

Energetics and the evolution of body size in small terrestrial mammals

J. R. SPEAKMAN

Department of Zoology
University of Aberdeen
Aberdeen AB9 2TN, UK

Synopsis

Many species of very small terrestrial mammals exhibit clinal patterns in their body size, often with larger individuals predominating in populations from higher latitudes (Bergmann's law). Classically, this pattern has been explained as reflecting the advantageous surface-to-volume ratio of larger animals, which provides them with a thermoregulatory advantage in colder regions, because it reduces their energy demands. Attempts to expand on this energetics explanation are, however, fraught with difficulty. A major problem relates to the fact that it is not possible to speculate on the direction of selection on body size by considering costs alone. However, when both costs and gains are considered there is a range of potential effects, which depend critically on the interspecific scaling relationships of energy gains and energy costs. Since these traits may vary in time, in space, and across species, general predictions from the energetics hypothesis of the direction of selection on body size are therefore not possible, and a wide range of directional effects of latitude on size is therefore predicted (and observed). It is generally the case that, within a species, mass explains less than 50% of the individual variation in metabolic energy expenditure. This low explained variation raises the question of why some individuals sustain high rates of metabolism, when this would be likely to make them more susceptible to failure in achieving an energy balance. In wood mice, *Apodemus sylvaticus*, we have found a correlation between basal metabolic rate (BMR) and the thermogenic capacity (noradrenaline-induced metabolic rate). These latter data suggest that animals which might be at a disadvantage in terms of achieving an energy balance might be at an advantage in terms of achieving a heat balance under severe temperature conditions. This indicates a more complex involvement of energetics in the phenomenon of overwinter survivorship than is addressed by models of energy balance alone.

Introduction

Miniature terrestrial mammals exhibit a high degree of individual variability in their body masses, with coefficients of variation, across populations of a given species, often exceeding 30% of the mean mass. Such high coefficients of variation

Given this background, it is widely believed that Bergmann's law describes an adaptive response, which has an explanation rooted in energetics. In this paper I will explore several theoretical attempts to elaborate on the link between energetics and the evolution of clines in body size, in these small mammals. This analysis will illustrate the complexity of deriving predictions from the energetics hypothesis, and the key roles played by several factors, for which, in most circumstances, we have no information. In the second section of the paper I shall present some empirical data which illustrate the difficulties of generating realistic theoretical models, and suggest that the role of energetics during overwinter survival may be considerably more complex than these models suggest.

Theoretical models

Models based on surface-to-volume effects on energy demands

If I take a kettle of boiling water and pour it into two cups, one of which holds 10 times more than the other, and then allow them to cool down, the temperatures in both cups will decline exponentially towards the ambient temperature. However, the water in the larger cup will cool more slowly than the water in the small cup. The reason for this difference is that heat is exchanged over the surface of the vessels and the larger cup has a lower surface-to-volume ratio. This means that the heat loss, relative to the volume of water, is lower in the large cup and, thus, it cools down more slowly. If we reverse this argument, and consider instead how much heat we would need to put into the two different-sized vessels in order to maintain them at a constant temperature—like an animal attempting to maintain a constant body temperature—the greater surface-to-volume ratio of the small vessel means that for each gram of water in that cup, we need to put in more heat than for the larger cup. This difference gets greater as ambient temperature declines (Fig. 1a).

Measurements made on animals of their thermoregulatory responses, in relation to declining temperature, support this simple Newtonian cooling model. For example, in Fig. 1(b), I present data on resting energy demands as a function of ambient temperature for two black mice (strain: C57/BL10), one of which was 47% heavier than the other. The pattern of energy demands and the differences between the smaller and larger individual match exactly the expectation from the Newtonian cooling model (Fig. 1a). The gradient of the line relating metabolic energy demands (W/g) to temperature, is called the whole-body thermal conductance. Several studies have demonstrated that the mean whole-body thermal conductance of populations of animals increases as they get smaller. Brown & Lee (1969), for example, examined 10 populations of wood rats (genus *Neotoma*) and found a large decrease in whole-body thermal conductance with increased size of the subjects (see Fig. 1c).

The physical heat balance model presented above is beguilingly simple to accept. For a long period it was considered that the energetics explanation of

Bergmann's law was that larger animals had more favourable surface-to-volume ratios, which gave them a selective advantage over smaller individuals, in terms of heat balance, as it became colder. This effect was therefore believed to result in the observed size clines. For example, Brown & Lee (1969: 337) interpreted their observed trend in thermal conductance of wood rats (Fig. 1c) in this way, when they stated 'Large wood rats have a selective advantage in cold climates . . . because their smaller surface-to-mass ratio . . . permit[s] them to conserve metabolic heat.'

