

PROPER EXPRESSION OF METABOLIZABLE ENERGY IN AVIAN ENERGETICS

MICHAEL R. MILLER

AND

KENNETH J. REINECKE

ABSTRACT.— We review metabolizable energy (*ME*) concepts and present evidence suggesting that the form of *ME* used for analyses of avian energetics can affect interpretation of results. Apparent *ME* (*AME*) is the most widely used measure of food energy available to birds. True *ME* (*TME*) differs from *AME* in recognizing fecal and urinary energy of nonfood origin as metabolized energy. Only *AME* values obtained from test birds fed at maintenance levels should be used for energy analyses. A practical assay for *TME* has shown that *TME* estimates are less sensitive than *AME* to variation in food intake. The *TME* assay may be particularly useful in studies of natural foods that are difficult to obtain in quantities large enough to supply test birds with maintenance requirements. Energy budgets calculated from existence metabolism should be expressed as kJ of *AME* and converted to food requirements with estimates of metabolizability given in kJ *AME*/g. Energy budgets calculated from multiples of basal metabolic rate (a component of maintenance energy), however, should be expressed as kJ of either *TME* or net energy depending on ambient temperature. Energy units should be stated explicitly to improve comparability and in some cases accuracy of energy analyses.

Metabolizable energy (*ME*; see Appendix for explanation of this and other abbreviations) is a measure of the energy available to birds from their diet (Vohra 1966). In avian energetics, *ME* is used to convert daily energy budgets (*DEB*; see, e.g., King 1974, Kendeigh et al. 1977) to weight of food required to supply energy needed by individuals or populations (Kendeigh et al. 1977, Wiens and Dyer 1977). *ME* has been used in this way for *DEBs* based on "existence metabolism" (*EM*; Kendeigh et al. 1977) and multiples of basal metabolic rate (*BMR*; King 1973, 1974, Ricklefs 1974, Prince 1979).

ME can be expressed as either apparent (*AME*) or true (*TME*) metabolizable energy (Harris 1966). The form of *ME* used in modeling calculations has almost always been *AME*, although not often specified as such (Ricklefs 1974, Wiens and Dyer 1975, 1977, Craig et al. 1979, Prince 1979, Raveling 1979, Ashkenazie and Safriel 1979, Sugden et al. 1981). *AME* has been the traditional measure of *ME* in studies of birds because, until recently, standard feeding trials did not separate total excretory energy into independent estimates of fecal plus urinary energy (*FE* + *UE*) and of metabolic fecal plus endogenous urinary energy (fecal and urinary energy of nonfood origin; *FE_m* + *UE_e*; Sibbald 1976). However, *TME* correctly recognizes *FE_m* and *UE_e* as metabolized energy (Harris 1966, Owen and Rei-

necke 1979) and is, therefore, a more direct measure of energy availability. Our purposes here are to provide a brief review of *ME* concepts and to show that the form of *ME* used for energetics analyses can affect interpretation of results.

AME is usually estimated with data obtained from test birds confined in metabolism cages. The birds are fed experimental diets over a number of days during which total food ingested and excreta voided are measured. This is the total collection method (Vohra 1972). Bomb calorimetry is used to determine the energy content of food and excreta, and *AME* (in kJ/g) is calculated from the equation:

$$AME = [(GE_i)(Q_i) - (GE_e)(Q_e)]/Q_i \quad (1)$$

where *GE_i* and *GE_e* = the gross energy density of food that is eaten (intake) and excreta (in kJ/g), and *Q_i* and *Q_e* = the quantity of food eaten and excreta produced (in g). Alternatively, a nondigestible chemical (Vohra 1972) or crude fiber (Almquist and Halloran 1971) can be used as a tracer to relate excreta production to food intake:

$$AME = GE_i - (\%T_i/\%T_e)GE_e \quad (2)$$

where *%T_i* and *%T_e* = percent tracer in the food and excreta. Expressions of energy availability that use digestive efficiency (Ashkenazie and Safriel 1979, Raveling 1979), assimilation efficiency (Ricklefs 1974), or metabolizable en-

TABLE 1. Apparent (AME) and true (TME) metabolizable energy values of selected foods assayed with roosters.

