

BIRDS AND MAMMALS ON AN INSECT DIET: A PRIMER ON DIET COMPOSITION ANALYSIS IN RELATION TO ECOLOGICAL ENERGETICS

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Abstract. Applying physiological measures of energy metabolism to problems in animal ecology and behavior usually requires knowledge of the composition of the diet and how it is digested. Using published values of insect composition, and making assumptions about digestibility of various components, I estimate that an average diet of flying insects yields about 24.2 kJ/g. About 84.4% of this energy is assimilable (EA), and the energy metabolized (EM) is about 75.9% in mammals and 71.2% in birds. I have provided tabulated values for the composition of insects, as well as gas exchange and energy values for the combustion of proteins, fats, and carbohydrates, as a reference for calculating energy values for other diets of insects.

Key Words: Energetics; conversion factors; insectivory; digestion; assimilation; physiology; protein; fat; carbohydrate.

By combining techniques of physiology and behavioral ecology researchers can frame ecological questions about animal activities in terms of the real currencies of energy and time. Although methods such as whole-animal respirometry have long been used to obtain laboratory data, which may be extrapolated to the field, recent technological advances have allowed physiological ecologists to obtain data directly from free-living animals. Techniques such as radio-telemetry (e.g., Cochrane 1980) and the use of labeled isotopes such as doubly labeled water, which allow for the measurement of turnover rates of various body materials (e.g., Lifson and McClintock 1966, Nagy 1983), are now being used routinely by ecologists. For example, Bell et al. (1986) combined laboratory and field measurements of energy consumption by California leaf-nosed bats (*Macrotus californicus*) to demonstrate the importance of roost site temperature selection in the bats' ability to balance both energy and water budgets during the winter. In another example, Flint and Nagy (1984) measured the cost of flight in the Sooty Tern (*Sterna fuscata*) and related the importance of flight adaptations to energy balance during the reproductive season.

A frequent problem in such studies is a dearth of appropriate conversion factors relating rates of gas exchange to rates of energy consumption. Measurement of gas exchange through respirometry or the use of doubly labeled water provides a direct correlate of energy metabolism, but requires appropriate conversion factors to express the results in units of energy. Such conversions depend upon the diet of the animal (see Karasov, this volume). In particular there are few useful data on the gross nutrient composition of insects which contain a high proportion of protein. A further problem in insect diets is the presence of

large amounts of chitin which is generally indigestible.

Much of the early work in the area of energetics stems from studies of domestic livestock (e.g., cattle, horses, and sheep; Brody 1945, Maynard and Loosli 1969). Although such conversion factors may be appropriate for other herbivores, they cannot be applied directly to carnivores or insectivores. Most birds and mammals include arthropods, principally insects, in their diets, and many species are entirely insectivorous. Insects are very high in protein and very low in carbohydrate, which renders useless the commonly applied tables of energy conversions and respiratory quotients (R.Q.) based upon grazing animals, which omit the use of protein as an energy source.

There are few data on insect nutrient composition. The energy conversion factors for insectivorous animals can usually be traced back to a few references, and the problem of chitin content has seldom been addressed. In this paper I: (1) summarize what is known about the general aspects of insect composition as it is relevant to energetics studies of insectivorous animals; (2) demonstrate the derivation of energy conversion factors which can be applied to a specific case if details of the diet are known; and (3) provide a ready reference source of appropriate conversion factors based on the average composition of insects.

THE COMPOSITION AND ENERGY CONTENT OF AN AVERAGE INSECT

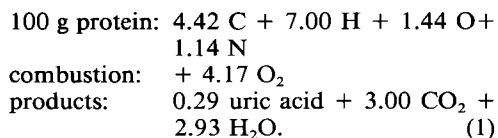
Data tabulated by Redford and Dorea (1984) and Spector (1958) on the gross composition of a variety of insects suggest that insects are consistently high in nitrogen and low in carbohydrate (Table 1) and average 70–75% water (2.33–3.00 ml/g dry mass). Thus we may assume that an average insect contains 2.33 ml H₂O/g dry

mass, and that the dry mass composition is 10.4% nitrogen, 15.5% fat, and 5.0% ash (Kurta et al. 1989) and yields approximately 22 kJ/g dry mass through combustion (Table 2). These values can be used to demonstrate the derivation of conversion factors for energetics studies.

