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Energetics of Foraging

DIGESTION IN BIRDS: CHEMICAL AND PHYSIOLOGICAL DETERMINANTS AND ECOLOGICAL IMPLICATIONS

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Abstract. I review the utilization efficiencies of wild birds on various foods. Average apparent metabolizable energy coefficients (*MEC**; [food energy − excreta energy]/food energy) according to type of food consumed are: nectar, 0.98; arthropods, 0.77; vertebrate prey, 0.75; cultivated seeds, 0.80; wild seeds, 0.62; fruit pulp and skin, 0.64; whole fruits (including seeds), 0.51; herbage, 0.35. The observed differences in *MEC** can be explained largely on the basis of differences in food composition. Fruits and herbage were utilized less efficiently than predicted on the basis of composition alone, possibly because of (1) underestimation of the refractory component of food (i.e., cell wall), (2) the presence of plant secondary chemicals, or (3) features of the digestive system, such as short digesta retention time and/or low enzyme levels.

The digestive system's efficiency in extracting food energy or nutrients is directly related to three variables: (1) digesta retention time; (2) rates of hydrolysis, fermentation, and absorption; and (3) digestive tract surface area and volume. Because these components act in concert, it is best to evaluate digestive system function in an integrated fashion. I present three examples: (1) efficiency is apparently depressed in frugivores because digesta retention time is relatively short and no compensation occurs in rates of hydrolysis and absorption; (2) herbivores must eat large amounts of food, but a compensation appears to be an increase in digestive tract volume; and (3) the presence of caeca in herbivores enhances extraction efficiency by affecting all three variables.

Digestion is important in avian ecology at the level of individuals, populations, and community structure by affecting resource removal rate, and possibly by constraining the rate of production and affecting niche width.

Key Words: Efficiency; food composition; intestine; metabolizable energy; nutrition.

Avian digestion is of interest to biologists because it is one of the factors that mediates birds' interactions with their environment. Foraging time and resource removal rate, for example, are functions of feeding rate. Feeding rate in turn is related to digestion so that for birds in steady state, feeding rate is equal to energy requirement, divided by energy value of food times the efficiency of its utilization. In addition to such ecological relations, avian digestion poses challenging problems for physiologists with the added virtue that certain aspects of the avian digestive system make birds useful models for the study of digestion in general.

I review here four topics related to digestion that have special relevance for avian biologists. First, the utilization efficiencies (a general term I use for various expressions of digestibility and metabolizability; see next section) of wild birds eating wild foods are comprehensively reviewed. The summaries and accompanying analyses should enable biologists to evaluate when they can substitute reasonable estimates for more accurate data obtained at the cost of new feeding trials.

Second, I consider the major chemical features of wild foodstuffs that determine or affect the efficiency with which a bird utilizes foods. I use a simple deterministic model of digestion based on food composition to identify important features of foods that should be measured or studied more intensively in the future.

Utilization efficiency is also affected by properties of the bird. Several recently developed models of digestion identify those particular attributes of the bird that determine digestive efficiency (Sibly 1981, Karasov 1987, Penry and Jumars 1987). Those features, their mode of action, and their interrelations are reviewed in several examples.

While the first three topics deal primarily with utilization efficiency, the fourth topic is broader. I consider how digestion rates might limit energy intake and hence rates of growth and reproduction. Also, the design and degree of adaptability of the gastrointestinal tract may determine diet diversity and hence niche width. These approaches about digestion operating as a possible constraint in ecology may represent an important direction for future research in avian digestion.

METHODS AND TERMS

UTILIZATION EFFICIENCIES

Measuring digestive efficiency in birds is a problem because the feces, which represent primarily undigested residue of food, are mixed in the cloaca with urine. Thus, the difference between the intake and excretory loss rates of dry matter, energy, or nutrients is more

TABLE 1. LIST OF SYMBOLS AND THEIR DEFINITIONS AND UNITS

Symbol	Definition	Units[a]
A_i	Ash concentration food	Proportion of dry mass
AMC^*	Assimilated mass in coefficient (apparent), eq. 2	Proportion of food dry mass
E_c	Endogenous loss of energy	kJ/day
E_m	Endogenous loss of mass	g/day
E_N	Endogenous loss of nitrogen	g/day
F	Fraction absorbed	Proportion
GE_i	Gross energy content of food	kJ/g dry mass
GE_e	Gross energy content of excreta	kJ/g dry mass
GE_R	Gross energy content of refractory material in food	kJ/g dry mass
J	Absorption rate	grams or moles per minute
MEC	Metabolizable energy coefficient (true)	Proportion of food energy
MEC^*	Metabolizable energy coefficient (apparent), eq. 1	Proportion of food energy
MEC^*_p	Predicted metabolizable energy coefficient (apparent), eq. 6	Proportion of food energy
N_i	Nitrogen concentration of food	Proportion of dry mass
Q_e	Rate of excreta production	g/day
Q_i	Rate of food intake	g/day
R_i	Proportion of food refractory to chemical digestion	Proportion of dry mass
T	Mean retention time of digesta	min
V	Amount of nutrient in the gut	grams or moles

[a] Rates can be expressed as g/day or g day^{-1} (kg body mass)$^{-1}$. All masses are dry matter basis.

properly called an apparent assimilable or metabolizable fraction (apparent because it is uncorrected for endogenous losses). In the case of energy, division of this quantity by the gross energy intake yields the apparent metabolizable energy coefficient (MEC^*; Kendeigh et al. 1977):

$$MEC^* = (GE_iQ_i - GE_eQ_e)/GE_iQ_i = 1 - (GE_eQ_e/GE_iQ_i) \quad (1)$$

where GE_i and GE_e equal, respectively, the gross energy content (kJ/g dry mass) of the food (intake) and excreta, and Q_i and Q_e equal, respectively, the food intake rate and excreta production rate (g/day) (Table 1). Miller and Reinecke (1984) present a good review of the various expressions of digestibility and metabolizability used in the literature.

In some studies only the flux of dry matter is determined and this yields useful information on the digestive efficiency of the bird; the apparent assimilated mass coefficient (AMC^*):

$$AMC^* = (Q_i - Q_e)/Q_i = 1 - (Q_e/Q_i) \quad (2)$$

One can see that the utilization efficiencies MEC^* and AMC^* differ according to the magnitude of GE_e/GE_i, with MEC^* being the larger value. AMC^*'s are most often reported for digestion trials involving herbage or fruit. From studies where both have been determined (see Appendix 1 and Worthington 1983) I found that, for herbage and fruit, MEC^* could be estimated (on average) from AMC^* by adding 0.03. I used this manipulation in some cases because MEC^* is the more desirable quantity considering our interests in the energetics of feeding.

MEC^* and AMC^* are usually determined in feeding trials with captive birds in which Q_i and Q_e are measured, that is, total collection trials. An alternative method is to use an inert substance as a tracer to relate excreta production to food intake:

$$MEC^* = [GE_i - (\%T_i/\%T_e)GE_e]/GE_i, \text{ or} \quad (3)$$

$$AMC^* = 1 - (\%T_i/\%T_e) \quad (4)$$

where $\%T_i$ and $\%T_e$ equal, respectively, the percent tracer in the food and excreta. In the laboratory one can mix the tracer into the food (e.g., Duke et al. 1968), but it is also possible to use naturally occurring tracers. The virtue of this technique is that it can be applied to a free-living bird if the diet is accurately known and food and excreta can be representatively sampled. Following Marriott and Forbes' (1970) finding that the apparent digestibility of crude fiber in lucerne chaff by Cape Barren Geese (consult the tables in the Appendix for scientific names not presented in the text) was negligible, numerous researchers working with waterfowl have used the inert marker technique and calculated AMC^* using crude fiber (e.g., Halse 1984, Miller 1984), lignin (e.g., Buchsbaum et al. 1986), and cellulose (e.g., Ebbinge et al. 1975) as the inert marker. Because waterfowl do ferment some cell wall (see following sections of this paper), this approach can lead to underestimation of AMC^*. Moss and Parkinson (1972) and Moss (1977) used Mg as an inert marker in a study of captive and free-living Red Grouse eating heather, and concluded that free-living birds digested the heather more efficiently than captives eating the same food. In this case Mg was probably not truly inert, but rather Mg absorption by the intestine was equalled by excretion in urine.

This latter study underscores the difficulty in measuring a utilization efficiency that applies to the ecological situation. Captives fed formulated rations before feeding trials with wild foods need to be conditioned to the new wild foods. For example, when American Robins were first switched from a formulated fruit-mash ration to crickets, their MEC^* was 15% lower than it was after they had fed on crickets for three days (0.59 vs. 0.70, $P < 0.001$; Levey and Karasov 1989). Such lags in efficiency of digestion following a diet

switch might be just a day if adaptations of digestive enzymes or nutrient absorption mechanisms are involved, or many days if changes in gut structure are involved (Miller 1975, Karasov and Diamond 1983). Allowing adequate time for adaptation to a new ration may be especially critical in studies of herbivores, in which changes in gut structure (Savory and Gentle 1976, Hanssen 1979), and hence presumably gut function, may be necessary to utilize a new food efficiently. In the wild, grouse gradually increase their intake of resinous forage well before they must rely upon it during midwinter (Bryant and Kuropat 1980).

The utilization coefficients *MEC** and *AMC** are considered "apparent" because they are not corrected for fecal and urinary endogenous losses of dry matter and energy. The endogenous component of excreta includes endogenous urinary nitrogen (the lowest level of N excretion attained under basal conditions even in the absence of protein intake) and dry matter and energy from bacteria or sloughed-off cells and secretions of the alimentary tract. One can determine the "true" metabolizability of a ration by correcting excretory losses for this endogenous component (Sibbald 1976), and this is often done in poultry science because "true" metabolizability is a more direct measure of energy availability. In chickens the endogenous energy loss (E_e) was about 21 kJ $kg^{-0.75}$ day^{-1}, or expressed as dry mass (E_m) 1.8 g $kg^{-0.75}$ day^{-1} (Guillaume and Summers 1970, Sibbald 1976). In Graylag Geese E_e was 14.4 kJ $kg^{-0.75}$ day^{-1} (Storey and Allen 1982). The correction equation for "true" *MEC* from *MEC** is $MEC = MEC^* + E_e/([Q_i][GE_i])$ (Guillaume and Summers 1970), while that for "true" *AMC* from *AMC** would be $AMC = AMC^* + E_m/Q_i$.

Apparent coefficients are generally 0.01–0.03 below "true" coefficients, and if Q_i is well below the level required for maintenance then differences can exceed 0.03 (Miller and Reinecke, 1984). Miller and Reinecke (1984) cautioned investigators to use *MEC**'s only from test birds fed at maintenance levels, though calculations with actual data in Appendix 1 show that this is unnecessarily conservative. They also discussed why the use by ecologists of apparent *MEC*'s in energetics studies is approximately correct.

Retention Time of Digesta in the Gut

There is a certain minimum duration for a digestion trial if utilization efficiency is to be measured accurately. Marked particles of food tend to clear the digestive tract in an exponential fashion in birds eating such diverse foods as nectar (Karasov et al. 1986), fruit and insects (Karasov and Levey 1990), and seeds and herbage (Duke et al. 1968, Herd and Dawson 1984). For exponential clearance, the time to clear 98% of a marked meal is equal to about four times the mean retention time (i.e., the mean residence time of marker particles) (Karasov et al. 1986, Penry and Jumars 1987). More time is required for the metabolic processing of nutrients and excretion of urinary wastes, which are also included in a calculation of *MEC**. As discussed below, the shortest mean retention times found in birds are about 45 min in small frugivores and nectarivores, and these times increase with increasing body mass and for other foods. Thus, digestion trials that begin with fasted birds (even small ones) and last only 4–6 hr have a relatively high likelihood of yielding overestimates of *MEC** with rather high variability (according to differences between birds in the trial in mean retention and metabolic processing time). However, day-long digestion trials with American Robins and European Starlings fed crickets or fruits yield *MEC**'s with the same mean and variance as multi-day trials (Levey and Karasov 1989).

Some researchers record only the first appearance of marked food particles, which may be termed gut-passage time, gut transit time, and gut-passage rate.These and other measures, plus methods for their determination, are discussed in detail in Kotb and Luckey (1972), Warner (1981) and Van Soest et al. (1983).

