+ 0.79
<u>Tree Sparrow</u>					
Energy Consumed (kcal/day)	19.7 ^a	18.7 ^a	21.2 ^a	20.3 ^a	+ 1.07
Wgt. Diet Consumed (g/day)	5.0 ^a	5.0 ^a	6.4 ^b	6.7 ^b	+ 0.40
Excreta Energy Content (kcal/g)	4.3 ^a	4.2 ^a	4.2 ^a	4.2 ^a	+ 0.06
Energy Excreted (kcal/day)*	3.1 ^b	2.5 ^a	3.0 ^b	3.0 ^b	+ 0.15
Wgt. Excreta Produced (g/day)	0.7 ^b	0.6 ^a	0.7 ^b	0.7 ^b	+ 0.03
Metabolic Efficiency (%)	84.3 ^a	86.3 ^a	86.1 ^{a,b}	84.9 ^{a,b}	+ 0.61
Existence Energy (kcal/day)*	16.6 ^a	16.1 ^a	18.2 ^a	17.2 ^a	+ 0.98

* Corrected for weight loss

Appendix, Table 3. Mean dry weight of excreta produced, energy consumption, and derived energetic calculations and standard errors for 10 mourning doves during 5 2-day trials. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE	TRIAL					STANDARD ERROR
	1	2	3	4	5	
Energy Consumed (kcal/day)	39.5 ^a	44.4 ^{a,b}	53.8 ^c	63.5 ^d	51.2 ^{b,c}	± 3.21
Wgt. Diet Consumed (g/day)	8.3 ^a	9.2 ^{a,b}	11.2 ^b	13.3 ^b	11.9 ^b	± 0.91
Excreta Energy Content (kcal/g)	4.32 ^b	4.32 ^b	4.30 ^{a,b}	4.30 ^{a,b}	4.26 ^a	± 0.02
Energy Excreted* (kcal/day)	6.3 ^a	7.6 ^{a,b}	9.8 ^b	12.6 ^c	9.0 ^b	± 0.87
Wgt. Excreta Produced (g/day)	1.6 ^a	1.9 ^{a,b}	2.3 ^b	2.9 ^c	2.2 ^b	± 0.18
Metabolic Efficiency* (%)	84.6 ^b	83.3 ^{a,b}	81.8 ^{a,b}	79.5 ^a	82.4 ^{a,b}	± 1.62
Existence Energy* (kcal/day)	33.2 ^a	36.8 ^{a,b}	44.0 ^{b,c}	50.9 ^c	42.3 ^b	± 2.79

* Corrected for weight loss

Appendix, Table 4. Semi-free-living energies and related calculations as influenced by diet for cardinals in outdoor flight pens. Values are derived from 3-bird group means summed over 5 trials in each of 2 test pens. Standard deviations or standard errors do not appear with some values due to lack of replications. Laboratory-determined values have corresponding standard errors. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE	DIET	
	Sunflower	Millet
Diet Energy Content (kcal/g)	6.4 ^b \pm 0.16	4.4 ^a \pm 0.11
Metabolic Efficiency (%)	79.4 ^a \pm 1.31	85.1 ^b \pm 1.31
Metabolizable Energy (kcal/g)	5.1 ^b \pm 0.07	3.7 ^a \pm 0.07
Total Dry Wgt. Diet (g)	2130	1892
Remaining Dry Wgt. Diet (g)	895	706
Total Pen Dry Wgt. Diet Consumed (g)	1235	1186
Dry Wgt. Diet Consumed/Bird/Day (g) (21 days total, 5 birds/pen/day)	11.7	11.3
Gross Energy Diet Consumed/Bird (kcal/bird)	72.8	49.9
Metabolized Energy (kcal/bird)	57.8	42.4
Semi-Free-Living Energy (kcal/day)	33.3	22.3
Existence Energy (kcal/day)	24.5 ^a \pm 2.30	20.1 ^a \pm 2.30
Percent Over Existence Energy (%)	136	111