Nitrogen is frequently converted to protein by multiplying by 6.25 (i.e., protein, on average, is 16% nitrogen by molecular weight; Brody 1945); however, this simple conversion ignores the fact that chitin ($C_8H_{13}O_3N$) is 6.9% nitrogen, most of which is indigestible. Chitin is difficult to isolate and analyze (Rudall 1963). Wigglesworth (1965) estimated that 33% of the dry mass of an average insect is cuticle. Wigglesworth further indicated that endocuticle made up, on average, 16.5% of dry mass and contained approximately 9.9% chitin, while exocuticle made up 13.2% of dry mass and contained only 2.9% chitin. Combining these values gives an approximate total chitin content of the average insect of 12.8% of dry mass, or 3.8% of wet mass. Thus, about 8.5% of the nitrogen in our average insect, or 0.88% of its dry mass, is bound in chitin. Jeuniaux (1961) suggested that some vertebrates possess chitinase complexes capable of breaking down chitin; however, it is doubtful that this would have a significant effect on the energy or nitrogen yield of insects in most cases (but see Karasov, this volume). Therefore, nitrogen bound in protein amounts to about 9.5% of dry mass. Using our estimate of 16% nitrogen in most proteins, we arrive at a value of 59.5% protein in the dry mass of an average insect. These values assume that most of the rest of the composition of cuticle, consisting of waxes and binding proteins, is both digestible and available to the animal under study. Combining these values we may further estimate, by subtraction, that approximately 7.2% of the dry mass of an average insect is carbohydrate.

PROTEIN

There are, to my knowledge, no data available on the composition of proteins in insects. The average protein consists of 53% carbon, 7% hydrogen, 23% oxygen, and 16% nitrogen, and yields 23.64 kJ/g by bomb calorimetry (Brafield and Llewellyn 1982). Other published values of energy yields for actual proteins range from 22 to 24 kJ/g. Amino acids yield from 13 to 28 kJ/g. Most nitrogenous waste in birds is in the form of uric acid, $C_5H_4O_3N_4$; thus



The energy yield from the digestion of 1 g of protein can be determined by subtracting the energy required to create the required amount of uric acid to excrete the nitrogen in the protein. The heat of combustion of uric acid is 11.5 kJ/g, (CRC 1986), thus

$$\begin{array}{l} 23.64 - [(0.29 \times 168 \times 11.5)/100] \\ = 18.04 \text{ kJ}. \end{array} \quad (2)$$

Similarly, we can use equation (1) to calculate the volume of oxygen consumed and the amount of carbon dioxide evolved in the digestion of one gram of protein. To calculate these values we use the gas laws, which state that one mole of a gas fills a volume of 22,400 ml at standard temperature and pressure (STP). Thus the volume of carbon dioxide produced is

$$\begin{array}{l} (3.00 \text{ moles} \times 22,400 \text{ ml/mole})/100 \text{ g} \\ = 672.0 \text{ ml CO}_2, \end{array} \quad (3)$$

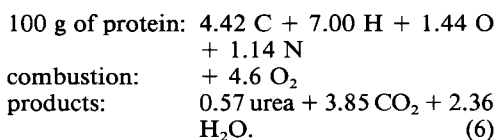
and the volume of oxygen consumed is

$$\begin{array}{l} (4.17 \text{ moles} \times 22,400 \text{ ml/mole})/100 \text{ g} \\ = 934.1 \text{ ml O}_2. \end{array} \quad (4)$$

The metabolic water produced in the combustion of 1 g of protein is

$$\begin{array}{l} (2.93 \text{ moles} \times 18 \text{ g/mole} \times 1 \text{ ml/g})/100 \text{ g} \\ = 0.527 \text{ ml H}_2\text{O}. \end{array} \quad (5)$$

In most mammals the nitrogenous waste product is urea (NH_2)₂ CO, heat of combustion = 10.53 kJ/g, (CRC 1986), thus



Following through the same calculations as above, the digestion of 1 g of protein by a mammal requires 1030.4 ml O₂ and yields 20.03 kJ of free energy, 862.4 ml CO₂, and 0.425 ml metabolic water.