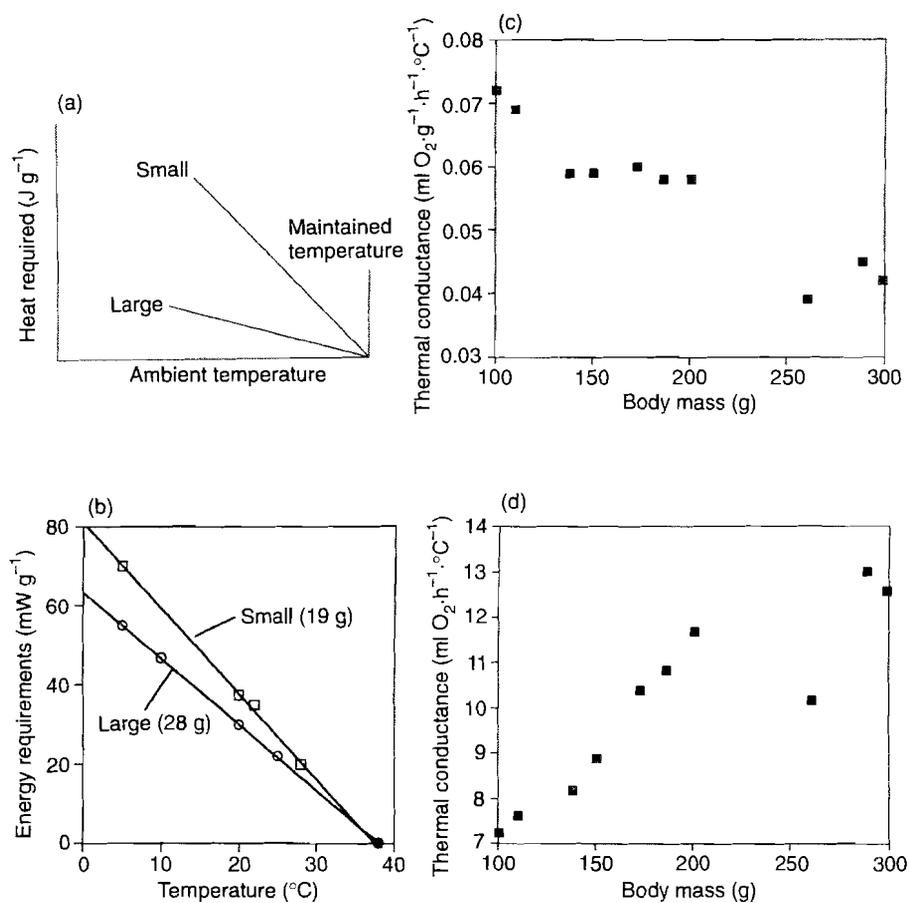


Fig. 1. (a) Theoretical energy requirements to sustain the temperature of two vessels of water which have different volumes, and hence surface-to-volume ratios, as a function of ambient temperature. The larger vessel, with smaller surface-to-volume ratio, requires less energy per gram to maintain its temperature. (b) Energy requirements of two mice of the same strain which differ in their body mass, as a function of temperature. Observed demands match closely the theoretical prediction from the heat balance model (in 1a). (c) Thermal conductance measured for wood rats (*Neotoma*) in relation to body mass (from Brown & Lee 1969). (d) Thermal conductances of wood rats recalculated on a whole-animal rather than on a per-gram basis.

Despite the fact that there are at least three problems with this explanation, elaborated below, which have been known since at least 1950 (Scholander, Walters, Hock, & Irving 1950; McNab 1971) it is still possible to find references in the literature to size clines and to Bergmann's law being the consequence of favourable surface-to-volume ratios of larger individuals (e.g. Davenport 1992).

The three problems with this explanation are as follows. Firstly, it is unclear from the model why there is ever a selective advantage to being small. If we examine the metabolic energy demands illustrated in Fig. 1b, the line for the small animal never falls below the line for the larger animal. Although the selection favouring large size will be less intense at warmer temperatures, it is clear from these curves that selection will never favour being small. Energetically this model predicts that it is always better to be bigger, whatever the temperature. The second problem is that energy demands are expressed in the model on a per-gram basis (cf. Fig. 1a-c). The rationale for expressing the energy expenditure per gram is that this supposedly normalizes the data for the effects of body mass. Even ignoring the fact that simply dividing a dependent variable by body mass will only normalize the mass effect if the gradient of the scaling relationship is 1.0 (Packard & Boardman 1987), the key question to be considered in this context is why this normalization is being performed at all. The question one is attempting to address, in the context of Bergmann's law, is the effect of body size on energy costs. It makes no sense, therefore, to perform before analysis a procedure which aims to remove the effect one is attempting to reveal! Moreover, the energy budget of an animal must be balanced on the basis of an entire animal, not per gram of animal. As McNab (1971: 846) pointed out 'Although weight-specific expressions are often convenient, it is important to realise that an animal does not live on a per-gram basis, but lives rather as an intact individual.' To illustrate the importance of this effect for the interpretation of thermoregulation data, consider the data for wood rats in Fig. 1(c) again. If these data are recalculated on a per-animal rather than on a per-gram basis, the direction of the relationship is completely reversed (Fig. 1d). Larger animals have greater whole-body thermal conductances. On a whole-animal basis, these data suggest that it would be energetically *disadvantageous* to be larger, which is the complete opposite of the interpretation by Brown & Lee (1969: see quote above) of the same data. The positive relationship between total energy costs and body size, despite larger animals having lower surface-to-volume ratios and generally better surface insulation, and the consequent inapplicability to surface-to-volume arguments in the explanation of Bergmann's law, were pointed out in the early 1950s (Scholander *et al.* 1950).

The third problem with this model is that it considers only energy demands. If energy balance is important to the selection of body size, it is also important to recognize that energy balance is the result not only of how much energy the animal is expending, but also how much energy it can acquire to meet those demands. Models, such as the surface-to-volume arguments presented above, which rely only on examining the effects of mass differences on energy costs, effectively

assume that body mass has no effect on the energy gains that the animals can achieve. This is likely to be a naive assumption.

Models based on energy costs and gains

Models which address both the energy demands and the energy gains of animals can be divided into two groups: those which consider the situation when food is present, which, to my knowledge, have not previously been explicitly modelled, and those which consider the situation when food is absent, which have been extensively considered. I will treat each of these situations separately.

