

Metabolic Constraints to Mammalian Energy Budgets¹

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An approach alternative to the conventional regression analysis of two-dimensional distribution of mammalian body sizes and metabolic rates is proposed. It is hypothesized that the actual species-specific energy budgets fill the space between physiological constraints functionally related to body mass. The allometric correlation between energy budgets and body mass is a side effect of this pattern. An attempt was made to identify and quantify the relevant constraining functions. The following allometric regressions, based on numerous literature data, were computed: minimum metabolism in hibernation $M_{\min} = 0.246 \times 10^{-3} W^{0.879}$; maximum aerobic metabolism $M_{\max} = 0.101 W^{0.887}$; maximum non-shivering thermogenesis $NST_{\max} = 0.112 W^{0.663}$; maximum total heat production $HP_{\max} = 0.168 W^{0.670}$; maximum rate of energy assimilation from food $A_{\max} = 0.214 W^{0.664}$; all metabolic rates in Watt, body mass (W) in grams. The theoretical scaling powers are 2/3 (surface) and 1 (mass). Thus, M_{\min} and M_{\max} seem to be limited by processes directly proportional to body mass, whereas other constraining functions depend on surface areas of morphological structures, e.g. surface area of the gut in the case of A_{\max} . The field energy budgets of mammals fit within these constraints but closely approach the limit for A_{\max} . Man avoided the physiological constraint of individual energy budget exploiting energy sources from outside the alimentary tract.

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1. INTRODUCTION

Bioenergetics is a domain well suited to exercise the search for universal, quantitative laws in biology. A good example of such attempts is the almost centennial debate on the factors affecting the relation between body size and metabolic rate in animal (Rubner, 1883). Since the concept of allometry was introduced (Brody & Proctor, 1932; Kleiber, 1932), power functions of the form: $M = aW^b$ (where M = metabolic rate and W = body mass) are notoriously being fitted to various sets of data and the debate continues as to the meaning of numerical values of the parameters a and b .

The variety of explanatory models proposed is amazing (cf. for example: McMahan, 1973; Ultsch, 1973; Apple & Korostyshevskiy, 1980;

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Gray, 1980; Heusner, 1982a, b, 1984; Feldman & McMahon, 1983; Frazier, 1984; Wieser, 1984; see also Peters, 1983 and Schmidt-Nielsen, 1984 for reviews). The individual deviations from the values predicted according to a formula are usually regarded as random effects, usually explained by some peculiarities of a given object (Poczopko, 1971; Müller *et al.* 1973; Henneman *et al.* 1983; to name just 3 examples). Recently, a more rigorous approach and a more advanced statistical analysis have been applied. The curves are still being fitted, but the analysis is not focused so much on the function parameters as rather upon the residual variation, which could explain some adaptive strategies of species or taxons (Hayssen & Lacy, 1985; Elgar & Harvey, 1987; McNab, 1986, 1988). The advantages and the drawbacks of such approaches have been repeatedly pointed out (Heusner, 1982a; Peters, 1983; Schmidt-Nielsen, 1984; Prothero, 1984, 1986; Wieser, 1984; McNab, 1988). Apart from the technical difficulties with statistics (Harvey & Mace, 1982; Seim & Saether, 1983; Smith, 1984; Weiner, 1985; Prothero, 1986; McNab, 1988), two problems should be mentioned:

Firstly, in the lack of data concerning the whole long-term energy budgets of free-living animals, the studies concentrate upon some more or less artificial bioenergetical indices, first of all the basal (standard) metabolic rates (BMR, SMR). On the other hand, however, the discussion concerns the ecological and evolutionary problems pertaining to natural situations of animals studied, *e.g.* adaptations to certain climates, habitats or food habits (Hart, 1962, 1971; McNab, 1980, 1986). This approach relies upon an explicit or implicit assumption that the bioenergetical index under study at least roughly scales to the total energy expenditure in the field. Based on reasonable theoretical considerations, this supposition still lacks good empirical evidence. Indeed, certain studies seem to cast some doubt on the validity of this fundamental assumption (Padley, 1985; Koteja, 1987).

Secondly, even if the above assumptions were allowed, one should not ignore the absolute value of the extent of residual variation (McNab, 1988). When keeping in mind the biological meaning of the difference in body size or in metabolic rate by one order of magnitude, one cannot treat such a variation as a "random noise", which merely scatters the variates around an imaginary line determined by the supposed strong, functional relationship.

Giving up the conventional regression analysis one can set the problem in quite another way. Let us assume that the actual species-specific energy budgets randomly fill a space between the constraints, which are the strictly determined functions of the body weight. If it were so, then one could also expect a correlation between these budgets and body

mass, but the parameters of a regression fitted to this scatter would be biologically meaningless. Instead, an identification and quantitative assessment of the constraining functions may be more productive.

2. THE DISTRIBUTION OF BODY SIZES AND METABOLIC RATES

The two-dimensional array determined by the axes of body sizes and energy budgets is only an extract of a multidimensional adaptive space, within which the natural selection operates. Various evolutionary strategies may put an organism into a certain position within this space. MacArthur & Wilson (1967) have distinguished the well-known r and K axis which concern the evolutionary strategies related to body size. Szarski (1983) proposed another axis extended between the extremes of the "frugal" (F) and "wasteful" (W) efficiency of resource use. More recently, Gnaiger (1987) independently developed a similar concept, mathematically rigorous and directly applicable to bioenergetics. He defined the evolutionary strategies of "power" (P) and "economy" (E).

Obviously, the evolutionary strategies of both axes correlate with many more parameters than metabolic rate and body mass, they are also most probably connected with each other. At any rate, it remains true that two individuals of the same size (equally positioned on the

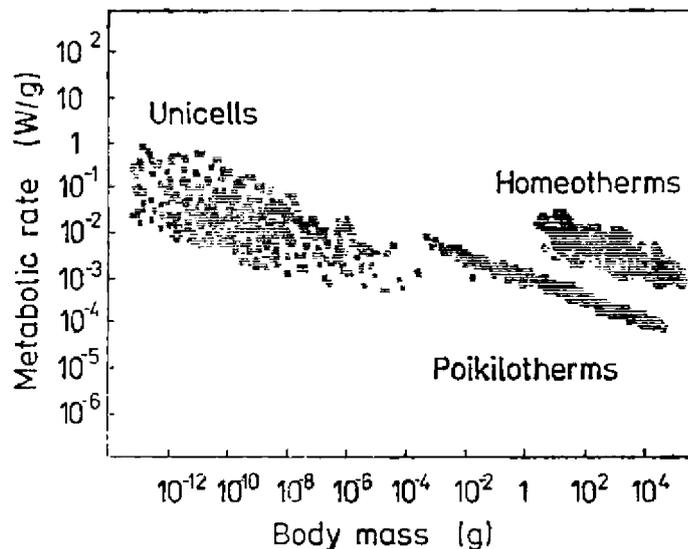


Fig. 1. Approximate, computer simulated distributions of metabolic rates of animals (double logarithmic scale). Based on regression equations and statistics of Robinson *et al.* (1985).

r — K axis) may employ more or less power ("wasteful" or "frugal" bio-energetic adaptations), as well as two individuals of the same energy budgets may be more r or more K strategists. The pursuit of a given strategy cannot continue infinitely: various physical and physiological constraints determine the space available for organisms of particular structural and functional properties.