UTILIZATION EFFICIENCIES OF WILD BIRDS EATING WILD FOODS

Major Patterns According to Food

Appendix 1 shows results from about 250 digestion trials in which either the particular food or the species of bird differs. In some cases a single species or closely related species was fed many different food types (e.g., Northern Bobwhites fed arthropods, seeds, and fruits; grouse species fed seeds, fruit, and herbage; passerine birds fed arthropods, seeds, and fruits). Inspection of those data suggests immediately that a large source of variation in utilization efficiency is the type of food consumed. Indeed, analysis of variance (ANOVA, using the arcsine of the square root of *MEC**) among all trials showed a highly significant effect of food ($F = 39.3$, $P < 0.001$). Accordingly, summarized in Figure 1 and Table 2 are estimates of *MEC** organized according to the following major food groups:

Nectar. Studies of nectarivores are in uniform agreement that utilization efficiency is practically 100%. Unfortunately, data are lacking for birds (e.g., passerine frugivores) in which nectar makes up a smaller proportion of the diet.

Arthropods and aquatic invertebrates. About three-fourths of the energy is apparently metabolized (Appendix 1, Bryant and Bryant 1988). Mealworms or domestic crickets have been used in studies with terrestrial arthropods, and the former yield higher utilization efficiencies than the latter, probably due to lower contents of cuticle (see below).

Vertebrates. I could discern no difference in *MEC** among trials where fish, mammal, or bird were offered to carnivorous birds. On average, about three-fourths of the energy in these foods is apparently metabolized.

Seeds. Sixty-two digestion trials were reviewed. Those trials conducted with cultivated seeds yielded significantly higher *MEC**'s ($P < 0.001$, ANOVA). About four-fifths of their energy was apparently metabolizable. When wild seeds were fed to nonpasserines, less than two-thirds of their energy was apparently metaboliz-

TABLE 2. UTILIZATION EFFICIENCIES AND ESTIMATED METABOLIZABLE ENERGY CONTENTS OF FOOD TYPES

Food type	N_1, N_2[a]	*MEC**			Energy content		
					GE_i[e] (kJ/g)		$(MEC^*) \times (GE_i)$[f] (kJ/g)
		$\bar{X}$[b]	SD[c]	95% C.I.[d]	$\bar{X}$	SD (N)	
Nectar (sucrose)	10, 4	0.98[A]	0.01	0.977–0.983	16.7	(1)	16.4
Cultivated seeds							
Passerines	9, 7	0.80[B]	0.05	0.76–0.83			17.0
Nonpasserines	17, 7	0.80[B]	0.08	0.76–0.83			17.0
All					21.3	4.3 (22)	
Arthropods	7, 6	0.77[B]	0.08	0.72–0.83	25.0	1.9 (4)	19.3
Vertebrates	20, 10	0.75[B]	0.07	0.72–0.79	23.6	2.0 (15)	17.7
Wild seeds							
Passerines	11, 5	0.75[B,C]	0.09	0.70–0.80			15.8
Nonpasserines	25, 7	0.59[D]	0.13	0.54–0.65			12.4
All					21.0	2.8 (27)	
Fruits							
Pulp and skin	31, 5	0.64[C]	0.15	0.59–0.70	19.6	3.4 (28)	12.5
Pulp and skin and seed	22, 9	0.51[D]	0.15	0.44–0.57	21.6	1.6 (10)	11.0
Herbage							
Bulbs and rhizomes	4, 4	0.56[C,D]	0.18	0.38–0.74	17.3	1.6 (2)	9.7
Grouse	19, 10	0.37[E]	0.08	0.33–0.40	21.5	0.8 (8)	8.0
Other	14, 6	0.33[E]	0.12	0.26–0.39	18.5	1.6 (6)[g]	6.1

[a] N_1 = number of feeding studies in which either food or bird species differed; N_2 = number of bird species. In some studies a bird species was fed different foods in separate feeding trials.
[b] Means with the same capitalized letter are not significantly different according to Duncan's Multiple Range Test on arcsine$\sqrt{MEC^*}$.
[c] SD on untransformed values of *MEC** with sample size equal to N_1.
[d] Confidence intervals were established using transformed values of *MEC** (arcsine$\sqrt{MEC^*}$) and the total sample size was taken to equal N_1.
[e] Gross energy content/g dry matter. Mean values from Appendix 1.
[f] Apparent metabolizable energy content/g dry matter.
[g] Excludes aquatic species fed to domestic ducks (Muztar et al. 1977).

able. Passerine species had higher *MEC**'s on wild seeds than nonpasserine species ($P < 0.001$, ANOVA) (Table 2), whereas there was no significant difference ($P > 0.4$) between the groups in digestion trials with cultivated seeds. Possible reasons for this might relate to phylogeny or body size.

Fruits. Small frugivores that are seed dispersers either egest or defecate seeds following ingestion of whole fruits. Consequently, most studies with passerine frugivores have determined the utilization efficiency on pulp and skin alone by subtracting the mass and energy value of seeds from that of whole fruit. In some other studies utilization efficiencies were determined on the basis of whole fruits, including seeds. Because seeds can make up a substantial fraction of the mass of the whole fruit (e.g., Sorensen 1984), and because they are relatively indigestible (Servello and Kirkpatrick 1987), one would expect that utilization efficiencies would be lower in the latter kind of digestion trial. This was indeed the case (Table 2). In those trials in which the *MEC** of pulp and skin alone was determined, about two-thirds of the energy was metabolizable; whereas, in those trials where the *MEC** of whole fruit was determined, about half of the energy was metabolizable ($P < 0.001$). Some larger fruit-eating birds partially digest the seeds, and in those cases *MEC**'s can be quite high (e.g., Willow Grouse eating cowberries apparently digested 81% of the total organic matter; Pullianinen et al. 1968).

Johnson et al.'s (1985) data set on frugivores was omitted from the above analysis because digestion trials were brief; fruit was presented to fasted birds for two hours and excreta were collected during those two hours and for an additional two hours. This might result in overestimation of *MEC**. Indeed, *MEC** for pulp and skin in these trials ($\bar{X} = 0.71$, SD = 0.13, N = 55) was significantly higher ($P < 0.01$) than for other trials with passerines fed pulp and skin (Table 2).

Herbage. Generally, species of grouse or waterfowl have been used in digestion trials with herbage (Appendix 1). The studies with Ostriches and Emus were excluded from Figure 1 and Table 2 because they were not performed with foods the birds might eat in the wild. There was no significant difference in *MEC**'s in trials with grouse species compared with trials with other

species of birds ($P > 0.5$), except that birds fed bulbs and rhizomes had significantly higher *MEC**'s ($P < 0.001$) than birds eating other kinds of herbage (leaves, twigs, buds) (Table 2). On average, birds apparently metabolized less than 40% of the gross energy in leaves, twigs, and buds. Sugden (1973) measured much lower *MEC**'s (sometimes negative values) for numerous plants fed to Blue-winged Teal but concluded that his methods yielded questionable values. He fed ducks that were not provided with grit, used test rations mixed with a reference ration, and calculated the *MEC** of the test ration by difference. The technique of mixing test and reference rations, which has been validated with chickens, was also used by Muztar et al. (1977) and they also calculated quite low values of *MEC** for ducks eating wild foods (Appendix 1). This technique may not work effectively for wild foods with low digestibilities.

For all these food groups the metabolizable energy per gram of food is the product of *MEC** and gross energy content (Table 2). On average an herbivore must ingest almost three times as much dry matter as an insectivore or carnivore to obtain the same amount of metabolizable energy.

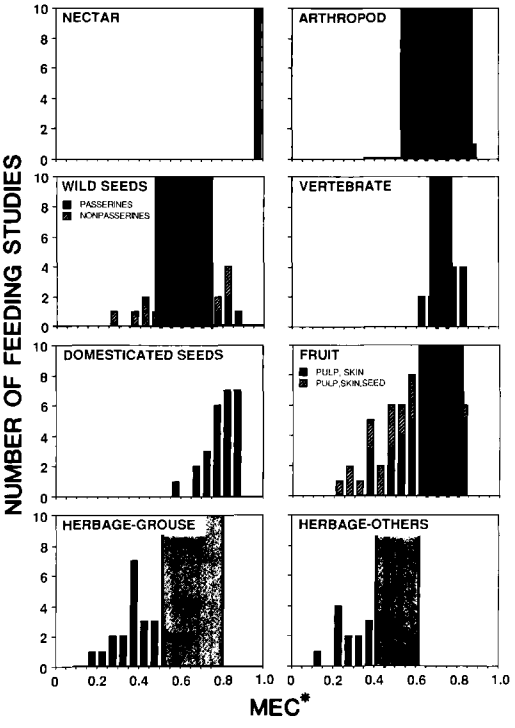

FIGURE 1. Comparison of apparent metabolizable energy coefficients (*MEC**) measured in feeding trials with predicted values based on chemical composition of foods. The frequency histograms (solid black or hatched bars) show the number of feeding trials (y-axis) which yielded the *MEC**'s listed on the x-axis. Data are from Appendix 1. The shaded grey boxes show the range of expected *MEC**'s which were predicted using a simple model which estimates $MEC^*_{predicted}$ based on the chemical composition of the food (see Food Chemistry section). Notice that fruit and herbage appear to be utilized less efficiently than predicted on the basis of food composition alone.

Other Factors Affecting Utilization Efficiency

There is considerable variation in *MEC**'s within each food type (Fig. 1). Some may be due to differences in composition between particular foods of a given type (e.g., growing vs. senescent vegetation, larval vs. adult arthropods; see Food Chemistry section), and some to individual variability (e.g., in age, reproductive condition; Moss 1983). How great are these effects?

Physiological condition. How might *MEC** vary with age or reproductive condition? When a bird is growing or gaining mass, *MEC** is expected to increase, because much ingested N (protein) is deposited as tissue, rather than being metabolized and excreted. For example, *MEC** was higher (by 0.04) in Long-eared Owls during the period of rapid feather growth (Wijnandts 1984). However, reproductive condition had no significant effect on *MEC** in Willow Ptarmigan (West 1968).

Young, developing birds might be less efficient than adults at extracting energy and nutrients; indeed, several studies have detected lower *MEC**'s in very young birds (e.g., by 0.12 in House Sparrows, Blem 1975; by 0.20 in Black-bellied Whistling-ducks, Cain 1976; see also Myrcha et al. 1973, Penney and Bailey 1970, and Dunn 1975). The *MEC** of Dunlin (*Calidris alpina*) chicks fed mealworms, ground beef, and oats was 0.57 (Norton 1970) which is lower than an expected value of 0.75 (Table 2). Thus, there is evidence that very young birds have immature guts and hence lower utilization efficiencies, but see Westerterp (1973) for an apparent exception. It would be interesting to know whether parents assist in digestion by softening food with mucous or predigesting it and then regurgitating it.

None of the digestion trials tabulated in Appendix 1, however, used very young birds and hence this is not an important source of variation in the analysis in Table 2.

Several studies (e.g., Bairlein 1985) have claimed that birds can adaptively modulate the efficiency of food utilization and thus, for example, undergo premigratory fattening without increases in energy intake or decreases in energy expenditure. Data apparently supporting this

TABLE 3. EXAMPLES OF VARIATION IN UTILIZATION EFFICIENCY AMONG DIFFERENT SPECIES EATING THE SAME FOOD[a]

Species	*MEC**
Corn	
Common Pheasant	0.83
Red-winged Blackbird	0.90
Graylag Goose	0.87
Northern Bobwhite	0.86
Sharp-tailed Grouse	0.86
Spur-winged Goose	0.78[b]
Alfalfa meal	
Graylag Goose	0.30
Mallard	0.32
Northern Pintail	0.33
Gadwall/Northern Shoveler	0.34
Spur-winged Goose	0.58[b]
University of Illinois Baby Chick Mash #521	
Hoary Redpoll	0.71
Common Redpoll	0.70
American Tree Sparrow	0.71
Variable Seedeater	0.74
Green-backed Sparrow	0.69
Blue-black Grassquit	0.80
Yellow-bellied Seedeater	0.79
White-throated Sparrow	0.67
Dickcissel	0.68
Sunflower seeds	
Great Tit	0.81
Northern Cardinal	0.74[c]
Evening Grosbeak	0.84
Northern Bobwhite	0.60[d]
Scaled Quail	0.86
House Sparrow	0.76[e]
10 species of passerines	0.82–0.91[e]
Wheat	
House Sparrow	0.72
Graylag Goose	0.78
Northern Bobwhite	0.70
Crickets	
American Robin	0.70
European Starling	0.70
Northern Bobwhite	0.83

[a] Data from Appendices 1 and 3.
[b] *MEC** estimated as *AMC** + 0.03 based on results from other species eating corn.
[c] Digestion trial possibly too short.
[d] Unclear whether shells were removed.
[e] S. N. Postnikov and V. R. Dol'nik in Kendeigh et al. (1977).

idea, however, could be artifacts of nutrient retention, as described above, or of the increased energy intake that occurs during premigratory fattening or reproduction. Because *apparent* rather than *true* utilization efficiency is usually measured, if there are endogenous losses of dry mass, energy, fat, carbohydrate, or other items, then increases in food intake will result in increases in apparent utilization efficiency for those components of the food, with no real change in true utilization efficiency. A convincing demonstration of this effect will require measurement of *true* utilization efficiency, or perhaps intestinal extraction efficiencies using isotopes or other methods.