The difference in nitrogenous waste products between birds and mammals has two important ramifications. The net energy yield from eating protein is approximately 11% higher in mammals than in birds. The benefit to birds of producing uric acid is in water savings: not only is there a slightly greater yield of metabolic water, but the higher solubility of uric acid reduces the amount of water lost in excretion. The other important difference is in the difference in gas exchange ratios (respiratory quotient, or R.Q.). A bird on a pure protein diet would have an R.Q. of approximately 0.72, while a mammal on the same diet would have an R.Q. of nearly 0.84. This difference in R.Q. might be of little importance in applying conversion factors to respiration.

TABLE 1. NUTRITIONAL QUALITY OF INSECTS (FROM REDFORD AND DOREA [1982] UNLESS OTHERWISE INDICATED)

	% H ₂ O (wet mass)	% ash (dry mass)	% nitrogen (dry mass)	% fat (dry mass)
Orthoptera				
Locust: (<i>Melanoplus</i> sp.)		5.6	12.0	7.2
(<i>Oxya</i> sp.)		3.8	10.8	7.2
(<i>Oxya</i> sp.)		6.5	12.2	5.7
(<i>Schistocerea paranensis</i>)		4.2	8.2	18.4
(<i>S. gregaria</i>)	70.6	8.7	10.2	13.5
(<i>Nomadacris septemfasciata</i>)		8.7	10.2	14.1
(<i>Locustana</i> sp.)	57.1		6.8	50.1
Cricket: (<i>Brachytrypes membranaceus</i>)	76	8.8	9.1	22.1
(<i>Gryllus domesticus</i>)	71	8.28	10.7	16.9
Cockroach: (<i>Blatta orientalis</i>) ^a	70.6			
(<i>Blattella germanica</i>) ^a				16.3
(<i>Periplaneta americana</i>) ^a	61			27.05
Coleoptera				
<i>Tenebrio molitor</i> (mealworm larvae)	66.4	6.9	8.72	32.7
<i>Lachnosterna</i> sp.: (larvae)	79.9	10.0	8.8	15.4
(adults)	69.4	5.2	10.5	16.0
<i>Polycleis equestris</i> (adult weevil)	51.8		10.1	4.6
<i>Sternocera orissa</i> (adults)	60.6		18.6	10.2
Lepidoptera				
<i>Galleria mellonella</i> (larvae)	56.1	1.82	4.92	61.5
<i>Bombyx mori</i> : (adult)	60.7	3.8	9.4	36.1
(adult)	80	5.2	8.7	3.9
(adult)				24
(larvae)	84.5		2.1	
<i>Antherea mylittal</i> (adult)	80	5.3	9.0	7.7
<i>Bombycomorpha pallida</i> (larvae)	82.2		9.4	34.3
<i>Cerina forda</i> (larvae)	79.6		9.3	27.9
Diptera				
<i>Musca domestica</i> : (pupae)		5.3	10.1	15.5
(pupae)		11.9	9.8	9.3
<i>Gasterophilus intestinalis</i> ^a	64.7			19.4
<i>Phaenicia sericata</i> ^a	79		12.5	
Hymenoptera				
<i>Apis mellifera</i> : (larvae)	77	3.0	10.7	16.1
(pupae)	70.2	2.2	14.7	8.0
(adult) ^a			12.2	18.0
<i>Carebara</i> sp.: (alate females)	60.0		1.2	23.8
(alate males)	60.0		4.0	3.3
<i>Carebara vidua</i> : (alate females)	60.0		3.0	59.5
(alate males)	60.0		10.1	8.3
<i>Camponotus rufipes</i> : (alate queen nymph)			22.90	
<i>Iridomyrmex detectus</i> : (alate females)				48.2
(alate males)				9.6
(worker)				18.8
<i>Tetramorium caespitum</i> : (alate females)	44.2			51.3
(alate males)	70.0			8.8
Isoptera				
Harvester termite (sp. unspecified)	77.5	12.09	10.62	7.69
<i>Macrotermes carbonarius</i> : (soldier)	76.5	3.66		
(worker)	72.4	31.67		
(alate)	59.5	1.60		
<i>Dicuspiditermes nemorosus</i> : (soldier)	80.6	3.52		
(worker)	72.2	48.73		
(alate)	56.1	1.76		