The empirical distribution of animal species within the two-dimensional space of metabolic rates and body sizes is three-modal (Hemmingsen, 1960; Phillipson, 1981; Robinson *et al.*, 1982): one cluster is composed of unicellular organisms, the other of multicellular ectotherms, and the third — of birds and mammals (Fig. 1). Within each group, the two variables correlate: larger animals tend to be energetically more "economical" ("frugal") than the small ones. The three groups differ in the relative metabolic level by an order of magnitude (Fig. 1). Apparently, various sets of constraints determine the space occupied by the three groups. The evolutionary strategy towards larger size and higher power (K and P selection) in unicells encounters an unsurmountable obstacle: the limited diffusion rate, because the relative surface of a cell decreases with increasing volume. The structural change that enabled an increase of the body size as well as of metabolic power consisted in the apportion of the body into many cells and the development of specialized tissues (Phillipson, 1981).

Even greater metabolic power could have been attained only after developing a stable and dangerously high body temperature (endothermy), a common characteristics of birds and mammals, which constitute the third cluster (Fig. 1). A survey of the factors constraining energy budgets of mammals is the aim of this study. The point of interest is the quantitative assessment of the limits set to energy budgets rather than the explanation of the underlying physiological mechanisms.

In the view of the pattern outlined above, the bivariate array of naturally variable energy budgets (or SMR's) and body weights is unsuitable to a standard regression analysis, for it represents a loose association (correlation) rather than a functional relationship (Harvey & Mace, 1982; Weiner, 1985). On the other hand, it is *a priori* postulated here that the physiological constraints to energy budgets are functionally related to body size. Assuming further that some morphological structures may be responsible for these relationships, the use of allometric regressions seems appropriate. All subsequent equations have been fitted by least-squares linear regressions in double logarithmic transformation, according to Zar (1974). The paucity of data prevents any deeper insight into the influence of taxonomy, life history, or seasonal acclimation on the functions studied. On the other hand, there are no grounds to as-

sume *a priori* that data should be segregated according to the supposed effects of that kind; quite on the contrary, it has been shown that extreme metabolic rates of marsupials do not differ from those of eutherians (Baudinette *et al.*, 1976; Dawson & Dawson, 1982). With a few exceptions, most of the data used here concern wild mammals.

3. EXTREME LEVELS OF MAMMALIAN ENERGY BUDGETS

A scrutiny of the actual distribution of mammalian energy budgets could help in outlining their limits and identifying the constraining factors involved. Unfortunately, the measurements of complete energy budgets in natural conditions, for a representative sample of more than 4000 extant species of mammals have not yet been completed. We will later return to the limited set of such estimates available so far.

However, keeping in mind the restrictions mentioned above, one can draw some conclusions examining the pattern of distribution of standard metabolic rates. (For the sake of simplicity all data originally reported as "basal", "standard" or "resting" metabolic rates at thermoneutrality and in postabsorptive state are pooled together and uniformly called "SMR"). Some six hundred such measurements for as many as about 450 species of mammals have been published so far. The sample is slightly biased due to the notorious inclination of researchers to study the rare

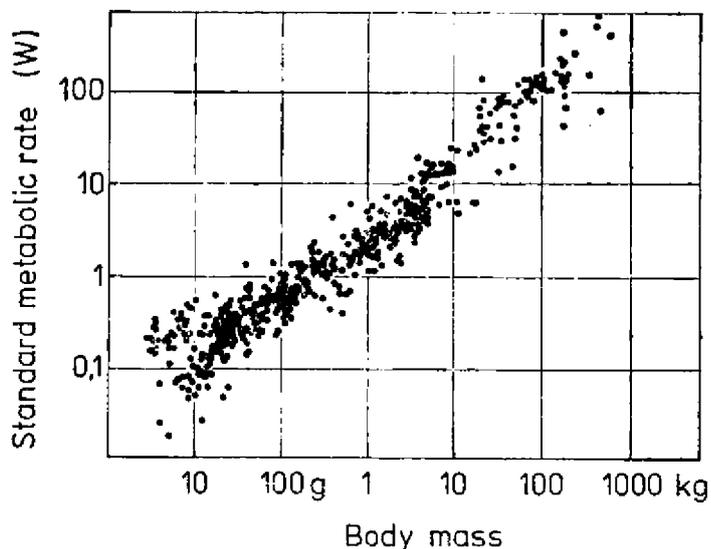


Fig. 2. Bivariate distribution of mammalian species according to their standard metabolic rates (Watt) and body masses (g, kg). Data collected from numerous sources (Weiner, unpubl.).

species of exotic taxons rather than the common ones. When plotting the standard metabolic rates against body weight on a double logarithmic scale, a following pattern emerges (Fig. 2): the span of body weights covers 6 orders of magnitude, with the smallest and largest mammals differing by about one million times, from several grams to thousands of kilograms. The extent of standard metabolic rates is smaller — about 4 orders of magnitude, from less than one to several hundreds Watt per animal. Metabolic rates are clearly correlated with body mass, but the variation is immense: over the whole span of body sizes, the variation of SMR's approaches one order of magnitude, *i.e.* the animals of the same body size may differ 10 times in their SMR's. Even more striking is the variation of body sizes *vs.* metabolic rates: the same level of SMR may characterize some species of mammals differing in size by the factor of 20 or 30. Such differences may hardly be attributed to the inaccuracy of measurements or to various experimental procedures. A power function with the exponent of 0.75 (3/4) fits quite well into the whole set of data, but one can also see that a straight line representing simple power function in a log/log transformation is not necessarily a good model for this peculiar distribution (Fig. 2). The lines of the best fit computed by various authors for similar sets of data differ slightly in their parameters and account for the variation of SMR's in 75% (Hayssen & Lacy, 1985), 80% (Elgar & Harvey, 1987) and 78% (McNab, 1988).

A set of field metabolic rates may have a similarly extended distribution, although its actual shape and coordinates are unknown. To determine its possible borderlines one should fit empirical equations to the extreme values of mammalian energy budgets as functions of the body mass. Such data are available for much smaller sets of mammalian species than these for SMR's. Moreover, each collection of data concerning a particular metabolic level contains a different selection of species, far from being representative for any group of mammals. Nevertheless, they may well be of use in an attempt to outline the approximate space available for mammalian energy budgets.

3.1. Energy Budgets at Minimum

It has been suggested that SMR may be used for comparisons as a lower limit of energy metabolism of a mammal (Poczopko, 1971; Taylor, 1982). This view has been strongly criticized because the standard laboratory conditions at which SMR is to be measured do not resemble any natural situation of a mammal. Moreover, in natural conditions mammals can spontaneously and revertibly reduce their metabolic rate far below the SMR, even for prolonged periods of time (when asleep,

torpid, estivating, or hibernating; Swan, 1974; Schmidt-Nielsen, 1984). Various kinds of controlled hypothermy are employed by quite a large fraction of mammalian species which economize on their energy expenses in this way. One can assume that if the natural selection were to favour the "frugal" strategy ("E-selection"; Szarski, 1983; Gnaiger, 1987), then the safe lower limit of energy budget can approach that attained by deep hibernators (Swan, 1974).

To estimate quantitatively where this lower extreme might be situated, the data on oxygen consumption of hibernating mammals have been gathered from literature (Table 1). Only the measurements taken at possibly low body temperatures, but close to the ones preferred in nature, were selected. They fit well to an allometric regression (Fig. 3):

$$M_{\min} = 0.246 W^{0.879}, r^2 = 0.95 \quad (1)$$

where M_{\min} is metabolic rate during deep hibernation (mW) and W is body mass (g).

Table 1

Metabolic rates of mammals during deep hibernation. All values recalculated into Watts using the following equivalents: 1 cm³O₂=20.1 J; 1 cal=4.184 J.

