Factors influencing the daily energy expenditure of small mammals

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All living processes utilize energy. Animals cannot perform essential behaviours, grow or reproduce without using energy. Moreover, even when animals are quiescent they still use energy to sustain homeostasis (e.g. maintaining ion gradients) and perform repair (e.g. DNA repair and protein synthesis). Two key factors have been recognized to inflict heavy demands for energy on animals. First, endothermy imposes enormous requirements when compared with exothermy (Nagy, 1987). The small endothermic bird phainopepla (*Phainopepla nitens*), for example, uses energy at about 40-fold the rate of an exothermic lizard of equivalent body mass (Weathers & Nagy, 1980). The second dominant factor is body size. Larger animals use more energy (Kleiber, 1932, 1961; Brody, 1945; Nagy, 1987, 1994). However, the disadvantageous surface:volume ratio of small animals means they expend energy at much greater rates relative to their body size. In consequence, it is not exceptional for a small mammal to ingest half its own body mass in food every day. Some small mammals must eat more than their own weight daily (for example, see Hawkins & Jewell, 1962; Hanski, 1985). For small endothermic animals, therefore, it is widely accepted that the demand for energy may place proximate and ultimate constraints on many aspects of their behaviour and life history (McNab, 1980; Henneman, 1983; Loudon & Racey, 1987; Tomasi & Horton, 1992). Because of this perceived importance, it is of interest to quantify the factors which influence the requirements for energy in free-living small animals.

In the present paper I will review the factors which influence the daily energy expenditure (and thus energy requirements) of small mammals as they go about their routine activities. Extant mammals range in body mass over about eight orders of magnitude, from the Etruscan shrew (*Suncus etruscus*) weighing 1·5–2·5 g to blue whales (*Balaenoptera musculus*) weighing up to 160 000 000 g (Rice, 1967). Any definition of 'small', therefore, is bound to be relatively arbitrary. I have selected as a cut-off a maximum size for inclusion of 2000 g. This size limit includes the lowest three orders of magnitude from the entire body mass range.

Factors which influence energy requirements may be subdivided into two different types: intrinsic factors and extrinsic factors. Intrinsic factors include the body mass of animals, their phylogeny, physiological traits such as their ability to reduce body temperature by falling torpid and whether they are reproducing or not, and finally behavioural traits such as their diet choice and locomotory behaviour. Extrinsic factors include aspects of the environment (e.g. temperature, humidity, rainfall, latitude and altitude), and social factors such as whether the animals engage in social thermoregulation by huddling (for example, see Karasov, 1983).

Some of these factors would be clearly expected to impose elevated demands on animals. Reduced ambient temperature, for example, might be anticipated to increase the energy expended by animals sustaining endothermy. If temperature continued to decline one might intuitively anticipate that the animal would not be able to sustain a continued elevation of its energy expenditure indefinitely and would ultimately die. Laboratory experiments clearly indicate that this is exactly what happens when small animals are exposed to severe cold (Horvath *et al.* 1948; Hart, 1953; Hart & Heroux, 1953). These

experiments suggest that there are physiological limits on the levels of sustainable energy expenditure. An interesting question then is what imposes such physiological limits, and whether such limits play an important role in the life histories and ecology of free-living animals (Weiner, 1987, 1989; Hammond & Diamond, 1997). It has been suggested, for example, that limits on thermoregulatory capacity and ability to sustain energy expenditure above certain levels may define the geographic distribution (northerly extensions of range) of endothermic animals (Root, 1988).

One theory concerning the sustainable limits to daily energy expenditure is that the limits are defined by a digestive bottle-neck (Drent & Daan, 1980; Weiner, 1987, 1989; Petersen *et al.* 1990; Hammond & Diamond, 1997). It has been suggested that animals are limited in their expenditure by the rates at which they can digest and process food. As the alimentary tract and associated organs have high metabolic rates they contribute a disproportionate amount to the total resting metabolic rate (RMR; Krebs, 1950; Daan *et al.* 1989; Konarzewski & Diamond, 1995). Thus, animals with high capacities for sustained metabolic rates also have high RMR. This leads to a link between sustainable metabolism and resting metabolism. The digestive bottle-neck is suggested to impose a limit on expenditure at about $6–7 \times$ RMR (Hammond & Diamond, 1992, 1997; Hammond *et al.* 1994). A second aim of the present paper, therefore, is to evaluate the link between daily energy expenditure and resting energy expenditure in the light of the 'digestive bottle-neck' hypothesis.

METHODS

There are several methods that can be used to quantify the daily energy demands of small mammals: time–energy budgets, food intake and doubly-labelled water (DLW). Time–energy budgets involve observing the behaviour and thermal environment of animals in the wild and quantifying the time interval that was spent in different activities and environments. By measuring the energy costs that are associated with each of these behaviours and thermal conditions, in the laboratory, the total daily energy expenditure can in theory be reconstructed by multiplying each time interval by its associated energy costs (Bakken, 1976; Goldstein, 1988). This method has been used frequently to quantify the daily energy demands of birds (for example, see Schartz & Zimmerman, 1971; Williams & Nagy, 1984), probably because they are generally diurnally active and relatively easily observed. Since many small mammals are nocturnally active they are less easily observed; hence, time budgets for this group tend to be more simplistic than budgets compiled for birds (for example, see Kenagy *et al.* 1989). Such simplicity, however, may introduce considerable inaccuracy in quantification of time interval spent expending energy at different levels. Even when budgets are relatively detailed there can still be large errors in the consequent estimates of daily energy expenditure (Weathers *et al.* 1984; Buttemer *et al.* 1986; Nagy, 1989).