Food	Food intake (g air-dried wt)	AME	TME	Difference between	Source of data
		(kJ/g air-dried wt)	(kJ/g air-dried wt)	AME and TME (%)‡	
Barley	30	11.51	14.02	18	Sibbald 1976
	30	11.51	12.93	11	Sibbald 1979a
Corn	30	13.65	16.49	17	Sibbald 1976
	30	14.82	16.24	9	Sibbald 1979a
	55*	15.24	16.91	10	Chami et al. 1980
Wheat	30	12.43	14.69	15	Sibbald 1976
	30	12.81	14.23	10	Sibbald 1979a
Oats	30	8.25	11.18	26	Sibbald 1976
	30	11.60	13.02	11	Sibbald 1979a
Milo	45*	13.90	15.91	13	Chami et al. 1980
Rice bran	40*	11.22	13.60	18	Chami et al. 1980
Soybean meal	35	9.42	11.72	20	Muztar and Slinger 1981
	35	11.68	12.64	8	Muztar and Slinger 1981
	35	10.47	12.39	15	Muztar and Slinger 1981
Alfalfa	20	5.86	7.70	24	Muztar et al. 1977
Cladophora sp.	23	1.76	2.80	37	Muztar et al. 1977
Lemna minor	21	4.23	4.69	10	Muztar et al. 1977
Potamogeton sp.†	24	1.59	2.64	40	Muztar et al. 1977
Vallisneria sp.†	25	2.55	2.85	11	Muztar et al. 1977

* Estimated.
 † Vegetative parts.
 ‡ (TME - AME)/TME × 100.

ergy coefficients (MEC; Kendeigh et al. 1977) are also "apparent" values because FE_m and UE_e are included as excretory energy in each case.

TME can be determined from total collection data by regressing total excretory energy [$GE_e(Q_e)$] on Q_i (Sibbald 1975). The regression is described by the linear equation $Y = a + bX$, where Y (in kJ) = $GE_e(Q_e)$, $X = Q_i$ (in g), $a = FE_m + UE_e$ (in kJ), and $b =$ energy voided as excreta per gram of food consumed (in kJ/g). Using this method, TME (in kJ/g) = $GE_i - b$. A direct method of determining TME was described by Sibbald (1976). Experimental and control birds are fasted for 24 h. The experimentals are then force-fed predetermined amounts of a test diet, and their excreta collected over the next 24–48 h (Sibbald 1979b). Control birds are either fasted for a comparable period or fed an energy source such as glucose that is completely absorbed (Dale and Fuller 1982). More precise results are obtained when each bird serves as its own negative control (Sibbald and Price 1980). Excreta from the control group estimates $FE_m + UE_e$ (Sibbald 1981), and TME (in kJ/g) is calculated using the equation:

$$TME = \{GE_i(Q_i) - [GE_{ef}(Q_{ef}) - GE_{ec}(Q_{ec})]\} / Q_i \quad (3)$$

where GE_{ef} and GE_{ec} = total energy density of excreta from fed and control birds (in kJ/g),

and Q_{ef} and Q_{ec} = the quantity of excreta from fed and control birds (in g).

TME and AME can be corrected to zero nitrogen balance so that ME values derived using birds with divergent nitrogen requirements (e.g., growing vs. mature) will be comparable. To do this, 34.4 kJ (8.22 kcal) are added to or subtracted from ME for each gram of nitrogen lost or gained to account for energy required in the excretion of urinary nitrogen (Harris 1966).

TABLE 2. Apparent (AME) and true (TME) metabolizable energy values of selected foods assayed with wild Mallards. Data from K. J. Reinecke and R. E. Kirk (unpubl).*

Food	Food intake (g air-dried wt)	AME	TME	Difference between
		(kJ/g air-dried wt)	(kJ/g air-dried wt)	AME and TME (%)†
Developer ration	5	7.17	11.72	39
	10	9.82	12.45	21
	15	10.10	11.62	13
	20	10.73	12.05	11
	25	10.68	11.59	8
	30	11.34	12.22	7
Corn	40	11.13	11.79	6
	5	11.64	15.62	26
	15	14.38	15.71	8
Wheat	25	15.09	15.89	5
	5	10.71	14.54	26
	15	12.57	13.85	9
	25	13.90	14.67	5

* Following the methods of Sibbald (1976).
 † (TME - AME)/TME × 100.

TABLE 3. Apparent (*AME*) and true (*TME*) metabolizable energy values of selected foods assayed with Embden Geese. Data from Storey and Allen (1982).

Food	Food intake (g air-dried wt)	<i>AME</i> (kJ/g air-dried wt)	<i>TME</i> (kJ/g air-dried wt)	Difference between <i>AME</i> and <i>TME</i> (%)*
Corn	50	16.81	17.86	6
Wheat (Era)	50	14.03	14.92	6
Oats (Moore)	50	13.87	14.74	6
Dehydrated alfalfa meal	50	5.18	6.10	15
Alfalfa haylage	25	6.78	8.76	23
Barley (Morex)	50	13.90	14.68	5
Rye (Rymin)	50	11.48	12.28	6
Soybean meal 1	50	13.41	14.19	5
Steamed, rolled oats	50	15.94	16.72	5
Milo	50	16.10	16.89	5
Corn oil	33	31.25	32.50	4
Animal/vegetable fat	33	28.66	29.03	1

* $(TME - AME)/TME \times 100$.