Species	Body mass (g)	Hibernation temperature (°C)	Metabolic rate (Watt)	References
<i>Tachyglossus aculeatus</i>	2500	5.5	0.418	15
<i>Nyctalus noctula</i>	24	4.3	0.003	77
<i>Pipistrellus pipistrellus</i>	7.4	4.3	0.001	77
<i>Myotis velifer</i>	12.9	5	0.005	124
<i>Erinaceus europaeus</i>	600	5	0.037	142
"	600	6	0.052	77
"	390	6	0.045	77
"	320	6	0.031	77
<i>Marmota flaviventris</i>	2500	5	0.251	30
<i>M. marmota</i>	2670	10	0.267	77
"	2140	10	0.214	77
<i>M. marmota</i> (juv.)	850	10	0.1	77
<i>M. marmota</i> (juv.)	800	10	0.093	77
<i>Cricetus cricetus</i>	305	6	0.051	77
<i>Citellus citellus</i>	275	7.8	0.027	77
"	165	6	0.015	77
<i>C. lateralis</i>	200	5	0.028	159
"	200	5	0.033	40
<i>C. undulatus</i>	650	5	0.109	62
<i>Glis glis</i>	130	9.2	0.01	77
"	100	8.7	0.008	77
<i>Eliomys quercinus</i>	89	5	0.014	77
"	72	6	0.012	77
<i>Muscardinus avellanarius</i>	23	10.1	0.005	77
<i>Zapus hudsonius</i>	26.5	5	0.007	103
"	20	5	0.004	103
<i>Z. princeps</i>	28	5	0.004	16

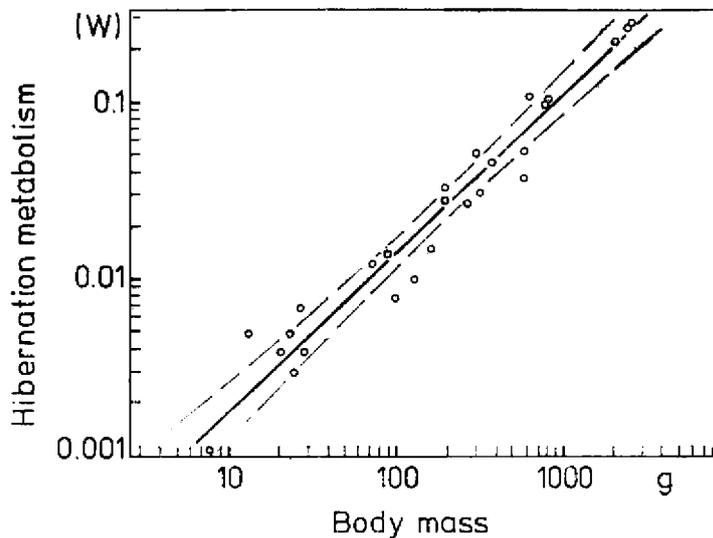


Fig. 3. Regression of mammalian minimum metabolic rate during hibernation (M_{\min} ; Watt) to body mass (W; g). Dashed lines: 95% confidence belts of regression.

3.2. Short-term Maxima of Energy Budgets

Much confusion reigns in the literature as to the meaning of the concept of maximum metabolic rate of animals. Extreme levels of the metabolic power output may be experimentally induced in endotherms by forcing either intense thermoregulation or muscular work (Taylor, 1982). In the first case, high cooling rates are required, and may be achieved by lowering considerably the air temperature in experimental chamber, or by substituting the medium in which the animal is submerged with the one of a much higher thermoconductivity: helium-oxygen atmosphere (Rosenmann & Morrison, 1974; Cygan, 1985) or water (Gajda, 1925). High muscular effort is most commonly provoked by forcing animals to run on a treadmill (Seeherman *et al.*, 1981). Regardless of the method used, the variable being actually measured most often is the rate of oxygen consumption. Thus, the results are referred to "maximal oxygen consumption" (Lechner, 1978; Prothero, 1979; Rosenmann & Morrison, 1974), "maximum aerobic capacity" (Langman *et al.*, 1981; Seeherman *et al.*, 1981; Hayes & Chappel, 1986), "maximal oxygen uptake" (Pasquis *et al.*, 1970). This value is often reported in relation to the resting ("basal" or "standard") metabolic rate as a "metabolic scope" (Dawson & Dawson, 1982).

Extreme metabolic rates developed by endotherms during intense thermoregulation, also measured by oxygen consumption, are often defined as "maximum thermogenic capacity" (Abbots & Wang, 1980; Wickler, 1980), "maximum cold-induced oxygen consumption" (Heldmaier *et al.*, 1982) or "maximum cold-induced heat production" (Wang, 1978). Dawson & Dawson (1982) and Hulbert *et al.* (1985) use the term "summit metabolic rate", synonymous to "maximal sustainable thermogenic response to cold" (Dawson & Olson, 1987), also induced by low ambient temperatures but believed to represent a method-independent maximum rate of oxygen consumption. On the other hand, Dawson & Carey (1976) preferred to call a similarly obtained value a "peak metabolic rate" which merely "closely approaches the summit metabolic rate" as it was defined by Giaja (1925). Some authors reserve the term "summit metabolism" for a prolonged cold-induced heat production, and "maximum metabolism" for muscular effort.

In earlier works, both methods of inducing high metabolic levels were used interchangeably, and the results were pooled together in comparative studies (Lechner, 1978; Prothero, 1979). Later on it became evident that the two methods may produce incompatible results (Seeherman *et al.*, 1981; Chappel, 1984). However, until recently these differences were regarded mostly as technical difficulties in obtaining a "true" maximum rate of oxygen consumption (Seeherman *et al.*, 1981; Taylor, 1982), although concerns were also expressed as to possible substantial differences in physiological processes underlying the increase of metabolic rates for thermoregulation and for mechanical work (Chappel, 1984; Hayes & Chappel, 1986; Taylor, 1982; Koteja, 1986). As far as the major interest is focused on the maximum rate of oxygen consumption *per se* (Weibel & Taylor, 1981; Seeherman *et al.*, 1981; Taylor, 1982), such distinction may be superfluous. On the other hand, when the metabolic rate is considered in terms of energy, and when the factors constraining the metabolic power of an animal are discussed, the choice of the experimental procedure may be crucial. Thus, the data for cold-induced thermogenesis and for muscular work should be segregated.

Another confusion may concern the two pathways of heat production in mammals: shivering (SH) and non-shivering thermogenesis (NST). In this last process the heat is quickly liberated in a purely chemical way of "uncoupled" oxidation, taking place first of all in the mitochondria of brown adipose tissue (Heldmaier *et al.*, 1985). Since NST is controlled by the sympathetic nervous system, it is relatively easy to activate it experimentally by injection of norepinephrine (Heldmaier, 1971) and to measure its maximum rate. Such data have been erroneously used as indices of maximum thermogenic metabolic rates (Prothero, 1979).

In fact, both metabolic pathways contribute to the total heat production in mammals, and their sum may be twice as high as the maximum rate of the NST alone (Böckler & Heldmaier, 1983).

All the above measures of high metabolic rates represent the so called "sustained metabolism", which is purely aerobic and may last for extended periods of time (at least minutes or tens of minutes in the case of muscular work, or as much as several hours of intense thermoregulation). In short bursts of intense muscular work this rate may be supplemented in mammals with the contribution of anaerobic metabolism. This combined power output may last for seconds only and is difficult to measure, so that the data are scarce. Taylor (1982) calls it "peak

Table 2

Maximum rate of non-shivering thermogenesis (NST). All values recalculated into Watts using the following equivalents: $1 \text{ cm}^3 \text{O}_2 = 20.1 \text{ J}$; $1 \text{ cal} = 4.184 \text{ J}$. (S) — summer; (W) — winter; (H) — data included in Heldmaier's (1971) regression.