Environmental conditions. There have been numerous studies with wild birds fed both wild foods and assorted poultry "mashes" in which air temperature was changed and sometimes photoperiod (Cox 1961, Brenner 1966, El-Wailly 1966, Brooks 1968, Kontogiannis 1968, West 1968, Owen 1970, Gessaman 1972, Cain 1973, Robel et al. 1979a, Stalmaster and Gessaman 1982, Wijnandts 1984). In about half of the studies, changes in these environmental variables had no significant effect on calculated *MEC**. In those studies in which significant effects were detected, no general patterns emerge except that the changes in *MEC** were generally small (i.e., <0.05). One exception to this generality is the study of Willson and Harmeson (1973) in which they found *MEC** to vary by as much as 0.13 in several digestion trials with seeds fed to passerines. The duration of their digestion trials (5–6 hours), however, was short compared to the probable mean retention time of seeds (>1.5 hours, see below) and this may be the source of the high variation, as discussed above. In studies in which changes in *MEC** have occurred with temperature, the graphical relationships between *MEC** and temperature were sometimes linear, sometimes concave, and sometimes convex. This mixed pattern would seem to rule out any unifying physiological explanation, such as decreased digesta residence time with increasing food intake.

DIFFERENCES IN UTILIZATION EFFICIENCY ASSOCIATED WITH PHYLOGENY

One suggestive piece of evidence that phylogenetic differences exist is that *MEC**'s for passerine species eating wild seeds were significantly higher than for nonpasserine species. But if one compares different species eating the same ration (Table 3), one usually finds that in most cases species have remarkably similar *MEC**'s. There are occasional outliers, some of which may be explained by methodological differences (e.g., Northern Bobwhites on sunflower seeds) or possibly errors (e.g., the substantially higher *MEC** of the Spur-winged Goose eating alfalfa meal is suspect), but others may reflect real physiological differences (e.g., Northern Bobwhites on crickets). Excluding outliers, the standard deviation among species eating the same food is about 0.04.

This measure of variation may also reflect differences among the studies in environmental conditions or methods.

This analysis corroborates my initial conclusion that probably the largest source of variation in observed utilization efficiencies is due to characteristics of food. Castro et al. (1989) concluded similarly. I do not mean to minimize the importance of the structural and functional characteristics of the birds themselves. Differences in *MEC** as large as 0.15 can occur in different species eating the same food (Table 3), and these may be associated with differences in anatomy and physiology. Also, there are few birds that can eat all types of food. Instead, there are several designs of guts that allow for effective utilization of from one to three of the food types. Presumably, this is the explanation for correspondence between food habits and gut morphology (e.g., Leopold 1953, Kehoe and Ankney 1985, Barnes and Thomas 1987).

In the following two sections of the paper, I elaborate upon the two themes of food chemistry and bird anatomy and physiology as determinants of utilization efficiency. First, I consider the chemical composition of the various food types and the manner in which it can determine utilization efficiency. As one cannot do this without making some assumptions about the physiological characteristics of the birds, I discuss those assumptions, and also attempt to define how particular anatomical and physiological attributes of the gastrointestinal tract affect utilization efficiency and allow its maximation, or optimization within certain constraints.

FOOD CHEMISTRY AS A SOURCE OF VARIATION IN UTILIZATION EFFICIENCY

A Simple Model of Utilization Efficiency Based on Food Chemistry

A simple model of digestion can illustrate the factors contributing to the large variation in utilization efficiencies within and among food types (Fig. 1) and highlight the topics where our knowledge is weakest. Comparison of model estimates with measured utilization efficiencies might reveal digestive adaptations or compromises. The model I present differs from others (e.g., Moss 1983, Servello et al. 1987) in being based upon principles of digestion and metabolism (rather than being empirically derived). Because it is more general (and therefore less accurate), its primary value may be heuristic and not predictive.

The excreta of a bird in steady state consists primarily of material of endogenous origin, undigested components of food (both organic and inorganic), and material of food origin that was absorbed, metabolized, and subsequently excreted by the kidneys (including food protein N as uric acid, urate, or urea where 1 g food N yields from 2.1 to 3 g of N-containing excretory product; see Bell, this volume). Detoxification products of plant secondary chemicals would also be included in this last component and will be considered later. If the food has an ash concentration A_i (proportion of dry mass), a N concentration of N_i, a certain proportion of R_i of its mass that is refractory to chemical digestion and absorption, and if the excretory product is uric acid (3 g excreted/g N consumed), then flux rates for the three components of excreta should be approximately accounted for as follows:

$$Q_e = E_m + Q_i(A_i) + Q_i(R_i) + 3(Q_i[N_i] - E_N) \quad (5)$$

The last component of the equation is the correction for N intake, which is incorporated into the equation primarily for birds eating foods with very high N_i (e.g., predators). It includes a new term E_N, the endogenous N loss. This N-correction is especially necessary for high N_i because the large amounts of N digested and absorbed will yield, after catabolism, appreciable amounts of excretory dry mass. E_N is subtracted from this N-correction because it has already been accounted for in E_m. Multiplying E_N by 3 implies that it is entirely uric acid whereas, in fact, some proportion of E_N might be urea, or endogenous protein N from the alimentary tract (e.g., sloughed cells).

In eq. 5 I have assumed that all of the nonrefractory portion of food is digested and absorbed, and this is often the case (some exceptions are discussed below). For example, intestinal extraction efficiencies for amino acids from soybeans averaged 93% in chickens (Achinewhu and Hewitt 1979). For glucose and sucrose, extraction efficiencies are ≥97% in nectarivorous birds (Karasov et al. 1986) and chickens (Sibbald 1976), and apparent extraction efficiencies for fat have been reported to be 93–94% in American Tree Sparrows (Martin 1968), 89–97% in Garden Warblers (Bairlein 1985) and 77–91% in chickens (Mateos and Sell 1981). Several species have been found to assimilate more than 95% of dietary wax (Obst 1986, Place and Roby 1986, Roby et al. 1986).

Substituting eq. 5 into eq. 1 allows one to derive an approximation for *MEC**, but first, energy equivalents must be assigned to R_i, N_i, and E_N (but not A_i because the energy content of ash is zero). To estimate the excretory energy loss per unit N consumed, one can use the energy

content of uric acid, 11.5 kJ/g (Bell, this volume). The same energy content will be applied to E_N, though some portion of this is probably protein. The energy content of refractory material in foods becomes a variable, GE_R. Incorporating these into eq. 5 and then substituting into eq. 1 yields:

$$MEC^*_p = 1 - [GE_R]R_i/GE_i - 34.5N_i/GE_i - (E_e - 34.5[E_N])/[GE_i][Q_i] \quad (6)$$

The number 34.5 is the product of 3 (grams uric acid/gram N excreted) and 11.5 (kJ/g uric acid) and thus has units of kJ excreted/g N excreted. If one assumes that only 75% of excreted N is in the form of uric acid (or urate) and 25% in the form of urea (with an energy content of 10.5 kJ/g; Bell, this volume), MEC^*_p is little affected (an increase of ≤ 0.016, depending upon N_i).

This equation predicts MEC^* based on four characteristics of food (R_i, GE_R, GE_i, N_i) and three characteristics of the bird (E_e, E_N, Q_i). All characteristics of the bird appear in the last term of the equation which tends to have a small effect on the calculation of MEC^*_p. Thus, the model implies that unless the N content of a food is very high, the major determinant of apparent utilization efficiency is the proportion of food that is refractory to chemical digestion. In applying the equation, one can use results from other birds to estimate E_e (e.g., 21 kJ $kg^{-0.75}$ day^{-1} in the chicken, see section Methods and Terms) and E_N (approximately 0.1 g $kg^{-0.75}$ day^{-1} in wild birds, Robbins 1983). The assumption that all birds will share similar E_e's is not unreasonable, considering that other kinds of endogenous losses (e.g., N, creatinine) in birds and mammals are predictable functions of $mass^{0.75}$. Also, even if E_e for a test species did differ substantially from the value for chickens, that usually would not have a large effect on the estimation of MEC^*_p, because the last term of the equation has a small effect on the calculation of MEC^*_p. But use of the chicken data underscores a large gap in our knowledge and emphasizes our current inability to correct accurately MEC^*'s to MEC's for almost any species but the chicken.

Food Composition as a Source of Variation in Utilization Efficiency

To understand the role of food composition in determining and affecting utilization efficiency, I will compare predictions of the equation for each food type with measured values of MEC^* (Fig. 1, Table 2). For Q_i in eq. 6, I used average feeding rates from Appendix 1 (in g $kg^{-0.75}$ day^{-1}): leaf and twig eaters, 65 ± 9 (SE); fruit-eaters, 55 ± 6; seed eaters, 52 ± 4; arthropod eaters, 59 ± 7; carnivores, 27 ± 2; and nectar, 74 (Calder and Hiebert 1983). I used average values for GE_i and N_i (Table 4), recognizing that such data may vary according to species of plant or animal sampled, phenological state, time of year, and so on. More difficult is estimating R_i, the proportion of a food that is refractory to chemical digestion. First, no single chemical assay perfectly separates the very digestible components of food from the highly indigestible components. Second, R_i for a food is not solely a function of the food but is also a function of the bird's digestive physiology. As an example, digestion of plant cell wall by geese has been reported to be negligible (Mattocks 1971, but see Buchsbaum et al. 1986), whereas some grouse and emus digest 15–35% of cell wall (Gasaway 1976b, Herd and Dawson 1984, Remington 1990). If we assume that all cell wall is refractory to digestion, we may be able to use eq. 6 to identify those instances when birds appear to digest a substantial fraction of the cell wall, based on comparatively high utilization efficiencies. Thus, developing expectations of extraction efficiency based on food composition is a first step in identifying physiological sources of variation in utilization efficiency.

A discussion of the comparisons of predicted and observed utilization efficiencies for each food type follows.

Nectar. Because nectar has no refractory material, negligible N, and I have assumed that all of the sugar is digested and absorbed, its MEC^*_p (0.986; from eq. 6) is just slightly below 1.0 due to endogenous energy losses. The predicted value is the same as the average observed value measured in 10 feeding trials (Table 2).

Vertebrate prey. I estimated MEC^*_p = 0.66–0.76 based on average N contents of vertebrate prey and a range of values for R_i (Table 4). I took R_i to be the proportion of ingested dry matter that was refractory to gastric digestion. This can be estimated based on the pellets egested by carnivores. In strigiforms, which egest pellets following gastric digestion, the ratio of pellet dry mass to ingested dry mass averages 0.13 ± 0.02 (SE) (N = 7 species of owls; Duke et al. 1975, 1976; Kirkwood 1979). In non-strigiform carnivores which pass more bone to the intestine and digest more of it, the ratio is slightly lower, 0.05 ± 0.01 (N = 11 species of hawks, falcons, eagles, and vultures; Duke et al. 1975, 1976; Kirkwood 1979). The energy content of egested material averaged 17.1 kJ/g which was used to estimate GE_R in the model.

All 20 measured values of MEC^* are within 0.09 of the predicted values (Fig. 1), indicating that most of the nonrefractory organic dry matter and hence energy in vertebrate prey can be digested and absorbed by carnivores.

