Small mammals: their productivity and population dynamics

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8. Ecological energetics of small mammals

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Small mammals have been a favorite subject for physiological studies for many years, but most studies have dealt with classical questions of mechanism under laboratory conditions and only in the past twenty to thirty years have physiologists concentrated on small wild mammals, attempting to investigate comparative adaptive strategies for coping with environmental circumstances. This new approach has developed into the field of physiological ecology (Dill *et al.*, 1964; Slonim, 1961). Many of the earlier studies dealt with temperature regulation and metabolism but did not necessarily place them into a field context.

Small mammal ecologists began to approach ecosystem and/or population function from the point of view of energy flow by the early 1960s (Golley, 1960; Odum *et al.*, 1962). With the advent of the IBP studies it became evident that relatively little information was available concerning small mammal productivity and energy flow. Thus the study of ecological energetics has developed and been greatly expanded in many countries. Such studies have drawn upon physiology and physiological techniques but have attempted to frame them into ecologically realistic conditions. Consequently, many papers on mammal energetics have been published during this past decade by IBP investigators and others. It is our desire to attempt a review and synthesis of these studies. The concepts of energy flow through animal populations have their origins in the physics of thermodynamics. The same thermodynamic concepts have been used successfully in developing general theories of growth (Lotka, 1956).

One of the most important concepts developed by ecosystem theory relates to energy flow through ecosystems. Indeed, much of the effort expended by IBP in synthesizing models has been based on the central theme of energy flow and analysis of the component parts through which such energy may cascade. Small mammals constitute one such component and thus analysis of energy flow through their populations has been one goal of the IBP. Although most studies indicate that a relatively small percentage of the total energy flux through a particular

ecosystem passes through the small mammal populations, they may function as control gates rather than major processors of energy.

Energy flow, or assimilation (A), can be described for an animal population by two well-known equations (Petrusewicz, 1967a): $A = P + R$ and $A = C - FU$, where P represents the amount of energy incorporated into animal tissue, R is the amount of energy used for maintenance or respiration, C is the energy of food intake and FU the amount of energy lost through feces and urine. These two general equations have been modified to define more precisely the balance of energy flow through small mammal populations (Golley, 1962; Grodziński et al., 1966):

$$A_T = K_b(\bar{N}B \cdot \theta_B) + M(\bar{N}B)_T \tag{8.1}$$

$$A_T = K_c(CW)_T - K_e(FU \cdot W)_T \tag{8.2}$$

where:

$\bar{N}$ = average numbers, or animal density,
B = mean biomass of an animal,
θ_B = turnover of biomass in the population,
M = metabolic rate, usually measured by gas exchange,
K_b = caloric value of the mammalian body,
K_c and K_e = caloric value of food and rejecta, respectively,
C = consumption (food intake) during a given time (units in W),
FU = feces and urine produce in the same time as C,
W = dry weight, or biomass, of food and excrement,
T = period of time for which energy flow balance is computed.

In order to determine the flow of energy through a small mammal population the parameters listed in either equation must be determined. Population numbers ($\bar{N}$), biomass (B) and turnover rate (θ_B) are determined from field studies. Within the restriction of present techniques most of the bioenergetic parameters are determined in the laboratory. Investigation of the bioenergetic parameters involves the study of respiration (metabolic rate; M), calorimetry (caloric values of mammalian production, food and excrements; K_b, K_c, K_e) and feeding balance (food consumption, feces and urine production; C, FU).

Our goal in this chapter is to cover three basic points concerning small mammal energetics. First, in order to relate small mammals to primary production, we shall discuss food utilization or consumption (how much energy small mammals consume and from what sources). Second, the energy which goes into small mammal production is important; this

relates to the amount of energy which small mammals provide for higher trophic levels. Thirdly, we will consider respiration since much of the energy processed by small mammals is used for maintenance. Cost of maintenance can also be determined from food assimilation.

Data and methods

Material and sources of data

Data for this chapter were gathered from a great variety of papers published primarily during the last decade in both American and European ecological and physiological journals. We have given special attention to information available in previous IBP publications. The IBP Handbook Series (Golley & Buechner, 1969; Petrusewicz & Macfadyen, 1970; Grodziński, Klekowski & Duncan, 1975) and previous proceedings of the IBP Small Mammal Working Group (Petrusewicz, 1967c; Petrusewicz & Ryszkowski, 1970; Palmén, 1971) have provided much relevant information. In addition, many recent texts and reviews on general animal bioenergetics have been useful in the preparation of our synthesis (e.g. Kleiber, 1961; Folk, 1966; Kalabukhov, 1969; Hart, 1971; Gessaman, 1973).

For the purposes of this paper it is important to define what we mean by a 'small mammal'. For our discussion we are restricting ourselves primarily to animals ranging in size from 3 to 300 grams. Furthermore, due to these size restrictions and the availability of sufficient data, we will consider only animals falling in the following taxonomic groups: Insectivora, Rodentia, Lagomorpha, and Carnivora. Only a few examples from Chiroptera were included.

Within these taxa, mammals gain food energy in a variety of ways each of which may modify the particular patterns and amounts of energy turnover or energy flow shown within populations of each species. For example, carnivores and insectivores feed from a different trophic level than do herbivores. Furthermore, their efficiencies of assimilation and the amounts of energy spent searching for food are different from herbivores. Within the herbivores, different feeding strategies necessitate different expenditures of energy. For example, seed eaters must, in a sense, hunt for their food, have larger home ranges (Brown, 1966), and thus conceivably spend more energy searching for food than do foliage-feeding herbivores such as microtine rodents (McNab, 1963).

Small mammals

Within the groups of mammals listed above, we find a variety of strategies for temperature regulation each of which may affect energy balance and energy flow somewhat differently. Mammals which remain homeothermic will expend more energy on maintenance than will those which demonstrate some degree of heterothermy. Many mammals show daily fluctuations in level of body temperature regulation, thus reducing the energy needed for maintenance during certain periods (Morhardt, 1970) while others show daily bouts of torpor (Bartholomew & Hudson, 1964); and of course, hibernators and estivators show reduced energy expenditure during part of the year.

Laboratory and field methods

A variety of techniques have been used for investigating the bioenergetics of small mammals (Golley, 1967). One of the concerns of the IBP has been to unify at least some basic techniques. This unification was attempted through an IBP training course in bioenergetics dealing primarily with the laboratory methods of calorimetry, respirometry and feeding ecology (Grodziński & Klekowski, 1968, Grodziński et al., 1975). Independent from the IBP some new field techniques have been introduced recently for studying homeotherm energetics under field conditions. These procedures include such techniques as radioisotopes, heavy water, and radiotelemetry (see Gessaman, 1973 for review).

Direct calorimetry. Most measurements of energy exchange between animals and their environment and, thus, their energy flow have been made using indirect measures of such things as oxygen consumption or carbon dioxide production. Such measurements give information about heat production and heat loss only if certain assumptions hold true (i.e., caloric equivalents of oxygen consumption, stability of body temperature and body heat content, etc.). Direct measures of such exchange are obviously desirable; however, simultaneous measures of heat production and loss have been few (Caldwell et al., 1966; Hammel et al., 1968). Investigators employing direct calorimetry used a simple animal calorimeter which consisted of a metal container lined with a net of thermocouples to measure direct heat loss. Due to the intricacy of construction and operation of direct systems, indirect calorimetry is probably a much better system to use in order to answer ecologically related questions about energy flow in animals.

Indirect calorimetry (respirometry). The indirect systems described here are much easier to operate than are direct measurement systems and allow more space in which the animals can operate during measurements (e.g., ADMR). Within the sorts of variation which we find in other parameters needed for calculating population energy flows, indirect systems do not provide unduly large sources of error even if RQ-values vary for oxygen–caloric conversions.

Closed circuit system respirometers. The simplest systems for measuring respiration (oxygen consumption) indirectly are closed system respirometers. The application of this technique depends simply upon physical gas laws. Animals are placed in closed containers with chemical agents to absorb CO_2 and water. As the animals consume oxygen, the CO_2 and water produced are absorbed and thus any change in volume (after appropriate temperature and pressure corrections) is due to the oxygen consumed. As oxygen is used, it may be replaced by adding specific aliquots, or through a tube attached to an oxygen reservoir, or one may simply monitor volume decreases.

