Energetics of small and large mammals

W. Grodziński & J. Weiner

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The bioenergetics of four herbivorous mammals with considerably different body sizes (22 g, 1.5 kg, 22 kg and 200 kg) were studied. These are the common vole (*Microtus arvalis*), wild rabbit (*Oryctolagus cuniculus*), roe deer (*Capreolus capreolus*) and elk (*Cervus elaphus canadensis*) respectively. Beginning with daily or fasting metabolic rate (ADMR/FMR), annual energy budgets (AEB) were constructed which also included the cost of thermoregulation, locomotory activity, SDA and reproduction. Annual energy budgets representing assimilation reached 22, 512, 2980 and 14940 MJ in vole, rabbit, roe deer and elk, respectively. Simulations of AEB's show some differences in budget structure (thermoregulation vs. activity); however there is a substantial similarity in the costs of female reproduction (20—30 % of total AEB). Small and large herbivorous mammals are characterized by a variety of life histories and foraging strategies (short and long life span, high and moderate reproduction, grazing and browsing, non-ruminant and ruminant digestion). Their populations, however, in terms of energy have similar influences upon terrestrial ecosystems.

W. Grodziński & J. Weiner, Department of Animal Ecology, Jagiellonian University, Karasia 6; 30-060 Kraków, Poland.

1. Introduction

Although mammalian energetics has been studied extensively only in last twenty years it has already undergone a major alteration of attitude towards its subject. During the IBP decade ecologists' attention was attracted to energy budgets, the main aim then being to estimate population productivity (Petrusewicz & Macfadyen 1970) while more recently the studies have concentrated upon evolutionary strategies in the energy budget partitioning into growth, maintenance, and reproductive efforts (Millar 1977, Randolph et al. 1977, Lavigne 1982). The components of energy budgets are regarded as traits which have evolved under various physical constraints and have been optimized by the natural selection.

The plentiful literature on mammalian energetics still remains deficient in studies summing up the data on energy budgets with respect to reproductive energy expenses. Generalizations are needed to enable any further exploration of the evolutionary patterns of reproductive effort in mammals. They may also help in making predictions about the population energy demands in various ecosystems. There are two possible ways of such generalizations, both already attempted: (1) an indirect reasoning which is based on the general patterns of changes in life-history parameters and morpho-physiological traits as related to the body weight. The current literature abounds in empirical allometric equations relating such parameters and traits to the body weight (Hart 1971, Blueweiss et al. 1978, Millar 1977, McNab 1980). The proposed functions differ in slope parameters (exponents) thus suggesting that the relative share of particular components of the entire energy budget might depend on body weight. (2) The second approach relies upon direct comparisons between the energy budgets studied in detail in particular species.

2. Size-dependent trends in energy budget partitioning

Maintenance requiremants. The components of maintenance energy budget related to body weight are described by a number of well known allometric equations, and therefore predicting the changes in energy budget partitioning with increasing body size of mammals seems relatively easy.

It is widely accepted that the basal metabolic rate in mammals is proportional to the 3/4 power of body weight (Hart 1971). It has also been convincingly shown (Hart 1971) that the overall thermal conductance, hence also the cost of thermoregulation at a given ambient

temperature, correlates well with the square root of
body weight (exponent 1/2). Also the cost of
locomotory activity (running at the given speed) seems
to increase with body weight powered to an exponent
slightly lower than 3/4 (Schmidt-Nielsen 1972). When
these exponents are compared, it appears quite obvious
that the relative cost of thermoregulation will decrease
whereas the share of locomotory activity and resting
metabolism will increase with increasing body weight.

Reproduction. The relative cost of reproduction
represents the most puzzling problem in the field of
animal energetics. The experimental measurements of
energy expenditures on reproduction in wild mammals
are still too scarce to facilitate any regression analysis.
There have been several attempts at deriving
relationships from morphological parameters and life-
history traits scaled to the body weight (e.g. Millar 1977,
Robbins & Robbins 1979, Lavigne 1982). Millar (1977)
and Robbins & Robbins (1979) provided the most
profound analyses of this type, taking into account such
species-specific variables as: weight at birth, litter size,
postnatal growth rate, age and weight at weaning, milk
production at the peak of lactation, etc. in relation to
adult body weight. Despite slightly different approaches
the authors arrived at similar conclusions that the
relative cost of reproduction decreases with increasing
body weight.

The conclusions derived from allometric analyses of
life-history variables suffer from ambiguities, however.
As pointed out by May (1980), the data used in
regressions show a great non-random variablility.
Variation in such parameters as proportionate weight at
birth seem to be weight-dependent and, moreover, these
relationships are often strongly modified by weight-
independent, sometimes non-energetic environmental
factors (Millar 1977, McNab 1980). For example the
share of thermoregulation and locomotion depends
greatly on ambient temperatures, time budget, and
behavioural patterns rather than on body weight alone.
There is no evidence that behavioural patterns are
related to body weight in a manner that would permit
allometric considerations.