Appendix, Table 5. Cardinal mean body weights and behavior variables with standard errors as influenced by quarter of the day in outdoor flight pens. Means are derived from 5-bird groups over 5 trials in 2 pens. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE	QUARTER				STANDARD ERROR
	1	2	3	4	
Flying (%)	6.0 ^b	4.4 ^b	3.6 ^b	1.9 ^a	± 0.64
Perching (%)	64.0 ^a	67.4 ^{a,b}	79.2 ^c	70.2 ^{b,c}	± 2.90
Maintenance (%)	0.6 ^a	1.3 ^a	1.1 ^a	2.8 ^a	± 0.89
Sitting (%)	4.9 ^a	4.4 ^a	1.6 ^a	5.7 ^a	± 1.38
Predator Scanning (%)	1.0 ^a	1.0 ^a	0.8 ^a	0.8 ^a	± 0.21
Drinking (%)	1.6 ^b	1.1 ^b	0.3 ^{a*}	0.7 ^{a,b}	± 0.37
Interspecific Interaction (%)	1.2 ^b	0.6 ^a	0.7 ^{a,b}	0.3 ^a	± 0.20
Nesting Behavior (%)	0.0 ^{a*}	0.0 ^{a*}	0.0 ^{a*}	0.2 ^{a*}	± 0.08
Foraging 1.5m From Feeder (%)	7.8 ^a	6.6 ^a	1.8 ^a	3.6 ^a	± 1.16
Feeding 1.5m From Feeder (%)	14.7 ^a	14.0 ^a	11.8 ^a	15.2 ^a	± 1.71

* Mean not different from zero ($P > 0.05$)

Appendix, Table 6. Cardinal mean body weights and behavior variables with standard errors as influenced by trial in outdoor flight pens. Means are derived from 3-bird groups in 2 pens. Values with a common superscript read across a row do not differ ($P < 0.05$).

VARIABLE	TRIAL					STANDARD ERROR
	1	2	3	4	5	
Bird Pretrial Weight (g)	43.0 ^b	43.7 ^b	42.7 ^b	40.5 ^a	40.6 ^a	± 0.61
Bird Posttrial Weight (g)	43.7 ^b	42.7 ^b	42.5 ^b	40.6 ^a	40.5 ^a	± 0.61
Flying (%)	4.9 ^a	3.2 ^a	3.2 ^a	3.6 ^a	5.0 ^a	± 0.71
Perching (%)	58.7 ^a	60.0 ^a	76.3 ^b	78.8 ^b	77.3 ^b	± 3.25
Maintenance (%)	1.8 ^{a*}	3.4 ^a	1.1 ^{a*}	0.4 ^{a*}	0.5 ^{a*}	± 1.00
Sitting (%)	2.8 ^{a*}	8.4 ^a	3.1 ^a	2.5 ^{a*}	4.0 ^a	± 1.54
Predator Scanning (%)	2.3 ^c	1.4 ^b	0.4 ^a	0.4 ^a	0.1 ^{a*}	± 0.24
Drinking (%)	1.1 ^a	1.4 ^a	1.0 ^a	0.6 ^{a*}	0.5 ^{a*}	± 0.41
Interspecific Interaction (%)	1.7 ^b	0.5 ^a	0.8 ^a	0.3 ^{a*}	0.3 ^{a*}	± 0.23
Nesting Behavior (%)	0.3 ^a	0.0 ^{a*}	0.0 ^{a*}	0.0 ^{a*}	0.0 ^{a*}	± 0.09
Foraging 1.5m From Feeders (%)	6.8 ^a	7.9 ^a	3.0 ^a	3.3 ^a	3.7 ^a	± 1.30
Feeding 1.5m From Feeders (%)	20.9 ^b	15.5 ^{a,b}	12.6 ^a	11.0 ^a	9.7 ^a	± 1.92

* Mean not different from zero

ENERGETIC RESPONSES OF AVIAN GRANIVORES TO WINTER
IN NORTHEAST KANSAS

by

THERESA WARNOCK SHUMAN

B.S., University of Illinois, 1980

AN ABSTRACT OF A MASTER'S THESIS

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The metabolic efficiency and semi-free-living energy cost assumptions of current avian energetics models were tested in winter in northeast Kansas using four sympatric sparrow species (cardinal, junco, tree sparrow, Harris' sparrow) and mourning doves. These energetics models form the basis for many areas of active avian research.

Additional assessment of sparrow responses to winter conditions involved three phases: 1) the effect of diet energy content on cardinal behavioral time allocations, 2) seed preferences based on energy content and handling time, and 3) the effect of trypsin inhibitor activity in seed diets on sparrow metabolic efficiencies and existence energies (energy required for weight maintenance in the absence of major activity).

Metabolic efficiency and existence energy data were used to interpret differential wintering and breeding season distributions of the four sparrow species.

The model assumptions of 70% metabolization of ingested food energy and of 40% requirement over existence for free-living conditions were not supported in this study. Metabolic efficiencies were in general at least 10% higher than the assumed value and semi-free-living requirements were at least 110% above existence levels. Diet energy content significantly shifted behavioral time allocations in cardinals but a combination of diet energy content and diet handling time was not found to be the sole predictor of sparrow seed preferences. Relative trypsin inhibitor activity in seed diets displayed a general relationship with sparrow metabolic efficiencies and existence energies.

Sparrow wintering and breeding distributions as well as migratory versus resident status followed a logical trend based a combined metabolic efficiency existence energy, and diet component explanation.