Two of the most widely used and effective systems are the Morrison respirometer (described in Morrison, 1951; and Morrison & Grodziński, 1968) and the Kalabukhov–Skvortzov respirometer (described in Kalabukhov, 1962).

The advantages of closed systems are that they are relatively inexpensive to develop and maintain and are fairly simple to operate. The major disadantage is that in some instances gas concentrations may reach low levels and affect metabolism of the animals being studied.

Open circuit systems. In an open flow system the animals are usually placed in a relatively small volume respirometer, ambient air is passed at a known rate of flow through this chamber and the concentrations of oxygen in the inflowing and outflowing gases are determined. The advantages of this system are its ease of operation, speed of response and accuracy. Among the best oxygen analyzers for use in such systems are those which utilize the paramagnetic properties of oxygen or thermoconductivity differences such as the Beckman analyzers or the Kipp and Zonen Diaferometer. It should be pointed out that there are a number of technical problems in using such systems. In addition to the problems of the logisitics and physics of setting up a flow system, one must consider problems of removing CO_2 from incoming gases and the use of appropriate equations for calculation of oxygen consumption (Depocas & Hart, 1957). Hill (1972) has recently re-evaluated problems of CO_2 in inlet and/or analyzed air streams and found that calculation

errors of up to 38 per cent can be made depending upon whether CO_2 is removed from inlet air or analyzed air. From Hill's analysis we would suggest that air going to the oxygen analyzer have CO_2 removed or flow rates be adjusted so that the volume fraction of oxygen in inlet air minus outlet air is greater than 0.00303. Such conditions will introduce an error of no more than 2 per cent which, considering the usual variation in oxygen consumption of a quietly resting mammal, is often of little significance.

Feeding trials. Studies of food utilization in mammals may be carried out on the intact animals *in vivo*, or outside them, i.e., *in vitro*. Digestibility *in vitro* is often employed when studying ruminants but is seldom used for studying non-ruminant small mammals.

In the nutrition studies of small wild mammals *in vivo* two methods are generally applied: the balance method and the tracer technique. The classical balance method is carried out in a metabolic cage, where all food consumed and all feces and urine produced are measured (Drożdż, 1966, 1968*b*). With such a method both digestibility and assimilation of energy, organic matter, or any nutrients can be determined. The tracer methods require addition of a marker (indicator substance) to food with subsequent analysis of its content in feces. Some colored markers can be used, e.g., chromic oxide, but recently radioisotopes such as ^{51}Cr (Petrides & Stewart, 1970) were successfully employed for small mammals. The tracer method may also utilize the natural ash content in food and excrement as a tracer. The analysis of ash content compares food and feces, and in the case of snap-trapped mammals it is limited to their stomach and colon contents (Johnson & Maxell, 1966; Johnson & Groepper, 1970). The latter technique has several limitations, but allows an estimation of digestibility of natural food by wild animals in their natural environment. All tracer methods will determine only digestibility (coefficient of digestibility) while the balance methods give both digestibility and assimilation.

Analysis of gross body composition and energy content. Some rather standard techniques have been applied by ecologists for determining the caloric value of production and for analysing body composition in animals. For total caloric values adiabatic bomb calorimetry has been utilized successfully (Gorecki, 1965*a*, *b*). Paine (1971) has reviewed the techniques and pitfalls associated with bomb determination, total ash or fat content of an animal. Fat can be determined by the Soxhlet ether

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extraction technique (Startin, 1969; Sawicka-Kapusta, 1970; Dawson, 1970), total ash by oxidation in a muffle furnace (Startin, 1969; Sawicka-Kapusta, 1970; Paine, 1971), and protein by the Kjeldahl method (as in Startin, 1969), using protein = 6.25 × nitrogen.

Because of individual and seasonal variation, ecologists have tried to develop techniques to gather average sample data from populations rather than simply measuring individual animals or parts of animals (Odum *et al.*, 1962).

Techniques for estimating metabolism in the field. For verifying models of energy flow through small mammal components of ecosystems and for getting some idea of what it costs small mammals to exist in the field, several methods have recently been devised for measuring metabolic rate of animals in the field. Such methods include: (1) radioisotope excretion rates, (2) $D_2^{18}O$ turnover rates and (3) bio-telemetry of heart rate. The strengths and weaknesses of most of these techniques have recently been reviewed (Gessaman, 1973). Most techniques are not completely satisfactory at present. To date no radioisotope excretion rates have been found to correlate well enough with metabolism to be used for field estimations of metabolic rate (Golley *et al.*, 1965; Wagner, 1970; Chew, 1971). Gessaman feels that the most promising technique is the $D_2^{18}O$ method; however, it is quite expensive, complicated and gives only a long-term average for integrated metabolic rate; and Mullen (1973) indicates that cost for isotopes becomes prohibitive for animals weighing more than 1 kg. Perhaps the technique that is next most promising is heart rate biotelemetry: however, we need much more data correlating heart rate and metabolic rate, especially during activity. Although involving expensive equipment, it is less expensive and involved than the $D_2^{18}O$ method but is limited to animals large enough to carry telemetry capsules. More work needs to be done in validating all of these techniques.

Bioenergetics parameters for energy budgets

Energy for maintenance (respiration)

In any discussion of maintenance energy turnover for mammals, three measures of metabolism are usually mentioned. These are basal metabolism (BMR), resting metabolism (RMR) and average daily metabolic rate (ADMR). For purposes of ecological investigations, basal metabolic rates are of little use due to the strict requirements for

their determination (Benedict, 1938). For example, it is very difficult to determine when a small mammal is post-absorptive; in fact, in the field they may never reach the state of being completely inactive and post-absorptive. Thus, for our purposes RMR and ADMR are much more useful measures of energy turnover. RMR refers to the metabolic rate of an animal at rest under a prescribed set of environmental circumstances. It is usually measured as an acute situation (i.e., responses over a period of 1 or 2 hours). ADMR necessitates at least a 24-hour measurement period, and is mean metabolic rate measured over that time under a prescribed set of environmental circumstances. Thus, it includes not only energy expended at rest but also in voluntary activity during the 24 hour period (Grodziński & Górecki, 1967). The energy components which are considered in each of these various measures of metabolism are summarized in Table 8.1.

Table 8.1. *Components of three metabolic measures*†

| | Components | | | |
Metabolic measure	Basal metabolism	Thermo-regulatory metabolism	Specific dynamic effect	Activity metabolism (locomotion)
Basal metabolic rate (BMR)	+	—	—	—
Resting metabolic rate (RMR)	+	+	+?	—
Average daily metabolic rate (ADMR)	+	+	+	+

† Modified from Gessaman (1973).

In the following we shall consider one model for energy budgets based upon RMR studies and one model based upon ADMR studies.

Basal and resting metabolism. There are many data available concerning the metabolic rates of mammals at rest under various ambient conditions. Many of these are summarized in Hart (1971) and in Kalabukov (1969). The relationships between body size and 'basal' metabolic rate has long been established (reviewed in Kleiber, 1961) although there are some groups of mammals which show slight variations (i.e., heteromyid rodents, fossorial rodents and some desert species show characteristically low metabolic rates while those for microtine rodents are high). Although we frequently refer to such values

as basal they are usually resting rates in thermoneutrality. It is not our purpose here to elaborate on the wealth of data available but merely to use the relationships correlating metabolic rate and body size generated from these data. 'Basal' metabolic rate can be estimated using the following formula which has been modified from the Brody–Proctor equation by Morrison *et al.* (1959).

$$BMR = 3.8 \ W^{-0.25} \tag{8.3}$$

with MR in cc $O_2/g \cdot h$, W in g.

Metabolism below thermoneutrality can be estimated if we know the relationship between metabolism and ambient temperature. This relationship is called thermal conductance and can be estimated from the allometric equation of Herreid & Kessel (1967):

$$TC = 1.05 \ W^{-0.50} \tag{8.4}$$

with TC in cc $O_2/g \cdot h \cdot °C$, W in g.

Hart (1971, p. 77) has recently reviewed the data relating to this relationship and derived a similar relationship.