Species	Body mass (g)	NST _{max} (Watt)	References
<i>Erinaceus europaeus</i>	733	7.16	71 (H)
<i>Sorex vagrans</i>	5.4	0.4	147
<i>Myotis lucifugus</i>	8.91	0.36	51
"	8.23	0.4	51
<i>Callithrix jacchus</i>	282.0	20.2	129
<i>Canis domesticus</i>	9950	82.21	109 (H)
<i>Spermophilus richardsoni</i>	400.0	18.87	1
<i>Reithrodontomys megalotis</i>	14.6	0.5	147
<i>Peromyscus leucopus</i> (S)	19.0	0.72	91
<i>Peromyscus leucopus</i> (W)	18.0	1.13	91
<i>Peromyscus maniculatus</i>	21.1	0.64	147
<i>Clethrionomys glareolus</i>	26.8	1.16	52 (H)
<i>Clethrionomys rutilus</i>	14.7	1.17	25
<i>Microtus montanus</i>	30.1	0.94	147
<i>Phodopus sungorus</i>	37.5	0.97	52 (H)
<i>Mesocricetus auratus</i>	114.4	2.57	52 (H)
<i>Meriones shami</i>	158.0	2.42	52 (H)
<i>Glis glis</i>	136.0	2.67	52 (H)
<i>Mus musculus</i>	33.4	1.29	52 (H)
<i>Rattus norvegicus</i>	300	4.96	57
"	301	3.53	88 (H)
"	336	3.73	88 (H)
"	369	6.82	21 (H)
"	378	5.38	72 (H)
"	100	1.94	2
"	150	2.56	2
"	200	2.97	2
"	250	3.1	2
<i>Cavia porcellus</i>	295	2.67	164 (H)
"	575	3.98	164 (H)
"	584	4.5	164 (H)
<i>Oryctolagus cuniculus</i>	3044	12.3	52 (H)

rate of aerobic and anaerobic metabolism" (usage different from the "peak metabolic rate" of Dawson & Carey, 1976).

Three categories of sustained metabolic rates are considered here: the maximum rate of norepinephrine-induced non-shivering thermogenesis (NST_{max}), the maximum total cold-induced heat production (shivering + non-shivering thermogenesis, HP_{max}), and the maximum aerobic capacity for muscular work (M_{max}). These high rates of energy expenditure may set upper limits for short-term energy budgets which may last for minutes or even hours or days, but need not necessarily to be balanced by the energy acquired from food.

Due to the well-established experimental protocol, the most uniform set of data is that concerning the non-shivering thermogenesis (NST), thoroughly reviewed by Heldmaier (1971), who also provided a regression equation relating maximum NST to body mass. Since that time more data have become available (Table 2), so that a new regression has been computed (Fig. 4):

$$NST_{max} = 0.112 W^{0.658}, \quad r^2 = 0.86 \quad (2)$$

where NST_{max} is maximum rate of norepinephrine-induced nonshivering thermogenesis (Watt) and W is body mass (g).

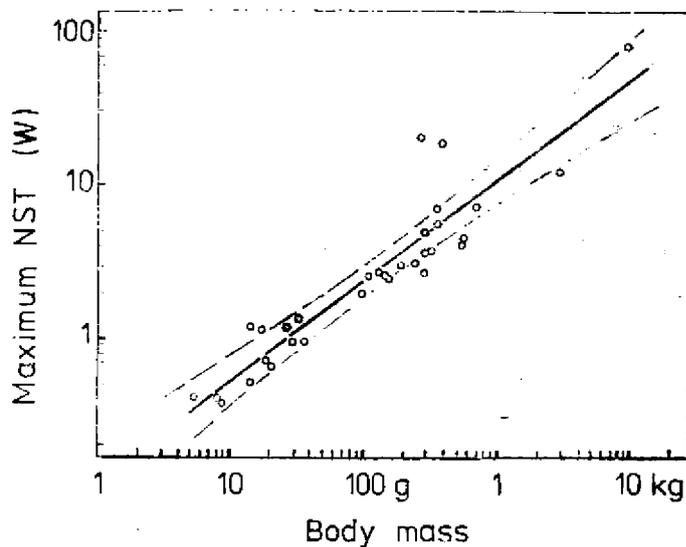


Fig. 4. Regression of maximum rate of non-shivering thermogenesis (NST_{max} ; Watt) to body mass (W ; g) in mammals. Dashed lines: 95% confidence belts of regression.

Table 3

Maximum cold-induced heat production. All values recalculated into Watts using the following equivalents: 1 cm³O₂=20.1 J; 1 cal=4.184 J. (S) — summer, (W) — winter. * — *Marsupialia*.

Species	Body mass (g)	Heat production (Watt)	References
<i>Planigale gilesi</i> *	10.1	0.62	19
<i>Dasyuroides byrnei</i> *	118.0	3.82	19
<i>Dasyuroides byrnei</i> (S) *	126.	4.85	137
<i>Dasyuroides byrnei</i> (W)	116.	4.42	137
<i>Sorex cinereus</i>	3.3	0.54	102
<i>Tamias striatus</i>	90.2	6.04	133
<i>Dipodomys merriami</i>	34.2	1.44	67
"	32.6	1.27	67
<i>Perognathus fallax</i>	19.7	0.95	67
"	21.2	0.93	67
"	17.6	0.82	67
<i>Liomys salvium</i>	45.1	1.12	67
<i>Peromyscus leucopus</i> (S)	19.	1.23	156
<i>Peromyscus leucopus</i> (W)	18.	1.96	156
<i>Peromyscus leucopus</i>	25.	1.66	135
"	23.	1.94	41
<i>Peromyscus maniculatus</i>	20.	1.21	13
"	23.	1.82	42
<i>Peromyscus eremicus</i>	18.4	0.81	67
"	19.1	0.81	67
<i>Peromyscus californicus</i>	41.3	1.17	67
<i>Baiomys taylori</i>	7.3	0.42	65
"	6.9	0.47	127
"	7.2	0.49	133
<i>Phodopus sungorus</i> (W)	26.4	2.02	54
<i>Phodopus sungorus</i> (S)	42.3	2.38	54
<i>Phodopus campbelli</i> (W)	24.0	1.9	155
<i>Phodopus campbelli</i> (S)	31.9	2.28	155
<i>Mesocricetus auratus</i>	98.	3.32	119
<i>Clethrionomys rutilus</i>	14.7	1.89	25
<i>Clethrionomys rutilus</i> (S)	28.	2.11	128
<i>Clethrionomys rutilus</i> (W)	15.	2.21	128
<i>Microtus oeconomus</i>	32.	2.23	127
<i>Ondatra zibethicus</i>	1100.	21.49	43
<i>Apodemus flavicollis</i> (S)	25.9	1.68	85
<i>Apodemus flavicollis</i> (W)	31.1	2.33	85
<i>Apodemus sylvaticus</i>	20.3	1.59	64
<i>Calomys ducilla</i>	16.0	1.25	127
<i>Calomys calosus</i>	48.0	1.82	127
<i>Notomys cervinus</i>	33.1	1.64	19
<i>Pseudomys gracilicaudata</i>	81.2	1.83	19
<i>Rattus norvegicus</i> (S)	250.	4.88	46
<i>Rattus norvegicus</i> (W)	281.	8.31	46
<i>Rattus norvegicus</i>	380.	6.79	58
"	385.	5.93	22
"	115.	3.09	33
"	400.	6.5	150
"	205.	5.24	133
"	253.	7.34	127
<i>Mus musculus</i>	18.5	1.11	33
"	29.5	2.27	127

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Table 3 — concluded.

<i>Mus musculus</i> feral	17.3	1.07	127
<i>Mus musculus</i> feral	17.0	1.17	127
<i>Oryctolagus cuniculus</i>	2540.	37.58	45
<i>Lepus americanus</i> (S)	1544.0	29.31	26
<i>Lepus americanus</i> (W)	1506.0	35.31	26

The data for maximum total heat production have been gathered from various sources (Table 3) and are much more diverse than the previous ones. They concern mammals exposed to low ambient temperatures, in air or in a mixture of helium and oxygen. Some values were explicitly reported by the authors as metabolic maxima, others were interpreted as such if the source contained an information that any longer exposure or any further lowering of ambient temperature lead to a decrease in metabolic rate or a collapse of experimental animals. The possible effects of seasonal acclimatization (Heldmaier *et al.*, 1985) were ignored.