Theoretically, *AME* and *TME* are related as follows (when expressed as kJ/g): (1) *TME* always exceeds *AME*, (2) *AME* varies with energy intake, (3) *TME* is independent of energy intake, and (4) *AME* approaches *TME* as energy intake increases. The first relationship can be inferred by comparing equations 1 and 3: endogenous losses are subtracted from excretory energy in calculating *TME*, but not *AME* (see Tables 1–3; and Harris 1966; Sibbald 1975). The other relationships can be inferred from the linear dependence of excretory energy on food intake, and from data which indicate that the rate of excretion of $FE_m + UE_e$ is constant under standard conditions (Sibbald 1975, 1976). *AME* values vary with food intake because intake levels determine the ratio between $(FE_m + UE_e)$ and $(FE + UE)$ in excreta (Table 2 and Sibbald 1975:Fig. 7). *TME* accounts for energy lost as $FE_m + UE_e$ and, therefore, is independent of food intake. Finally, if energy intake could increase indefinitely, the percentage of $(FE_m + UE_e)$ in excreta would approach zero and *AME* would, therefore, approach *TME*. However, food intake cannot increase without bounds, so there is a practical limit on the convergence of *AME* and *TME*. For example, if a 1-kg Mallard (*Anas platyrhynchos*) has a maintenance energy requirement of 2.5 *BMR* and $BMR = 314$ kJ/kg, then at maintenance (785 kJ) the difference between *TME* and *AME* would be about 3% of *TME* (cf. Sibbald 1975). This is because $FE_m + UE_e$ is approximately 22 kJ in the Mallard (K. J. Reinecke and R. E. Kirk, unpubl. data).

Differences between *AME* and *TME* illustrated in Tables 1–3 exceed 3% because determinations were made at intake levels below

maintenance. Differences in Table 1 are variable because the data are from several studies involving different foods and intake levels that were low relative to maintenance requirements of roosters (*Gallus gallus*, var. *domesticus*) weighing 2–3 kg. Differences in Table 2 decreased to 5–6% as intake levels of Mallards increased to 25–40 g. If the maintenance requirement of Mallards is about twice the highest experimental intakes, then differences between *AME* and *TME* should decrease proportionately and approach the predicted value of about 3%. Storey and Allen's (1982) data for domestic geese (*Anser anser*; Table 3) include two alfalfa diets which produced differences between *AME* and *TME* of 15 and 23%. Consumption of these diets was probably low relative to maintenance requirements because of the low *ME* values. Also, values for dehydrated alfalfa meal may have been affected by incomplete passage of this food through the digestive tract during the collection period (Sibbald and Price 1980). The mean difference for other foods consumed by these geese was about 5% and might have been lower if control birds had fed rather than fasted (Dale and Fuller 1982).

Thus, when feeding trials are conducted with foods that are readily accepted and ingested at levels that maintain body weight (e.g., Sugden 1971), differences between *AME* and *TME* may be as low as 3%. Unfortunately, *AME* values available in the literature have been determined by several different techniques at a number of laboratories and vary considerably even for the same foods (Sibbald 1977). Also, published values often are not accompanied with data concerning food intake which may be below maintenance levels, especially in the case of poorly digested foods. Caution should be used in selecting published *AME* values for use in avian energetics analyses. In general, investigators should use *AME* data derived only from test birds fed at maintenance levels. Variability of *AME* values makes determination of *TME* with regression equations like those developed by Sibbald (1977) and Muztar and Slinger (1981) of questionable value. Direct measurements of *TME* would provide more reliable estimates.

Traditional feeding trials used to determine *AME* values are often impractical for work with wild birds and natural foods because it can be difficult to collect or keep sufficient food to ensure that the birds' intake is at maintenance levels. Erratic or even negative *AME* values may result (e.g., Sugden 1973). In contrast, the *TME* assay of Sibbald (1976) is rapid, requires only small quantities of a test diet, includes a measure of endogenous losses, and

is independent of intake level. Because of these practical considerations and the sensitivity of *AME* estimates to intake levels, Sibbald's method should be of considerable value as "nutritional ecology" gains attention (Murphy and King 1982).