Average daily metabolism. ADMR measurements are made with the animals in large containers so that they can be active, have access to a nest and food and water (Grodziński & Górecki, 1967; Morrison & Grodziński, 1968). Consequently this measure contains basal metabolism, the metabolic equivalent of energy for thermoregulation and activity as well as the energy of SDA (specific dynamic action or the calorigenic effect of food).

Analyses of the relation of ADMR to body size in several species of voles, mice and squirrels have shown that it is intraspecifically allometric. However, the exponents for these intraspecific relationships (expressed as metabolism per whole animal) have been found to be close to 0.5 and not 0.75 which is the well-known exponent for BMR (Hansson & Grodziński, 1970; Grodziński, 1971*a, b*; Drożdż *et al.*, 1971; Górecki, 1971). Recently two general interspecific functions of ADMR against body weight were computed, one for small rodents and one for insectivores (French, Grant & Grodziński, unpublished data). These relationships were computed from 72 data points of ADMR for 36 species of rodents and 8 species of insectivores (Fig. 8.1). The regression line for rodents ranges from a 7 g pocket mouse (*Perognathus*) to a 370 g hamster (*Cricetus*) and the insectivore regression from a 3 g lesser shrew (*Sorex minutus*) to a 21 g short-tailed shrew (*Blarina*

brevicauda). The two equations have significantly different intercepts but the exponent is close to 0.50 in both cases (−0.57 and −0.46). By forcing the regressions into an average slope of 0.50 the following
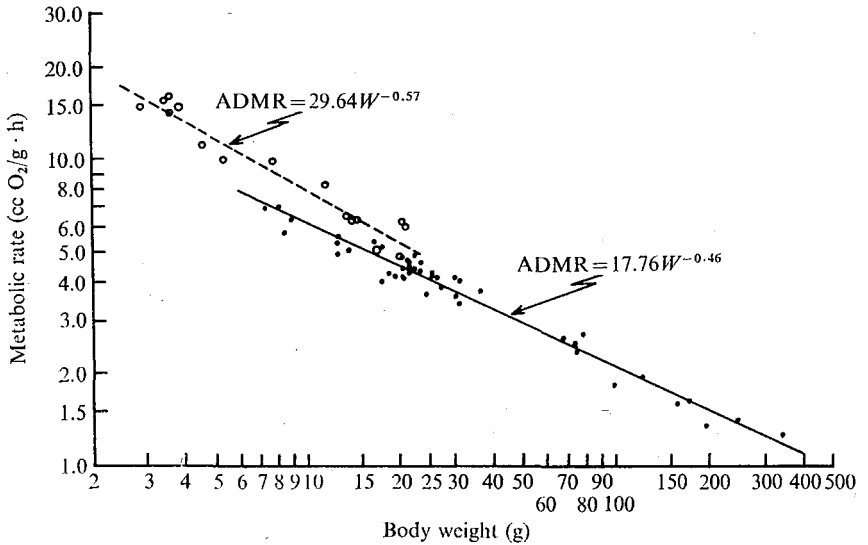

Fig. 8.1. ADMR as a function of body size in rodents (solid lines) and insectivores (broken lines). Data are taken from French ,Grant & Grodziński (see text).

equations were generated to predict ADMR for animals exposed to 20 °C:

$$\text{Rodent ADMR} = 19.94 \; W^{-0.50} \qquad (8.5)$$

$$\text{Insectivore ADMR} = 26.80 \; W^{-0.50} \qquad (8.6)$$

with ADMR in cc $O_2/g \cdot h$, W in g.

Physiologically ADMR is not a very well defined measurement; however, it is probably the most natural and ecological measure of metabolism possible under laboratory conditions.

Consumption and assimilation

Investigations of feeding ecology should provide answers to several questions important for studies of energy flow through small mammal populations; for example, what the food consumption by a small mammal is, what part of the consumed energy is assimilated and what fractions are passed on with rejecta, i.e., feces and urine. A more general question is that of how much food is available for small mammals in various ecosystems. This has been defined as 'that food which is

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easy to find and is being chosen and eaten by these animals' (Grod-ziński, 1968). The estimation of available food is usually based on some knowledge of mammalian food habits. The food habits of wild small mammals may be studied with various approaches, but should pre-ferably be determined both by analysis of stomach contents (or feces) and by applying food preference tests of choice ('cafeteria test'). The food available for rodents has already been estimated in several forest and grassland ecosystems. In various types of forests this constitutes only a few per cent (4 – 13 per cent) of the total primary plant produc-tion (Grodziński, 1968), but in the grassland ecosystems, including cultivated fields, a majority of the above-ground plant production can be considered as potential food for herbivorous grazing rodents (Golley, 1960; Grodziński *et al.*, 1966; Trojan, 1970; Batzli & Pitelka, 1971). Granivorous rodents have available only a small fraction of plant production (Odum *et al.*, 1962; Pearson, 1964).

The utilization of food energy is shown in a general scheme in Fig. 8.2. Note that the terminology employed by ecologists and nutritionists

CONSUMPTION; *C*
(Gross energy)

EGESTA, FECES; *F*
(Energy of feces)

DIGESTED ENERGY; *D*
(Digested energy)

EXCRETA, URINE; *U*
(Energy of urine)

ASSIMILATION; *A*
(Metabolizable energy)

RESPIRATION; *R*
(Respiration,
cost of maintenance)

PRODUCTION; *P*
(Energy of production)
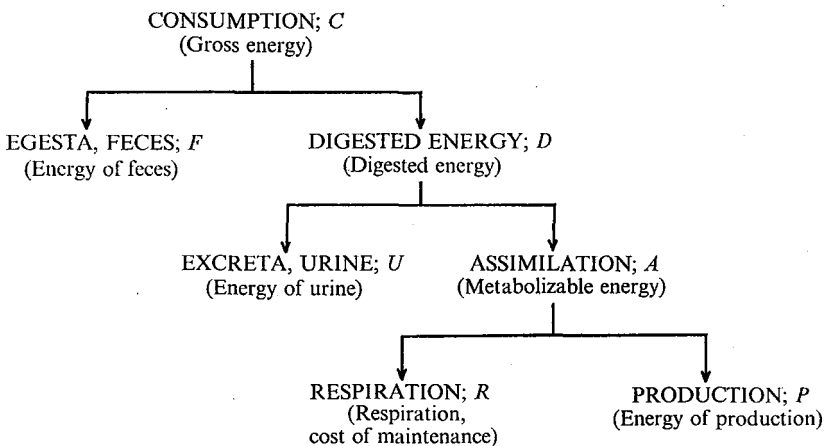
Fig. 8.2. A scheme of energy flow through a mammal and/or mammal population. Nutrition terminology is given in parentheses. Note that the terminology used by ecologists is slightly different (slightly modified from Drożdz, 1968).

is slightly different, but this is not of primary importance. It is clearly visible in this diagram that consumption (*C*) exceeds assimilation (*A*) by the amount of energy lost through feces and urine (*FU*). Thus, in order to calculate total consumption ecologists have recently studied assimil-ation and digestibility (or digested energy) in small mammals. We present in Table 8.2 a review of all the available data on digestibility and

Table 8.2. *Digestibility and assimilation of natural and laboratory foods in small mammals*: *as a percentage of gross energy, GE or organic matter, OM. B, balance method; T, tracer method; I, insectivore; C, carnivore; H, grazing herbivore; O, omnivore; G, granivore*

No.	Species	Body wt (g)	Feeding type	Method	As % of GE or OM	Digestibility coefficient		Assimilation coefficient		Reference
						range	av.	range	av.	
	INSECTIVORA									
	Soricidae									
1	*Sorex cinereus* Masked shrew	3.6	I	B	GE			93–95	94.0	Buckner, 1964
2	*Sorex arcticus* Arctic shrew	5.4	I	B	GE				88.0	Buckner, 1964
3	*Sorex araneus* Common shrew	8.5	I	B	GE		94.9			Hawkins & Jewell, 1962
4	*Microsorex hoyi* Pygmy shrew	3.5	I	B	GE				83.0	Buckner, 1964
5	*Cryptotis parva* Least shrew	3.6	I	B	GE		90.1		87.8	Barrett, 1969
6	*Neomys fodiens* European water-shrew	12.4	I	B	GE		92.5			Hawkins, & Jewell, 1962
7	*Blarina brevicauda* Short-tailed shrew	20.1	I	B	GE				80.0	Buckner, 1964
	CHIROPTERA									
	Vespertilionidae									
8	*Lasiurus cinereus* Hoary bat	23.6	I	B	GE		81.0			Brisbin, 1966
	CARNIVORA									
	Mustelidae									
9	*Mustela rixosa* Least weasel	60.0	C	B	GE		89.9			Golley, 1960