The allometric regression fitted to these data (Fig. 5) has an exponent close to the previous one:

$$HP_{\max} = 0.168 W^{0.970}, r^2 = 0.90 \quad (3)$$

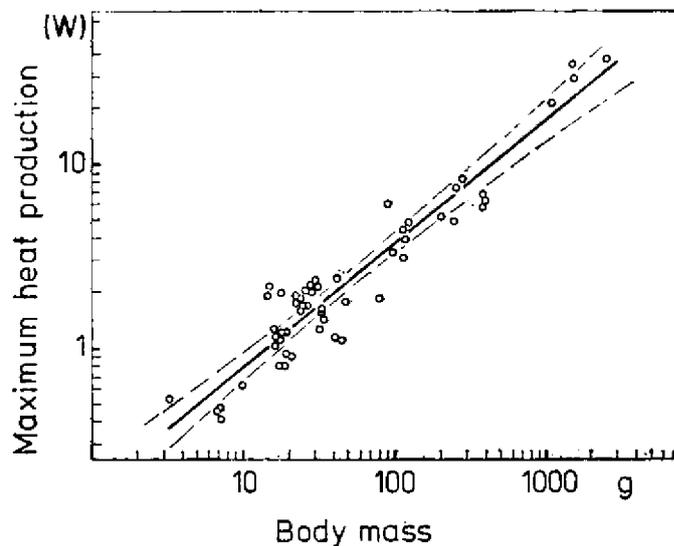


Fig. 5. Regression of maximum rate of total heat production (HP_{\max} ; Watt) to body mass (W ; g) in mammals. Dashed lines: 95% confidence belts of regression.

Table 4

Maximum aerobic metabolic rate in exercising mammals. All values recalculated into Watts using the equivalents: 1 cm³ O₂=20.1 J; 1 cal=4.184 J. * — *Marsupialia*; D — domesticated species; ? — no scientific name reported.

Species	Body mass (g)	Metabolic rate (Watt)	References
<i>Sminthopsis crassicaudata</i> *	15	1.09	6
<i>Antechinus flavipes</i> *	40	2.43	6
<i>Dasyuroides byrnei</i> *	115	5.78	6
<i>Dasyuroides viverrinus</i> *	1120	37.51	6
<i>Bettongia penicillata</i> *	1100	65.09	133
<i>Phyllostomus hastatus</i>	94	13.7	146
<i>Eidolon helvum</i>	315	23.77	11
<i>Hypsiprymna monstrosus</i>	258	25.13	11
<i>Pteropus poliocephalus</i>	465	26.94	11
"	629	40.17	11
<i>Homo sapiens</i>	68500	1158.66	29
"	65400	1307.02	4
"	81500	1524.13	4
<i>Canis familiaris</i> (D)	24000	803.87	12
"	10000	455.52	162
"	8300	150.88	15
"	25300	1357.27	87
"	21000	1113.69	133
<i>Canis latrans</i>	12400	764.79	151
<i>Canis lupus</i>	27550	1442.3	151
<i>Canis lupus</i> (?)	23300	1226.56	87
<i>Vulpes vulpes</i> (?)	4700	288.09	87
<i>Vulpes vulpes</i>	4610	281.15	151
<i>Mustela vison</i>	943.5	32.66	158
<i>Genetta tigrina</i>	1458	51.85	144
<i>Helogale parvula</i>	583	24.93	144
<i>Mungos mungo</i>	1151	46.84	144
<i>Panthera leo</i>	50000	837.36	14
"	57000	954.59	14
"	30000	602.9	133
<i>Equus caballus</i> (D)	677000	8578.98	9
"	105000	3393.82	133
<i>Madoqua kirkii</i>	4354	79.38	144
<i>Connochaetes taurinus</i>	98000	1459.02	144
<i>Kobus defassa</i>	114000	1804.68	144
<i>Taurotragus oryx</i>	217000	2632.66	144
<i>Nesotragus moschatus</i>	3500	112.93	144
<i>Gazella granti</i>	11200	200.7	144
<i>Capra hircus</i> (D)	21150	367.19	144
<i>Ovis aries</i> (D)	22650	351.51	144
<i>Bos indicus</i> (D)	160000	1482.69	144
"	254000	2509.74	144
<i>Sus scrofa</i> (D)	18500	578.34	133
<i>Baiomys taylorii</i>	7.2	0.63	133
<i>Tamias merriami</i>	75	2.96	161
<i>Tamias striatus</i>	90.2	7.19	133
<i>Peromyscus maniculatus</i>	20	1.14	13
<i>Mesocricetus auratus</i>	113	3.75	113
"	75	3.66	70

Continued on p. 17

Table 4. — concluded.

<i>Clethrionomys glareolus</i>	18.	1.24	69
<i>Microtus arvalis</i>	20.	1.59	69
<i>Dicrostonyx graenlandicus</i>	61	2.51	46
<i>Apodemus sylvaticus</i>	16.9	1.49	64
<i>Rattus norvegicus</i>	346	8.44	113
"	286	7.78	113
"	461	9.06	7
"	472	11.73	7
"	207	5.63	7
"	254	7.71	7
"	205	6.64	133
<i>Mus musculus</i>	34	1.9	113
"	27	1.86	41
<i>Ondatra zibethicus</i>	649	10.43	28
<i>Pedetes capensis</i>	3000	97.47	133
<i>Cavia porcellus</i>	868	18.8	113
"	959	19.11	113
<i>Oryctolagus cuniculus</i> (D)	2540	38	46

where HP_{max} — maximum total cold-induced heat production (Watt); W — body mass (g). A comparison of the equations (2) and (3) within the range of actual body masses of mammals leads to the conclusion that NST constitutes a relatively constant fraction, about 50%, of the maximum total heat production. A slight tendency to the decrease of its share in larger animals, which may be inferred from the difference of exponents, is statistically insignificant.

The maximum rates of aerobic metabolism in exercising mammals have been investigated intensely and in detail within a framework of a well designed team project (Taylor & Weibel, 1981; Taylor *et al.*, 1981; Seeherman *et al.*, 1981; Taylor, 1982). The same authors provided the largest and most uniform collection of empirical data (Seeherman *et al.*, 1981; Taylor *et al.*, 1981), but even more information can be found in the literature (Table 4). An allometric regression was fitted to all these data (Fig. 6), yielding a following equation:

$$M_{max} = 0.101 W^{0.887}, r^2 = 0.97 \quad (4)$$

where M_{max} is maximum exercise metabolic rate (Watt) and W — body mass (g). The slope of this regression does not differ substantially from the one reported by Taylor *et al.* (1981) for a subset of the data used here, but it is considerably steeper than these for NST_{max} (eq. 2, Fig. 4) and HP_{max} (eq. 3, Fig. 5). The lines for M_{max} and HP_{max} converge at low body masses, which means that small mammals (up to a hundred grams) develop a similar maximum metabolic power both for mechanical work and for intense thermoregulation, whereas in larger mammals the