When food is present

Imagine a small animal species, individuals of which vary in their body mass. Relatively few studies have examined the effects of intraspecific variation in body mass on energy expenditure. The few studies which have been performed suggest that the effect of intraspecific differences in mass on basal or resting energy expenditure (per whole animal) is positive (Daan, Masman, Strijkstra, & Verhulst 1989; Earle & Lavigne 1990; Millar & Hickling 1990; Hayes, Garland, & Dohm 1992). Interspecifically there is some evidence that in small mammals and birds the total daily energy requirements follow a trend similar to that of basal metabolic rate, as a function of mass, but elevated approximately three to seven times above it (Drent & Daan 1980; Peterson, Nagy, & Diamond 1990; Bryant & Tatner 1991; Weiner 1992). We will assume that this linkage also pertains intraspecifically, although as yet no studies I am aware of have empirically verified this possibility. The basal and total daily energy costs as a function of body mass therefore follow two lines with a fixed ratio (Fig. 2). The exact position of the total cost line might be anticipated to vary with environmental conditions, so that when it is colder, for example, thermoregulatory costs would increase, and the line would be elevated. Conversely, when it is warmer, the total cost line would be lower. This is a simplistic view of the role of environmental variability on energetics. Intuitively it is attractive, because it accords with laboratory studies of the impact of temperature on resting energy demands: lower temperatures lead to greater resting energy demands (cf. Fig. 1b). However, studies in small birds suggest the link between daily energy demands and ambient temperature in the field may be considerably more complex. In the absence of similar information for small mammals, however, I will assume that decreases in temperature will elevate thermoregulatory demands and, thus, elevate total daily energy expenditure.

Consider now some different scenarios for the effects of intraspecific variation in body mass on energy intake. It is possible to imagine many different relationships between energy intake and body size. For example, increases in mass may have a very steep positive effect on energy gains, because, in competition over food resources, larger individuals may have a distinct advantage over smaller individuals. However, where food is abundant, and competition less likely, gains may be independent of mass. Finally, there may be situations where smaller individuals have greater gains than larger individuals. For example, small mustelids may be

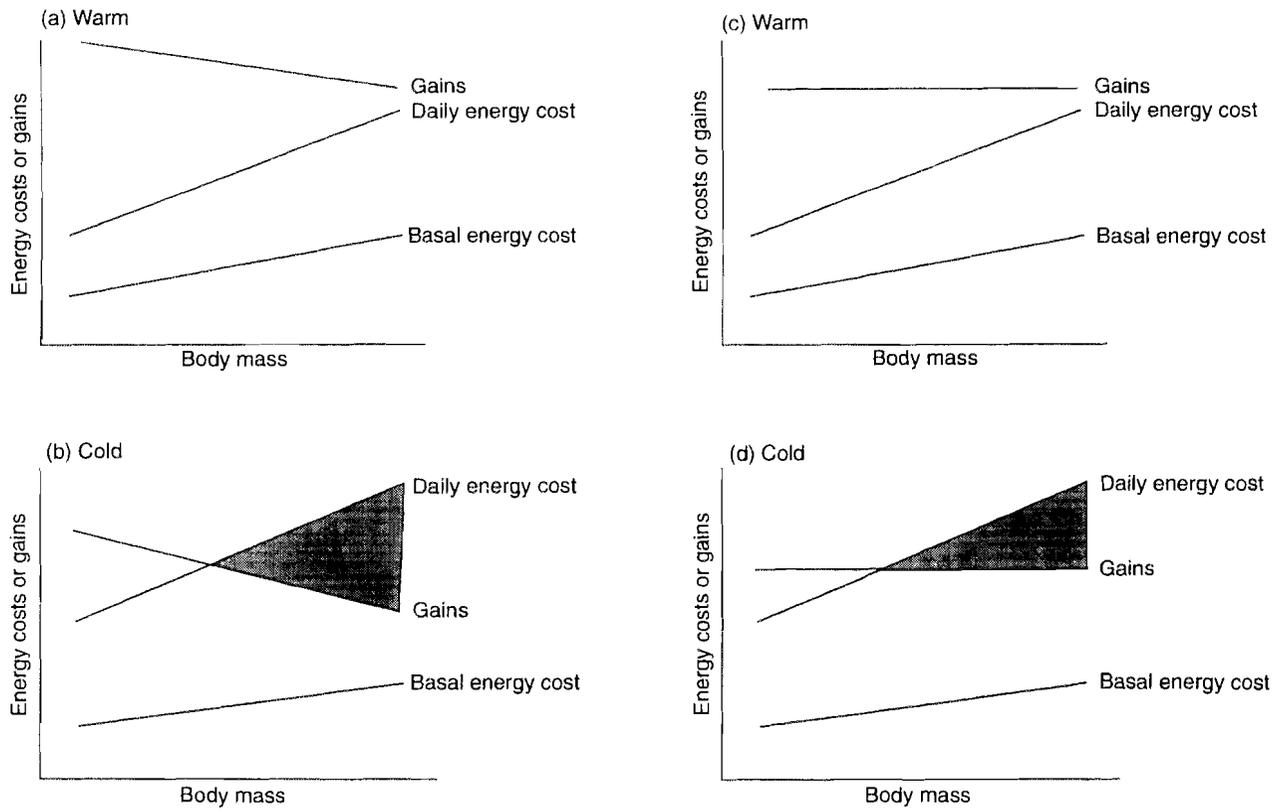


Fig. 2. Models of energy balance including relationships of both costs and gains to variations in body mass. In (a) it is warm and energy gains are negatively linked to body mass. In (b) it is cold and the gain line falls below the cost line for the larger individuals. This would lead to selection for small size. In (c) and (d) the gains are independent of body size. The same effects occur as when the relationship between size and gains is negative.

able to get down burrows with narrower entrances, and gain access to a prey resource which is not accessible to larger individuals (King 1991). In addition to these diverse effects of body mass, we might also imagine that environmental variation would play an important role in influencing the energy gains that animals might achieve. These effects might occur directly or they might occur indirectly because of effects of the changing environment on food availability.

