The Cost of Living: Field Metabolic Rates of Small Mammals

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I. SUMMARY

Energy is a universal currency that is required for all biological functions. It has been frequently suggested that the rates at which animals can expend energy are limited in some manner. These limits may be extrinsic, set by the availability of energy resources in the environment, combined with the inability of animals to harvest these resources effectively. Alternatively the limits may be set intrinsically by aspects of the animal’s physiology. Some evidence from field manipulations of birds and insects suggests that the limits are more likely to be intrinsic than extrinsic. Intrinsic limits may be set centrally (e.g. by capacities of the alimentary tract or the respiratory system’s ability to provide oxygen) or peripherally at the sites where energy is utilized (such as the muscles during exercise, brown adipose tissue during thermoregulation, or mammary tissue during lactation).

In the late 1980s it was widely believed that the intrinsic limitations were centrally mediated. In part this belief originated in observations that free-living energy demands of animals appeared to be linked to the level of their basal metabolic rates. This link was believed to arise because the major tissues contributing to basal metabolism are those that limit sustainable metabolism, namely the alimentary tract and associated structures such as the liver and kidneys. It was suggested that the physiological aspects of this linkage impose a limit on expenditure at around either 4x or 7x basal metabolism. Laboratory manipulations of lactating mice have confirmed a link between sustainable expenditure and basal metabolism but simultaneously cast severe doubt on the notion of a central limit, and it is currently more widely believed that limits on sustainable expenditure are set peripherally.

In this review I have summarized 185 measurements of the cost of living (daily energy expenditure or field metabolic rate) made on 73 species of small mammals (weighing less than 4 kg), using the doubly labelled water method. Field metabolic rate (FMR) was dependent on body mass, ambient temperature, and latitude of the study site. I confirmed that the effect of body mass remained when the phylogenetically independent contrasts of mass and RMR were calculated. There was a strong relationship between FMR and RMR. However, this relationship was much weaker when the shared effect of mass was removed. There was a significant relationship between the residuals of the phylogenetic contrast relationships of FMR and RMR to body mass. When the shared variance due to temperature and latitude was removed, the relationship was further weakened, and dependent only on two outlying data points.

Evidence supporting a link between FMR and RMR is very weak. The ratio of FMR to RMR averaged 3.4. The maximum ratio was 7.3 and the minimum was 1.6. Twenty per cent of values exceeded the postulated limit at 4x RMR. Most small mammals are working at well below their supposed physiological limits. In this sample there was no link between the ratio of FMR to RMR and body mass, and no evidence that the ratio was lower in the Chiroptera than in other orders.

The absence of these associations does not support the trade-off explanation for the observed discrepancy between habitual levels of expenditure and the supposed limits. Expenditures by semelparous marsupial mice were greater than the average ratio, supporting the trade-off hypothesis. There was a significant link between the ratio and diet. Small mammals exploiting more energy-abundant resources had greater ratios. These latter data support the extrinsic limitations hypothesis.

Overall these data provide no support for the notions of intrinsic physiological limits acting at either 4x or 7x RMR. Such limitations may be illusory. Independent evaluations of limits on performance from ultra-distance runners and migrating birds suggest that animals may be physiologically capable of expending up to between 9x and 15x RMR daily. They routinely do not do this because of limits imposed by the extrinsic supplies of energy and possibly trade-offs with future fecundity. In small mammals the former may be most important, but in other groups (for example, birds) trade-offs may dominate.

II. INTRODUCTION

A. The Importance of Energy in Living Systems

Living things are the most complex and organized structures that we are currently aware of. Chemically the elemental composition of living objects is not particularly noteworthy. It is the complexity and organization of these elements that sets the living and non-living apart. However, there is a potential downside to being so complex and organized: the second law of thermodynamics. This is the inexorable trend towards increased entropy in a closed system. Fortunately, living things are not closed systems. They are consequently able to maintain a high level of complexity and organization for a sufficient time to enable them to reproduce, and thereby propagate the genetic
information they are carrying into the future gene pool. They do this by taking materials from outside their own systems and using these materials to shore up and repair the perpetually decaying fabric of their organization. Eventually, however, once the propagation of genes has been completed, the rates of repair decline, but the rates of decay do not (Barnett and King, 1995). It has been calculated, for example, that the DNA in every cell is hit by oxidative damaging agents approximately $10^4$ times each day (Ames et al., 1995). Our capacity to repair this damage is considerably greater in our midlife than in later life (Barnett and King, 1995). Physiological attrition of our entire system consequently increases (Meyer et al., 1991) until eventually the organization becomes reduced to such an extent that the unspectacular amalgamation of elements becomes just that. It is no longer sufficiently organized to be classed as an animate object. Life and death are convenient points of reference along a continuum of complexity and organization. Life is the quasi-steady state in which the rate of repair matches the rate of degradation. Death is the unsteady state that results when it does not.