#	Species									Reference
10	*Mustela nivalis* Weasel Felidae		C	B	GE		82.6			Bobek & Grodziński (unpublished results)
11	*Lynx rufus* Bobcat	6250.0	C	B	GE		90.6		82.6	Golley *et al.*, 1965
	LAGOMORPHA Ochotonidae									
12	*Ochotona princeps* Pika Leporidae	171	H	T	OM	54–76	68.0			Johnson & Maxell, 1966
13	*Sylvilagus floridanus* Eastern cottontail	312.0	H	B	GE		60.0			Davis & Golley, 1963 (Golley & Amerson, unpublished results)
14	*Lepus europaeus* European hare	3800.0	H	B	GE	79.9–80.2	80.1	77.7–78.5	78.0	Myrcha, 1968
	RODENTIA Sciuridae									
15	*Eutamias minimus* Least chipmunk	34.0	G(O)	T	OM		75.2			Maxell, 1973
16	*Spermophilus richardsonii* Richardson's ground squirrel	303.0 250.0	O	B T T	OM OM OM	 79.9–82.4 	82.2 81.2 46.1			Johnson & Groepper, 1970 Maxell, 1973
17	*Spermophilus tridecemlineatus* Thirteen-lined ground squirrel	132.0 67.0	O	B T	OM OM		81.0 82.3			Johnson & Groepper, 1970 Maxell, 1973
18	*Spermophilus lateralis* Golden-mantled ground squirrel	270.0	O	T	OM		33.3			Maxell, 1973
19	*Cynomys ludovicianus* Black-tailed prairie dog	885.0	H	B B	GE OM		85.8 85.9			Hansen & Cavender, 1973
20	*Cynomys leucurus* White-tailed prairie dog	1050.0	H	T	OM		24.6			Maxell, 1973

Table 8.2 (*continued*)

No.	Species	Body wt (g)	Feeding type	Method	As % of GE or OM	Digestibility coefficient		Assimilation coefficient		Reference
						range	av.	range	av.	
	RODENTIA (*continued*)									
21	*Sciurus carolinensis*	520.0	O	B	GE		73.8		71.2	Ludwick *et al.*, 1968
	Gray squirrel									
	Gliridae									
22	*Glis glis*	147.0	G	B	GE	90.9–91.3	91.1	87.8–88.1	88.0	Gebczynski *et al.*, 1972
	Fat dormouse									
	Geomyidae									
23	*Thomomys talpoides*	73.0	H	T	OM		57.5			Maxell, 1973
	Northern pocket gopher									
	Heteromyidae									
24	*Perognathus fasciatus*	11.0	G	B	OM	95.1–95.3	95.2			Johnson & Greopper,
	Olive-backed pocket mouse			T	OM	93.2–95.2	94.2			1970
25	*Dipodomys ordii*	60.0	G	B	OM	95.1–97.7	96.4			Johnson & Greopper,
	Ord's kangaroo rat					91.1–93.1	92.1			1970
	Cricetidae	67.0		T	OM		88.3			Maxell, 1973
	Cricetinae									
26	*Oryzomys palustris*	37.0	O	B	GE	88–95	92.2			Sharp, 1967
	Marsh rice rat									
27	*Peromyscus maniculatus*	20.0	O	B	OM		77.0			Johnson & Groepper,
	Deer mouse			T	OM	85.8–89.5	87.0			1970
		22.0		T	OM		71.3			Maxell, 1973
28	*Peromyscus polionotus*	13.0	G	B	GE		93.9			Davenport, 1960 (after Davis & Golley, 1963)
	Old-field mouse									
				B	GE		87.0			Caldwell & Connell, 1968
29	*Onychomys leucogaster*	30.0	I	T	OM		62.2			Maxell, 1973
	Northern grasshopper mouse									
30	*Sigmodon hispidus*	100.0	H	B	GE		91.2		86.5	Golley, 1962
	Hispid cotton rat									

31	*Neotoma cinerea* Bushy-tailed wood rat Microtinae	297.0	H	T	OM		52.3			Maxell, 1973
32	*Clethrionomys glareolus* Red bank vole	23.0	O	B B	GE OM	77.4–92.9 75.8–90.7	86.8 84.9	72.0–88.7	82.9	Drożdż, 1968a, 1970 Drożdż, 1968a
		20.0		B	GE	86.2–88.5				Kaczmarski, 1966
33	*Clethrionomys gapperi* Southern red-backed vole	21.0	O	B T	OM OM	81.8–93.1	78.9 87.4			Johnson & Groepper, 1970
34	*Microtus arvalis* Common vole	22.0	H	B B	GE OM	70.4–92.3 74.5–94.0	81.3 84.3	65.2–89.7	77.5	Drożdż, 1968a, 1970 Drożdż, 1968a
		23.0		B	GE		91.0		8.77	Migula, 1969
35	*Microtus agrestis* Field vole		H	B B	GE OM	33.0–60.0 32.0–59.0	50.7 50.3			Hansson, 1971b, c
36	*Microtus oeconomus* Tundra vole	28.0	H	B	GE	68.7–73.9	71.3	67.2–71.4	69.3	Gebczynska, 1970
37	*Microtus pennsylvanicus* Meadow vole	46.0 29.0	H	B B T B	GE OM OM OM	82.2–89.8 72.0–76.3 43.0–62.9	86.0 81.1 74.2 51.7			Golley, 1960 Johnson & Groepper, 1970 Keys & Van Soest, 1970
38	*Arvicola terrestris* Water vole Muridae	74.0	H	B	GE	55.2–91.2	73.2	47.7–87.7	67.7	Drozdż et al., 1971
39	*Mus musculus* House mouse	16.0	O	B T	OM OM	91.0–94.8	79.5 92.9			Johnson & Groepper, 1970
40	*Apodemus flavicollis* Yellow-necked field mouse	27.0	G(O)	B B B	GE OM GE	81.4–92.2 82.8–89.5	88.2 86.3 90.0	78.7–90.9	86.1	Drożdz, 1968a, 1970 Drożdż, 1968a Turcek, 1956
41	*Apodemus agrarius* Striped field mouse Zapodidae	21.0	G	B B	GE OM	89.6–90.5 86.8–92.1	90.0 89.4	88.9–89.0	88.9	Drożdż, 1968a, 1970 Drożdż, 1968a
42	*Zapus hudsonicus* Meadow jumping mouse Castoridae	16.0	O	B T	OM OM		71.5 94.8			Johnson & Groepper, 1970
43	*Castor canadensis* American beaver	12998.0	H				69.0			Cowan et al., 1957 (after Davis & Golley, 1963)

assimilation in 43 species of non-ruminant small mammals. This list contains data on the utilization of both natural and laboratory food. The data have been determined in different trials by the balance method (B) and the tracer method (T). In the first case both the coefficient of digestibility and coefficient of assimilation as a percentage of gross energy (GE) are known. With the second method only the digestibility coefficient as a percentage of organic matter or dry matter (OM) was determined. The digestibility of energy and of organic matter is usually quite similar. We outlined data for 43 small mammals: 29 rodent species, 7 insectivores, 3 lagomorphs, 3 carnivores and 1 chiropteran. It is difficult to analyze such a long list of heterogeneous data and for this reason all species have been divided, according to feeding habits, into four general categories: (1) grazing herbivores, (2) omnivores, (3) granivores, and (4) insectivores and carnivores (Table 8.3, Fig. 8.3). It should be recognized that these are artificial divisions based upon the major feeding habits of the particular rodent, as most rodents are surely omnivorous. These main feeding types among wild mammals have been previously distinguished by Davis & Golley (1963). Animals fall into a particular category due in part to the anatomy of their digestive tract and in part to the availability of particular foods to them. All non-ruminant herbivores must have a large caecum.