Arthropod prey. I estimated MEC^*_p = 0.53–0.86 based on an average N content for arthropods and a range of values for R_i (Table 4). The

TABLE 4. CHEMICAL CHARACTERISTICS OF FOODS THAT AFFECT UTILIZATION EFFICIENCY

Food type	R_i[a]	N_i[a]	GE_i[b] (kJ/g)	GE_R (kJ/g)
Nectar (sucrose)	0	0	16.7	0
Vertebrate prey	0.04–0.17[c]	0.122[d]	23.1	17.1[e]
Arthropods	0.01–0.5[f]	0.086[g]	24.5	18.0
Cultivated seeds		0.02[h]	21.5	16.7[i]
Wild seeds	0.18–0.53[j]	0.01–0.028[j]	21.5	16.7[i]
Fruit, pulp and skin	0.09–0.34[k]	0.01[l]	19.5	16.7[i]
Fruit, pulp and skin and seeds	0.40[m]	0.01[m]	21.6	16.7[i]
Herbage eaten by grouse	0.22–0.6[n]	0.015[o]	21.6	16.7[i]
Herbage eaten by other birds	0.38–0.61[p]	0.015[o]	18.2	16.7[i]

[a] Proportion of dry mass.
[b] From Table 1.
[c] Range for 18 species from Duke et al. (1975, 1976) and Kirkwood (1979).
[d] Average for 12 species of vertebrates from Ricklefs (1974b).
[e] Average from three digestion trials from Duke et al. (1973) and Kirkwood (1979).
[f] Bernays (1986).
[g] Ricklefs (1974b) and Vonk and Western (1984). See also Bell (this volume).
[h] Five species of grains from Ricklefs (1974b).
[i] The average energy content of carbohydrate.
[j] Short and Epps (1976).
[k] Range of NDF's for six species (Levey and Karasov, unpubl., and Servello and Kirkpatrick 1987); average was 0.26.
[l] Average for 18 species from Sorensen (1984), Worthington (1983) and Levey and Karasov (unpubl.) ($\bar{X}$ = 0.013, SD = 0.007).
[m] Average for 50 species from Short and Epps (1976) and Servello et al. (1987).
[n] Gasaway (1976a), Remington (1983, 1990), Servello et al. (1987), Servello and Kirkpatrick (1987).
[o] Most values in the literature for leaves and twigs range 0.01–0.02 (Mattson 1980), though leaves of herbaceous plants sometimes exceed 0.04 (e.g., Servello and Kirkpatrick 1987).
[p] Buchsbaum et al. (1986).

primary material in arthropods refractory to chemical digestion is probably the cuticle, which may comprise 1–50% of dry matter (Bernays 1986). Because cuticle is composed of a mix of chemicals (primarily chitin and protein plus some lipids), I took its energy content to be 18 kJ/g.

Measured values of MEC^* (Fig. 1) for arthropods cluster at the higher end of the range of predicted values. This is not because the arthropods used in the digestion trials had low cuticle contents. Three of the trials used orthopterans, which have cuticle contents of about 50% of dry matter (Bernays 1986). Evidently not all of the cuticle is refractory to digestion, as had been assumed. Some components of cuticle (e.g., lipid waxes and soluble protein) are probably quite digestible while others (e.g., chitin and tanned protein [sclerotin]) are more refractory. The extent to which chitin (up to 60% of the cuticle's dry mass; Fraenkel and Rudall 1947) can be digested by birds has been practically unstudied. One Red-billed Leiothrix (*Leiothrix lutea*) was reported able to digest 56.8% of the chitin in dead mealworm larvae added to its diet (Jeuniaux and Corneluis 1978).

If one assumes that birds digest about 50% of ingested cuticle, then the predicted values of MEC^*_p range from 0.7 to 0.86. This yields very good agreement with measured values of MEC^*. Thus, I conclude that most noncuticular protein and fat in arthropods can be digested and absorbed, as well as a substantial fraction of the cuticle.

Seeds. For wild seeds I estimated MEC^*_p = 0.53–0.83 based on a range of N contents and a range of values for R_i (Table 4). As a reasonable estimate of R_i in vegetation (seeds, fruits, leaves, twigs, buds, storage organs), I used the cell wall content, determined by measuring that proportion of plant dry matter that is insoluble in neutral detergent, and correcting it for its ash content (i.e., neutral detergent fiber [NDF]; Goering and Van Soest 1970, Demment and Van Soest 1985).

Most measured values of MEC^* (Fig. 1) for seeds fall within the predicted range, indicating that little fermentation of cell wall occurs. In those cases where measured MEC^*'s fall below the predicted range, perhaps seeds with even higher cell wall contents were used than I assumed in Table 4.

Because MEC^*'s of wild seeds tend to be lower than for cultivated seeds, we might expect that wild seeds have higher cell wall contents. In fact, the amount of crude fiber (a poorer index to cell wall than NDF) in 20 species of seeds in southern forests (Short and Epps 1976) appears to be about four times greater than in commercially available seeds (Conley and Blem 1978). Possible differences in chemical makeup and hence digestibility between wild and domestic seeds merits further study.

Fruits. For wild fruits I estimated MEC^*_p = 0.67–0.89 based on an average N content and a range of values for R_i (Table 4). Surprisingly, many measured MEC^*'s fall below the predicted range (Fig. 1). That is, the utilization efficiency

on fruits is lower than might be predicted by assuming that birds digest and absorb all of the nonrefractory portion of food and none of the cell wall. There are several possible explanations. One, NDF underestimates refractory fiber (Neilson and Marlett 1983). If fruits have a large amount of pectin, gums, or mucilages (i.e., carbohydrates soluble in neutral detergent but nevertheless refractory to digestion), then use of NDF to estimate R_i will result in overestimation of MEC^*_p. This applies to herbage and seeds as well, though possibly to a smaller extent because soluble fiber tends to comprise a smaller proportion of total fiber in cereal products and vegetables (Anderson and Bridges 1988). Two, fruits may contain secondary chemicals (Herrera 1982) that might reduce utilization efficiency. Three, the anatomy and physiology of fruit-eaters results in less-than-complete digestion and absorption of even the nonrefractory sugars, fats, and proteins in fruit, as discussed below.

Herbage eaten by grouse and other birds. Herbivores appear to have lower utilization efficiencies than might be expected (Fig. 1). The predicted range for MEC^*_p was based on the assumption that all cell wall was refractory to digestion. Because some grouse and waterfowl digest 15–35% of cell wall (Buchsbaum et al. 1986, Gasaway 1976b, Remington 1990), I expected that the model would underestimate observed utilization efficiencies, but just the opposite occurred.

In some cases the values in Table 4 that I used to calculate MEC^*_p may have differed considerably from actual values in foods used in feeding trials to measure MEC^*. More importantly, a factor not considered in the model was plant secondary chemicals, which could complicate prediction of forage digestion in three ways (Robbins 1983): (1) in a forage analysis secondary chemicals can be extracted as a part of the neutral detergent soluble fraction and therefore be considered digestible, when in fact they may have little or no nutritional value; (2) secondary chemicals may interfere with digestion and absorption of the highly digestible fraction; and (3) high energy detoxification products of secondary chemicals can appear in excreta, thereby inflating the energy excretion and lowering MEC^*. I suspect that at least one of these reasons explains the apparent difference between expected and observed MEC^*'s in, for example, grouse eating leaves and twigs. Servello et al. (1987) found that total phenols averaged 0.05 of dry mass in mixed rations of wild plants fed to Ruffed Grouse. Furthermore, the accuracy of their predictions of utilization efficiency based on forage analysis was increased when they incorporated a parameter for phenol content into their equation predicting MEC^*. The grasses eaten by waterfowl probably have lower levels of secondary chemicals, such as tannins and resins, than do the leaves, twigs, and buds eaten by grouse (Rosenthal and Janzen 1979). Buchsbaum et al. (1986) found that phenols averaged 0.03 of organic matter in three species of grasses eaten by geese.

Buchsbaum et al. (1986) found that lipid (ether-soluble material) was the major energy source in the grasses eaten by geese (estimated to comprise 44% of total plant kJ), but that its apparent digestibility was low (average 36.3%). Is this an effect of plant secondary chemicals, short digesta retention time, or slow rates of fat digestion?

Waterfowl eating rhizomes have higher MEC^* values, but these foods have much lower cell wall contents (Van Soest and Robertson 1976). For example, tubers eaten by Canvasbacks had only 16% cell wall and their MEC^* was 0.79 (Takekawa 1987).

Summary. One can rank the food types from Table 2 according to expected utilization efficiency based on their average chemical composition (Table 4). The ranking for MEC^*_p is nectar > cultivated seeds > vertebrate prey ≅ arthropods ≅ wild seeds ≅ fruits > herbage. This predicted ranking compares well with the ranking of food types according to measured MEC^* (Table 2): nectar > cultivated seeds ≅ arthropods ≅ vertebrates > wild seeds ≅ fruits > herbage. For half of the food types the model predictions agree fairly well with the averages from empirical studies. Agreement was poorer for: (1) arthropods, for which the prediction underestimated the observed probably due to an incorrect assumption that all cuticle is refractory to digestion; and (2) fruit and herbage where the observed is less than the predicted, perhaps due to (a) underestimation of R_i, (b) the presence of secondary chemicals in plants, or (c) anatomical or physiological attributes of the birds resulting in less-than-complete digestion and absorption of even the nonrefractory sugars, fats, and proteins in foods. Overall, food composition can tell us a lot about the efficiency with which birds can utilize food. But difficulties remain in predicting what proportion is indigestible, based on plant chemical characteristics such as fiber and secondary compounds.

GASTROINTESTINAL TRACT STRUCTURE AND FUNCTION AS A SOURCE OF VARIATION IN UTILIZATION EFFICIENCY

Several properties of digestive anatomy and physiology affect a bird's digestive efficiency for a particular food by determining what propor-

tions of the refractory and nonrefractory parts of food are digested and absorbed (see also Ziswiler and Farner 1972 and McLelland 1979). These include the surface area and structural complexity of the gastrointestinal tract, aspects of motility that affect the retention time of digesta, and the digestive tract's capacity for chemically breaking down macromolecules and subsequently absorbing their constituents. Probably none of these properties is static, but may be affected by food intake rate or the quality of the food. Also, because these components of the digestive system act in concert, it is best to evaluate them together when possible.

Two tools are needed in order to evaluate how a difference in form or function affect digestive efficiency. One is a model that identifies those attributes of the digestive system that determine digestive efficiency, and shows how they are related to each other. The second is an understanding of how the attributes vary with body size, because without this it becomes difficult even to identify species with notable differences in form or function.

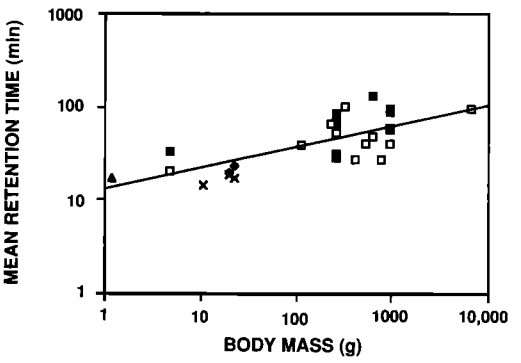

FIGURE 2. Mean retention time of food in the digestive tract as a function of mass of bird. Symbols represent different foods fed in the digesta retention trials (Appendix 2): (■) seeds; (⊡) leaves or bird chow; (◆) arthropods; (▲) nectar; (×) fruit. All data were fit to the equation $Y = 29.37X^{0.215 \pm 0.039}$ ($P < 0.001$). Retention time of seeds significantly exceeded that of leaves (or chow) by an average of 1.7 times ($P < 0.001$; analysis of covariance).

A Simple Model of Digestive Efficiency Based on Anatomy and Physiology

The proteins and complex carbohydrates in food are hydrolysed by the digestive enzymes of saliva, gastric juice, pancreatic juice, gastrointestinal secretions, and intestinal cell membranes to yield small peptides, free amino acids, and monosaccharides. These smaller molecules are then absorbed, mostly in the small intestine. The fraction of ingested nonrefractory material in food that is absorbed is directly related to the mean residence time of digesta in the gut, and the rate of hydrolysis and absorption (Penry and Jumars 1987). Absorptive efficiency for sugars and proteins can be viewed as follows (Karasov 1987):

$$F \propto (T)(J)/V \qquad (7)$$

where F is the fraction absorbed, T is the mean retention time (in minutes), J is the absorption rate (grams or moles per min) (either hydrolysis or absorption might be the limiting step; Diamond and Karasov 1987), and V is the amount of nutrient in the gut (grams or moles), which is a function of gut volume and nutrient concentration. In some birds that ferment refractory materials, there is an additional chamber for digestion either proximal (e.g., Hoatzins, *Opisthocomus hoatzin*; Grajal et al., 1989) or distal (e.g., cecal digesters) to the small intestine, and its efficiency can be similarly modeled (Penry and Jumars 1987). The parameters T and V constrain intake Q_i because it is positively related to gut volume and inversely related to retention time (Sibly 1981, Demment and Van Soest 1985, Penry and Jumars 1987):

$$Q_i \propto V/T \qquad (8)$$

We use this model to evaluate the significance of apparent digestive adaptations or trade-offs in birds. Some of the examples involve comparisons of birds differing in body size. If we know how the relevant variable covaries with body size, we can approximately correct for this difference.

Allometry of Digestive Tract Form and Function

Retention time. Calder's (1984) and Demment and Van Soest's (1985) contention that digesta retention times should increase with body mass$^{0.25}$ is supported by an analysis of available data (Fig. 2; Appendix 2). There is, however, considerable variability independent of body size. Some is due undoubtedly to differences in methods for estimating mean retention time, and to differences in diet. For example, retention times for seeds exceed those for vegetation by 70% (analysis of covariance, $P < 0.005$), in part because hard substances take longer to clear the crop and stomach (Swanson and Bartonek 1970, Custer and Pitelka 1975). In hummingbirds 13% of mean residence time for the entire gut could be accounted for by residence in the crop (Karasov et al. 1986). A comparison of whole gut mean retention and crop clearance times for seeds and arthropods (Appendix 2; Swanson and Bartonek 1970, Custer and Pitelka 1975) indicates that for

birds eating insects and seeds, most of mean residence time for the entire gut occurs in the crop.