Automobiles are also fairly complex structures. They are not quite so organized and complex as living things, but at a lower level they illustrate the need of any organized system to be continually maintained. Left alone, without any maintenance, automobiles gradually decay, until eventually they fail to function as vehicles any more. Maintenance of complexity in a car, or a living system, requires two distinctly different activities to be performed continuously, and two distinct types of material are involved. Anyone who has had a car repaired at a garage will be familiar with these two separate activities when they have received a bill separated into the costs for parts and labour.

Parts and labour are the two things that all organized systems need: materials (parts) to repair damaged components of the existing system, and the energy (labour) to perform the work necessary to remove the damaged pieces and replace them with undamaged bits. Living systems require nutrients in the form of macronutrients, such as protein and fat, or micronutrients, such as vitamins and trace elements. It is important, however, to distinguish between the elements of nutrition that concern replacement of the essential building blocks of the system (parts) and the nutrients whose role is to supply the energy necessary to integrate the building blocks into the system as it is repaired (labour). The requirement for energy to sustain the complexity and organization of life is a distinct requirement from the needs for specific essential building blocks. Energy is often called a nutrient, but I think this usage obscures the very real difference between energy and other essential aspects of the diet. I think this confusion arises in part because animals can mobilize parts of their body that have been taken in as essential building blocks and use them to provide energy, if they require to do so. Normally, however, this is only a desperate response to a shortage of energy intake in the diet. It is a bit like selling the seats in your car to pay for some petrol—a measure that would work if needed, but not something you would (could) do every day. By using this analogy I do not mean to imply that animals do not store energy in their bodies for use at some later time, as most animals do store energy in their bodies as lipids, and withdraw these reserves to cover shortfalls in the external food supply. In the above analogy this is equivalent to the petrol in the fuel tank, not the seats.

Energy is required by animals not only to sustain the complexity of their systems, it is also required to allow them to perform work and also to maintain homeostasis. Animals perform work whenever they do anything at that involves movement. During movement animals transform chemical energy into kinetic energy, potential energy and heat. Ultimately the kinetic and potential energy also becomes heat. This requirement for energy includes all the movement going on inside the animal: pumping of the heart, breathing in and out, contracting the alimentary tract, as well as all the more visible and audible aspects of movement such as running, jumping, fighting, copulating, singing and flying. All movements made by living things, no matter how trivial, require energy to be performed.

Animal systems also generally exist a long way from natural equilibria. Animals maintain non-equilibrium ionic potentials in their cells, for example, and their body temperatures are perturbed from the levels they would reach if the system were left to reach equilibrium. To maintain these non-equilibrium states, animals must also use energy, for example to operate ionic pumps in cells to sustain the ionic gradients (Swaminathan et al., 1982, 1989; Poehlman et al., 1993). The ubiquitous demands for energy to fuel all biological processes means that energy is a fundamentally important currency of life (Kleiber, 1961; Bartholomew, 1982; Brafield and Llewellyn, 1982; Blaxter, 1989; McNeil Alexander, 1999).

**B. Limitations on Animal Energy Expenditure**

On 16 June 1999, during the Tsiklitiria International Track Meeting in Athens, Greece, the 100-m sprint for men was won by the American Maurice Greene in a time of 9.79 s. This was the fastest time that a human being had ever covered the distance entirely under their own steam (and without the assistance of drugs—the Canadian Ben Johnson has also clocked this time but his run is not formally recognized as a record). Several animal species are also capable of making very fast sprints of short duration. Cheetah (*Acinonyx jubatus*), for example, can sprint at speeds approaching 75 km h$^{-1}$ for short periods. Measurements of energy expenditure during sprints by cheetah suggest it might be as high as 50 times the resting metabolic rate (RMR), measured inside the thermoneutral zone (Taylor, 1974). Rheas (*Rhea americana*) also expend energy at over 35× RMR when sprinting (Bundle et al., 1999).
In the Athens games the 400-m sprint race was run in 44.7 s. This was also a remarkable running feat, but it was not a world record. The fastest that an athlete has ever run 400 m was in Seville, Spain, in 1999 when Michael Johnson covered the distance in 43.18 s. Although it covers four times the distance, Johnson's record is 4.02 s slower than four times the 100-m record time set by Greene. The 400-m athlete cannot sustain the same power output as a 100-m athlete even though the race still lasts for well under 1 min. This phenomenon is further exemplified by the fact that, despite the potential hindrance of baton changes, the 4 × 100-m relay (37.4 s) is run almost 6 s faster than a single person can run 400 m. (It is run faster than four times the 100-m race because athletes have running starts at three of the four sections).