Crissey *et al.* (1997) have detailed some of the problems which are associated with quantification of food intake in primates. In small mammals these same problems apply, but are generally compounded by the problem of watching the animals in darkness. Radioisotope-elimination methods may provide a route around these problems (Baker *et al.* 1968; Chew, 1971; Baker & Dunaway, 1975; Green & Dunsmore, 1978; McLean & Speakman, 1995), but the same tracers have seldom been used on more than a small sample of species, and comparability across techniques has not been demonstrated.

Because of the paucity of data derived using time–energy budget and food-intake methods, and the fact that such methods may not be of sufficient accuracy, I have restricted

the present review to measurements made using the DLW method. The DLW method is an isotope-elimination technique which was developed in the 1950s (Lifson *et al.* 1955). It works on the principle that a label of O in body water will be eliminated from the body because of the flow of water through the body and CO_2 production, while a label of H will be eliminated only by water flow. Consequently, a measure of CO_2 production is possible from the difference in elimination of the two labels (Lifson & McClintock, 1966; Nagy, 1980). There are many protocols for application of the technique (Speakman, 1997), but the one most frequently used to assess energy expenditures of small animals is a two-sample methodology in which the animal is injected with isotopes, bled after a short time interval to derive an initial level of isotopes in the body and then released into the wild. After a further time interval (24–48 h) the animal is recaptured and a final sample of blood taken. The measurement derived from this protocol is of CO_2 production over the interval between the two samples when the animal is in the field and, thus, it is generally referred to as field metabolic rate (FMR). Validation studies of the method suggest that in small mammals it provides on average an estimate of CO_2 production which differs from the true CO_2 production assessed by indirect calorimetry by about 3 % (Speakman, 1997). A review of studies in which comparisons of behaviour between labelled and unlabelled individuals have been undertaken indicates that the method does not adversely affect the behaviour of animals under most circumstances (Speakman, 1997).

The first application of the DLW method to a wild small mammal was a study of the pocket mouse *Perognathus formosus* in 1970 (Mullen, 1970). I have reviewed the literature published between 1970 and March 1997 on daily energy expenditure of small mammals measured using the DLW technique. In many studies, measurements have been made on groups of animals in different conditions, for example, between summer and winter, and between different physiological states (such as pregnancy and lactation). One might anticipate that these factors would be associated with changes in daily energy expenditure. I therefore included multiple measurements from each study where information was available. Generally such multiple measures include different individuals sampled at different times of year. In total, from fifty-four separate studies I obtained ninety-two measurements of FMR on a total of fifty-two species. To these I have added three measurements from unpublished studies from my own laboratory making a total of ninety-five measurements of fifty-four species.

The data-set included several phylogenetic groups, but was dominated by sixty-five measurements made on twenty-nine species of Rodentia. The remaining measurements included seven measures on six species of Chiroptera, four measurements on three species of Carnivora, twelve measurements on eleven species of Marsupialia, five measurements on four species of Insectivora and two measurements on a single species of Lagomorph. These animals had been measured in a wide range of geographical conditions, from hot arid deserts through the temperate-zone woodland and grassland to the arctic tundra. Surprisingly, there was only one measurement from tropical regions (von Helversen & Reyer, 1984), which concerned the nectarivorous bat (*Anoura caudifera*). None of the measurements involved animals in hibernation and, thus, these trends apply only to mammals sustaining continuous endothermy.

In addition to measurements of FMR, I have also compiled, from the publications, data on the body masses of the individuals involved in the measurements, latitude of the study site, shade ambient air temperature during the measurements and diet selected by the animals. Occasionally shade ambient air temperatures were not cited, but if a date and location were known I obtained the ambient temperatures from *The Encyclopedia of Climatology* (Oliver & Fairchild, 1984).

RESULTS AND DISCUSSION

The data reviewed are summarized in Table 1.

Variation in field metabolic rate with body mass

There was a significant positive relationship between $\log_e$ FMR (kJ/d) and $\log_e$ body mass (g; Fig. 1). The best-fit regression (least squares) explained 86·9 % of the variation in energy expenditure. The gradient of this relationship (0·622) differed significantly from an anticipated scaling exponent of 0·81 (Nagy, 1987). Given the fact that the data were converted to log values before analysis and the r^2 was only 0·869, there was considerable residual variation around this fitted line. I removed the observed mass effect by taking residuals to this relationship. I then examined the effect of other factors on these residuals (residual $\log_e$ FMR).

Latitude

Residual $\log_e$ FMR was associated with latitude (Fig. 2). A third-order polynomial fitted the data (residual $\log_e$ FMR = 0·563 − 0·0483latitude + 0·0000371latitude^2 − 0·00000040latitude^3; r^2 0·366, F 14·6, $P < 0·001$), but given the scarcity of data from the tropics such a sophisticated model is probably unwarranted. It is clear, however, that residual $\log_e$ FMR increases as one travels to progressively higher latitudes above 25 °N or S. Whether FMR also increases as one moves from these latitudes towards the equator requires more data on the metabolism of tropical animals.

It seems very unlikely that this effect is an intrinsic aspect of latitude. Day length was unlikely to be a covariable factor, since these data have been compiled across sites and seasons in both hemispheres. Thus, measurements at high latitudes (70 °N) include measures of animals in midsummer and midwinter which are continuously light and dark respectively. Furthermore, examination of one latitude (35 °) reveals a range of estimates which almost equals the entire range across the other latitudes. This alone indicates that other factors probably produce the overall latitude effect.