Measurements of digesta retention in birds eating vertebrates are not directly comparable with the values in Appendix 2. Meal-to-pellet intervals (the time between ingestion of prey and egestion of pellets of undigestible material) are generally 10–20 hours (Duke et al. 1968, Balgooyen 1971, Duke et al. 1976, Rhodes and Duke 1975).

Anatomical measurements of the small intestine. At least three anatomical measurements of the small intestine are useful within the context of equations 7 and 8: intestinal length and surface area, because hydrolytic or absorptive measures are usually expressed per cm length intestine or per cm^2 nominal area (which excludes the area of villi and microvilli), and gut volume, because of its relation to retention time and intake. In a simple tube the three are related: $(4\pi)(\text{volume})(\text{length}) = (\text{area})^2$. How do these scale with body mass?

In tetraonids, small intestine length scales with $\text{mass}^{0.32}$ in species eating the same type of food (calculated from Leopold 1953). Mass of gut contents scales with $\text{mass}^{1.0}$ (Moss 1983), and volume probably scales in the same manner. Given these allometries, intestinal surface area might be expected to scale with $\text{mass}^{0.66}$. In mammals intestinal nominal surface area has been reported to scale with $\text{mass}^{0.63}$ (Karasov 1987) and $\text{mass}^{0.75}$ (Chivers and Hladik 1980). Too few data are available for a separate analysis in birds. For purposes of comparing birds of different sizes I shall normalize intestine length to $\text{mass}^{0.33}$, intestine surface area to $\text{mass}^{0.66}$, and intestine volume to $\text{mass}^{1.0}$.

Absorption rate per unit intestine. In mammals, reptiles, and fish rates of absorption of sugar and amino acid/cm^2 intestine are independent of body size (Karasov 1987). This was also the case in a small sample of birds (7 species) ranging in size from 3.2 to 700 g (Karasov and Levey 1990).

Examples of Trade-offs or Adaptations in Digestive Physiology

Low digesta retention time in frugivores. Retention time is relatively short in frugivorous birds (Herrera 1984b, Karasov and Levey 1990; Appendix 2, Fig. 2). The digestion model predicts that in the absence of a compensatory increase in hydrolysis or absorption rate, a decrease in digesta retention should result in a decrease in digestive efficiency. There is evidence for such a decrease in highly frugivorous Phainopepla (Walsberg 1975), Cedar Waxwings (Martinez del Rio 1989), and manakins (Worthington 1983), as well as in the previous comparison of predicted and observed utilization efficiency (Food Chemistry section).

Table 5 presents a detailed analysis of the effect of short retention on digestive efficiency by comparing the fruit-eating waxwing and nectarivorous hummingbird. These species are compared because they both digest solutions containing monosaccharides and disaccharides (nectar or juice of fruit), and entirely comparable data sets based on identical methodology are available (Karasov et al. 1986, Martinez del Rio et al. 1989). Waxwings, being larger, have longer small intestines with much greater nominal surface area. But when normalized to scaled body mass, intestine lengths are similar, and intestinal surface area is slightly greater in the hummingbird. Waxwings have shorter mean retention times, and, when corrected for body mass, the difference appears to be two-fold. A unit area of hummingbird intestine absorbs glucose seven times faster than that of the waxwing. Given the shorter retention time and lower glucose absorption rate (per cm^2 or per $g^{0.66}$), one would predict that digestive efficiency in the waxwing may be less than that in the hummingbird when the birds eat meals with very high glucose concentrations.

Digestive efficiencies have been measured in both species using radiolabeled glucose (Karasov et al. 1986, Martinez et al. 1989). When fed high glucose concentrations (585 mM for the hummingbird, 806 mM for the waxwing), the waxwings absorbed significantly less of the glucose than the hummingbirds (0.92 vs. 0.97, $P < 0.001$). The difference is not due to the difference in the glucose concentration; hummingbirds eating even more concentrated sugar solutions still extract more than 97% (Appendix 1). Instead, the difference is due to the relatively lower retention time and absorptive rate in the waxwing. Differences between the two species become even greater for the digestion of sucrose, because it is a two-step process of hydrolysis followed by absorption, and the overall rate is less than that of absorption alone (Martinez del Rio, pers. comm.). Thus, when waxwings and hummingbirds were fed meals containing sucrose (respectively, 439 mM and up to 2000 mM), the former had a much lower digestive efficiency (0.62 vs. 0.98; value for hummingbirds from Hainsworth 1974).

Thus, it appears that frugivores are characterized by relatively short digesta retention times which, in some cases, compromise their ability to extract nonrefractory components of their food. Presumably there is some compensating advantage to short digesta retention. Sibly's (1981) model suggests that the net rate of energy intake (a function of $Q_i \times F$) might be maximized when T is shorter than the time necessary to achieve maximal absorptive efficiency.

Large gut volume in herbivores. It has been argued that, because of the demands of flight, the mass of the digestive tract in birds should be

TABLE 5. COMPARISON OF DIGESTIVE SYSTEM FORM AND FUNCTION IN RUFOUS HUMMINGBIRDS AND CEDAR WAXWINGS IN RELATION TO EXTRACTION OF GLUCOSE FROM A MEAL

	Body mass (g)	Intestine length		Intestine area		Mean retention time		Rate of absorption[a]	Extraction efficiency (%)
		cm	$cm/g^{0.33}$	cm^2	$cm^2/g^{0.66}$	min	$min/g^{0.25}$	nmole min^{-1} cm^{-2}	
Rufous Hummingbird	3.2	5	3.4	1.2	0.6	48	36	942	97
Cedar Waxwing	35	12.4	3.8	17.4	1.7	41	17	127	92

[a] Maximal rate of carrier-mediated glucose uptake across the luminal surface of the gut; average for the proximal, mid, and distal gut (from Karasov et al. 1986, Martinez del Rio et al. 1989, Karasov, unpubl. data).

minimized. But how much gut is enough? It is possible to deduce an answer using models of digestion (Sibly 1981, Penry and Jumars 1987).

Because refractory material lowers the metabolizable energy content per gram food, more must be consumed to obtain the same amount of metabolizable energy. Equations 7 and 8 indicate that if Q_i increases, then to maximize utilization efficiency animals eating food with higher R_i should have larger digestive chambers and a longer digesta retention time. To maximize the rate at which digestive products are formed, digestive chamber size should increase (cf. eq. 5.3, Sibly 1981).

What actually happens when R_i is increased experimentally? Savory and Gentle (1976) added sawdust or cellulose to a conventional ration fed to Japanese Quail (*Coturnix japonica*) and measured feeding rate, utilization efficiency, modal retention time (*sensu* Warner 1981), and digestive tract dimensions after at least 10 weeks. Daily food intake increased and compensated almost exactly for the dilution of the nonrefractory portion of the food, and neither the rate of dry matter digestion (in g/day) nor the utilization efficiency of the nonrefractory portion of the food decreased. These changes were effected without any major change in modal retention time, but the size of the colo-rectum, small intestine, and caeca increased significantly. Other studies with ducks (Miller 1975) and woodpigeons and starlings (reviewed in Sibly 1981) have demonstrated increases in intestinal length of up to 40% when birds were switched to high R_i diets. Thus, as the models predict, a response to increased R_i is larger digestive chambers.

In the wild these changes occur as birds undergo seasonal diet shifts to foods with higher R_i (Davis 1961, Moss 1974, Drobney 1984, Gasaway 1976a). Diet shifts probably account for the differences sometimes seen in intestine lengths between wild and captive birds (reviewed in Sibly 1981) because the captives are usually fed commercial rations with lower R_i.

The proximate mechanism for the intestinal enlargement in most of these cases is probably hyperphagia (Karasov and Diamond 1983), as birds attempt to compensate for caloric dilution (higher R_i) or lower gross energy content in the food. Increased food intake during cold weather or reproduction may have similar effects (Drobney 1984).

The generalization that gut volume should be greater in birds that eat foods with high R_i does not appear to hold for frugivores. For example, four highly frugivorous species in the body mass range 14–35 g (Cedar Waxwings, Phainopepla, and two manakins; Walsberg 1975, Worthington 1983) have small intestine lengths of 13 ± 0.7 (SE) cm, whereas in eight species of less frugivorous or nonfrugivorous birds in that size range they average 19.3 ± 1.2 cm (Herrera 1984b). Herrera (1984b) did not detect a significant difference in gut length between the more frugivorous and less frugivorous species that he studied.

Selective retention of digesta in herbivores. The proportion of refractory material that is microbially fermentated is directly related to gut volume and reaction rate and indirectly related to digesta flow rate (Penry and Jumars 1987). The presence of caeca enhances fermentation by affecting all three variables: caeca increase gut volume; decrease digesta flow rate; and increase reaction rate.

Among gallinaceous birds, the proportionally largest variation among species in lower gastrointestinal tract structure is in the caeca, which are generally at least twice as long in browsers as seed-eaters (Leopold 1953). In some species the caeca selectively retain smaller particles and solutes, while larger particles pass down the large intestine. (For a discussion of the evidence for, and mechanism of, this selective retention see Fenna and Boag 1974, Clemens et al. 1975, Gasaway et al. 1975, Bjornhag and Sperber 1977, Hanssen 1979, Sperber 1985.) Thus, in Rock Ptarmigan, which have well-developed caeca, the mean retention time of a liquid marker greatly exceeds that of a solid marker (Appendix 2; see the pheasant also) whereas in the Emu, which lacks enlarged caeca, the markers travel through the digestive tract at approximately the same rate (Appendix 2). Selective retention probably increases the fermentation rate by effectively in-

creasing nutrient concentrations and the surface area available for attack by the microbes.

While a large proportion of the NDF (neutral detergent fiber) that enters the caeca may be fermented there (up to 98% in Blue Grouse; Remington 1990), only a small proportion of the total in the food actually enters (< 33% in Blue Grouse). Thus, estimates of the proportion of total dietary NDF actually digested are less than 40% (Food Chemistry section). Because food NDF values are generally less than 50–60% of dry matter, one might expect that NDF digestion provides for less than 25% of the maintenance energy requirements of cecal digesters. Estimates (cf. Gasaway 1976b) have generally been below this.

A caecum is not required for effective digestion of cell walls. Because of the relationship between mean retention time of digesta and body mass (Fig. 2), larger birds will tend to retain digesta long enough for significant fermentation to occur if the symbiotic microbes are present in the small or large intestine. This is the case in Emu in which the major site of fermentation is the distal section of the small intestine (Herd and Dawson 1984), and possibly in geese (Buchsbaum et al. 1986). Additionally, Herd and Dawson (1984) point out that if bonds between hemicellulose and lignin are hydrolyzed by gastric acid or pepsin, the solubilized hemicellulose is fermented more rapidly than other fiber components of the cell wall.

THE INTERPLAY BETWEEN DIGESTION AND ECOLOGY

The discussion so far has emphasized the utilization efficiency of birds consuming their natural foods, and those features of food composition and bird anatomy and physiology that affect that efficiency. The ecological significance of this efficiency is that it influences both the feeding rate and hence foraging time of the bird, as well as the impact of the bird on its environment through its rate of depletion of resources.

My emphasis on efficiency should not be taken to mean that this aspect of digestion is most important with regard to natural selection. Bird guts do not necessarily operate in a manner that maximizes digestive efficiency; the maximization of the rate of energy gain per gram of food and concomitant minimization of digesta volume may sometimes occur at the expense of digestive efficiency (Sibly 1981, Penry and Jumars 1987). Frugivores may provide an example of this. Neither should my emphasis on efficiency be taken to mean that this is the only context in which digestion has implications for ecology. The following are two examples of interplay between digestive physiology and ecology that suggest how digestion can constrain important aspects of an animal's ecology.

Digestive Constraints on Rates of Production

Because the maximum energy available for growth, storage, and reproduction is the difference between the maximal rate of metabolizable energy intake and the energy expended for maintenance, intake could limit productive processes (Kendeigh 1949, West 1960, Porter and McClure 1984). Unfortunately, data are virtually lacking on the maximal level, what determines it (e.g., food availability, foraging rate, digestion rate), and whether it actually operates as a limit in the wild.