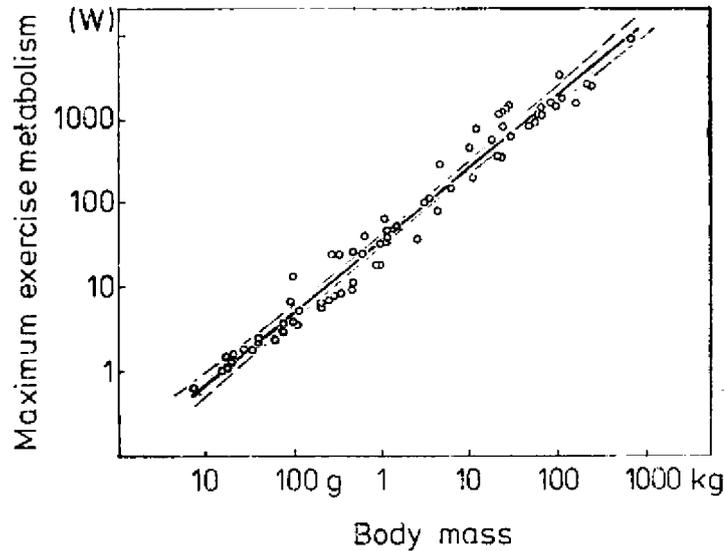


Fig. 6. Regression of maximum rate of aerobic metabolism of exercising mammals (M_{\max} ; Watt) to body mass (W; g). Dashed lines: 95% confidence belts of regression.

power output for muscular exercise may be as much as 5 times larger than that for heat production. This conclusion, however, must be taken with caution, because no experimental data on HP_{\max} in large mammals can be obtained.

3.3. Long-term Energy Budgets: Limits Set by Energy Assimilation Rate

In the long run, the energy expenditure must be balanced by the energy assimilated from food. Thus, the physiological factors that restrict the energy assimilation rate are also responsible for the limitation of total energy budgets in longer periods of time. A quantitative assessment of the upper limit to energy assimilation seems to be of key importance in the understanding of ecological and evolutionary optimization of animals' energy budgets (Karasov, 1986). However, a survey of literature reveals that relevant empirical data are astonishingly scarce. Kleiber (1933, cited after Kleiber 1961) was probably the first to tackle this problem and to demonstrate that this limit, in several species of domesticated animals, lays at the level of about 5-fold their fasting metabolic rate. In a more purposeful manner and with a clear under-

standing of the ecological and evolutionary implications of this concept, Kendeigh (1949, 1973; Morris & Kendeigh, 1981) designed and conducted experiments to estimate indirectly the upper limit of energy budgets in wild birds and a mammal ("potential energy" or "maximum potential metabolism" according to Kendeigh's original nomenclature).

More recently, Kirkwood (1983) made an attempt to estimate the limit to metabolizable energy intake as a function of body mass in homeotherms. To this end he pooled diverse data on birds ($n=12$) and mammals ($n=9$), mostly on domesticated species, that had been observed in peculiar situations causing extremely high ingestion rates. The collection contains, for example, geese fed by force, horses at heavy work, a man realimentated after undernutrition, and a number of fast-growing young animals. None of these figures has been obtained for the purpose of measuring maximum energy assimilation rates, yet the function derived by Kirkwood (1983) may serve well as a first approximation.

The maximum rate of energy assimilation can, however, be measured directly, in artificial laboratory conditions as well as in natural situations. One of the possibilities is to measure long-term energy budgets of small mammals burdened with high metabolic costs of thermoregulation. Such experiments have been made with bank voles *Clethrionomys glareolus* (Piątkowska & Weiner, 1987), and Djungarian hamsters *Phodopus sungorus* (Weiner, 1987a, b). The results clearly demonstrate that the possible rate of energy acquisition can only be much lower than the rate of short-term energy expenditure. Moreover, the ability to assimilate energy from food may undergo significant and relatively fast changes (acclimatization), adjusting to any long-lasting increase in energy expenditure (e.g. as caused by lowered ambient temperature or lactation). These changes are limited and revertible, which suggests that the increased assimilation capacity is connected with considerable metabolic costs.

It is not entirely clear which physiological modifications make up such a nutritional acclimatization. It is doubtless, however, that the increase of gut size, and particularly of its internal surface is of a key importance (Sibly, 1981). Numerous studies have demonstrated the occurrence of seasonal changes in mammalian gut size, which apparently follow the seasonal changes in nutritional requirements (Myrcha, 1964, 1965; Gębczyńska & Gębczyński, 1971; Hoffman, 1982). Strong evidence also exists for the influence of an increased energy budget (or decreased nutritional value of food) upon gut morphology (Gross *et al.*, 1985; Green & Millar, 1987). It is obvious, therefore, that the internal surface area of the alimentary tract, and especially of the small intestine,

constitutes a bottleneck for energy budget of an animal (Musacchia & Barr, 1969; Sibly, 1981; Karasov, 1986). Small wonder, then, that the evolutionary transition from ecto- to endothermy was accompanied by a 10-fold increase of the area of the gut (Karasov *et al.*, 1985, 1986; Diamond, 1987). This major morphological evolutionary change is similar in its character to the one that differentiates unicells from multicellular organisms: a leap increase of contact surfaces, which enables an enormous amplification of metabolic power.

Table 5

Maximum rate of energy assimilation from food (A_{\max}) in female mammals at peak lactation. * Recalculated from the rate of energy consumption, assuming 82% efficiency of energy assimilation.

Species	Body mass (g)	A_{\max} (Watt)	References
<i>Clethrionomys glareolus</i>	24.5	2.01	73
<i>Clethrionomys gapperi</i>	26.8	2.66	68 *
<i>Microtus arvalis</i>	25.4	2.03	98
<i>Microtus pennsylvanicus</i>	29.4	3.59	68 *
<i>Microtus pinetorum</i>	30.1	1.54	90
<i>Mus musculus</i>	28.0	1.55	108
<i>Peromyscus leucopus</i>	25.0	2.19	99 *
<i>Peromyscus maniculatus</i>	25.4	2.02	100 *
"	24.0	2.89	139
<i>Phodopus unsgorus</i>	34.0	1.21	133
<i>Sigmodon hispidus</i>	126.0	2.3	123
"	169.0	4.4	93
<i>Sciurus niger</i>	875.3	25.56	48
<i>Oryctolagus cuniculus</i>	4100.0	49.02	112
<i>Capreolus capreolus</i>	20000.0	174.47	Weiner, unpubl.
<i>Odocoileus hemionus</i>	52000.0	321.85	131

The supposed metabolic cost prevents, however, an infinite increment of gut size, both in evolutionary and ecological time scales. Data gathered so far suggest that, in mammals, the ultimate maximum energy assimilation, *i.e.* including the effects of acclimatization, can be achieved by females at peak lactation (Weiner, 1987a, b). At that period the females usually run into negative energy balances, despite maximized rates of food consumption. Thus, the relatively numerous measurements of energy assimilation rates at peak lactation published so far make up a homogenous database, which can be used to outline the ultimate upper limit to the long-term energy budgets. The relevant empirical data gathered from literature ($n=16$, Table 5) yielded an allometric regression (Fig. 7):

$$A_{\max} = 0.214 W^{0.684}, r^2 = 0.95 \quad (5)$$

where A_{\max} is the maximum rate of energy assimilation from food (Watt) and W is body mass (g). The slope coefficient does not differ significantly from the theoretical value of $2/3$ (Table 6), which indicates the geometric character of this relationship (the surface area of the gut limiting assimilation rate).

The above equation is pretty close to that obtained from much less homogenous data by Kirkwood (1983): $A_{\max} = 0.137 W^{0.72}$ (Fig. 7). The single estimate of "maximum potential metabolism" in *Peromyscus maniculatus* (Morris & Kendeigh, 1981) does not exceed much the confidence limit of the regression (Fig. 7).