For each different scenario, for the direction of the effect of body mass on energy gains, there would be a series of cost and gain curves the precise location of which would depend on the environmental conditions. The juxtaposition of these cost and gain functions would define whether an individual, of a given body mass, would make an energy balance or not, in that environment, in those particular conditions. For simplicity let us imagine two contrasting environmental conditions: when it is warm and when it is cold. We will assume that these two conditions have opposite effects on energy costs and gains—warmth decreasing costs and increasing potential gains and cold increasing costs but decreasing gains. If we overlay the energy gain patterns on the variation in energy costs we can reveal the situations in which animals are likely to achieve energy balance, fail to achieve energy balance or make an energy surplus. From these patterns of net gain, and net loss, we could thus infer the likely direction of selection on body mass, as a result of energetics (Fig. 2a–d).

In Fig. 2(a) and (b), energy gains are negatively related to body mass. In warm conditions (Fig. 2a) the gain curve always lies above the cost curve. Consequently, in this situation, both large and small animals could make an energy surplus, which would be somewhat larger for the smaller animal. However, in cold conditions (Fig. 2b) the small animals continue to make an energy balance (gains above costs) but large animals fail to do so (gain line falls below the cost line: shaded area). If these cold conditions persisted for any period of time the larger animals in this population would perish. Selection would favour the smaller individuals. In Fig. 2(c) and (d), the energy gains are independent of body size. The pattern of change in costs and gains in this situation is similar to that when gains are negatively related to body size and the consequences are the same: selection will favour smaller individuals. Several previous studies have also suggested that the lower absolute energy costs of small individuals (implicitly combined with an inferred independence of energy gains from body size, as in Fig. 2c) would favour small size in winter (Merritt & Merritt 1978; Ure 1984; Millar & Hickling 1990; Merritt & Zegers 1991). This effect has been suggested to explain the observation that many small mammals reduce their body size during winter (Dehel's phenomenon).

In Fig. 3(a) and (b), the relationship between energy gains and body mass is very steeply positive. This situation might pertain, for example, if there was strong competition for food resources and larger individuals competed favourably. In this situation, it is the smaller individuals which make a loss when it is cold (Fig. 3b: gain line below cost line) and the larger individuals which continue to achieve a positive energy balance. Selection in this situation would be likely to favour larger individuals. Finally, in Fig. 3(c) and (d), the gain line is also positive, but this