Within these feeding categories the average digestibility and assimilation were computed using the original data. In some species, for which only the digestibility coefficient was available, the assimilation coefficient was estimated by subtracting from digestibility 2–3 per cent for the energy lost as urine. Grazing herbivore species, like many voles and lagomorphs, have the lowest level of digestibility and assimilation (av. 65–67 per cent). A higher level of utilization of food energy is represented by various omnivores such as mice, some voles, ground squirrels, etc. (av. 75–77 per cent). The highest digestibility and assimilation is reached by granivore rodents (dormice, pocket mice and field mice) as well as insectivores and also some carnivores. In these animals assimilation approaches 90 per cent, and in small shrews it may even be slightly higher.

Digestibility and assimilation depend on many factors, but primarily upon the quality of food itself. Bulky food is less digestible than concentrated food and hence the laboratory chow employed in many feeding trials has a very high percentage assimilation. Thus, data based on such experiments may be of limited use for ecologists. Digestibility also depends on the chemical composition of the food, mainly on the

Table 8.3. *Digestibility and assimilation of natural foods in small mammals, as percentage of energy or organic matter consumed*

Feeding type	Number of species (number of data used)	Digestibility coefficient (%)	Assimilation coefficient (%)
Grazing herbivore	14 (14)	67	65
Omnivore	10 (12)	77	75
Granivore	6 (8)	90	88
Insectivore	9 (9)	–	85
Small shrews	6 (6)	–	90
Carnivore	2 (2)	90	–

Grazing herbivores (14) — 65 — 67

Omnivores (12) — 75 — 77

Granivores (8) — 88 — 90

Insectivores & Carnivores (11) — 86 — 91
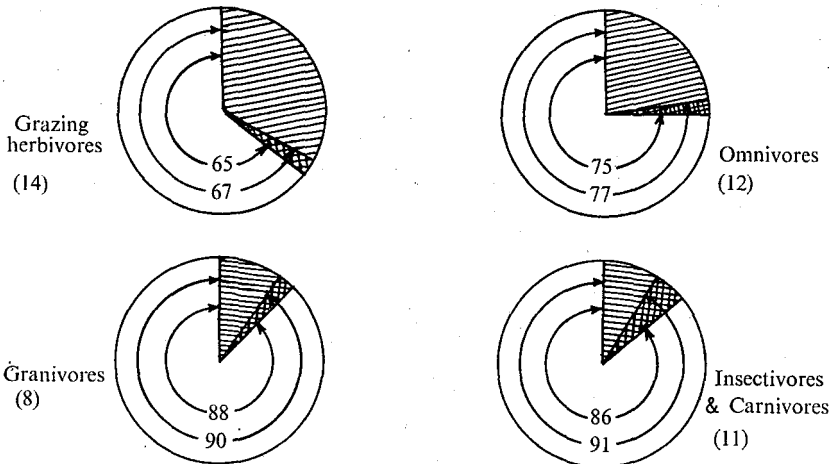
Fig. 8.3. Utilization of food energy by small mammals. The top number on each scheme is the coefficient of assimilation and the bottom number the coefficient of digestibility. Both numbers are given as percentages. The lined areas represent energy lost with feces and the cross-hatched areas energy lost through urine.

content of poorly digested fiber which is found in cell wall constituents, CWC (Van Soest, 1966). Out of this fraction only cellulose and hemi-cellulose are utilized while lignin is not digested, so digestibility is a function of the lignin content of the food. Low protein content, or high content of mineral constituents, e.g., silica or calcium, are other factors limiting digestibility. Another well-known relationship is represented by the effect of the amount of consumed food on its utilization. Finally, the age of a small mammal and its physiological state may to some extent be relevant.

Small mammals

Estimation of the consumption of the whole population may be based upon the assimilation coefficients discussed here. In such computations we usually start with assimilation determined as a sum of production and respiration. The simplest way of estimating total consumption is by adding energy of feces and urine to assimilation. In general the average coefficients can be employed for different categories of small mammals (i.e., by adding to the assimilation of herbivores 35 per cent, omnivores 25 per cent, granivores 12 per cent, insectivores and carnivores 10–15 per cent). This is a 'desperate' and very inaccurate estimation, and the real one should be based on more specific data (Table 8.2) There is a great need for analysis of food utilization in natural conditions since this parameter is critical for computations of the total energy flow. Estimation of food assimilation could also be used to determine the cost of maintenance (R) in small mammals. If an animal does not change body weight during a feeding trial (i.e., $P = 0$) and also does not change the composition of its body, we can consider assimilation as respiration (R). Such an approach has been used by several investigators (Odum *et al.*, 1962; Sharp, 1967; Drożdż, 1968*b*). This approach to the investigation of energy assimilation is basically the same as that outlined for nutrient assimilation by Gentry *et al.* in Chapter 9. Comparison of results from both feeding trials and respirometric studies show fairly close agreement. The feeding method usually gives higher estimates than those using respiration, especially in ADMR tests. Animals studied in metabolic cages do not have nests available and this may explain part of the reasons for higher estimates (Drożdż, 1968*b*).

Modifiers of energy expenditure

Size. The effect of body size on the metabolic rate of small mammals was previously discussed on pp. 181–2. In general, the smaller the mammal, the greater the metabolic rate. The power function of this relationship is different, however, for BMR or RMR and for ADMR.

Shape. Brown & Lasiewski (1972) have shown that in extreme cases the shape of mammals can affect their metabolic requirements. Long thin weasels (*Mustela frenata*) when placed under cold stress at 5 °C have metabolic rates 50–100 per cent greater than that of normal-shaped mammals of the same weights. Their metabolic coefficient or thermal conductance (TC) is about 50 per cent greater than that predicted by the equation of Herreid & Kessel (1967).

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Reproduction conditions. A great many studies have shown that the energetic cost of lactation in cows is high. However, relatively little information is available concerning the energetic cost of reproduction in small mammals. To our knowledge, in small wild mammals, only three rodent species have been studied recently (Kaczmarski, 1966; Trouan & Wojciechowska, 1967; Migula, 1969; Myrcha *et al.*, 1969). (see Table 8.4). In both mice and voles a slight increase in energy

Table 8.4. *Additional energy requirements of reproducing females during gestation and lactation (values recalculated from references)*

Rodent species	Percentage increase†		Reference
	Assimilation	Respiration‡	
Clethrionomys glareolus Bank vole	57.8	49.4	Kaczmarski, 1966
Mus musculus House mouse	77.7	64.7	Myrcha *et al.*, 1969
Microtus arvalis Common vole	82.5	69.3	Migula, 1969
	80.5	69.4	Trojan & Wojceichowska, 1969
Average	72.3	61.2	
Correction factor (rounded off)	1.70	1.60	

† In comparison with non-reproducing females of the same body sizes.
‡ Respiration represents assimilation minus production of litters including placentae and fetal membranes.

requirements during pregnancy has been found and a very great increase in energy cost during lactation (Fig. 8.4). Reproduction can increase metabolic cost (respiration) by 50–70 per cent.

Having such an effect on metabolism, reproduction can be quite an important factor in the energy budgets of small mammal populations. However, the magnitude of the effect on a population basis depends upon the number of reproducing females and the length of the breeding season.