The question of the cost of reproduction is even more
complicated. Reproductive patterns are not subjected to
the physical constraints in a direct way, as it takes place
in the case of the components of maintenance energy
budgets. The evolutionary optimization of the cost of
reproduction within the total energy budget may rely
upon a trade-off between particular components, or on
some adaptations to increase the total energy budget
(Mattingly & McClure 1982). The amount of energy
spent for particular life activities, as well as the total
energy budget of an animal is strongly affected by such
factors as environmental conditions (latitude), habitat
(e.g. fossorial vs. above-ground), foraging strategy
(herbivory or granivory vs. carnivory, etc.), mode of
postnatal development (altricial vs. precocial), etc. The
particular life-history traits are evidently inter-related
(May 1980, McNab 1980, Zeveloff & Boyce 1980) and
thus some compensatory effects may occur which
cannot be assessed using the allometric functions
computed for single variables.

It appears that the analysis of allometric relations of

life-history, physiological and morphological traits may
provide but too generalized, qualitative, verbal
statements about the tendencies in energy budget
partitioning. This may be enough for generating
interesting hypotheses, but is far insufficient to yield a
satisfactory, especially quantitative conclusion.

The aim of this study was to attempt the other
approach which is based on comparisons between the
species-specific energy budgets, calculated from the
empirical data for particular species rather than from
general equations. The number of such budgets,
including the original estimates of reproductive energy
expenses, is very limited. Those that exist are hardly
comparable, due to differences in computational
procedures. For these reasons we have used only four
budgets designed in a similar manner, only for the
females, from comparable sets of experimental data, and
covering a large span of body weights (five orders of
magnitude). To offset the effect of different life
strategies, the species chosen are grazing or browsing
herbivores of the temperate zone. These are: European
common vole *Microtus arvalis*, European wild rabbit
Oryctolagus cuniculus, roe deer *Capreolus capreolus*, and
American elk *Cervus elaphus canadensis*. Three of these
budgets (for vole, rabbit, and elk) have been partly
published elsewhere (Grodziński et al. 1977, Weiner
1975, Bobek, Kunelius & Weiner, ms.), while that for
rabbit was computed for this study.

3. Structure of energy budgets

The annual energy budgets (AEB) considered here consist of the
following elements: (1) resting metabolic rate (RMR — roughly: the
sum of BMR and SDA), (2) cost of thermoregulation (THERM), (3)
cost of locomotory activity (ACTIV), (4) cost of female
reproduction (REPR). Constant body weight of females was
assumed. In large mammals the compensatory effect of total heat
production on the thermoregulatory expenditures was considered.
The cost of maintenance (i.e. the sum of resting metabolism,
thermoregulation, and activity) was calculated from respirometric
measurements with the field data on behaviour and ambient
temperature also taken into account. Cost of reproduction was
estimated from the data on biomass production in gestation, growth
rate and respiration of sucklings, and the efficiency of milk
production and milk digestion. The energy budgets were carefully
refined using computer simulations.

4. Energy budget partitioning in small and large mammals

The structures of energy budgets of the four species
involved are compared in Table 1. In all cases, the
resting metabolism including SDA constitutes a major
part, ranging from about 40 to more than 60 % of the
annual energy budget (AEB). The cost of
thermoregulation is unexpectedly low, decreasing from a
mere 4 % in voles to none in elks. In other words, when
endothermy is once established, resulting in a high rate
of basal metabolism, the additional costs of
thermoregulation may no longer be an important factor
in the yearly energy budget. In some instances, however,
this expense may be much higher, e.g. in an arctic
lemming (Karasov 1981) the cost of thermoregulation
may reach as much as 50 % of maintenance
requirements.

Table 1. Annual energy budget (AEB) partitioning in four species of mammals (in MJ; percent proportion of AEB in parentheses).

	Body weight	Maintenance			Reproduction				Total	Annual energy budget
		RMR	THERM	ACTIV	Gesta-tion	Lacta-tion	Produc-tion	Respi-ration		
Microtus arvalis	22 g	12.5 (56.4)	0.9 (4.0)	2.5 (11.2)	1.2 (5.7)	5.0 (22.6)	3.2 (14.6)	3.0 (13.7)	6.2 (28.3)	22.1
Oryctolagus cuniculus	1500 g	202.6 (39.5)	3.2 (0.6)	156.8 (30.6)	11.5 (2.2)	138.5 (27.0)	105.4 (20.6)	44.3 (8.7)	150.0 (29.3)	512.5
Capreolus capreolus	22 kg	1580.2 (53.0)	8.9 (0.3)	626.1 (21.0)	72.5 (2.4)	702.7 (23.6)	539.8 (18.1)	235.4 (7.9)	775.2 (26.0)	2990.4
Cervus elaphus canadensis	200 kg	9509.0 (63.6)	0.0 (0.0)	2624.3 (17.6)	236.1 (1.6)	2569.1 (17.2)	1935.6 (13.0)	869.6 (5.8)	2805.2 (18.8)	14938.5

Reproduction constitutes the second largest part of energy budgets (20 to 30 % of the AEB). Lactation involves from 80 to 92 % of the costs of reproduction (17 to 27 % of the total AEB). Activity costs range from 11 to 30 %. Up to one-fifth of the whole AEB of a reproducing female is incorporated in the tissues of foetuses, and in milk. The efficiency of such production is lowest in the vole and elk (13—14 %, Table 1), while it attains a maximum in the rabbit (20.6 %).