Ambient temperature

High latitudes are generally colder (Oliver & Fairchild, 1984), thus a potential covariate of latitude was ambient air temperature. In this data-set, temperature was correlated with the latitude of the study site (r 0·56). There was a significant negative relationship between residual $\log_e$ FMR and air temperature (Fig. 3). The least-squares-fit regression equation (residual $\log_e$ FMR = 0·282−0·018temperature) explained 26·0 % of the variation in the residual $\log_e$ FMR. In colder conditions, animals had higher residual $\log_e$ FMR. Such a relationship would be anticipated, from a simple thermostatic model of endothermic function, but this differs from the relationship found in endothermic birds (Bryant, 1997). Possibly, mammalian budgets are less dominated by the high costs of flight activity and the covariant effects of ambient temperature on activity levels. Small terrestrial mammals expend relatively trivial amounts of energy on locomotion (Garland, 1983; Peters, 1983) and, thus, thermoregulatory effects may dominate their energy budgets. Unfortunately, there are insufficient data available for bats to make a comparison with birds using a mammal which has the same high activity costs.
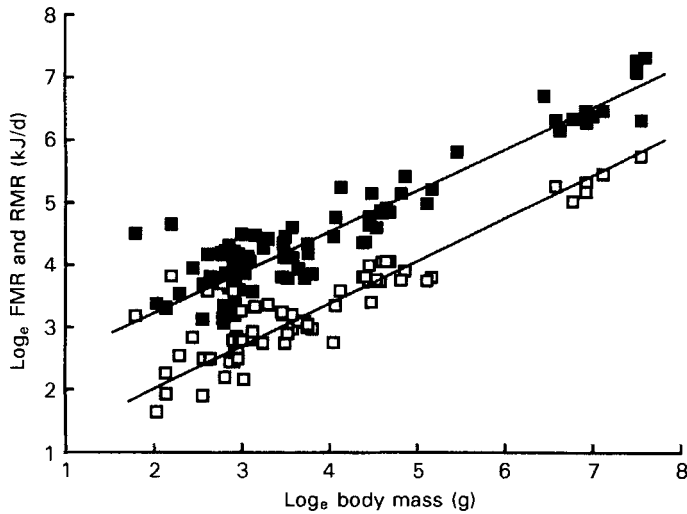
Fig. 1. Log$_e$ field metabolic rate (FMR; ■) and log$_e$ resting metabolic rate (RMR; □) v. log$_e$ body mass (g) for small mammals weighing less than 2000 g (data shown in Table 1).

Although intuitively appealing, the effects of ambient air temperature are surprising because animals generally expose themselves to ambient air temperatures for relatively short periods of time. Microclimates in the microhabitats they occupy may bear only scant resemblance to the shade ambient air temperature. For example, insectivorous bats around Aberdeen (57 °N) at summer ambient air temperatures of 10–15 ° spend almost their entire day in communal roosts where the ambient temperature is generally in excess of 25–30 ° (J. R. Speakman and P. A. Racey, unpublished results). In contrast, many desert-living rodents at very high ambient temperatures hide in cool burrows throughout the day and emerge to forage only at night. Thus, the temperatures they routinely experience are
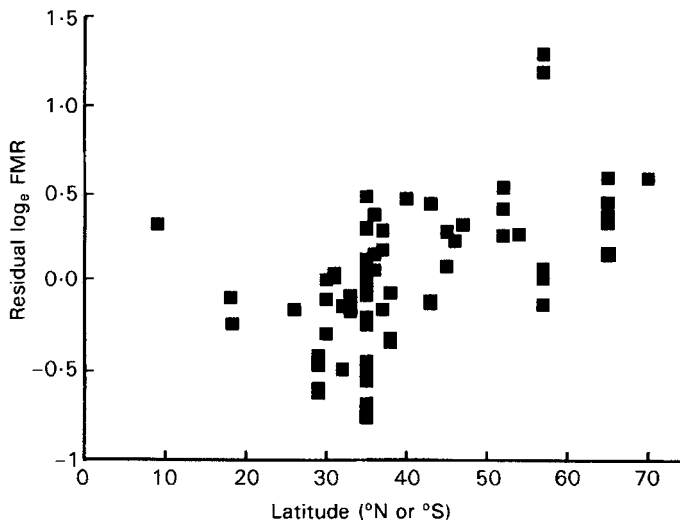

Fig. 2. Residual log$_e$ field metabolic rate (FMR; after the effect of body size was removed) v. latitude for small mammals weighing less than 2000 g.

Table 1. *Measurements of body mass (BM; g), field metabolic rate (FMR: kJ/d), resting metabolic rate (RMR: kJ/d) and FMR:RMR in a sample of small mammals weighing less than 2000 g*