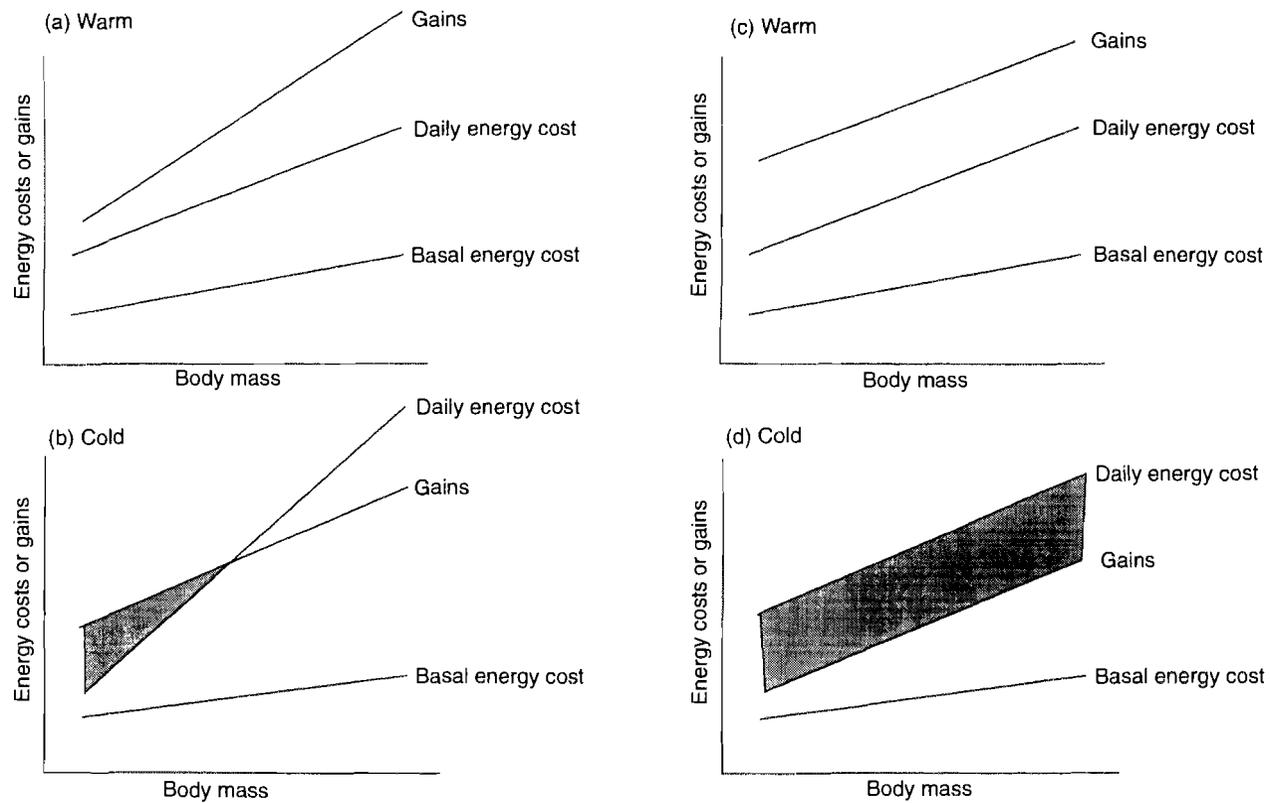


Fig. 3. Models of energy balance including relationships of both costs and gains to variations in body mass. In these examples the gains are positively related to body mass. In (a) it is warm and energy gains are strongly positively linked to body mass. In (b) it is cold and the gain line falls below the cost line for the smaller individuals. This would lead to selection for large size. In (c) and (d) the gains are positively related to body size and increase at the same rate as costs. Consequently net gains are independent of body size.

time has the same gradient as the cost line. In this circumstance, in warm conditions (Fig. 3c) all the animals would make an energy gain, but in cold conditions (Fig. 3d) all the animals would make an energy loss. Consequently, there would be no clear selection on body size as a result of the energetics.

Given this framework, where the effects of changes in environmental conditions affect the elevation of the relationships between energy (costs and gains) and body mass, it is only a small step to imagine more complex scenarios where the gradients of the relationships are also affected by environmental conditions. For example, when it is warm, gains might be negatively related to mass and selection might favour smaller individuals. However, when it is cold, intense competition might result, favouring the larger individuals. This model could lead to size clines as a function of ambient temperature and, hence, latitude, with larger individuals dominating populations where it is colder. It is important to point out that this is one of many potential theoretical effects. There is no reason to favour this latter model over other theoretical treatments where exactly the opposite trends are predicted: with larger animals selected in the warm and smaller individuals favoured in the cold.

These theoretical models suggest that selection on body size will depend critically on the relationships of energy costs *and* energy gains to body mass and how these relationships change with changing environmental conditions. As far as I am aware, no study has yet been performed on a mammal which has elucidated these relationships. The complexity of these models suggests that there is no *a priori* reason to expect from energetics that body mass would increase with increases in latitude. A myriad of different patterns of size-selection as a function of latitude are possible, depending on the cost and gain functions, and how these alter with latitudinal changes in the environment.

When food is absent

When animals have no food available to them they must rely on energy-conservation mechanisms to reduce their energy costs, and their stored fat reserves to supply this energy. As animals will put energy-conservation mechanisms into effect, energy costs will be generally lower than when food is present and they are actively feeding. The amount of time that animals could remain alive while functioning at this low level (called their fasting endurance) would depend on how large their fat reserves were, in relation to how rapidly they were burning them up. The critical factor influencing fasting endurance is therefore the balance of the relationship between energy costs and body size, and the relationship between fat storage and body size. Many studies have observed that the amount of fat that animals can store in their bodies increases disproportionately with body mass (Calder 1984). It has been generally suggested that this increase with size in potential fat storage exceeds the increased energy costs of maintaining a larger body. Consequently, there is a positive relationship between the potential fasting endurance and body size (Rosenzweig 1968; Searcy 1980; Calder 1984; Lindstedt & Boyce 1985; Millar & Hickling 1990). This positive relationship suggests that, in the absence of food, selection will favour larger individuals. Periodic absence of

food has been suggested to be a phenomenon linked to the severity of winter. Therefore the fasting endurance model appears to provide a potential mechanism explaining the size clines of increasing body mass with latitude (reference cited above).

Complete absence of food, however, is unlikely to be a prolonged occurrence. Even for animals which must endure frequent fasts, there must also be times when food is available, between the fasting periods. The actual direction of selection on body size, for animals which must cope with periodic complete fasts, will therefore be a trade-off between the selection pressures during the times when food is available and those when it is not available (Speakman 1992, 1993). As I have indicated above, we can expect virtually any pattern of selection when food is available, depending on the exact dynamics of the cost and gain curves. Consequently, even when food is periodically absent and the fasting endurance hypothesis suggests that selection would favour larger individuals, the total direction of selection, including periods when food is and is not available, could be positive or negative or could favour some intermediate size where the benefits in the fasting phase are not offset by the disadvantages in the feeding phase (e.g. as suggested by Campbell & Slade 1993 for cotton rats, *Sigmodon hispidus*, in Kansas). There is no unambiguous pattern in the direction of selection which can be anticipated, without specific information on the energy costs and gain relationships, as a function of body mass, for a particular situation.

Millar & Hickling (1990) used the fasting endurance model to generate predictions of the likely patterns of body size selection, as a function of periodic food shortage. I have suggested, however, that these predictions are flawed, because they take into account only the direction of selection during the periods of time when food is not available (Speakman 1992, 1993). The intervening periods between fasts are considered only to the extent that there must be sufficient time for all animals to replenish their fat reserves to the maximum capacity. This scenario, however, is only likely if the effect of mass on energy balance during interfasting periods is neutral (Fig. 3b). If other patterns of costs and gains occur, it is possible to envisage selection during the fasting period being strongly reinforced (e.g. if the pattern was like that in Fig. 3a) or, conversely, completely reversed (e.g. if the pattern was like that in Fig. 2a or c).