TABLE 1. CONTINUED

	% H ₂ O (wet mass)	% ash (dry mass)	% nitrogen (dry mass)	% fat (dry mass)
<i>Homalotermes foraminifer</i> : (soldier)	78.3	21.48		
(worker)	74.0	46.03		
(alate)	52.2			
<i>Orthognathotermes gibberorum</i> : (nymph)				19.72
(worker)	71.35	61.00	2.55	
(soldier)	71.90	26.30	7.54	
<i>Syntermes dirus</i> : (nymph)				22.00
(worker)	79.65	17.05	6.91	3.40
(soldier)	74.0	5.90	11.89	1.75
<i>Grigiotermes metoecus</i> : (nymph)				21.41
(worker)	66.35	59.90	2.99	1.51
<i>Procornitermes araujoi</i> : (nymph)				24.12
(worker)	78.10	16.10	5.42	3.45
(soldier)	78.40	10.05	8.68	4.56
<i>Termes</i> sp. (no caste specified)	44.5	5.3	6.0	50.5
<i>Macrotermes falciger</i> (alates)	34.2	10.9	6.31	41.9
<i>Trinervitermes geminatus</i> : (worker)	80.0	7.2		
(major soldier)	73.0	3.6		
(minor soldier)	80.0	8.9		
(alate)	50.0	2.3		
<i>Basidentitermes potens</i> : (workers)	61.0	71.0		
(soldiers)	69.0	4.5		
<i>Macrotermes bellicosus</i> : (workers)			10.0	<25
(soldiers)			9.4	<35
(alates)			6.5	52.8
<i>Velocitermes paucipilis</i> : (worker)	70.35	12.70	7.32	
(soldier)	69.50	10.85	9.28	
<i>Cortaritermes silvestri</i> : (worker)	77.80	8.50	7.78	6.85
(soldier)	70.95	6.70	6.78	14.40
<i>Nasutermes</i> sp.: (worker)	77.80	11.30	7.14	3.59
(soldier)	72.70	8.75	8.39	2.31
<i>Armitermes euamignathus</i> : (worker)	73.60	46.05	3.34	
(soldier)	73.85	38.00	3.93	
<i>Cornitermes cumulans</i> : (worker)	77.70	36.00	4.27	2.65
(soldier)	78.10	6.45	8.85	4.29

* Data from Spector (1958).

metry studies on species with low-protein diets; however, insectivorous species may obtain as much as 60% of their energy from the combustion of protein, and the difference in digestive physiology between birds and mammals becomes more significant.

The assimilation rate (or digestibility) of protein depends upon both the protein and the animal in question. Drodz (1975) gave a range of digestibility of 75–99%. Karasov (1982) indicated that the digestibility of insect (cricket) protein was about 95%.

FATS

The size of the fat body in insects varies by stage of life cycle as well as taxonomic affinity (see Gilbert 1967). Total lipid content may range from 5.3–85.4% total dry mass. In many studies of insectivorous animals the total energy content

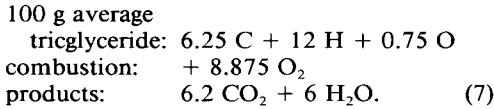
of an insect meal is derived from analysis of mealworm (*Tenebrio molitor*) samples, in which fat content may be as high as 50–60% dry mass. In social insects, such as wasps and termites, reproductive forms tend to have extremely high fat contents and low water contents compared to larvae or workers. Most adult insects have fat contents in the range of 10–25% dry mass.

Similarly, the fatty acid content of insect fats is variable (summarized in Barlow 1964). For example, most Homoptera appear to have a high proportion of myristic acid (14:0), with very little fats of longer chains and very little unsaturated fatty acid content. In contrast, most coleoptera have a high proportion (50–75%) of unsaturated 18-carbon fatty acids. There are insufficient data on different taxa or on variation in fatty acid content with stage of life cycle to make other generalizations.