Species*	Reference*	BM	FMR†	RMR‡	FMR:RMR
Marsupialia					
Tarsipes rostratus	Nagy et al. (1995)	9.9	34.4	12.7	2.71
Sminthropsis crassicaudata	Nagy et al. (1988)	16.6	68.7	9.0	7.63
Antechinus stuartii	Nagy et al. (1978)	25.7	72.0	15.6	4.61
Antechinus stuartii	Green et al. (1991)	33.0	86.4	15.6	5.54
Phascogale calura	Green et al. (1989)	33.5	61.9	–	–
Petaurus braviceps	Nagy & Suckling (1985)	123.5	172.5	42.8	4.03
Gymnobelideus leadbeateri	Smith et al. (1982)	129.0	226.0	49.7	4.55
Pseudocheirus peregrinus	Nagy (1987)	717.0	556.0	192.7	2.88
Petauroides volans	Foley et al. (1990)	1018.0	532.0	206.5	2.58
Bettongia penicillata	Green (1989)	1100.0	593.0	–	–
Isoodon obesulus	Nagy et al. (1991)	1230.0	644.0	235.0	2.74§
Settonix brachyurus	Nagy et al. (1990)	1900.0	548.0	310.0	1.77‖
Chiroptera					
Pipistrellus pipistrellus	Racey & Speakman (1987)	7.6	29.3	5.2	5.63
Myotis lucifugus	Kurta et al. (1989)	8.5	27.6	9.6	2.87
Plecotus auritus	Speakman & Racey (1987)	8.5	27.0	6.9	3.91
Anoura caudifer	von Helversen & Reyer (1984)	11.5	51.9	17.0	3.05
Macrotus californicus	Bell et al. (1986)	12.9	22.8	6.7	3.40
Eptesicus fuscus	Kurta et al. (1990)	20.8	47.6	–	–
		17.4	75.3	–	–
Rodentia: Mice					
Mus musculus	Nagy (1987)	13.0	39.8	12.1	3.29
Mus domesticus	Mutze et al. (1991)	14.0	45.1	12.1	3.73
Mus musculus	Rowe-Rowe et al. (1989)	19.3	65.1	12.1	5.38
Peromyscus crinitus	Mullen (1971a)	13.4	40.1	11.9	3.37
Peromyscus leucopus	Randolph (1980)	19.4	36.5	16.3	2.24
Peromyscus leucopus	Munger & Karasov (1989)	18.2	53.1	16.3	3.26
		19.6	58.3	16.3	3.56
		20.2	62.2	16.3	3.82
Peromyscus maniculatus	Hayes (1989a)	20.6	56.1	8.7	6.45
Peromyscus maniculatus	Hayes (1989b)	18.4	68.4	11.5	5.95
		17.6	46.3	11.5	4.03
Apodemus sylvaticus	N. Corp, M. L. Gorman and	22.0	58.1	16.5	3.52
	J. R. Speakman	18.9	54.7	17.3	3.16
	(unpublished results)				
Pseudomys albocinereus	Nagy (1987)	32.6	62.2	–	–
Acomys cahirinus	Degen et al. (1986)	38.3	51.8	22.3	2.32
Acomys russatus	Degen et al. (1986)	45.0	47.6	19.7	2.42
Praomys natalensis	Green & Rowe-Rowe (1987)	57.3	86.6	15.8	5.48
Perognathus formosus	Mullen (1970)	18.6	29.2	13.4	2.18
Perognathus formosus	Mullen & Chew (1973)	19.2	53.2	13.4	3.97¶
Sekeetamys calurus	Degen et al. (1986)	41.2	44.0	22.0	2.00
Rats					
Dipodomys merriami	Mullen (1971b)	35.9	61.8	19.7	3.14
Dipodomys merriami	Nagy & Gruchacz (1994)	33.9	44.0	18.2	2.41
Dipodomys microps	Mullen (1971b)	58.6	117.4	28.5	4.12
Psammomys obesus	Degen et al. (1991)	175.7	184.5	44.9	4.10**
		165.6	146.3	42.3	3.46**
Voles and lemmings					
Clethrionomys rutilus	Holleman et al. (1982)	13.6	64.9	35.8	1.81††
		18.3	58.0	35.8	1.62
		15.9	66.1	40.3	1.64
		16.1	64.3	40.3	1.56
Clethrionomys glareolus	Daan et al. (1990)	23.4	88.0	28.0	3.14‡‡

(Continued)

Table 1. (*continued*)

Species*	Reference*	BM	FMR†	RMR‡	FMR:RMR
Microtus arvalis	Daan *et al.* (1990)	20·0	90·0	26·1	3·45§§
Microtus agrestis	Daan *et al.* (1990)	27·2	83·0	28·9	2·87‖‖
Microtus pennsylvanicus	Berteaux *et al.* (1996*a*)	32·3	77·5	24·5	3·16
Microtus pennsylvanicus	Berteaux *et al.* (1996*b*)	35·6	100·4	24·5	4·10
Arvicola terrestris	Grenot *et al.* (1984)	85·8	118·9	54·6	2·18
Lemmus trimucronatus	Peterson *et al.* (1986)	62·0	191·4	36·2	5·29
Gerbils					
Gerbillus allenbyi	Degen *et al.* (1992)	22·8	35·6	18·7	1·90¶¶
Gerbillus pyramidium	Degen *et al.* (1992)	31·8	45·2	25·6	1·77¶¶
Squirrels and chipmunks					
Ammospermophilus leucurus	Karasov (1981)	97·5	130·6	41·9	3·12
		85·5	104·3	41·9	2·49
		79·9	79·2	45·5	1·74
		82·1	79·6	45·5	1·75
Tamais striatus	Randolph (1980)	93·1	99·3	43·2	2·30
Thomomys bottae	Gettinger (1984)	99·4	126·6	57·9	2·19
		108·2	127·7	57·9	2·21
		103·9	135·9	57·9	2·35
Spermophilus saturatus	Kenagy *et al.* (1989)	224·0	232·0	97·4	2·40
		231·0	263·0	97·4	2·70
		256·0	248·0	107·8	2·30
		174·0	159·0	79·5	2·0
		215·0	289·0	93·2	3·1
		241·0	205·0	102·5	2·0
	Kenagy *et al.* (1990)	232·0	336·0	90·8	3·7
Spermophilus parryi	Daan *et al.* (1990)	630·0	817·0	–	–
Carnivora					
Vulpes cana	Geffen *et al.* (1992)	874·0	568·1	151·2	3·76***
		1016·0	640·2	175·8	3·64***
Bassariscus astutus	Chevalier (1989)	752·0	472·0	–	–
Vulpes velox	Covell *et al.* (1996)	1990·0	1488·0	–	–
Insectivora					
Sorex areneus	Poppitt *et al.* (1993)	9·0	104·8	45·6	2·30
		6·0	90·3	24·0	3·76
Microgale dobsoni	Stephenson *et al.* (1994)	42·6	77·1	20·1	3·84†††
Microgale talazaci		42·8	66·5	21·0	3·17†††
Talpa europea	S. L. Frears, M. L. Gorman and J. R. Speakman (unpublished results)	87·7	173·0	29·9	5·79
Lagomorpha					
Lepus californicus	Shoemaker *et al.* (1976)	1800·0	1416·0	–	–
		1800·0	1175·0	–	–

* Multiple entries under a given species or reference involve animals measured in different seasons or at different stages of reproduction.