Season: acclimatization. The season of the year affects the metabolism of many small mammals. There has been considerable confusion in the literature regarding this topic. Part of this confusion arises from the manner in which data are gathered and the terminology associated with such studies (see Hart, 1971, pp. 41–5). Acclimation refers to changes

resulting from exposure to controlled variables (usually one at a time and, for our purposes, usually temperature) in the laboratory. Acclimatization refers to modifications in the animal stimulated by seasonal changes in the field. There have been a great many studies concerning the effects of prolonged exposure to cold temperatures, but very few studies of seasonal acclimatization. In general, acclimation to cold temperatures elicits higher metabolic rates at all temperatures. Unfortunately this is not a consistent response and may vary not only
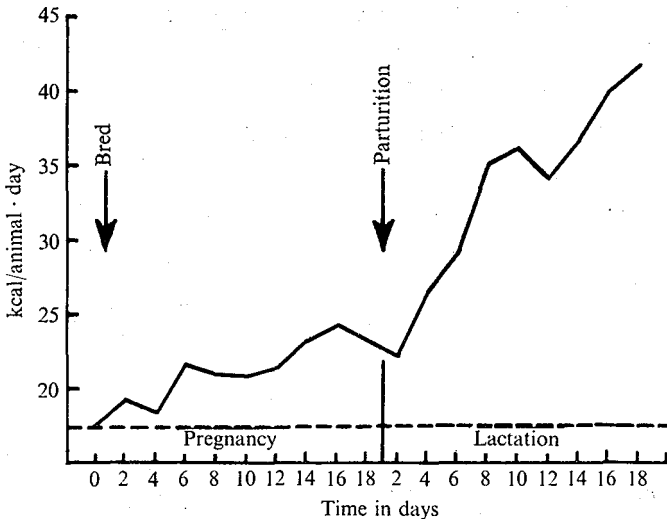
Fig. 8.4. Energy requirements of reproducing female bank voles (*Clethrionomys glareolus*) during gestation and lactation. The dotted line shows the normal energy requirements for a non-pregnant female of the same size (from Kaczmarski, 1966).

between species but within species (see Hart, 1971, p. 43 for review). However, for animals in the field we are dealing with acclimatization not acclimation. In several studies of acclimatization it has been pointed out that it frequently involves modification of heat conserving mechanisms, whereas acclimation involves increases in heat production. In fact, in certain species we find metabolism at any given test temperature may be lower in 'winter' animals than in 'summer' animals (Grodziński & Górecki, 1967; Hart, 1971). Results of acclimatization studies make any generalizations about increases or decreases in metabolism with season very difficult and probably species specific. In most cases the variation in metabolism is not greater than 10–15 per cent and varies with exposure temperature (Hart & Heroux, 1963; Pearson, 1962).

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Habits. It has been pointed out that the habits of small mammals may influence the amount of energy they expend. McNab (1963) has suggested that croppers (mammals feeding on grasses or vegetative parts) have smaller home ranges than hunters (carnivores and seed eaters) and thus may spend less energy per day searching for their food. However, all indications are that metabolic rates relative to body size are similar in both groups. Thus any differences in energy expenditure would result from different rates of expenditure for activity and this will be discussed below.

Activity. Small mammals use considerably more energy in activity than rest and metabolism during activity may be 5–8 times as great as at rest (Wunder, 1970). Taylor *et al.* (1970) have shown that the net cost of running on the horizontal is a function of body size as shown in the following equation:

$$M_{run} = 8.46 \, W^{-0.40} \tag{8.7}$$

where W is in g, MR in cc $O_2/g \cdot m$.

This factor, M_{run}, is the slope of the relation between metabolism and velocity of running. Thus, given body size, we can predict the change in metabolism of a mammal as it runs at different velocities. In addition to these factors of size and velocity of running, the kind of activity an animal is engaged in will influence metabolism. Whether an animal is running up or down hill modifies its metabolic expenditure somewhat. Intuitively one feels that running up inclines necessitates a higher energetic cost for mammals than running on the level. However, Taylor *et al.* (1972) have presented evidence that the cost of running uphill may be size dependent. This is further substantiated by the work of Wunder & Morrison (1974). Thus our capacity to estimate the physiological cost of activity is becoming fairly precise. However, in order to put these data into an ecological context, we need to know how much time an animal spends in activity and at what level of activity. These sorts of data are few.

We suggest much more information is needed on the time budgets of mammals in the field. Since most small mammals are nocturnal and secretive, such data will probably have to be generated via telemetric studies.

Duration of daily activity in small mammals (activity out of the nest) and the main patterns of their activity have been reviewed by Saint Girons (1966).

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Behavioral thermoregulation. Behavioral thermoregulation is best developed in and important for small mammals rather than large forms. During exposure to cold (times of high energy expenditure), small mammals can modify their heat loss and thus conserve energy by huddling together and using a more favorable microclimate such as a nest. Daily activity may also be adjusted to take advantage of the least stressful time of day, especially regarding temperature (Pearson, 1960; Erkinaro, 1971). By storing food for winter small mammals gain two advantages. They will have food available during times of food shortage and will need to spend little time searching for food during adverse weather (Muul, 1968).

Underground nests of small mammals provide quite constant thermal environments (Daniel, 1964; Hayward, 1965b; Brown, 1968) on a daily basis; however, the temperature level may shift slightly from season to season. It has been shown experimentally that the presence of a nest can considerably reduce the energy expenditure of small mammals (Sealander, 1952; Pearson, 1960; Hudson, 1964; Trojan, 1970; Tertil, 1972).

Although there are no field studies, laboratory measurements indicate that small mammals may reduce metabolism during exposure to cold if they are allowed to huddle in groups. The magnitude of the decrease in metabolism due to huddling varies with the species studied (Ponugaeva, 1960) and may range from about 5–45 per cent. The decrease in metabolism is usually a function of the size of the group of animals, but, as group size increases above certain levels in various species, metabolism again increases due to antagonism and additional activity (Prychodko, 1958; Górecki, 1968; Fedyk, 1971).

Although the specific effects of nest insulation and huddling on metabolic rate are relatively small when taken as a percentage change, these factors are quite important when considering daily energy budgets since most small mammals may spend much of their time huddling in a nest. The effects of these phenomena are manifested in a daily energy budget by modifying the temperatures of exposure for the animals.

Energy of production

The theoretical aspects of the energy of production in small mammals have been discussed in Chapter 7 by Petrusewicz & Hansson. Production includes both energy which goes into growth and that which goes into reproduction.

Energy which goes into growth is difficult to measure and most investigators simply consider the increase in weight of an organism and the caloric value for that tissue. Such values can be expressed in several ways (kcal/g fresh weight, kcal/g dry weight, or kcal/g ash weight) and the value used depends on the question being asked. Energy values of growth and animal tissue have been summarized by Górecki (1965*a*, 1967), Sawicka-Kapusta (1970) and Fleharty *et al.* (1973). Body composition may change throughout the year and investigators should correct for this (see Fleharty *et al.*, 1973 for discussion).

The second pathway for production energy is that into reproduction. Few values exist for the energy content of litters and reproductive structures (see Kaczmarski, 1966; Fleharty *et al.*, 1973). However, for a correction, one need know only the energy content of litters and reproductive structures and the biomass of these.

Energy budget models

In dealing with energy flow in small mammals we are, at present, limited to looking at various components of flow and adding or integrating these together (see (1.1), (1.2)). In energy flow through small homeothermic animals, production (P) compared to respiration (R) consists of only about 2 per cent of assimilation (Grodziński & Górecki, 1967; Turner, 1970). Grodziński & French have recently reviewed all available data for 44 populations of small mammals and found that the mean production efficiency of small rodents is 2.3 per cent and of small shrews 0.7 per cent. Thus one of the major components of most energy flow models is an estimate of R.

Gessaman (1973) has reviewed the various models generated to date for estimating small mammal energy flow. These are summarized in Table 8.5.

Some of the earliest models of energy flow in small mammals simply used BMR × 2 as an estimate of energy requirements under field conditions (Golley, 1960). Following these early models some modifications were introduced. Pearson's (1960) model was one of the first to attempt to account for various ecological parameters and included the effects of huddling, nest insulation and a factor for activity. MacNab (1963) presented a model which described R for a deer mouse, although the model has general application to other mammals. Metabolism is described as a function of temperature, time at that temperature and whether the animal is active or not. For the purposes of the model a day

Table 8.5. *Models of mammalian energy budget and factors they include*

Authors of model	Body size	Temperature		Nest insulation	Huddling	Sex	Activity	Light/ dark	Season
		Outside	In nest						
Pearson (1960)	−	+	+	+	+	−	+	−	−
McNab (1963)	−	+	−	−	−	−	+	−	−
Grodzinski & Górecki (1967)	+	+	+	+	+	+	+	−	+
Trojan & Wojcieckowska (1969)	+	+	+	+	+	+	+	+	+
Chew & Chew (1970)	−	+	+	−	−	−	+	−	−
Newman (1971)	+	+	−	−	−	+	+	−	+
Randolph (1973)	−	+	+	−	−	−	+	−	+

is divided into a sinusoidal function of high temperature, low activity (daytime) and low temperature high activity (night time). The activity for activity energetics needs to be fed in as maximum to minimum following the sine-wave function. In addition, one needs, independently, to feed into the model the thermal conductance of each animal studied.