Ruminants are the classic example of animals whose food intake can be limited by digestive anatomy. Similarly, the intake of brassica by Woodpigeons (*Columba palumbus*) (Kenward and Sibly 1977) and nectar by hummingbirds (e.g., Rufous Hummingbird; Karasov et al. 1986) is apparently limited by the rate at which these foods can be processed. Such a digestive bottleneck can explain why hummingbirds spend so much time perching between feeding bouts (> 75% of activity time), as they are waiting for their crop to empty. Feeding or foraging rate may also be limited by internal food-processing rate in some frugivores that swallow fruits whole (Levey 1987b).

Drent and Daan (1980) suggested that the evolution of some life history traits reflects in part the maximum energetic or work capacity of parents. For example, if the costs of feeding more nestlings are reflected in higher levels of energy expenditure, then perhaps the maximum intake which must match that expenditure has been an important constraint in evolution of clutch size. To evaluate this idea, one can estimate energy expenditure in the field (using doubly labeled water or time-energy budgets), but there is no established upper bench mark with which to compare field metabolic rates, as there is a lower bench mark (standard or basal metabolic rate). Nor is it clear how one might best measure experimentally the maximal rate.

Kendeigh (1949) and his colleagues used cold stress as an experimental manipulation to measure the maximum rate of metabolizable energy intake. They estimated these maxima in several species of birds maintained at temperatures very near or at the lower limit of their long-term temperature tolerance (Appendix 3). Work with White-throated Sparrows suggested that when the birds were exposed to temperatures below the lower limit of tolerance, they apparently died of starvation (body fat was substantially reduced).

Also, for this species, forced activity increased the lower lethal temperature, but the maximum rate of intake of metabolizable energy did not change (Kontogiannis 1968). While these data suggest that the primary limitation to energy metabolism under these conditions is the rate food can be consumed and digested, at least one other interpretation is possible: that heat generation by muscles is inadequate at the lower limit of tolerance, and the resultant hypothermia causes secondary dysfunction of digestion (Ricklefs 1974b).

Could these measures of maximal intake be used as an upper bench mark against which field metabolic rates could be compared? It may seem incongruous to compare field metabolic rates measured in the breeding season with those measured under conditions of cold and exercise, but cold and exercise should be seen merely as the most practical device for forcing a sustained elevated metabolic and feeding rate. In fact, field metabolic rates of birds in the breeding season tend to fall just below the maximum intake values (Fig. 3). I think that this approach has utility, and that considering the data available, one cannot rule out the possibility that digestive limits on the maximal rate of energy intake were important in the evolution of life history traits.

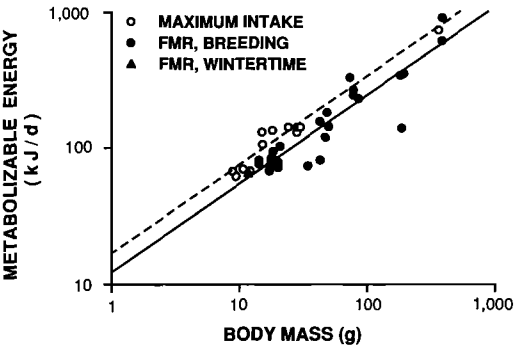

FIGURE 3. Comparison of estimates of maximum rate of energy intake with measures of energy expenditure during two periods of the annual cycle during which expenditure is likely to be particularly high. Maximum intake rates are from Appendix 3. Metabolic rates of free-living birds (field metabolic rates [*FMR*] measured with doubly labeled water) during the breeding season are from Nagy (1987). The single measurement of wintertime FMR is for the Black-capped Chickadee (*Parus atricapillus*) in Wisconsin (Brittingham and Karasov, unpubl. data). The slopes did not differ significantly whereas the intercepts did ($P < 0.005$; analysis of covariance). Data for maximum intake were fit to the equation $Y = 16.4X^{0.65}$, $r = 0.99$; for *FMR*, $Y = 12.1X^{0.65}$, $r = 0.92$.

Digestive Constraints on Niche Width

Digestive processes, when rigidly fixed by genotype, can limit a bird's ability to exploit other foraging opportunities via phenotypic adjustment (Karasov and Diamond 1988). Even when adjustment is possible, as in the case of alterations in gut morphology with change in diet, a key question is what are the limits of adjustment, and are they dictated by the foods most frequently eaten (Miller 1975, Barnes and Thomas 1987)? Also, do birds choose foods according to their ability to digest them and, if so, what are the physiological and ecological mechanisms?

Preferences of fruit-eating birds for various sugars may be determined by their abilities to digest them. In behavioral tests, European Starlings and Cedar Waxwings preferred glucose and fructose to sucrose (Schuler 1983, Martinez del Rio et al. 1988, Martinez del Rio et al. 1989). In starlings, the sucrose aversion is associated with an absence of the intestinal enzyme sucrase (Martinez del Rio et al. 1988), which hydrolyses sucrose into fructose and glucose. Too much unabsorbed sucrose in the intestine can cause severe osmotic diarrhea (Sunshine and Kretchmer 1964), and this may provide the sensory cue that leads to aversion. In waxwings the low preference for sucrose is associated with low digestive efficiency due to low levels of sucrase activity relative to digesta retention time (Structure and Function section). Perhaps these low sucrose preferences, which seem to have a physiological basis, affect fruit selection such that the birds favor those containing monosaccharides.

In some mammals the capacity to hydrolyse and absorb sugar and protein is enhanced by greater concentrations of these nutrients in the diet (reviewed in Diamond and Karasov 1987, Karasov and Diamond 1988). If starlings had this regulatory ability, then their sucrase deficiency would not be fixed, they would not necessarily get diarrhea when they eat sucrose, and they would not have an aversion to it that affected their food choice. But because the diet fed the starlings contained some sucrose, they still had negligible sucrase activity; yet, their ability to adaptively increase sucrase activity is apparently limited (Karasov and Diamond 1988). Thus, the starling's inability to digest sucrose, and hence its sucrose aversion, may set a limit to its ecological niche.

Krebs and Harvey (1986) suggested that such digestive constraints in ecology might be more widespread than previously thought. This suggests opportunities for ecologically-oriented research on avian digestion, beyond those studies dealing with the chemical and physiological determinants of digestive efficiency.

ACKNOWLEDGMENTS

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APPENDIX I. UTILIZATION EFFICIENCIES OF WILD BIRDS EATING VARIOUS TYPES OF FOODS

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q[b] (g/day)	GE[c] (kJ/g)	*AMC**	*MEC**	Source
Nectar								
Black-chinned Hummingbird (*Archilochus alexandri*)	3.2		0.5 M sucrose			0.98		Hainsworth (1974)
			1.0 M sucrose			0.98		
			2.0 M sucrose			0.99		
Rufous Hummingbird (*Selasphorus rufus*)	3.2		0.585 M sucrose			0.97		Karasov et al. (1986)
Blue-throated Hummingbird (*Lampornis clemenciae*)	7.9		0.5 M sucrose			0.98		Hainsworth (1974)
			1.0 M sucrose			0.99		
			2.0 M sucrose			0.98		
Brown Honeyeater (*Lichmera indistincta*)	~9.0		0.8 M sucrose	16.7			0.98	Collins et al. (1980)
			1.2 M sucrose				0.99	
			1.6 M sucrose				0.99	
Arthropods								
Coal Tit	~8.4		Mixed arthropods	2.4	24.4	0.48	0.67	Gibb (1957)
(*Parus ater*)	8.3	0	Mealworms	2.1	27.6	0.71	0.86	
Blue Tit (*P. caeruleus*)	11.3	−0.74	Mealworms	1.9		0.63	0.84	Gibb (1957)
Garden Warbler (*Sylvia borin*)	~20		Mealworms (+elderberries 2×/week)	2.6		0.64		Bairlein (1985)
European Starling (*Sturnus vulgaris*)	71	0	Domestic crickets	5.9	23.2	0.56	0.70	Levey and Karasov (1989)
American Robin (*Turdus migratorius*)	79	0	Domestic crickets	6.5		0.55	0.70	Levey and Karasov (1989)
Northern Bobwhite (*Colinus virginianus*)	178		Domestic crickets		24.7		0.83	Robel et al. (1979a)
Aquatic invertebrates								
African Black Oystercatcher (*Haematopus moquini*)	~50	gaining	Intertidal polychaeta (*Pseudonereis variegata*) and Rock mussels (*Choromytilus meridionalis*)				0.72	Hockey (1984)
	589	~0	Limpet (*Patella granularis*)				0.73	
Lesser Scaup (*Aythya affinis*)	820		Shrimp *Gammarus*		14.7		0.87	Sugden (1973)
Vertebrates								
White Ibis (*Eudocimus albus*)	<100	growing	Sardines plus shrimp				0.85	Kushland (1977)
	700	~0	Anchovies plus shrimp				0.80	
Eurasian Kestrel (*Falco tinnunculus*)	204	0	Day-old cockerel (*Gallus domesticus*)	9.2	24.6	0.51	0.71	Kirkwood (1979)
Common Barn-Owl (*Tyto alba*)	262	0	Day-old cockerel (*Gallus domesticus*)	10.7		0.54	0.73	Kirkwood (1979)
Long-eared Owl (*Asio otus*)	293	0	Lab mice in aviary	~10[e]			0.75[e]	Graber (1962)
			Wood Mouse (*Apodemus sylvaticus*)		21.7		0.79	Wijnandts (1984)

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
			Lab mouse (*Mus musculus*)		25.1		0.79	
			House sparrow (*Passer domesticus*)		21.8		0.68	
			Common vole (*Microtus arvalis*)		23.5		0.68	
			Shrews (*Soricidae*)		22.7		0.62	
			Harvest mouse (*Micromys minutus*)		23.8		0.61	
Broad-winged Hawk (*Buteo platypterus*)	413	0	Lean venison		22.4	0.51	0.74	Mosher and Matray (1974)
Great Horned Owl (*Bubo virginianus*)	1615	0	Mice	26.6	26.3	0.68	0.85	Duke et al. (1973)
			1-day-old turkey poults	26.4	26.8	0.71	0.85	
Snowy Owl indoors (*Nyctea* outdoors *scandiaca*)	1970	0	Lab rats				0.70	Gessaman (1972)
	1818						0.76	
Wood Stork (*Mycteria americana*)	2100	0	Frozen whiting fish	64.6	24.6		0.79	Kale (1964)
Cape Gannet (*Morus capensis*)	2755	0	Anchovy	100.0	22.4	0.54	0.74	Cooper (1978)
Bald Eagle (*Haliaeetus leucocephalus*)	3892	−0.2	Chum Salmon (*Oncorhynchus keta*)	63.4	24.4	0.54	0.75	Stalmaster and Gessaman (1982)
	3952	~0	Black-tailed Jackrabbit (*Lepus californicus*)	79.8	19.0	0.54	0.75	
	3924	+0.1	Mallard Duck (*Anas platyrhynchos*)	84.8	24.8	0.67	0.85	
Seeds								
Coal Tit	8.7	−0.3	Scots pine	2.1		0.59	0.81	Gibb (1957)
(*Parus ater*)	9.5	0	Ground nuts (peanuts)	1.8		0.61	0.81	
Blue Tit (*Parus caeruleus*)	10.2	−0.4	Ground nuts (peanuts)	2.2		0.59	0.77	Gibb (1957)
	10.4	−1.25	Scots pine	1.8		0.56	0.75	
Great Tit	17.9	−0.73	Scots pine seeds	3.3	25.7	0.64	0.78	Gibb (1957)
(*Parus major*)	19.2	−1.56	Sunflower	3.1	26.5	0.65	0.81	
	19.6	−0.36	Cob nuts	3.4	27.2	0.65	0.78	
	19.8	−0.71	Ground nuts (peanuts)	3.6	30.1	0.67	0.88	
Song Sparrow	20.8		Foxtail				0.89	Willson and
(*Melospiza melodia*)			Smartweed				0.55	Harmeson
			Hemp				0.83	(1973)
			Pigweed				0.69	
House Sparrow (*Passer domesticus*)	27	~0	Husked wheat	4.7	16.8	0.71	0.72	Weglarczyk (1981)
Eurasian Skylark (*Alauda arvensis*)	40		Barley grain		18.2	0.49	0.81	Green (1978)
Northern Cardinal	44		Foxtails		20.0		0.73	Willson &
(*Cardinalis cardinalis*)			Smartweed		20.1		0.71	Harmeson
			Hemp		24.7		0.73	(1973)
			Ragweed		30.8		0.73	
			Sunflower		22.0		0.74	
Evening Grosbeak (*Coccothraustes vespertinus*)	55.1	~0	Sunflower seeds		30.4		0.84	West and Hart (1966)
Gambel's Quail	144	+0.3	89% commercial grass seed	8.4	19.0		0.60	Goldstein and Nagy (1985)
(*Callipela gambelii*)			9% *Encelia* seed 2% arthropod		18.0			