† The cited reference is the source of the FMR measurements.

‡ Unless indicated, the RMR was obtained from the same reference as the FMR. RMR measurements were made on animals at rest at thermoneutrality, but not necessarily of post-absorptive individuals.

§ Hulbert & Dawson (1974).

‖ Kinnear & Sheild (1975).

¶ Glazier (1985).

** Degen (1993).

†† Rosenman *et al.* (1975).

‡‡ Kaczmarski (1966).

§§ Migula (1969).

‖ ‖ M. S. Johnson and J. R. Speakman (unpublished results).

¶¶ Haim & Izhaki (1993).

*** Noll-Banholzer (1979).
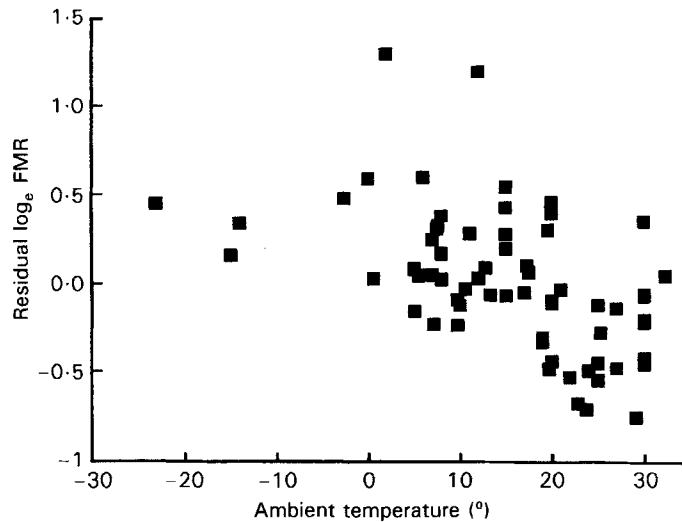
††† Stephenson & Racey (1993).

Fig. 3.　Residual $\log_e$ field metabolic rate (FMR; after the effect of body size was removed) v. ambient air temperature for small mammals weighing less than 2000 g.

considerably lower than the reported average air temperature. These effects may explain why the relationship, although significant statistically, was quite diffuse and had an r^2 of only 0·260.

Together body mass and temperature explained 87·7 % of the variation in FMR. I then removed both the body mass and temperature effects to explore the effects of some nominal variables on the residual variation.

Phylogeny

Residual $\log_e$ FMR (excluding mass and temperature effects) differed significantly between different phylogenetic groups (Fig. 4). Rodents had lower residual FMR than average, whilst bats and marsupials had slightly higher than average residual FMR. The Carnivora and Insectivora both had residual $\log_e$ FMR which were substantially above the average, but in both groups the sample was small. These groups also have elevated basal rates of energy expenditure (McNab, 1980, 1986). However, high FMR in bats and marsupials, with low FMR in rodents, does not match the pattern of variation in BMR in these groups (McNab, 1986).

Diet

Insect-eating animals had higher than average residual $\log_e$ FMR and granivores had lower than average residual $\log_e$ FMR once the effect of mass and temperature had been removed (Fig. 5). For insect-eating animals this effect was independent of phylogeny, since there were bats, rodents, Carnivora and Insectivora represented in the group. The granivores in this sample were exclusively rodents, the majority of which live in desert regions. The apparent effect of eating grains on residual $\log_e$ FMR, therefore, may reflect more a response to low food availability rather than that of feeding on grains. Nagy & Gruchacz (1994) observed that kangaroo rats (*Dipodomys merriami*) increased their metabolic rates in midwinter when they switched their diets from mostly grains to feeding on vegetation, which matches the observed trends across species. However, in this latter case, the switch
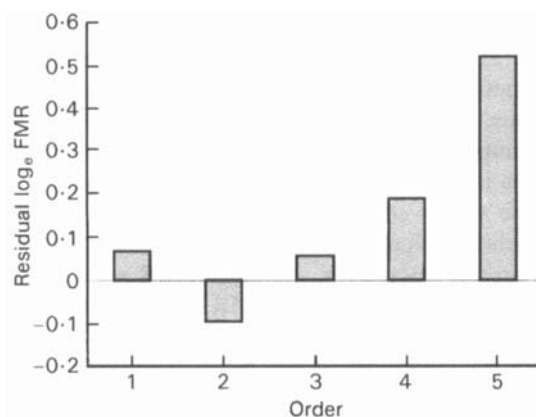
Fig. 4. Residual $\log_e$ field metabolic rate (FMR; after the effects of body size and ambient air temperature were removed) as a function of the phylogenetic order of the animals. 1, Chiroptera; 2, Rodentia; 3, Marsupialia; 4, Carnivora; 5, Insectivora.

in diet was coincident also with the coldest time of year, which also might have elevated the energy expenditure. The bias in the present sample towards desert rodents may also explain the lower than average residual FMR linked with the group of rodents as a whole (Fig. 4).