In addition to the models outlined in Table 8.5, Porter & Gates (1969) have approached animal energetics in a slightly different fashion introducing the new concept of climate space for animals.

It is our intent now to discuss in detail *only two* models of small mammal energetics and then to add some comments on the concept of climate space. One model was based on resting metabolic rate (RMR) and then another developed from average daily metabolic rate (ADMR).

RMR model

Early in the development of small mammal energetics, resting metabolism was used by some investigators for computing energy flow (Wiegert, 1961; Grodziński, 1961). Trojan (1970) modified the RMR approach to construct a more complex ecological model. The most complete model to date which is based upon RMR is that presented by Chew & Chew (1970); however, it still has two limitations. They have no simple way of estimating the cost of activity and they need to feed in metabolic data specific to the animal with which they are working.

Wunder (1975) has designed a generalized model to estimate R in small mammals given: (1) body size, (2) air temperature, (3) degree of running activity. The model takes the following general form:

$$R = \alpha M_B = M_{TR} + M_A, \tag{8.8}$$

where α is a coefficient to modify metabolism for the posture associated with activity (Schmidt-Nielsen, 1972a), M_B is basal metabolism, M_{TR} is metabolism associated with temperature regulation below thermoneutrality and M_A is metabolism due to activity. The mathematical form for the model is:

$$R = \alpha(3.8W^{-0.25}) + 1.05W^{-0.50}[(38 - 4W^{+0.25}) - T_A]$$
$$+ (8.46W^{-0.40})V, \tag{8.9}$$

where α is as above, W is weight in grams, T_A is ambient temperature and V is velocity of running in km/h.

This model coupled with estimates of ambient conditions in the field and estimates of time budgets can thus be used to estimate energy flux through an individual over time.

The ADMR model

Starting with measurements of average daily metabolic rate (ADMR) a model of daily energy budgets (DEB) was constructed for small mammals, mainly for small rodents. This model initially represented the cost of maintenance (i.e., respiration) of an animal of mean body weight (Grodziński, 1966; Grodziński & Górecki, 1967). Later, however, it was based on intraspecific functions of the allometric type describing the relationship between ADMR and body size in different species of voles, mice, and squirrels (Grodziński *et al.*, 1970; Hansson & Grodziński, 1970; Grodziński, 1971*a*; Drożdż *et al.*, 1971).

These budgets describe the respiration of adult animals, assuming that they do not change their body weight in the course of one day, i.e., that their production is equal to zero. Such DEBs represent the sum of the energy expenditure during the time the animal spends in its nest and in the period of activity out of the nest, together with additional costs of maintenance connected with female reproduction. Owing to the seasonal nature of reproduction and also to seasonal changes in activity and temperature outside the nest, these budgets were computed separately for different seasons, or at least for winter and summer days. Corrections added in these budgets to the empirical value of ADMR are limited to two alone, namely: (1) additional heat production for thermoregulation when the animal is active outside the nest, and (2) additional energy requirements of reproducing females (Grodziński, 1971*a*).

The daily energy budget of small mammals was recently developed by J. Weiner (Grodziński & Weiner, unpublished data) in the form of a general formula which utilizes interspecific equations describing relationships between ADMR and body size in small mammals, see (8.5) and (8.6). The general formula for a DEB based on the ADMR of small mammals has the form:

$$\text{DEB} = \text{ADMR} + \text{f}\left[\text{TC}(t_k - t_a)\right] + \text{CR}(\text{RP} \cdot \text{TR}), \qquad (8.10)$$

where f is the fraction of day spent outside nest, TC the thermo-conductance, t_k the lower critical temperature, assumed to be 20 °C, t_a the ambient temperature, CR the coefficient of respiration increase in a pregnant or lactating female (which on the average amounts to 0.61 – cf. p. 191 and Table 8.4), RP the fraction of reproducing females in a

population and TR the duration of the breeding period as a fraction of one year. RP and TR may be assumed to amount to 0.2 and 0.5, respectively.

ADMR in (8.10) for rodents may be replaced by (8.5) while TC may be taken from (8.4) or from the following formula given by Hart (1971):

$$TC = 0.1094 \ W^{-0.499} \approx 0.1097 \ W^{-0.5}, \tag{8.11}$$

with TC in kcal/g·day·°C, W in g.

Upon substituting (8.5) and (8.11) together with constant coefficients into (8.10) and after transforming the equation and unifying various units we obtain an equation specific to rodents:

$$DEB = [2.437 + f(2.3278 - 0.1164 \ t_a)] \ W^{-0.5} \tag{8.12}$$

with DEB in kcal/g.day, t_a in °C, W in g, and f dimensionless.

From (8.12) we may easily calculate the approximate respiration for each rodent species if we know its body weight W, the fraction of the day, f, that it spends in activity beyond the nest, and the temperature, t_a, of its environment. An analogous specific relation may also be written for insectivores starting with expression (8.6), although the data for assessing such corrections are inadequate in their case. Formula (8.12) involves the formal averaging of female reproduction costs over all the individuals in the population for an average day of the year. This is a simplification which admittedly facilitates the computation of a yearly energy budget for a whole population (see section on population models, p. 204).

The exponent in the equation (-0.50) gives values in kilocalories per unit of body weight in grams. If we simply change its sign we obtain the number of kilocalories per whole animal. Equation (8.10) written in its general form allows us to make adjustments to specific conditions in determining the DEB if only we know the necessary parameters, both physiological and populational.

Budgets representing only respiration or assimilation may easily be generalized to represent total consumption by adding the energy of feces and urine to the initial value (Drożdż *et al.*, 1971).

Daily and yearly energy budgets

Perhaps the simplest way to approach calculation of the daily energy budget (DEB) of an individual mammal is to envision the budget as the sum of its component parts. Thus DEB can be represented as:

$$DEB = R + P. \tag{8.13}$$

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As mentioned above, for adults, except reproducing females, P is quite small relative to R. Thus the primary influence of P on DEB is through reproducing females and growing young. Grodziński & Górecki (1967) have suggested that P might be easiest to calculate on a population basis using a yearly time scale. However, R can be estimated for an animal using either the ADMR or RMR model. If the RMR model is used, R will be a function of the amount of time the animal is resting or active and the ambient conditions under which such behavior occurs. Since the model of (8.9) can give estimates of metabolism for very short periods of time, the R of a DEB can be envisaged as the sum of a variable metabolism for a day:

$$\text{Daily } R = \sum_{i=1}^{24} R. \qquad (8.14)$$

If P is calculated on a daily basis, then

$$\text{DEB} = \sum_{i=1}^{24} R + \sum_{i=1}^{24} P. \qquad (8.15)$$

For a seasonally cumulative budget one needs to know: (1) does the animal become torpid, and if so for how long, to what degree and under what ambient conditions; (2) how ambient conditions change in the field; (3) how the behavior of the animal may change from season to season (huddling, use of nest, moult, etc.); and (4) if the animal is a female, one needs to know how long she is pregnant and/or lactating. A yearly energy budget (YEB) can then take the following form

$$\text{YEB} = \sum_{i=1}^{365} \text{DEB} \qquad (8.16)$$

To calculate such a budget for day-by-day conditions would be quite tedious. Muul (1968) has constructed a seasonal energy budget for flying squirrels. Gebczynski *et al.* (1972) have done the same for a dormouse and Randolph (1973) presented a yearly model for short-tailed shrews (*Blarina*). Grodziński & Górecki (1967) have suggested that at least two seasons (summer and winter) should be considered if constructing a yearly budget.

It is interesting to note here that Mullen & Chew (1973) have compared estimates of metabolism for *Perognathus formosus* calculated from the model of Chew & Chew (1970) and from measurements of $D_2{}^{18}O$ in free-living animals. The results are quite similar. Using their estimates of temperature exposure, time of exposure and the activity correction

suggested by Chew & Chew for this 20 g mouse, we can compare their results with an estimate from the model presented in (8.9). We compared estimates for only 2 months, October and July. The estimate for October (using Chew & Chew's model) is 126.9 cc O_2/g·day and our estimate is 127 cc O_2/g·day. Their estimate for July is 66·3 cc O_2/g·day and our estimate is 61 cc O_2/g·day.