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q[b] (g/day)	GE[c] (kJ/g)	*AMC**	*MEC**	Source
Northern Bobwhite	178		Sunflower		25.3		0.60	Robel et al.
(*Colinus virginianus*)			Showy partridgepea		19.4		0.52	(1979a)
			Giant ragweed		23.8		0.76	
			Prostrate lespedeza		20.7		0.69	
			Pin oak acorn meat		21.1		0.55	
			German millet		18.7		0.78	
			Korean lespedeza		20.7		0.63	
			Soybean		23.2		0.68	
			Wheat		18.3		0.70	
			Western ragweed		22.2		0.73	
			Black locust		20.8		0.51	
			Smartweed		18.9		0.51	
			Thistle		23.5		0.48	
	190	−4.1	Partridgepea (*Cassia nictitans*)	7.3	19.4		0.38	Robel and Bisset (1979)
	190	+0.33	Corn	15.0	18.9	0.82	0.86	Robel et al.
		+0.19	Sorghum	16.7	18.0	0.85	0.86	(1979b)
		−0.54	Hemp	14.8	23.3	0.29	0.45	
		−0.91	Shrub lespedeza	14.6	21.0	0.40	0.54	
		−3.53	Acorn	8.6	21.8	0.49	0.57	
		−4.1	Switchgrass	8.2	19.0	0.26	0.41	
Scaled Quail	194	−0.2	Sorghum	13.1	18.0		0.87	Saunders and
(*Callipepla squamata*)		+1.1	Sunflower chips	10.6	25.5		0.86	Parrish (1987)
		+0.4	Hybrid amaranth	14.1	18.8		0.84	
		−0.2	Pearlmillet pennisetum	12.6	18.8		0.84	
		~0	Amaranth	12.8	18.8		0.82	
		−0.6	Dwarf sorghum	12.1	18.4		0.75	
		−1.1	Canary grass	10.5	19.3		0.74	
		−0.4	Sand dropseed	15.2	18.0		0.68	
		−1.5	Blackwell switchgrass	11.2	19.7		0.65	
		−2.1	Bulk switchgrass	10.1	19.7		0.62	
		−0.8	Korean lespedeza	10.7	19.3		0.61	
Northern Shoveler	513							
(*Anas clypeata*)								
Gadwall	653	+1.4	Barnyard grass seeds	55	18.7		0.66	Miller (1984)
(*Anas strepera*)								
Northern Pintail	678							
(*Anas acuta*)								
Black-bellied Whistling-duck	682		Sorghum	37			0.85	Cain (1973)
(*Dendrocygna autumnalis*)								
Ring-necked Pheasant								
(*Phasianus colchicus*)								
juvenile hens	753	~0	High lysine corn	33.6	18.6	0.81	0.83	Labisky and
adult hens	900	−0.1	High lysine corn	28.6		0.80		Anderson (1973)
Sharp-tailed Grouse	950	~0	Corn	31.8	19.1		0.86	Evans and Dietz
(*Tympanuchus phasianellus*)								(1974)
Spur-winged Goose	2940	+0.03	Corn	93		0.75		Halse (1984)
(*Plectropterus gambensis*)								
Graylag Goose	4600		Ground corn		19.3		0.87	Story and Allen
(*Anser anser*)			Barley		18.3		0.76	(1982)
			Wheat		18.0		0.78	
Eastern Wild Turkey	4222	0	Water oak acorns (*Quercus nigra*)			0.57		Billingsley and Arner (1970)
(*Meleagris gallopavo silvestris*) hens			Wild pecans (*Carya illinoensis*)			0.27		
Fruit								
Red-capped Manakin	14		*Byrsonima crassifolia*		20.3		0.55	Worthington
(*Pipra mentalis*)								(1983)

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
			Guatteria amplifolia		18.6		0.40	
			Palicourea elliptica		18.4		0.53	
			Hasseltia floribunda		17.4		0.50	
			Doliocarpus major		16.8		0.78	
			Coccolaba mazanillensis		16.4		0.84	
			Anthurium clavigerum		16.4		0.76	
			Psychotria marginata		16.2		0.65	
			Psychotria horizontalis		15.5		0.61	
			Psychotria deflexa		15.2		0.76	
			Doliocarpus dentata		16.7		0.83	
Golden-collared Manakin (*Manacus vitellinus*)	17		*Heliconia latispatha*		21.0		0.81	Worthington (1983)
			Byrsonima crassifolia				0.38	
			Guatteria amplifolia				0.58	
			Palicourea elliptica				0.57	
			Hasseltia floribunda				0.51	
			Doliocarpus major				0.79	
			Anthurium brownii				0.49	
			Coccolaba mazanillensis				0.80	
			Anthurium clavigerum				0.37	
			Psychotria marginata				0.70	
			Psychotria horizontalis				0.58	
			Pyschotria deflexa				0.70	
Red-eyed Vireo (*Vireo olivaceus*)	18		*Prunus serotina*				0.83	Johnson et al. (1985)
			Smilacina racemosa				0.83	
			Sambucus canadensis				0.90	
			Vitis vulpina				0.89	
House Finch (*Carpodacus mexicanus*)	21.4		Mistletoe				0.62[f]	Walsberg (1975)
Phainopepla (*Phainopepla nitens*)	26.7		Mistletoe	4.2[f]	22.1[f]		0.49[f]	Walsberg (1975)
Gray-cheeked Thrush (*Catharus minimus*)	30		*Prunus serotina*				0.46	Johnson et al. (1985)
			Phytolacca americana				0.78	
Cedar Waxwing (*Bombycilla cedrorum*)	31		Mixed fruits (*Sorbus* sp., *Viburnum* sp., *Ligustrum* sp., *Phellodendron sachalinense*)				0.37[f]	Holthuijzen and Adkisson (1984)
Hermit Thrush (*Catharus guttatus*)	31		*Menispermum canadense*				0.62	Johnson et al. (1985)
			Smilax lasioneura				0.54	

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
			Arisaema				0.61	
			Polygonatum commutatum				0.76	
			Prunus serotina				0.74	
			Smilax hispida				0.71	
			Phytolacca americana				0.71	
			Euonymus atropurpurea		23.4		0.75	
			Celtis occidentalis				0.75	
			Smilacina racemosa				0.63	
			Cornus racemosa				0.80	
			Sambucus canadensis		21.1		0.67	
			Vitis vulpina				0.72	
Swainson's Thrush (*Catharus ustulatus*)	32		*Polygonatum commutatum*				0.65	Johnson et al. (1985)
			Prunus serotina				0.66	
			Lindera benzoin				0.72	
			Phytolacca americana				0.75	
			Smilacina racemosa				0.74	
			Cornus racemosa				0.68	
Veery (*Catharus fuscescens*)	33		*Polygonatum commutatum*				0.73	Johnson et al. (1985)
			Prunus serotina				0.77	
			Lindera benzoin				0.76	
			Phytolacca americana				0.89	
			Celtis occidentalis				0.74	
			Smilacina racemosa				0.90	
			Sambucus canadensis				0.82	
			Vitis vulpina				0.88	
Gray Catbird (*Dumetella carolinensis*)	39		*Parthenocissus quinquefolia*				0.42	Johnson et al. (1985)
			Polygonatum commutatum		18.5		0.40	
			Prunus serotina				0.58	
			Lindera benzoin		26.7		0.66	
			Phytolacca americana				0.59	
			Smilacina racemosa		18.6		0.66	
			Cornus racemosa		28.4		0.82	
			Vitis vulpina		18.4		0.83	
Wood Thrush (*Hylocichla mustelina*)	50		*Lindera benzoin*				0.85	Johnson et al. (1985)
European Starling (*Sturnus vulgaris*)	71	−3.7	Mixed fruits (grape, viburnum, dogwood)	5.2	20.2	0.56	0.55	Levey and Karasov (1989)
Brown Thrasher (*Toxostoma rufum*)	72		*Parthenocissus quinquefolia*		23.4		0.46	Johnson et al. (1985)
			Prunus serotina		17.0		0.45	
			Lindera benzoin		26.7		0.62	
			Phytolacca americana		18.7		0.81	
American Robin (*Turdus migratorius*)	77		*Menispermum canadense*		20.8		0.41	Johnson et al. (1985)
			Smilax lasioneura		19.7		0.51	

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
			Polygonatum commutatum				0.69	
			Prunus serotina				0.76	
			Smilax hispida		18.6		0.76	
			Phytolacca americana				0.74	
			Celtis occidentalis		18.6		0.79	
			Smilacina racemosa				0.81	
			Cornus racemosa				0.77	
	79	−2.6	Mixed fruits (grape, viburnum, dogwood)	7.0		0.57	0.57	Levey and Karasov (1989)
Eurasian Blackbird (*Turdus merula*)	91		Elder			0.90	0.82	Sorensen (1984)
			Bramble			0.87	0.80	
			Hawthorn			0.68	0.66	
			Sloe			0.81	0.58	
			Dogrose			0.45	0.47	
			Ivy			0.80	0.83	
Northern Bobwhite (*Colinus virginianus*)	178		Smooth sumac		21.8[f]		0.28[f]	Robel et al. (1979a)
			Rose hips		20.3[f]		0.42[f]	
			Osage orange		23.5[f]		0.63[f]	
			Dogwood		25.1[f]		0.59[f]	
Rock Ptarmigan (*Lagopus mutus*)	420		Berries of *Vaccinium myrtillus*			0.61[f]		Moss (1973)
			Berries of *Empetrum* sp.			0.49[f]		
Willow Ptarmigan (*Lagopus lagopus*)	550		Cowberries (*Vaccinium vitis-idaeu*)	19.2[f]			0.81[f]	Pullianinen et al. (1968)
Ruffed Grouse (*Bonasa umbellus*)	550		Mixed fruits (sumac, grape, autumn eleagnus)				0.48[f]	Servello et al. (1987)
Sharp-tailed Grouse (*Tympanuchus phasianellus*)	950	−3.7	Wood's rose	63.3[f]	20.6[f]		0.72[f]	Evans and Dietz (1974)
		+4.2	Fleshy hawthorn	92.3[f]	19.9[f]		0.39[f]	
		~0	Russian olive	59.6[f]	20.9[f]		0.48[f]	
		~0	Silver buffalo berry	48.9[f]	20.7[f]		0.64[f]	
		+1.8	Western snowberry	39.9[f]	20.6[f]		0.51[f]	
Eastern Wild Turkey (*Meleagris gallopavo silvestris*) hens	4,222	0	Sugarberry (*Celtis laevigata*)			0.23[f]		Billingsley and Arner (1970)
			Chufa (*Cyperus esculeutus*)			0.53[f]		
			Greenbrier (*Smilax rotundifolia*)			0.22[f]		
			Dogwood (*Cornus florida*)			0.30[f]		
			Spicebush (*Lindera benzoin*)			0.56[f]		
			Grape (*Vitis aestrivalis*)			0.41[f]		
Leaves, twigs, buds, bulbs								
Eurasian Skylark (*Alauda arvensis*)	40		Wheat leaf				0.58	Green (1978)
White-tailed Ptarmigan (*Lagopus leucurus*)	360		Willow, birch, alder			0.45		Moss (1973)
Hazel Grouse (*Tetrastes bonasia*)	400		*Betula* sp., *Salix* sp., *Chosenia* sp., *Alnus* sp.			0.38		A. V. Andreev cited in Moss (1983)