The relationship between field metabolic rate and resting metabolic rate

For seventy-three of the eighty-nine measurements (forty-five species) I compiled information on RMR for the animals that had been involved in the FMR measurements. It is well established that RMR is also strongly dependent on body mass (Kleiber, 1932, 1961; McNab, 1980, 1986). In this sample, the effect of mass on RMR followed a line parallel to the measured FMR (gradient 0·601, not significantly different from the gradient for FMR (0·622); analysis of covariance: F 0·18, P 0·676) but at a lower elevation (intercept 1·13, significantly lower than the intercept for FMR (2·09); analysis of
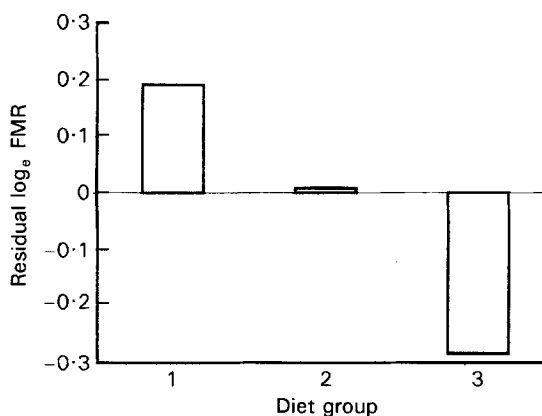

Fig. 5. Residual $\log_e$ field metabolic rate (FMR; after the effects of body size and ambient air temperature were removed) as a function of the diet grouping of the animals. 1, Insectivorous animals; 2, herbivorous animals; 3, granivorous animals.

covariance: F 766·51, $P < 0.001$; Fig. 1). Since the plots are log-based, this implies that anticipated FMR are on average a multiple of the anticipated RMR. This might be true simply as an epiphenomenon of both scaling relationships having the same gradient for independent reasons. Thus, the fixed ratio FMR:RMR might reflect only the general pattern of covariation of both traits with body mass. An interesting question then is the extent to which residual variations in FMR are linked to residual variations in RMR.

In this sample, there was a strong positive relationship between residual FMR and residual RMR (both residuals calculated removing the effect of mass but not temperature) (Fig. 6). The least-squares-fit regression, residual FMR = 0·015 + 0·448 residual RMR, explained 26·9 % of the variation in residual FMR. Animals which had higher FMR than expected for their mass also had higher than expected RMR. I will illustrate this point using two species measured in my laboratory at Aberdeen. The common shrew (*Sorex areneus*) weighs approximately 8–10 g and has a daily energy requirement in the wild, measured by DLW, of on average 90 kJ/d (Poppitt *et al.* 1993). This expenditure is considerably higher than the expected FMR for an animal weighing 8 g which is 29 kJ/d (Fig. 1). Its RMR at thermoneutrality, however, is 24 kJ/d (Poppitt, 1988) which is also substantially above the expected level for an animal of this size. The brown long-eared bat (*Plecotus auritus*) also weighs 8–10 g and lives sympatrically with the shrew. Both shrew and bat feed on insects. In Aberdeen, the bat expends 27 kJ/d on FMR (Speakman & Racey, 1987). This is approximately what one would predict for a small mammal of this body mass. It is interesting to note that the FMR of the bat is similar to the RMR of the shrew. The RMR of the bat (Webb *et al.* 1992) is only 7 kJ/d which is again in line with the expectation for an animal of this size.

The link between FMR and RMR could reflect several different processes. In the remainder of the present paper, I will use the data-set accumulated for small mammals to evaluate these processes and to propose an alternative explanation for the link. The first possibility is that the effect is an artefact of lack of independence. FMR is not an independent measurement from RMR because part of FMR is RMR. Thus, even if the amount expended in the field over and above RMR was constant, across all animals there would still be a positive correlation between the residuals, because one would in effect be
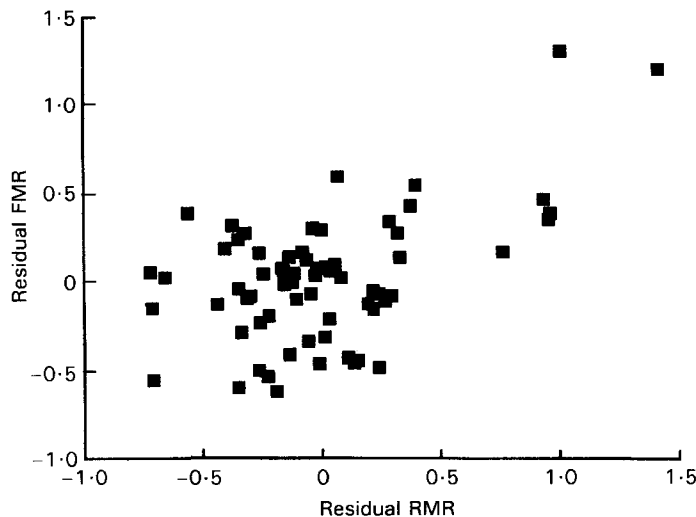

Fig. 6.   Residual $\log_e$ field metabolic rate (FMR) *v.* residual $\log_e$ resting metabolic rate (RMR) (both with effects of body mass but not ambient air temperature removed) for small mammals weighing less than 2000 g.

correlating RMR with itself. However, if one examines the relationship between residual FMR minus RMR and residual RMR the same trends exist (not shown). Examination of the examples of the shrew and bat mentioned previously illustrates this point. The difference between FMR and RMR for the shrew (66 kJ/d) substantially exceeds the difference between FMR and RMR of the bat (20 kJ/d). Moreover, the values for FMR–RMR are correlated with the values for RMR. It is not the case, therefore, that FMR–RMR is invariant. Hence, the correlation between residual FMR and residual RMR does not entirely reflect shared variation in RMR.