Climate space

One very important approach to modeling energy flow has received relatively little attention from students of small mammal ecology. This is the study of models of heat balance in terrestrial vertebrates approached with heat transfer equations (Birkebak *et al.*, 1966; Birkebak, 1966; Porter & Gates, 1969; Beckman *et al.*, 1971).

Porter & Gates (1969) have defined what they call the climate space of an animal. In essence, they have generated mathematical models, based on heat transfer theory and physiological data, for defining the environmental limits within which animals may function. They can then simulate changes in environmental parameters and predict animal limits and behavior. At present the models have been most refined for the desert iguana, *Dipsosaurus dorsalis*, a poikilotherm. However, personal communications with Porter indicate that models describing energy balance between mammals and their environment are possible.

One powerful advantage of such models is that they would allow one to stimulate environmental change and estimate changes in energy balance and thus in energy flow. Although not appropriate for model building at present this approach may be quite important in the next five to ten years.

Estimation of metabolic rate in the field

To date no studies estimating metabolic rate of small mammals in the field by means of the $D_2^{18}O$ technique have been responsible for generating models of energy flow. Mullen (1970, 1971*a,b*) has investigated field metabolism in two species of kangaroo rats, a pocket mouse, and the canyon mouse. Table 8.6 summarizes his results, showing only slightly higher metabolic rates in winter than in summer months.

Mullen & Chew (1973) compared estimates of energy flow in *Perognathus formosus* generated by indirect and direct techniques. The indirect technique was to use the model of Chew & Chew (1970) based

on laboratory studies on metabolism and estimates of field time budgets. The other estimate was a direct integrated measure of metabolism by the $D_2{}^{18}O$ technique. Comparisons were calculated over several months and a fair agreement was found (10–20 per cent). Mullen & Chew suggest that one reason this agreement was so close is that they feel *Perognathus formosus* acts in the laboratory much as it does in the field, and a large component of the energy flow is due to thermoregulation. Thus they conclude that for species which are not especially active

Table 8.6. *Metabolism (expressed as cc $O_2/g \cdot day$) of free living small mammals determined by $D_2{}^{18}O$. All data recalculated from Mullen (1970, 1971a, b).*

Month	Perognathus formosus (20 g)	Dipodomys merriami (36 g)	Dipodomys microps (57 g)	Peromyscus crinitus (13 g)
January	–	61	–	129
February	168	107	105	220
March	162	146	96	–
April	151	100	148	–
May	–	–	–	–
June	–	–	133	–
July	77	–	70	–
August	83	44	–	–
September	100	73	–	–
October	160	122	12†	–
November	128	73	16†	129
December	–	98	86	–

† Suspected torpor.

indirect and direct estimates may be similar, but for species which may behave very differently in the field, estimates may be in error if calculated by the indirect model techniques.

In addition to the use of heavy water various radioisotopes have been studied as possible methods for estimating field metabolism. To date, however, none appear to be very promising (see Sawby, 1973, for discussion and review).

Other investigators have attempted to use biotelemetry of heart rate as a means to estimate metabolism in the field. At present none of the systems tried have been successful, as heart rate is only one of several parameters determining oxygen delivery to the tissues (see various chapters in Gessaman, 1973, for discussion).
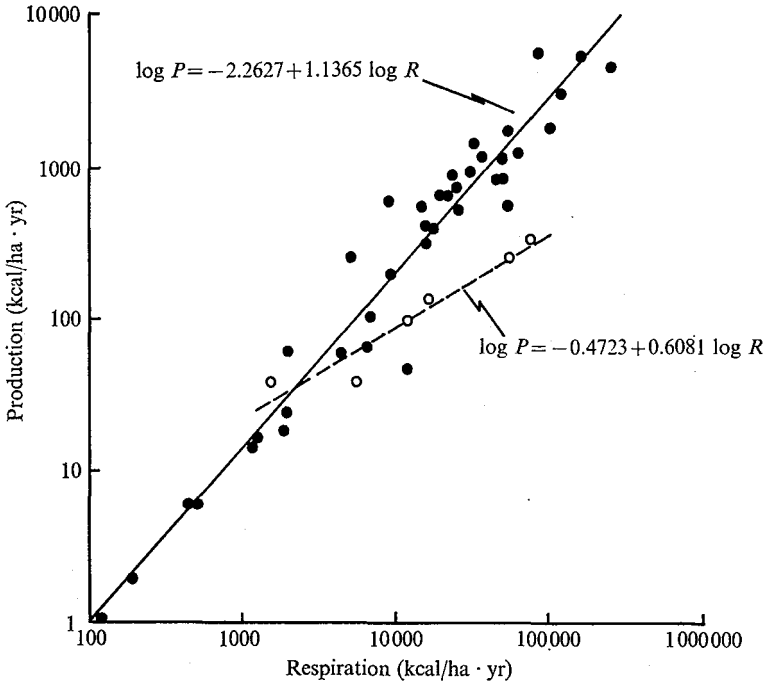
Fig. 8.5. Population production (*P*) described as a function of respiration (*R*) in rodents (solid line) and insectivores (broken line). Data points are for 44 populations of small mammals from Europe and North America. From Grodziński and French (unpublished data).

Table 8.7. *Effects of errors in estimates on energy budgets*

	Type of error	Size of error	Error as % *R*
(*A*)	In *R* components		
	(1) Estimating level of activity. (Largest error when level is low but estimated high.)	0.9–2.1 km/h	2–10
	(2) Amount of time running	—	5–15
	(3) Temperature when out of nest. (Depends on time out of nest: our limits 4–8 hrs.)	10 °C	6–12
	(4) Time out of nest. (Low error if little time spent running, high error if much time running.)	4–8 h	6–12
	(5) Temperature of nest. (Depends on amount of time in nest.)	5 °C	12–17
(*B*)	In *P* estimates		
	Depends directly on the degree of error in estimating number of animals breeding and breeding period, but will affect only *P*.		
(*C*)	In *N* estimates		
	These errors will affect DEB in direct relation to the magnitude of their error and will affect both *P* and *R*.		

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Small mammals

Population models

To expand energy budget estimates to the population level we need simply to sum the DEB values for all individuals in the population (usually considered by cohorts of age/body size):

$$DEB_{pop} = \sum_{i=1}^{n} DEB \qquad (8.17)$$

where n = number in population.

In order to sum correctly we need to know: (1) the number of individuals in the population and the population age structure; (2) the levels of activity and conditions under which individuals are operating; and (3) the fraction of the population which is reproducing and length of the breeding season. Again the yearly budget for a population can be generated from a summation of the DEB_{pop}:

$$YEB_{pop} = \sum_{i=1}^{365} DEB_{pop}.$$

Summations of this sort have been used in several computations of energy flow through small populations in different ecosystems (Grodziński *et al.*, 1970; Chew & Chew, 1970; Grodziński, 1971*a*; Hansson, 1971*a*). As suggested above, production is more easily estimated separately and then added to respiration to give estimates of assimilation (see Chapter 7). In some 'desperate' cases P can be estimated as some small proportion of R using either of two formulae developed recently for small rodents and small insectivores (Fig. 8.5).

In order to assess the effects of errors in estimating various parameters involved in the calculation of energy budgets, we have listed the possible magnitude that these errors might have on energetic estimates (Table 8.7). These values were generated using the model in (8.9) and varying the parameters of time, temperature and level of activity. By comparing model estimates for R with values in the literature the model has an overall accuracy level of about 10–20 per cent (Wunder, 1975).

Most errors in estimating conditions which the animals are exposed to will only affect certain percentages of an R estimate. Errors in estimation of the fraction of the population breeding will affect the overall energy budget through mis-estimates of P and will depend directly on how far the breeding estimate is wrong. Errors in estimating the total population number will affect both P and R directly in relation to the magnitude of their error. Given the sorts of variance placed on population estimates (see Chapter 2) we suggest that this is the largest source of error in population energy budget estimates.