Hickling & Millar (1993) have suggested that my critiques (Speakman 1992, 1993) of their predictions from the fasting endurance model (Millar & Hickling 1990) are unscientific. They argue that they have developed a hypothesis and derived predictions from that hypothesis, which are open to testing and falsification, as required by the hypothetico-deductive scientific method (Popper 1962). In contrast, they suggest that my argument is that, because the predictions may be falsified, they are untenable. However, this is a misinterpretation of my criticisms. My critique of their predictions is not that they might be falsified, but that they do not derive from the hypothesis. The hypothesis which underlies the fasting endurance model is that energetics has played a role in the evolution of body size. From this hypothesis, Millar & Hickling (1990) derived the fasting endurance

model and generated a series of predictions. However, because they assumed a particular model for what pertains in the periods when food is available, the predictions they generated do not necessarily follow from the original hypothesis concerning the role of energetics in body-size evolution. My argument is that because these predictions do not reflect the original hypothesis, any attempt to falsify them will also not test the original hypothesis.

An analogy may clarify what I mean. Imagine a hypothesis that the earth is not a flat plate, but is actually spherical, like a ball. To test this hypothesis, using the hypothetico-deductive method, the falsifiable prediction might be made that, if the Earth is spherical, all the people living in Australia will have to walk around on their heads. A visit to Australia, to test this prediction, reveals that they do not. What does this mean? I have developed a hypothesis, generated a falsifiable prediction from it, tested the prediction against data, and falsified it. Therefore the Earth must be flat. In this analogy it is very clear what is wrong. The prediction does not stem from the hypothesis. Although it is less obvious, this is the same problem with the Millar & Hickling (1990) predictions. The predictions they generate do not test the hypothesis that energetics has played a role in the evolution of body size, or even the hypothesis that fasting endurance leads to selection in favour of larger body size. It is possible to collect data which completely falsify the predictions made by Millar & Hickling (1990) and yet both these hypotheses may still be correct, because selection on size may be dominated by what is happening when food is available, rather than what happens when it is not.

In summary, even when food is periodically absent, the expected direction of selection on body mass as a result of energetics is not immediately obvious. Various patterns of body mass, as a function of latitude, could be expected to occur and trends of increasing size with latitude are possible, but not particularly anticipated, from the energetics models. Since Rensch (1936) suggested that 81% of North American mammals conform to Bergmann's law, this might indicate that energetics has, in fact, not played a dominant role in the evolution of body size—despite the intuitive appeal of such interpretations. This was also suggested by Scholander (1955), who suggested that the observed variation in body size in most clines was physiologically unimportant for heat balance.

More recent reviews, however, have cast doubt on the figure of 81% derived by Rensch (1936). McNab (1971), for example, found that only 32% of species conformed to Bergmann's law and that the opposite trend, of animals becoming smaller at greater latitudes, was observed as frequently in the data he reviewed. Close examination of the data compiled by McNab (1971) reveals many complex trends. To illustrate these, consider the shrew *Blarina brevicauda*. At latitudes less than 30°N this species has a negative trend of body mass with latitude (opposite to Bergmann's law). Between 30 and 45°N the trend is positive, strongly supporting Bergmann's law. However, at latitudes above 45°N, there is no significant relationship. Geist (1987) also re-examined data on body size and latitude in mammals and came to the conclusion that Bergmann's law was generally inapplicable to the trends observed, which were more often than not complex

functions of latitude showing both positive and negative relationships over different latitudinal ranges. Although the existence of these complex patterns could not be used as evidence to support the energetics models, they are consistent with the expectation from the energetics models, whereas rigid conformity with Bergmann's law would not be.

Empirical data

The models derived above, relating energy costs and gains to body mass, all implicitly assume that body mass has a significant positive effect on basal and daily energy expenditure, explaining the majority of the variation in energy demands under standard conditions. This implicit assumption derives from studies which describe the effect of body mass on energy demands across species (e.g. Kleiber 1961). These interspecific relationships are generally very strong, with variations in mass typically explaining more than 90% of the variation in energy expenditure. Although there have been many hundreds of studies in which metabolic rates of several individuals of a given species have been measured and in which the individuals must have varied in their body masses, these studies seldom present the relationship between the measured metabolic rate and body mass, preferring to eliminate the mass effect by using mass-specific values or a derived scaling exponent, before seeking some other effect. Where relationships are presented, however, they reveal that individual variation in body mass, within a species, explains far less of the variation in energy expenditure than is routinely found in interspecific studies. This is partly because of the range of masses found within a species, compared with that across species. Nevertheless, when plots of energy expenditure against body mass are examined, it is the residual variation in energy demands across animals of varying body mass that is far more striking than the effect of mass itself. Four previously unpublished plots of basal energy expenditure as functions of individual variations in body mass across three different species illustrate this point (Fig. 4). In these plots the variations in body mass explain less than 50% of the variation in energy demands. This is not an effect unique to my laboratory. Reviewing data from several other studies of small mammals reveals similar low coefficients of determination (e.g. Glazier 1985; Earle & Lavigne 1990; Hayes *et al.* 1992; Konarzewski & Diamond *in press*).