A second possibility is that the relationship between sustainable metabolic rates (i.e. FMR) and RMR comes about because both are linked to the digestive capacity of the alimentary tract (Drent & Daan, 1980; Weiner, 1987, 1989; Petersen *et al.* 1990); the so-called digestive bottle-neck hypothesis. It is suggested that levels of sustainable expenditure are constrained by the amount of energy that an animal can process through its alimentary system. Different alimentary systems can cope with processing different amounts of energy, which leads to different limits in the achievable FMR. However, the maintenance costs of the alimentary system are related to its processing capacity. In addition, the alimentary system contributes a disproportionate amount to the animal's total RMR (Daan *et al.* 1989; Konarzewski & Diamond, 1995). Thus, animals which have high processing capacity, and thus high FMR, also have high RMR, leading to a fixed ratio between the two variables of approximately 6·0–7·0 (Drent & Daan, 1980; Weiner, 1987; Petersen *et al.* 1990; Hammond & Diamond, 1997).

There has been some debate as to whether the actual physiological upper limits are imposed by the alimentary system (the central-limits hypothesis), or alternatively by aspects of the peripheral sites where energy expenditure actually occurs (the peripheral-limits hypothesis; McDevitt & Speakman, 1994; Koteja, 1996). A third idea is that capacities of the peripheral and central systems are closely matched by the process of symmorphosis (Taylor & Weibel, 1981). Whichever model is adopted, a close link between FMR and RMR is anticipated, but in the peripheral-limits model, levels of maximal FMR will vary with the mode of energy expenditure, whereas in the central-limits hypothesis they will not.

Hammond & Diamond (1992, 1997) and Hammond *et al.* (1994) have pushed laboratory mice to extreme levels of energy expenditure. These experiments have established that at extremes of temperature stress, lactation and combinations of cold and lactation, mice expend energy at different total rates, supporting the peripheral-limits model. Yet the link between daily energy requirement (measured as food intake) and RMR remains fixed at between 6 and $7 \times$ RMR (supporting the digestive bottle-neck and/or symmorphosis ideas).

The digestive bottle-neck hypothesis makes predictions which can be tested using the data available from small mammals. It predicts that the ratio FMR:RMR should cluster around the limiting level of $6–7 \times$ RMR. This is because if an animal had an elevated energy expenditure which took its FMR beyond the $6–7 \times$ RMR limit it would have to respond by increasing the capacity of its alimentary system. This increase would lead to an increase in the RMR to maintain the ratio between the two (for an example of this, see Speakman & McQueenie, 1996). If the animal reached some limit in the capacity of the alimentary system to respond to the energy expenditure, the animal could draw on reserves for a short period but ultimately would have to reduce expenditure to match the $6–7 \times$ RMR level. On the other hand, if an animal experienced a reduction in its energy demand to below $6–7 \times$ RMR, it could scale back the capacities of the alimentary system so that the RMR would drop and the ratio RMR:FMR would again remain fixed at about $6–7 \times$ RMR.

In the current data-set this prediction is not verified. A frequency plot of FMR:RMR values (Fig. 7) reveals that the peak ratio is between 2·0 and 3·0, and relatively few animals expend energy around the supposed physiological limit of about 6–7 × RMR. The mean value for FMR:RMR was 3·27 when including all the data (SE 0·15, *n* 74), and 3·36 when including a single value for each species (SE 0·19, *n* 45). This indicates that small mammals in the field are routinely expending energy at rates substantially below the supposed physiological maximum of 6–7 × RMR. Similar distributions and average ratios have been reported in reviews of the literature for birds (Bryant & Tatner, 1991; Koteja, 1991; Nagy, 1994) and reptiles (Christian *et al.* 1997).

It is unlikely that the failure to find an FMR:RMR of 6–7 × RMR is because the formulation of the bottle-neck hypothesis relates to the ratio, energy intake:RMR rather than the ratio, energy expenditure (FMR):RMR. Energy expenditure is generally lower than intake because not all ingested energy is assimilated and available for use as metabolizable energy. Using food intake rather than FMR would thus elevate the observed values for FMR:RMR. Digestive efficiencies of small mammals, however, tend to be uniformly high, independent of their diverse dietary intakes. Thus, small insectivores digest approximately 75–90 % of their food intake (Speakman & Racey, 1989; Barclay *et al.* 1991), whilst small herbivores absorb about 75–90 % of their food intake (Drozdz, 1968; Foley, 1987; Hammond & Wunder, 1991; Corp *et al.* 1997). These values, if typical across the board, would elevate FMR:RMR from 3·3 to approximately 3·6–4·5. Digestibilities would need to be uniformly low, at about 50 %, to elevate the mean to the supposed physiological limits. Low digestibilities, however, may explain why some animals appear to have extremely low FMR:RMR of about 1·1–1·5.

Why do small mammals not work harder?

Given the strong evidence that physiological limits to expenditure do exist in the laboratory situation (Weiner, 1987, 1989; Hammond & Diamond, 1992, 1997; Hammond *et al.* 1994; Speakman & McQueenie, 1996), it is interesting to consider why the current data suggest
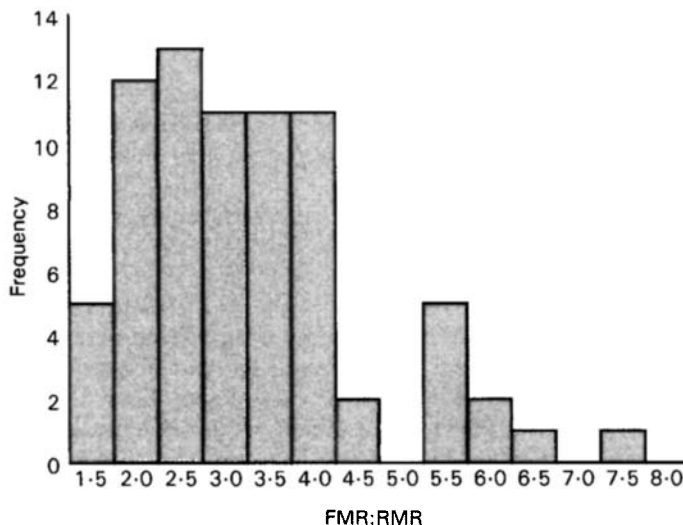