4. ALLOMETRY OF ENERGETIC CONSTRAINTS

According to the results presented above, two kinds of physiological upper limits to energy budgets may be distinguished: short-term limits (maximum thermogenesis, activity metabolism) and an ultimate long-

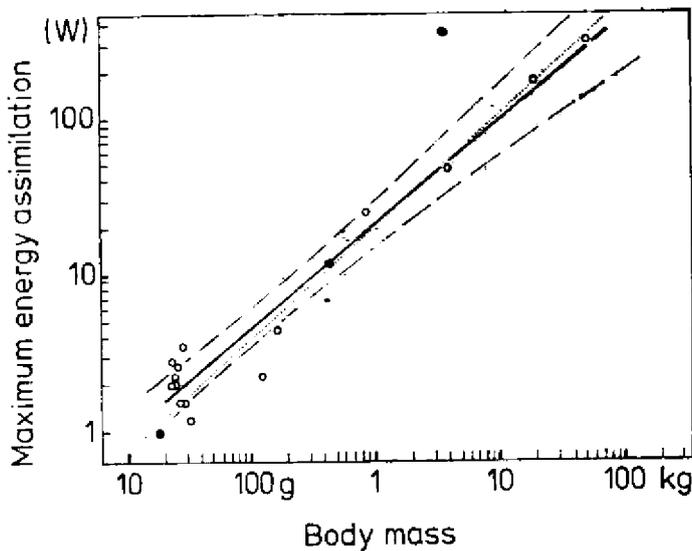


Fig. 7. Regression of maximum rate of energy assimilation of lactating females (A_{\max} , open circles; Watt) to body mass (W ; g). Dashed lines: 95% confidence belts of regression. Dotted line: the Kirkwood's (1983) estimate of A_{\max} . Closed circle: single estimate of A_{\max} in *Peromyscus maniculatus* (Morris & Kendeigh, 1981).

Table 6

Differences between the allometric regressions representing metabolic constraints to energy budgets of the form: $M = aW^b$, where M — metabolic power (Watt), and W — body mass (g); n — number of entries; r^2 — coefficient of determination; $S_{y \cdot x}$ — standard error of estimate; s_b — standard error of regression coefficient b . Equal superscripts denote groups of exponents statistically undistinguishable at the level of 1% (ANCOVA, SNK-test; Zar, 1974). The significance of differences between empirical exponents and theoretical constants have been assessed by t -test (Zar, 1974).

Metabolic function	Regression parameters						Significance of differences between exponents and constants:		
	n	r^2	$S_{y \cdot x}$	a	b	s_b	0.667	0.75	1.00
Minimum metabolic rate in hibernation M_{\min}	27	0.95	0.154	0.246×10^{-3}	0.879 ¹	0.040	$t=5.25$ $p<0.001$	$t=3.19$ $p<0.01$	$t=2.99$ $p<0.01$
Maximum aerobic exercise metabolism M_{\max}	67	0.97	0.199	0.101	0.857 ¹	0.019	$t=10.04$ $p<0.001$	$t=5.63$ $p<0.001$	$t=7.58$ $p<0.001$
Field energy budget (Nagy, 1987, recalculated)	74	0.95	0.205	0.057	0.734 ²	0.021	$t=3.25$ $p<0.01$	$t=0.78$ NS	$t=12.88$ $p<0.001$
Maximum non-shivering thermogenesis NST_{\max}	32	0.86	0.203	0.112	0.653 ²	0.048	$t=0.296$ NS	$t=2.05$ $0.01 < p < 0.05$	$t=7.31$ $p<0.001$
Maximum total heat production HP_{\max}	55	0.90	0.143	0.168	0.670 ²	0.031	$t=0.36$ NS	$t=1.929$ $0.01 < p < 0.02$	$t=8.84$ $p<0.001$
Maximum rate of energy assimilation A_{\max}	16	0.95	0.173	0.214	0.664 ²	0.040	$t=0.07$ NS	$t=2.18$ $0.01 < p < 0.05$	$t=8.49$ $p<0.001$

term limit: maximum rate of energy assimilation. The ultimate lower limit of energy budgets is probably situated at the minimum metabolic rates of hibernating mammals, although empirical values may be higher.

The empirical power functions relating these extreme values of energy budgets to body mass have various exponents (Table 6). The maximum activity and the minimum hibernation metabolic rates both have the exponents of over 0.85, differing significantly from the hypothetical "mass" and "surface" scaling power exponents (1 and 2/3, respectively), as well as from the esoteric SMR exponent of 3/4 (Table 6). This may indicate a relatively large contribution of some morphological structures or quantities, directly proportional to body mass, to the factors constraining these two extreme metabolic rates. These two borderlines are virtually parallel, so that within the whole range of mammalian body sizes the short-term energy budgets may potentially vary by two orders of magnitude: about 300 to 400 times. It is noteworthy that the so called "metabolic scope for activity", i.e. the ratio of maximum metabolic rate to SMR, was believed to be a constant of about 10 (Hemmingsen, 1960; Taylor, 1982) although it recently became clear that in certain species this index may be as high as 30–40 (Langman *et al.*, 1981; Koteja, 1987).

The remaining functions: maximum non-shivering thermogenesis, maximum total heat production and maximum rate of energy assimilation from food yield the slope coefficients statistically indistinguishable from 2/3 (Table 6), and therefore suggesting that they scale to the surface area of some morphological structures. The homogeneity of the slopes of these functions (Table 6) may also lead to the conclusion that physiological adaptations pertaining to processes of energy acquisition from food and of energy use for thermoregulation are "symmorphic", i.e. optimally adjusted to each other so that they "satisfy but not exceed the requirements of the functional system" (Taylor & Weibel, 1981). The metabolic effort connected with maintaining a constant body temperature in cold ambients usually lasts for prolonged periods of time. It is therefore obvious that this energy expenditure cannot depend on body reserves, but rather has to be currently balanced with energy assimilated from food.

In contrast to the situation described above, the short-term constraint for maximum aerobic metabolism has a much steeper slope than the long-term constraint for energy assimilation (Table 6, Fig. 8). In large mammals (10–100 kg) the instantaneous rate of energy expenditure may exceed 2 to 5 times the average rate of energy assimilation, while in small ones (10–100 g) both maximum rates are similar (cf. equations 4 and 5, Fig. 8). Energy reserves in mammalian body tend to scale

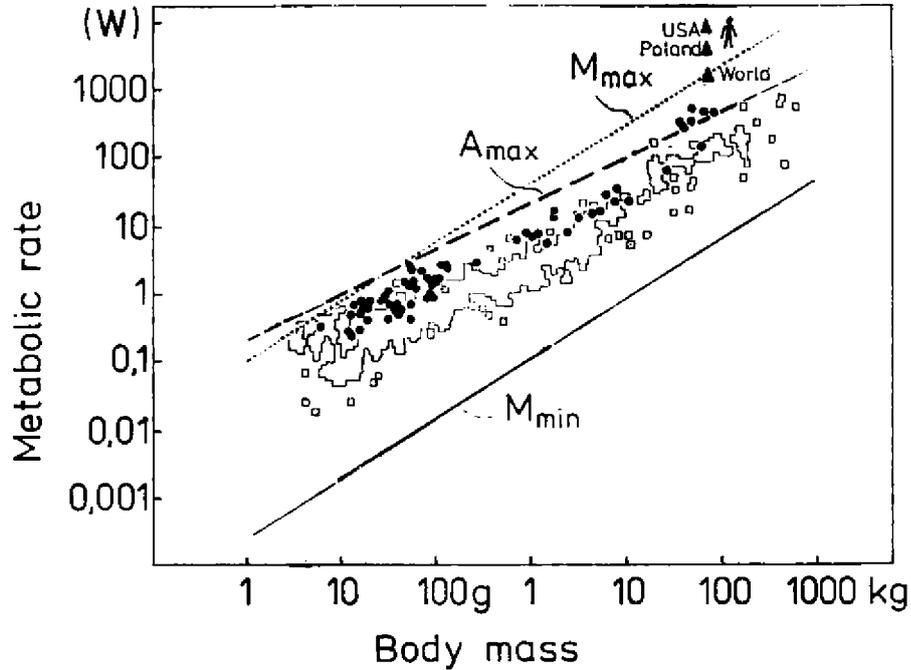


Fig. 8. Constraints to mammalian energy budgets: M_{max} (dotted line)=maximum rate of aerobic metabolism; A_{max} (dashed line)=maximum rate of energy assimilation from food; M_{min} (solid line)=minimum rate of metabolism during hibernation. Closed circles: field metabolic rates of mammals (from Nagy, 1987); open squares: standard metabolic rates (cf. Fig. 2); closed triangles: average individual use of energy in various human populations (from Rocznik Statystyki Międzynarodowej, 1987).

isometrically (Schmidt-Nielsen, 1984) or even hypermetrically to body mass (Pitts & Bullard, 1968, obtained an exponent of 1.2 when regressing total fat content to the body mass in mammals). Thus, large mammals may temporarily afford deeply negative energy balances thanks to their relatively large body reserves, whereas smaller animals have to rely upon current supply of energy from food.