This high degree of variation between individuals, which is not related to body mass, raises some interesting questions in the context of the models attempting to relate selection on body size to energetic costs and benefits. Consider the data for the Orkney vole illustrated in Fig. 4(c). For Orkney voles of intermediate mass (35–40 g) some individuals have basal metabolic rates (0.7 W) which are over twice as great as the basal metabolic rates of other individuals of the same body mass (0.3 W). Variations in body mass, at this level, appear to have much less effect on the basal metabolic rate than other intrinsic factors. Focusing attention

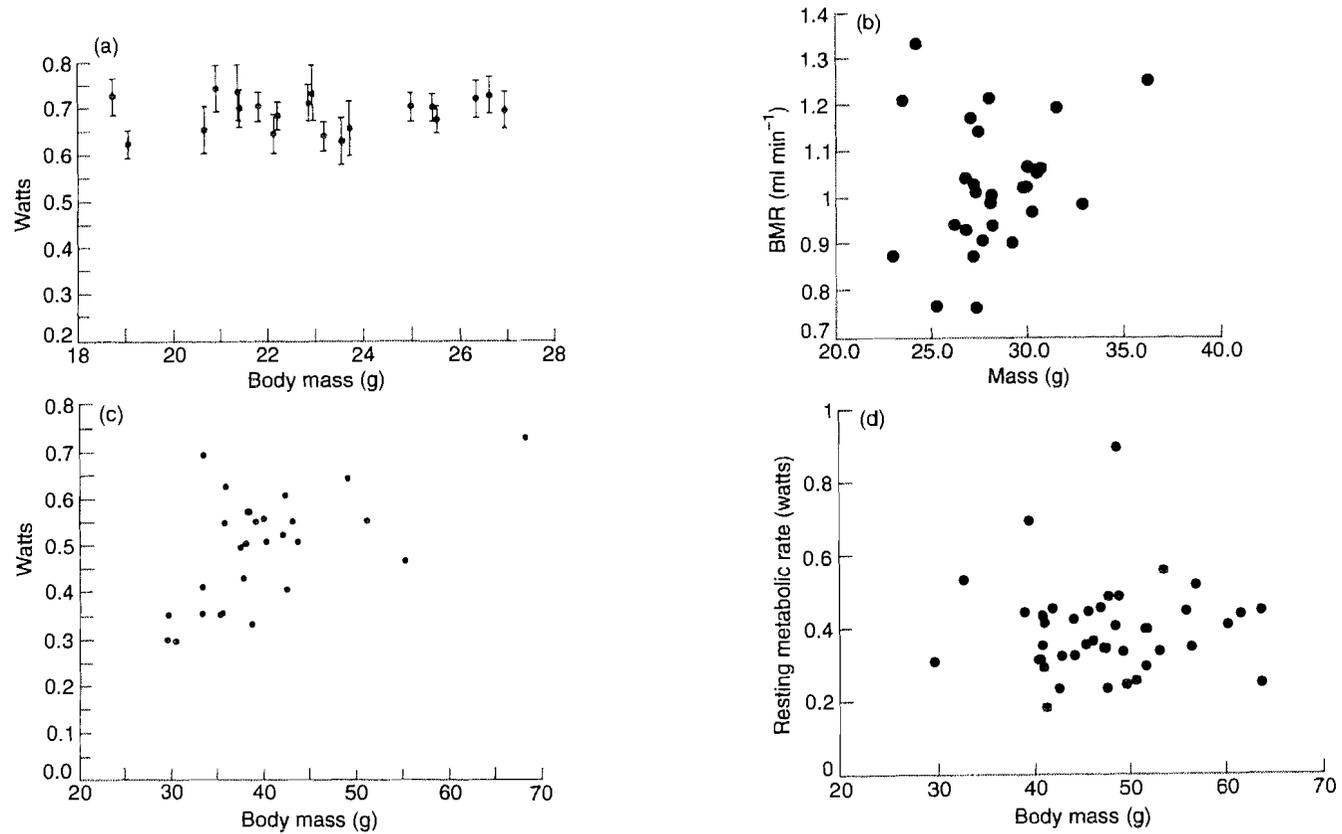


Fig. 4. Relationships between basal metabolic rates and body mass for four groups of small rodents. (a) C57/BL10 mice (J. R. Speakman unpubl.), (b) MF1 mice (S. C. Thomson, M. Johnson, & J. R. Speakman unpubl.), (c) Orkney voles (*M. arvalis*) (J. R. Speakman unpubl.) and (d) Djungarian hamsters (*Phodopus sungorus*) (J. Garvin & J. R. Speakman unpubl.). In all cases body mass does not explain a large amount of the variation in the basal metabolic rate.

on the effects of body mass (as the only intrinsic variable incorporated into the above models) may therefore obscure more interesting questions. It is pertinent to ask, for example, what benefit is derived by the individuals of a given mass which maintain very high basal energy demands? Intuitively, one might anticipate that high levels of BMR would be disadvantageous because they would commit the animal in question to a high rate of food intake. If there was a food shortage, therefore, the animals with lower metabolic rates would appear more likely to achieve an energy balance.

There are, however, a whole series of potential benefits which might be associated with a high basal metabolic rate and which might offset this hypothetical disadvantage. Animals with greater basal metabolism at a given mass might be more able to take in and digest food and, thus, have elevated gains as well as elevated costs. They may be more aggressive and, thus, more likely to compete favourably for food as it becomes scarce. In some small birds, for example, it has been suggested that there is a link between metabolic rate and dominance, independent of the effects of mass, but studies of the link between basal metabolism and dominance in small mammals are currently lacking.

In the last part of this paper I want to consider one further potential energetic benefit which may be linked to individual variation in basal metabolic rate. That is the link of basal metabolism to thermogenic capacity. When animals are placed in the cold, in the laboratory, they increase their thermogenic capacity. A direct consequence of this enhanced thermogenic capacity is that if the animals are subsequently exposed to extremely cold temperatures they survive longer than animals which have had no pre-exposure. Another effect which occurs in synchrony with the enhanced thermogenic capacity, when animals are exposed to the cold, is that their BMR increases. In short-tailed field voles (*Microtus agrestis*) we have shown recently that the increase in BMR is not linked with hypertrophy of the alimentary tract, but rather appears to be more closely linked to changes in the concentration of the uncoupling protein in the brown adipose tissue (McDevitt & Speakman 1994), which is the principal locus of the enhanced thermogenesis (Foster & Frydman 1979).