Fig. 7. Frequency of field metabolic rate (FMR):resting metabolic rate (RMR) values among small mammals weighing less than 2000 g.
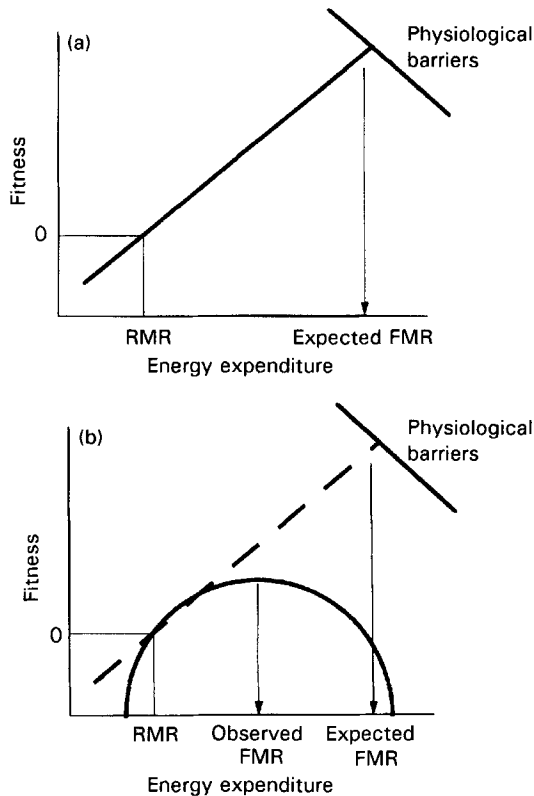
Fig. 8. (a) Hypothetical model presumed to underlie the digestive bottle-neck hypothesis. Increases in energy expenditure are presumed to be linked to increases in fitness. The only limits placed on continued increase in expenditure and fitness are physiological barriers which result in an expected field metabolic rate (FMR) around 6–7 × resting metabolic rate (RMR). (b) Suggested alternative model which explains why most small mammals do not expend energy at their physiological capacities. The relationship between fitness and energy expenditure is curved (——) rather than linear (– – –). Thus, increases in FMR towards the supposed physiological barriers do not result in increased fitness. Most animals utilize FMR:RMR which optimize energy expenditure but maximize fitness (observed FMR).

that small mammals almost never operate at these supposed capacities in the wild. The reason is, I think, a flaw in the underlying rationale of the bottle-neck idea. The bottle-neck hypothesis implicitly assumes that there is a positive monotonic relationship between energy expenditure and fitness. Thus, animals that expend more energy obtain greater fitness benefits (Fig. 8(a)). The only factor that is supposed to prevent them from achieving greater expenditures, and thus greater fitness, is the capacity of their alimentary systems. Different animals are inferred to reach different absolute levels of expenditure because the physiological limits in their systems differ, but the ratio RMR:FMR at the limit is presumed to be fixed. This has been characterized as a trade-off between activity and maintenance costs (Hammond & Konarzewski, 1996).

I suggest that the implicit positive link between fitness and energy expenditure in the digestive bottle-neck hypothesis is its flaw. Rather than a positive relationship, I suggest a more realistic relationship between fitness and energy expenditure is probably curved (Fig. 8(b)). If an animal expends energy on a daily basis at RMR or below, it will have a fitness of 0 or below, as it would be expending insufficient energy to go out and forage. Greater

expenditures of energy would be attached to greater fitness, as assumed in the bottle-neck hypothesis. However, I suggest beyond a certain level of expenditure, further increases lead to a levelling off in fitness gains, and ultimately a reduction. Thus, by working at the physiological maximum rate of energy expenditure the resultant fitness would be considerably lower than at the optimum level of energy expenditure.

I suggest that animals expend energy at rates substantially below the supposed physiological limits because of the nature of this fitness–expenditure relationship. I further suggest that the unexpected diversity of values for FMR:RMR (from 1·1 to 6·5) may reflect the precise nature of this trade-off in different species. In addition, the nature of the trade-off may vary with different modes of energy expenditure and, thus, within a species the FMR:RMR might vary substantially with season and reproductive state (as observed by Nagy (1994) in larger mammals). This model indicates that knowledge of the maximum physiological capacities of animals, and whether these are a consequence of peripheral or central constraints, may actually provide little elucidation of why animals expend energy in the wild at the levels they do.

An analogy may clarify these concepts. I have a car. If I drove my car as fast as I possibly could, it would go at about 105 miles/h (175 km/h). If I were to take my car to a mechanic the vehicle could be examined to determine exactly what was imposing this limit. It might be some element in the fuel-injection system (a central limit) or some aspect of the transmission of power from the combustion engine to the drive mechanism (i.e. a peripheral constraint), or one of many other peripheral reasons. Knowledge of the limits to the mechanical performance of my car, however, would be very unlikely to shed any light on why the average speed at which my car routinely travels on the roads is between 30 and 70 miles/h.

I am suggesting that small mammals routinely live their lives at well below their physiological capacities, in the same way that we drive our cars at well below their mechanical capacities. Examining the nature of physiological limits in animals is an interesting problem, in the same way that establishing the mechanical limits of automobile performance is also of interest. It is clearly, however, a different question from that of why animals have the levels of expenditure they do (or why drivers routinely drive at the speeds they do). I suggest greater progress on the latter problem will come about by examining the nature of the relationship between energy expenditure and fitness, rather than focusing exclusively on maximal limits.

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