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
Rock Ptarmigan (*Lagopus mutus*)	420		Bulbils of *Polygonum*			0.50		Moss (1973)
			Catkins of *Betula pubescens*			0.19		
			Willow and birch			0.37		
	460		*Betula* sp., *Alnus* sp.			0.42		A. V. Andreev cited in Moss (1983)
Willow Ptarmigan/Red Grouse (*Lagopus lagopus*)	500		Willow and birch			0.44		Moss (1973)
hens, wild			Heather (*Calluna*		22.1	0.52	0.50	Moss (1977)
cocks, wild			*vulgaris*)	63		0.46	0.44	
captives			Heather	65		0.26		
captives			Heather	47		0.37		
cocks, captive	600	−0.8	Heather	71	22.2	0.27		Moss and Parkinson (1972)
			Blueberry stems (*Vaccinium myrtillus*)	67.8		0.30	0.31	Pullianinen et al. (1968)
	600		*Chosenia arbutifolia*			0.35		A. V. Andreev cited in Moss (1983)
Northern Shoveler (*Anas clypeata*)	513	+0.9						
Gadwall (*Anas strepera*)	653	+0.9	Alfalfa pellets	43.9	17.6		0.34	Miller (1984)
Northern Pintail (*Anas acuta*)	678	+0.9	Alfalfa pellets		17.6		0.33	Miller (1974)
Ruffed Grouse (*Bonasa umbellus*)	550	−2.8	Aspen male flower buds		20.9		0.18	Hill et al. (1968)
			Grape leaves plus greenbrier leaves				0.43	Servello et al. (1987)
Spruce Grouse (*Dendragapus canadensis*)	575	−0.3[e]	*Pinus contorta* needles	40.4	21.9	0.27	0.30	Pendergast and Boag (1971)
Sharp-tailed Grouse (*Tympanuchus phasianellus*)	950	−5.0	Plains cottonwood buds	21.5	22.5		0.46	Evans and Dietz (1974)
Canvasback (*Aythya valisineria*)	964		American wild celery winter buds (*Vallisneria americana*)	27.6	16.1	0.75	0.79	Takekawa (1987)
Black Grouse (*Tetrao tetrix*)	1000		*Betula* sp.			0.35		A. V. Andreev cited in Moss (1983)
Blue Grouse (*Dendragapus obscurus*)	1040	+0.5	Doulgas-fir needles	87	21.0	0.35		Remington (1990)
		−1.2	Lodgepole pine needles	74	21.5	0.34		
		−2.1	Subalpine fir needles	52	21.7	0.30		
		−1.1	Engelmann spruce needles	64	20.1	0.26		
Brant (*Branta bernicla*)	1600		*Spartina patens* (Gramineae)		18.3	0.45	0.51	Buchsbaum et al. (1986)
			S. alterniflora		19.5	0.10	0.34	
Barnacle Goose (*Branta leucopsis*)	1687		*Lolium perenne*		18.7	0.33		Ebbinge et al. (1975)
			Mixed grasses			0.22		
Lesser Snow Goose (*Anser caerulescens*)	2500		Bulrush rhizomes (*Scirpus americanus*)	66–137		0.28	0.36	Burton et al. (1979)
Spur-winged Goose (*Plectropterus gambensis*)	2940	+0.04	Rabbit pellets	164		0.55		Halse (1984)
Mallard (*Anas platyrhynchos*)	3600		Alfalfa		17.4		0.32	Muztar et al. (1977)
			Cladophora		8.3		0.30	
			Duckweed (*Lemna minor*)		17.5		0.15	

APPENDIX I. CONTINUED

	Body mass					Utilization efficiency[d]		
	$\bar{X}$ (g)	%/day[a]	Diet	Q_i[b] (g/day)	GE_i[c] (kJ/g)	*AMC**	*MEC**	Source
			Watermilfoil		7.6		0.23	
			Pondweed		11.6		0.23	
			Vallisneria americana		12.9		0.22	
Cape Barren Goose (*Cereopsis novaehollandiae*)	3680		Dried lucerne	298		0.26		Marriott and Forbes (1970)
Canada Goose (*Branta canadensis*)	4000	0	*Spartina alterniflora* (Gramineae)		19.0	0.25	0.30	Buchsbaum et al. (1986)
	4000	0	*Juncus gerardi* (Juncaceae)		20.0	0.19	0.40	
Common Capercaillie (*Tetrao urogallus*)	4600		*Pinus sylvestris*			0.33		A. V. Andreev cited in Moss (1983)
Graylag Goose (*Anser anser*)	4600		Dehydrated alfalfa meal		17.5		0.30	Story and Allen (1982)
			Alfalfa haylage		17.6		0.38	
Tundra Swan (*Cygnus columbianus*)	6650	−2.3	Timothy grass		15.5		0.40	McKelvey (1985)
Trumpeter Swan (*C. buccinator*)	10,650	−2.4	Rhizomes of *Carex lyngbei*		18.4		0.56	
Emu (*Dromaius novaehollandiae*)	38,000		Grain and vegetable offal					Dawson and Herd (1983), Herd and Dawson (1984)
			Diet 1	~750		0.60	0.64	
			Diet 2	~459		0.62	0.64	
			Diet 3	~628		0.60	0.68	
Ostrich (*Struthio camelus*)	80,700	−1.4	Lucerne, coarsely milled, H_2O deprived	290	16.6	0.17	0.28	Withers (1983)
	95,400	~0	Lucerne, coarsely milled, ad lib H_2O	1780		0.34	0.43	

[a] Change in body mass during feeding trials.
[b] Feeding rate, g dry matter/day.
[c] Gross energy content per gram dry matter.
[d] Definitions in Table 1.
[e] Recalculated by Wijnandts (1984).
[f] For whole fruit including seeds. All other values in table are for whole fruit minus seeds.
[g] Two other wild-caught birds maintained weight eating *Pinus* needles for 2 mo.

APPENDIX II. MEAN RETENTION TIMES, OR APPEARANCE TIMES OF DIGESTA MARKERS IN BIRDS

Species	Body mass (g)	Diet	Appearance time (min) 5%	50%	95%	Source
Leaf and twig eaters						
Common Canary (*Serinus canarius*)	15	Turnip leaves	31[d]	59[f]		Malone (1965)
Rock Ptarmigan (*Lagopus mutus*)	460	Game chow	78[b] 288[c]	114 594	618 1554	Gasaway et al. (1975)
Canvasback (*Aythya valisineria*)	964	Wild celery buds		189[a]		Takekawa (1987)
Red-breasted Goose (*Branta ruficollis*)	1120	Grass	80[d]	91		Owen (1975)
Mallard (*Anas platyrhynchos*)	1150	*Elodea* (algae) cattail	48[d] 84[d]	84[f] 150[f]		Malone (1965)
Ring-necked Pheasant (*Phasianus colchicus*)	1400	Turkey breeder pellets	90[b]	300[f]	510[g] 2100[h]	Duke et al. (1968)
Barnacle Goose (*Branta leucopsis*)	1905	Grass	52[d]	78		Owen (1975)
Lesser Snow Goose (*Chen c. caerulescens*)	2500	Bulrush rhizomes	58[a]	120	192	Burton et al. (1979)
Spur-winged Goose (*Plectropterus gambensis*)	2940	Rabbit pellets	108[a]	138	210	Halse (1984)
Cape Barren Goose (*Cereopsis novaehollandiae*)	3680	Lucerne		78	132	Marriott and Forbes (1970)
Graylag Goose (*Anser anser*)	4600	Grass		120		Mattocks (1971)
Emu (*Dromaius novaehollandiae*)	38,000	Grain plus vegetable offal	132[b] 108[c]	282 234	822 444	Herd and Dawson (1984)
Seed eaters						
Common Canary (*Serinus canarius*)	15	Commercial seeds	58[d]	95[f]		Malone (1965)
Chipping Sparrow (*Spizella passerina*)	11.5	Cracked corn	62[a]			Stevenson (1933)
Field Sparrow (*Spizella pusilla*)	13.7	Cracked corn	101[a]			Stevenson (1933)
Song Sparrow (*Melospiza melodia*)	20.6	Cracked corn	102[a]			Stevenson (1933)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	41.6	Cracked corn	92[a]			Stevenson (1933)
Mallard (*Anas platyrhynchos*)	1150	Maize Oats Wheat	168[d] 126[d] 90–210[a]	246[f] 192[f] ~210		Malone (1965) Malone (1965) Clark et al. (1986)
Spur-winged Goose (*Plectropterus gambensis*)	2940	Maize	315[a]	384	450	Halse (1984)
Graylag Goose (*Anser anser*)	4600	Corn Wheat Oats Rice hulls		258[a] 168[a] 174[a] 282[a]		Storey and Allen (1982)
Arthropod eaters						
Scarlet Tanager (*Piranga olivacea*)	29	Beetle and moth larvae, mealworms	85[a]			Stevenson (1933)
European Starling (*Sturnus vulgaris*)	71	Crickets		56[c]		Levey and Karasov (unpubl. data)
American Robin (*Turdus migratorius*)	79	Crickets		65[c]		Levey and Karasov (unpubl. data)
American Black Duck (*Anas rubripes*)	904	Blue mussels			50[d]	Grandy (1972)
Mallard (*Anas platyrhynchos*)	1150	Crayfish	66[d]	86[f]		Malone (1965)
Nectar eaters						
Rufous Hummingbird (*Selasphorus rufus*)	3.2	Sugar water	<15[c]	48	180	Karasov et al. (1986)
Fruit eaters						
Red-capped Manakin (*Pipra mentalis*)	14	Tropical fruits	22[d]			Worthington (1983)

APPENDIX II. MEAN RETENTION TIMES, OR APPEARANCE TIMES OF DIGESTA MARKERS IN BIRDS

Species	Body mass (g)	Diet	Appearance time (min) 5%	50%	95%	Source
Golden-collared Manakin (*Manacus vitellinus*)	18	Tropical fruits	21[d]			Worthington (1983)
Phainopepla (*Phainopepla nitens*)	26.7	Mistletoe	29[d]			Walsberg (1975)
Cedar Waxwing (*Bombycilla cedrorum*)	31	Dogwood	23[a]			Holthuijzen and Adkisson (1984)
		Red cedar	12[a]			
Cedar Waxwing (*Bombycilla cedrorum*)	35	Fruit mash		41[c]		Martinez del Rio et al. (1989)
European Starling (*Sturnus vulgaris*)	71	Wild grapes	14[c]	53		Karasov and Levey (1990)
American Robin (*Turdus migratorius*)	79	Wild grapes	16[c]	48		Karasov and Levey (1990)
Eurasian Blackbird (*Turdus merula*)	90	Elder	26[d]			Sorensen (1984)
		Bramble	39[d]			
		Hawthorne	32[d]			
		Sloe	19[d]			
		Dogrose	29[d]			
		Ivy	30[d]			

Times shown are times of appearance of 5%, 50%, and 95% of marker fed to animals, or else mean retention time (roughly equivalent to time until appearance of 50% of a marker) determined by another method. The marker or method is indicated by a superscript: [a]dye, [b]particulate marker, [c]liquid marker, [d]fragments of food, [e]meal to pellet interval, [f]midpoint between appearance of first and last marker, [g]portion not digested in caecum, [h]portion digested in caecum.

APPENDIX III. MAXIMUM RATES OF INTAKE OF FOOD AND METABOLIZABLE ENERGY IN BIRDS

Species	Mass	Diet	*MEC*[a]	Q_i Maximum[a] (g/day)	Q_i Maximum relative to normal[b]	Metabolizable energy intake Maximum (kJ/day)	Metabolizable energy intake Maximum relative to *BMR*[c]	Source
Yellow-bellied Seedeater (*Sporophila nigricollis*)	8.9	Univ. Ill. #521 chick starter feed	0.79	5.1	1.59	68	3.84	Cox (1961)
Blue-black Grassquit (*Volatinia jacarina*)	9.3	Univ. Ill. #521 chick starter feed	0.80	4.4	1.52	62	3.39	Cox (1961)
Variable Seedeater (*Sporophila aurita*)	10.8	Univ. Ill. #521 chick starter feed	0.74	5.0	1.52	69	3.39	Cox (1961)
Zebra Finch (*Poephila guttata*)	12	Laying ration for chickens	0.77	5.4	1.59	67	3.05	El-Wailly (1966)
Hoary Redpoll (*Carduelis hornemanni exilipes*)	15	Univ. Ill. #521 chick starter feed	0.71	10.3	2.94	130	5.03	Brooks (1968)
Common Redpoll (*Carduelis flammea*)	15	Univ. Ill. #521 chick starter feed	0.70	9.1	2.28	105	4.07	Brooks (1968)
American Tree Sparrow (*Spizella arborea*)	18	Univ. Ill. #521 chick starter feed	0.71	10.7	2.05	134	4.55	West (1960)
House Sparrow (*Passer domesticus*)	24	Univ. Ill. #393 chick mash	0.85	8.9	1.85	144	3.97	Kendeigh et al. (1977)
White-throated Sparrow (*Zonotrichia albicollis*)	28	Univ. Ill. #521 chick starter feed	0.67	10.9[d]	1.63	130[d]	3.20	Kontogiannis (1968)
			0.67	11.6	2.14	143	3.52	
Dickcissel (*Spiza americana*)	30	Univ. Ill. #521 chick starter feed	0.68	12.6	1.88	143	3.35	Zimmerman (1965)
Blue-winged Teal (*Anas discors*)	360	Duck Growena	0.75	>53	>2.43	>748	>4.76	Owen (1970)
Black-bellied Whistling-duck (*Dendrocygna autumnalis*)	782	Sorghum	0.85	87	2.29	1282	4.67	Cain (1973)

[a] Highest intake (g dry mass/d) measured at temperature very near or at the lower limits of temperature tolerance.
[b] Normal intake measured at 20–24°C.
[c] Basal metabolic rate (*BMR*) from Lasiewski and Dawson (1967).
[d] Maximum value under experimental condition of low temperature plus forced exercise.