TABLE 2. WATER AND ENERGY CONTENT OF VARIOUS INSECTS (FROM CUMMINS AND WUYCHECK [1971] UNLESS OTHERWISE NOTED; ALL ADULT UNLESS OTHERWISE NOTED)

Order Family	KJ/g (dry mass)	% H ₂ O (wet mass)	Source
Orthoptera	22.18		
Acrididae	21.25		
Gryllidae	25.1		Karasov (1982)
Tettigoniidae	22.80		
Ephemeroptera	22.88		
	22.09		Maxson and Oring (1980)
	23.26		Maxson and Oring (1980)
Heptageniidae	23.37		
Ephemeridae	20.44	85	
Odonata			
Lestidae	20.74	79.6	
Agrionidae	22.59		
Libellulidae	24.52		
Gomphidae	12.69	81.6	
Coleoptera			
Hydrophilidae	22.47		
Tenebrionidae	24.48		
(larvae)	29.71	61	Sall (1979)
(pupae)	28.87	67	Sall (1979)
(adults)	27.61	64	Sall (1979)
(larvae)	27.56	46.6	O'Farrell et al. (1971)
Elateridae	22.76		
Coccinellidae	24.48		
Chrysomelidae	21.85		
Trichoptera			
Limnophilidae	19.30		
Hydropsychidae	22.53	81.2	
Megaloptera			
Corydalidae	21.80		
Diptera	17.89		
Chironomidae	22.69	79.8	
	21.42		Maxson and Oring (1980)
	21.25		Maxson and Oring (1980)
(larvae)	22.25	85.8	
(adults)	23.73	73.8	
Culicidae	20.65		
	23.01		Kunz (1987)
Drosophilidae	24.25		
Calliphoridae	24.13		
Stratiomyidae	12.00		
Tipulidae	25.52		Kunz (1987)
Hemiptera			
Cercopidae	23.59		
Dictyoptera			
Blattellidae	22.58		
Hymenoptera	19.37		
Formicidae	19.03		
Apidae	20.37		
Lepidoptera	21.25		Kunz (1987)
Mixed Insects	22.09		
	23.81	76.3	Nagy et al. (1978)
		63.5	Carpenter (1969)

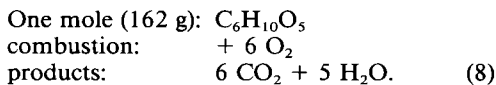
The caloric value of fatty acids increases with both length of carbon chain and degree of saturation. An average triglyceride contains 75% carbon, 12% hydrogen, and 12% oxygen by weight, and yields 39.54 kJ/g. The end products of the combustion of lipids are carbon dioxide and water, thus



Thus, the digestion of 1 g of average triglyceride yields 39.54 kJ, 1400 ml CO₂, and 1.08 ml metabolic H₂O, and requires 1988 ml O₂. The R.Q. for the combustion of pure fat is about 0.70. The digestibility of fats may also be assumed to be about 95% (Drodz 1975).

CARBOHYDRATES

Carbohydrate is often ignored in insect analysis even though it may occur in large quantities. Kirby (1963) suggested that as much as 33% of the entire dry mass of an insect may be glycogen in some larval forms, that glucose may be found at concentrations of up to 30 mg/100 ml blood, and that trehalose may occur at concentrations of 1500–6000 mg/100 ml blood. The calculations presented above suggest that about 7.2% of dry mass of an average insect is carbohydrate. The combustion of pure carbohydrate results in the production of carbon dioxide and water, and the R.Q. for such reactions is 1.0. The energy yield for the combustion of a variety of carbohydrates shows remarkable uniformity (15.5–17.5 kJ/g) regardless of molecular weight or complexity. Therefore, for our purposes we may assume that all insect carbohydrate is in the form of glycogen (C₆H₁₀O₅)_n, thus



The energy yield for the combustion of glycogen is 17.52 kJ/g. Combustion of 1 g of glycogen yields 0.556 ml of metabolic water and 830 ml of CO₂, and requires 830 ml of O₂. The digestibility of carbohydrate is at least 95% (Drodz 1975).