5. WITHIN LIMITS AND BEYOND

As has been mentioned above, no representative sample of natural, complete energy budgets of mammals is available. A few dozen of such data, which can be found in literature, have been derived by a variety of methods, most commonly being compiled from laboratory measurements of various metabolic rates, supplemented with some field data

and based on numerous assumptions (Grodziński & Wunder, 1975; Wunder, 1975; Grodziński & Weiner, 1984; Hudson & White, 1985; Król, 1985). As accurate as many of them can be, these diverse and indirect estimates can hardly be used for comparative purposes. However, as many as 74 species have already been subjected to empirical measurements of energy expenditures in the field, using the isotopic method of "doubly labelled water" (see Nagy, 1987, for a recent review). The sample includes mammals of the size from several grams to above 100 kg. This collection, again, is far from being representative. Not only is the choice of species totally incidental, but also the eco-physiological situation of the individuals studied is varied and sometimes poorly defined. The number of replicates for each species are low, and the variation for each specific average is poorly estimated or unknown, although some data suggest strikingly large variations (Nagy, 1987). Nevertheless, these estimates of mammalian field metabolic rates are technically the most accurate and the most uniform of all. If nothing else, this collection carries a message that some mammals, at some natural conditions, do have certain metabolic rates.

When plotted on a graph (Fig. 8), most of the field metabolic rates fall somewhat below the line representing the maximum rate of energy assimilation from food (A_{max}). Only the largest species studied (seals, a deer, and a kangaroo) had the field metabolic rates slightly exceeding the assimilation constraint. In large animals, however, it is difficult to assess if the energy budget was balanced during the relatively short period of field experiment.

This pattern seems to corroborate a previous conclusion (Weiner, 1987a, b) to the effect that natural energy budgets tend to approach a maximum which is determined by the highest possible rate of energy assimilation from food. An allometric regression forced through all these points has an exponent of 0.73 (Nagy, 1987; Table 6), similar to most of the exponents calculated by various authors for mammalian SMR's (Kleiber, 1961; Hayssen & Lacy, 1985; Elgar & Harvey, 1987; McNab, 1988). This effect, however, may incidentally result from fitting curves to the sets of variates which randomly fill a space confined by strictly determined functions.

The energy used to cover all expenditures of an animal must penetrate first through the walls of alimentary tract. In comparison to unicells and multicellular ectotherms, mammals accomplished a very high efficiency of digesting food and extracting valuable components out of it. An expansive evolutionary strategy (W or P strategy, according to Szarski, 1983; and Gnaiger, 1987; respectively) implies a maximization of metabolic power. When the constraint on limited surface area of the

gut is met, any adaptation that allows for taking advantage of energy sources from outside of an organism may instantly be favoured by natural selection. Human evolution apparently followed this path. From the ecological point of view, the use of fire, wind, and running water, as energy sources enhancing survival and reproduction, could have had a more important contribution to the evolutionary success of man than the invention of artificial tools and weapons. Interestingly, the increment of human energy budget, as compared to that of a mammal of the same body size, apparently was not much greater than these of the transitions between unicells and multicellular ectotherms, and between ecto- and endotherms: about one order of magnitude. Even today, the power used by an average human being inhabiting the Earth amounts to 1.7 kW, including the exploitation of all energy resources, from firewood to atomic energy (Rocznik Statystyki Międzynarodowej, 1987). This is slightly less than 10 times the average metabolic rate, and less than the power developed by athletes at extreme muscular efforts (Fig. 8). In some regions of the world, however, the use of energy by an "average citizen" is much higher, reaching for example 4.2 kW in Poland and 8.9 kW in the USA (Fig. 8; Rocznik Statystyki Międzynarodowej, 1987). The question remains unanswered if this extravagant life strategy is being favoured, or disfavoured, by the action of natural selection.

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METABOLICZNE OGRANICZENIA BUDŻETÓW ENERGETYCZNYCH SSAKÓW

Streszczenie

Rozmaite strategie ewolucyjne zwierząt mogą zmierzać albo do wysokich wydatków energetycznych, albo do oszczędnego wykorzystywania zasobów (dobór

typu "P(ower)" lub "E(conomy)", podobnie jak rozmaite strategie popierają mniejsze lub większe rozmiary ciała (dobór typu r i K ; Ryc. 1). Działanie doboru naturalnego w obu tych kierunkach napotyka ograniczenia fizjologiczne lub morfologiczne. Skutkiem rozmaitych adaptacji przeciętne budżety energetyczne różnych gatunków przybierają losowe wartości, wewnątrz zakresu ograniczonego przez owe czynniki, które są funkcjonalnie związane z wielkością ciała. Ubocznym skutkiem tego faktu jest alometryczna korelacja tempa metabolizmu i masy ciała ssaków (Ryc. 2). Podjęto próbę zidentyfikowania i ilościowego oszacowania czynników ograniczających budżety energetyczne ssaków. Zebrano z literatury dane o skrajnych wartościach budżetów energetycznych (Tabele 1—5) i obliczono ich regresje do ciężaru ciała. Otrzymano następujące równania: minimalne tempo metabolizmu hibernacji $M_{\min} = 0,246 \times 10^{-3} W^{0,870}$ (Ryc. 3); maksymalne tempo metabolizmu wysiłkowego $M_{\max} = 0,101 W^{0,887}$ (Ryc. 4); maksymalne tempo termogenezy bezdreszczowej $NST_{\max} = 0,112 W^{0,059}$ (Ryc. 5); maksymalne tempo termogenezy całkowitej $HP_{\max} = 0,168 W^{0,070}$ (Ryc. 6); maksymalne tempo asymilacji energii z pokarmu $A_{\max} = 0,214 W^{0,064}$ (Ryc. 7); wszystkie tempo metabolizmu w Watach, ciężar ciała (W) w gramach. Porównanie empirycznych wykładników potęg z teoretycznymi wartościami wykładników funkcji skalujących dla powierzchni ($2/3$) i objętości (1) sugeruje (Tabela 6), że M_{\min} i M_{\max} ograniczone są przez procesy metaboliczne w znacznym stopniu związane z masą ciała, podczas gdy pozostałe funkcje ograniczające uzależnione są od powierzchni struktur morfologicznych, np. tempo asymilacji energii ograniczone jest powierzchnią przewodu pokarmowego. Budżety energetyczne ssaków mierzone w terenie metodą izotopową mieszczą się wewnątrz tych ograniczeń, ale zbliżają się do granicy wyznaczonej przez A_{\max} (Ryc. 8). Człowiek uniknął fizjologicznych ograniczeń budżetu energetycznego dzięki wykorzystaniu strumienia energii omijającego jego przewód pokarmowy.