If enhanced thermogenesis during cold acclimation is linked to increased BMR, is it possible that natural variation in BMR is linked with variation in thermogenic capacity? One measure of thermogenic capacity is the increase in the metabolic rate following injection of noradrenaline (NA) which activates brown adipose tissue. We have recently collected some data in wood mice (*Apodemus sylvaticus*) which indicates that this is indeed the case. Individual variation in the basal metabolism of wood mice is possibly linked to the NA-induced metabolic rate of the same individuals (Fig. 5a: McDevitt, Haim, Thomson, & Speakman in prep.). This effect is found, not only in the raw relationship, which could reflect the covariation of both factors with body mass, but also in the residuals of both factors to body mass (Fig. 5b). Therefore animals of a given mass, which have a higher than expected basal metabolic rate for their mass, appear also to have a greater than expected thermogenic capacity for their mass.

These observations suggest that individual animals may pursue different

thermoregulatory strategies when entering the winter. At one extreme animals may opt for a low BMR/low thermogenic capacity option. This might be predicted to be a favourable strategy when conditions are relatively mild, food relatively abundant, and populations low so that competition is reduced. These animals might be most likely to make an energy balance because of their low energy demands. However, if there was a very cold period these animals would die, not from an inability to meet an energy balance, but rather from a lack of metabolic power. In contrast, at the other extreme, animals might opt for the high BMR but high thermogenic capacity strategy. This might make it hard for them to achieve an energy balance, particularly under conditions of food shortage, but they would be more likely to have sufficient metabolic power to survive periods of intense cold. Since cold acclimation takes approximately 10–20 days to develop in the laboratory, switching between strategies would not be a viable option for an animal suddenly confronted with a prolonged period of intense cold.

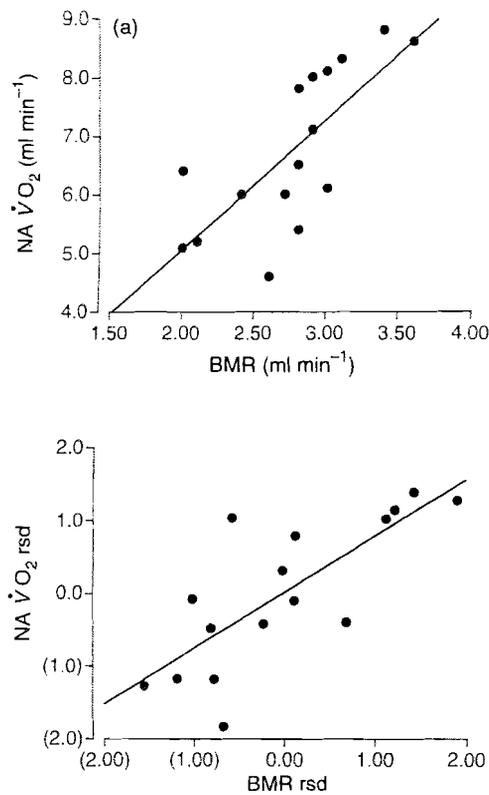


Fig. 5. The relationship between noradrenaline induced metabolic rate (NA $\dot{V}O_2$) and basal metabolic rate (BMR) in wood mice (*A. sylvaticus*) (from R. M. McDevitt, A. Haim, S. C. Thomson, & J. R. Speakman unpubl.). In (a) raw values for both parameters are used and in (b) the residuals of the parameters to the relations with body mass are plotted. In both cases there was a significant positive relationship.

These findings add a novel dimension to the role of energetics as a factor influencing winter survival of small rodents. Studies which have attempted to elucidate how energetics might impact on winter survival have, to date, concentrated entirely on the problem of achieving energy balance. A second problem, however, may be that of achieving heat balance and, thus, of having sufficient metabolic power to generate adequate internal heat to achieve heat balance under extreme conditions. Our data for the wood mouse (Fig. 5 a and b) indicate that the solutions to these two problems may interact negatively. This negative interaction leads to some extremely interesting possibilities for trade-offs in energetic strategies adopted by animals as they enter the winter. It also indicates that the role of energetics as a factor influencing overwinter survival may be considerably more complex than models based on energy balance alone would predict.

Conclusions

Models of energy balance based on costs alone cannot predict the effects of energetics on the selection of body size. Using both costs and gains it is possible to envisage a variety of effects of energetics on body mass which might result in selection for larger or smaller individuals depending on the exact relationships at any particular site. At present the crucial parameters necessary to construct a prediction of the likely effects of energetics on size selection are not available for any small terrestrial mammal. Size clines as a function of latitude can be predicted by using energetics models, but the direction of the cline is not always expected to be positive. A diversity of patterns can be predicted, and this corresponds with the trends observed in nature. Observations of the relationship between metabolic rate and size within species reveals that mass variations generally explain less than 50% of the variation in metabolism. Having a high metabolic rate for one's mass would superficially appear disadvantageous in terms of meeting an energy balance. Animals with higher than anticipated metabolic rates may, however, derive other advantages, one of which could be enhanced thermogenic capacity. There may therefore be a trade-off between capacity to achieve an energy balance and capacity to achieve a heat balance. This suggests that the relationship between energetics and overwinter survival may be considerably more complex than models based on energy balance alone predict.

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