The results of these calculations for the digestion of protein, fat, and carbohydrate in a typical insect suggest that, while the total energy content of such an insect based on combustion is 24.2 kJ/g dry matter, assimilable energy (EA) is 84.4%, and metabolizable energy (EM) is only 75.9% for mammals and 71.2% for birds (Table 3). Dry matter assimilation is approximately 78%. The combined R.Q. for a bird on a diet of mixed

insects is approximately 0.76, and the consumption of 1 g of mixed insects results in the bird's producing 637 ml CO₂. For a mammal on the same diet R.Q. is 0.81, and the CO₂ yield would be 750 ml/g insects. Karasov (this volume) reported a mean EM for birds on an arthropod diet of 77%, but included studies using mealworms. Omitting those studies reduces the mean (N = 4 studies) EM to 73%.

THE EFFECTS OF USING INAPPROPRIATE CONVERSION FACTORS

We can now consider the effects of using inappropriate conversion factors, or ignoring the importance of protein and chitin in a diet of insects. I will use as an example hypothetical data on a 9.0 g little brown bat (*Myotis lucifugus*). If this bat is found, through doubly labeled water studies, to produce 1224 ml CO₂/day we could use the conversions for mammals (Table 3) to estimate its daily energy expenditure (DEE) at

$$(18.35/750) \times 1224 = 29.9 \text{ kJ/day.} \quad (9)$$

We can further estimate that this bat's daily food intake would be

$$\begin{aligned} 1224/750 &= 1.63 \text{ g dry insects/day} \\ &= 1.63/0.3 \\ &= 5.4 \text{ g fresh insects/day.} \end{aligned} \quad (10)$$

However, if we were to use the conversion factors for birds by mistake we would obtain values of 33.1 kJ/day (11% too high) for DEE and 6.4 g fresh insects/day (18.5% too high).

Another common mistake is to ignore chitin content. If all of the nitrogen found in insect samples were bound in protein, we would overestimate the proportion of protein in the diet by about 9% (10.4% nitrogen \times 6.25 = 65% protein). Using the resulting conversion factors we would estimate that our bat had a DEE of 29.6 kJ/day (only 1% too low), but our estimate of daily food intake would be about 4.8 g fresh insects/day, or about 11% too low.

A third mistake would be to assume, as we often do for plant-eating animals, that no protein is metabolized to produce energy. This would only overestimate DEE by about 9%, but would overestimate daily food intake by about 187%! An appreciation of the nitrogen metabolism of the animal and the digestibility of the diet are just as important as the actual energy content of the diet in obtaining accurate estimates of energy metabolism and food intake.

I present the conversion factors in this paper as a starting point for studies in which the principal prey are adult insects. Similar values may be derived for other diets using the tables or additional data. In some cases more precise con-

TABLE 3. SUMMARY OF CONVERSION FACTORS FOR BIRDS AND MAMMALS ON A DIET OF INSECTS

Component	Mass/g dry mass		kJ/g dry mass			
	Gross	Assimilated	Gross	Assimilated	Metabolized	
					Birds	Mammals
Protein	0.595	0.565	14.06	13.36	10.19	11.32
Chitin	0.128	0.000	2.71	0.00	0.00	0.00
Fat	0.155	0.147	6.13	5.82	5.82	5.82
Carbohydrate	0.072	0.069	1.28	1.21	1.21	1.21
Inorganic	0.050	0.000				
Totals	1.000	0.781	24.18	20.40	17.22	18.35

Dry Matter Assimilation (DMA) = 78.1%.

Energy Assimilation (EA) = 20.40/24.18 = 84.4%.

Energy Metabolization (EM) = 17.22/24.18 = 71.2% for birds
 = 18.35/24.18 = 75.9% for mammals.

versions might be obtained through careful feeding studies and diet analysis; however, I suggest that in most cases the errors in such studies are comparable to those in simply deriving conversion factors from published values of insect composition. However, it must be noted that there is a great deal of variation in Tables 1 and 2. Some caution is obviously needed in using the numbers in these tables, and larger sample sizes are needed for many insect groups; what is needed is a broader data base on the general composition of different taxa of insects that can be

generally applied to feeding studies. The processes of digestion and nitrogen excretion might be expected to be constant enough that individual studies of digestibility may be unnecessary.

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