No clear tendency appears in energy budget structure in respect to the body weight. The costs of thermoregulation were the only ones to show a rapid decrease with increasing body weight, while other components varied. The limited number of entries does not allow any but a tentative allometric analysis of these budgets. The total AEB's, however, fall almost exactly on a straight line when plotted on a double logarithmic scale, and the regression calculated yields the following equation:

$$\text{AEB (MJ animal}^{-1}\text{ year}^{-1}) = 2.56\ W^{0.71},$$

where W is adult body weight in grams. Similarly, the RMR relation to body weight follows the equation:

$$\text{RMR (MJ animal}^{-1}\text{ year}^{-1}) = 1.19\ W^{0.73},$$

which shows that the total energy budget equals approximately 2RMR, almost independently of body weight. The line representing costs of reproduction appears to be less steep (exponent 0.67), which in turn suggests a decrease in the costs of reproduction within AEB with increasing body weight. However, as seen from Table 1, the reproduction and activity costs may well reach a maximum at medium body sizes rather than to decrease steadily.

Nevertheless, much more information on species-specific energy budgets is needed, before firm conclusions about the general trends in energy budget partitioning can be drawn. Ironically, when searching through the literature on mammalian energetics one gets an impression that the attention paid to the particular components of energy budgets remains in a negative correlation with the relative importance of these components. Until recently, only five studies have been devoted to the experimental measurements of energetics

of reproduction in wild mammals, all five concerning small rodents (see Mattingly & McClure 1982, for a review).

5. Energetics at individual and population levels

All the four mammalian species discussed are strictly herbivorous consumers. Common vole, rabbit and both deer species are characterised, however, by different life histories and foraging strategies (short and long life span, high and moderate reproduction, altricial and precocial development, grazing and browsing food habits, non-ruminant and ruminant digestion). Their populations differ in density and biomass, and especially in the occurrence of fluctuations in population numbers. Voles and also wild rabbits are well known for population outbreaks, whereas deer numbers are usually stable.

Population energetics of these herbivores can be discussed in more detail on the basis of data on the common vole and roe deer in Southern and Western Poland. Voles cycle on wheat fields with an amplitude from 9 ind./ha during a normal year to 62 ind./ha at an outbreak; the same cycle in alfalfa fields reaches 7—15 times higher densities (Grodziński et al. 1977). Roe deer numbers in lowland forests varied from 0.05—0.35 ind./ha with the mean at about 0.15 ind./ha (Pucek et al. 1975, Bobek 1980). In terms of biomass standing crop, this represents 0.16—1.1 kg/ha in voles and 1.1—8.0 kg/ha in roe deer.

Energy flow (assimilation) through such populations computed on the basis of AEB's described in this paper range between 551 and 4435 MJ ha⁻¹ year⁻¹ for voles and 140—980 MJ ha⁻¹ year⁻¹ for roe deer (as recalculated from Grodziński et al. 1977, Bobek & Perzanowski, ms.). When a vole population during a normal year is compared with a deer population of a mean density their energy flow (A) and total consumption (C) could be quite similar (A = 551 and 420 MJ ha⁻¹ year⁻¹; C = 917 and 700 MJ ha⁻¹ year⁻¹; Grodziński et al. 1977, Bobek & Perzanowski, ms.). This supports the idea expressed by Damuth (1981) that energy use by a population of a mammal is independent of its body size.

Nevertheless, more distinct differences appear during analysing efficiency of production in energy flow through populations of small and large herbivorous mammals. In common vole the population efficiency of net production in comparison with respiration (Pn/R) is the highest among herbivorous rodents reaching 7.43 % (Grodziński & French 1983), whereas in roe deer populations it could be estimated as 3.24 % (Bobek & Perzanowski, msc.). The production efficiency in populations of voles and deer does not appear to be explicitly related to the efficiency of female reproduction (production/respiration) as derived from their

individual energy budgets (16.8 % and 22.1 %, cf. Table 1). It even seems that they might be inversely correlated, and the differences could have reflected their various demographic patterns and post-weaning growth rates.

Other differences between small and large herbivorous consumers concern their impacts on vegetation and depend mainly on their various foraging strategy and mobility (Petrusewicz & Grodziński 1975). Voles and rabbits grazing in grasslands could exploit vegetation affecting it heavily and rather locally around their nests; by contrast deer browsing in woodlands affect vegetation by selective feeding spread over large areas.

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