Furthermore, models of individual and population food requirements involving estimates of *ME* are subject to error if *AME* and *TME* are not used correctly. For example, in order to estimate the amount of food necessary to meet a bird's *DEB*, energy available from the diet should be expressed as *AME* when the *DEB* is based on *EM*, because units are consistent, i.e., food required (in g) = Energy required (in kJ *AME*)/Energy available (in kJ *AME*/g). On the other hand, use of *TME* with the same *DEB* (kJ *AME*/day) would underestimate food requirements because *TME* is larger than *AME*. However, when *DEB* is based on multiples of *BMR*, use of *AME*, *MEC*, and digestive or assimilative efficiencies (all kJ of *AME*) will overestimate food requirements for the same reason; *TME* is more appropriate in this case. Potential errors in the resulting estimates are directly proportional to the differences between *AME* and *TME* (e.g., Tables 1-3).

A further distinction must be made in cases where *DEB* is calculated from multiples of *BMR*. Because *BMR* is a component of maintenance energy (Harris 1966), it should be expressed as kJ of net energy (*NE*). *NE* is the difference between *TME* and specific dynamic effect (*SDE*) or heat increment of feeding; it provides energy for maintenance (e.g., *BMR*) and production (e.g., tissue growth; Harris 1966, Owen and Reinecke 1979: Fig. 1). When ambient temperatures are above a bird's lower critical temperature (T_{lc}), energy from *SDE* is dissipated as heat, but when temperatures fall below T_{lc} , *SDE* replaces energy that would otherwise be required for thermoregulation (Kendeigh et al. 1977). Ideally, *DEB* calculated from *BMR* should be converted to food requirements using *NE* values when temperatures are above T_{lc} and with *TME* values at lower temperatures. Unfortunately, *NE* is difficult to estimate and even the poultry industry operates with an *ME* system (National Research Council Subcommittee on Poultry Nutrition 1977). Ideally, investigators should use *TME* in this case and, if necessary, consider adjustments for *SDE* (see Ricklefs 1974:168). In practice, however, *AME* is approximately correct because the differences between *AME* and *TME*, and between *TME* and *NE*, are compensating errors. Finally, the comparability, and in some cases accuracy, of energetics analyses will improve if units of energy are stated explicitly.

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U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Wildlife Research Field Station, 6924 Tremont Road, Dixon, California 95620. Address of second author: U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Vicksburg Field Station, Rm. 509, 820 South Street, Vicksburg, Mississippi 39180. Received 6 May 1983. Final acceptance 24 May 1984.

APPENDIX 1. Glossary of selected abbreviations used (in order of their appearance).

Abbreviation	Definition
ME	Metabolizable energy
AME	Apparent metabolizable energy
TME	True metabolizable energy
DEB	Daily energy budgets
EM	Existence metabolism
BMR	Basal metabolic rate
FE	Fecal energy
UE	Urinary energy
MEC	Metabolizable energy coefficients
NE	Net energy
SDE	Specific dynamic effect

RECENT PUBLICATIONS

Birds of Fiji, Tonga and Samoa.—Dick Watling. 1982. Millwood Press. 176 p. \$39.95 U.S. plus \$4.55 surface postage. Source: Millwood Press Ltd., 291b Tinakori Road, Thorndon, Wellington, New Zealand. This book opens with an ornithological history and a good discussion of avifaunal composition and ecological isolation for the birds of its region. Beautiful oblique aerial views of islands and habitats are presented. Part 2 offers 15 good color plates of paintings by Chloe Talbot-Kelly. Part 3 contains species accounts of land birds, including common, local, and scientific names, descriptions, song, habitat and some behavior. This section is well-illustrated with food and habitat plants, insects, identification aids, and adequate maps of distribution. In contrast, Part 4 summarily dismisses the sea and shore birds with silhouettes and abbreviated species accounts. Glossary. Excellent bibliography of 245 entries. Checklist of birds in the Fiji region. Indices of scientific, English and local names. This work covers a larger area from a more professional point of view than the book by Muse and Muse (noted below). Ornithologists who intend to work in these islands are reminded to see

Amerson, Whistler, and Schwaner's report (noticed in *Condor* 85:391).—J. Tate.

The birds and birdlore of Samoa.—Corey and Shirley Muse. 1982. Pioneer Press, Walla Walla, Washington. 156 p. Paper cover. No price given. More than just a list of the birds of a group of sixteen tropical islands in the western Pacific, this small paperback also provides an interesting ornithological history, numerous legends and proverbs, and more. The loss of native forests and a burgeoning human population are documented and clearly of concern. The bird list is divided into sections on seabirds; migrants and visitors; and waterfowl, marsh and land or forest birds. For each species, a common name, Samoan name, size, description, similar species, seasonal status, habitat and birding locations are usually provided. A useful section on suggestions for birding in Samoa and notes on the language contribute greatly to the value of the book. It appears better suited for the birder than Watling's book (noted above). List of citations, bibliography, photographs, and illustrations by Norman Adams.—J. Tate.