Figure 1 shows a plot of the speeds averaged during current (1999) world records for men running different distances, against the duration of the races. This figure demonstrates that there is a progressive decline in the speeds achieved by world record-breaking athletes as the distance and duration over which they run increases.

**Fig. 1.** Maximum running speed (m s⁻¹) attained by men in competitive athletics events as a function of log₂ duration (s) of the event. There is a progressive decrease in the achieved maximum speeds. The pattern of decline follows four distinct phases, which appear to reflect different physiological limitations on the capacity to expend energy.
NADH and simultaneously converting some ADP to ATP. The production of lactate therefore allows a greater rate of production of ATP than by oxidative phosphorylation alone. Measurements of lactate accumulation, however, suggest that this route can be sustained for only about 3–4 min. Thereafter the production of ATP is supported entirely by oxidative phosphorylation. This corresponds to the third phase in the relationship of running speed to duration (Figure 1, line C).

Readers who have competed in marathon events may be surprised that the curve relating record speeds to duration gives no indication of a decline in performance at around 1.75 h. For many amateur marathon runners this represents a time when substrate availability appears to decline, and the runner appears to hit a ‘wall’ where sustaining further activity at the same pace is extremely difficult. The absence of this phenomenon in the world record data may, however, only suggest that individuals capable of performing at world record levels do not hit this limit until much later. Measurements of substrate utilization suggest that there is a progressive shift, from using predominantly glycogen, to predominantly fat, to fuel oxidation as duration of exercise increases (Edwards et al., 1934). The ‘wall’ probably reflects exhaustion of glycogen reserves and difficulty in mobilizing fat at the same high rate as glycogen. Many marathon athletes pre-load their systems with carbohydrate to boost their glycogen stores before performing to prevent hitting this substrate limitation before the end of the race.

Competitive human running events, which are commonly competed for in international games, last a maximum of 2.5 h. The pattern of speeds for these records establishes that physiological barriers limit energy expenditure over these time periods. Extrapolation of Figure 1 (line C) suggests that if a competitive event existed that involved running continuously for 24 h, and if no further substrate changes occurred, humans could probably sustain a running speed of about 4.0 m s⁻¹ and the race would cover a distance of about 346 km. This would be equivalent to eight sequential marathons in a single day.

The furthest distance ever run to date (1999) in 24 h was 295.03 km. A Greek called Yiannis Kouros in Canberra, Australia, achieved this on 1–2 March 1997. The discrepancy between the predicted and observed distances may indicate that further changes in substrate utilization occur after 2.5 h (possibly a delayed ‘wall’ effect; Figure 1, line D), or it may be that this event is less keenly competed for than the events of shorter duration. We do not know for certain how much energy Yiannis Kouros expended during his 24-h record-breaking run. However, we can make an estimate because there have been many studies of the energy costs of human locomotion as a function of running speed. Given the distance he ran, and the time it took him, we know that Yiannis ran at an average speed of 3.4 m s⁻¹. Using the relationship between running speed and oxygen consumption (Margarin et al., 1963), a person sustaining this speed for 24 h would consume a total of about 5040 litres of oxygen. Assuming a respiratory quotient of 0.85 leads to a predicted energy expenditure of 101 MJ (see the section on Methods below and Appendix A for details of the methodology for measuring oxygen consumption and its conversion to energy expenditure). The human resting metabolic rate at thermoneutral is about 7.1 MJ per 24 h (Schmidt Nielsen, 1975) and thus Yiannis was probably expending energy at a rate of about 101.2/7.1 = 14.2 × RMR. This is probably the maximum level of energy expenditure that could be sustained over a 24-h period.

Numerous other animal species emulate this level of performance. Several species of migrating birds, for example, may fly continuously for protracted periods when they cross areas of open ocean. Barnacle geese (Branta leucopsis) migrating from the islands of Svalbard well above the Arctic Circle to spend the winter months in Scotland are a well studied example (Butler et al., 1998). Satellite tracking studies have shown that these birds take off from Svalbard and fly in several stages down the Norwegian coast, occasionally flying continuously for up to 14 h, until they reach their winter habitat in south-west Scotland (55°N) (Butler et al., 1998). Because flight is energetically expensive, with the energy costs normally ranging between 13 and 18 times resting metabolic rate (Tucker, 1966; Thomas, 1975; Masman and Klaassen, 1987; Rothe et al., 1987; Butler and Bishop, 1998; Winter and von Helversen, 1998), these animals are probably expending energy at this level for the majority of the duration of the trip. Measurements of heart rate in migrating barnacle geese (Butler et al., 1998) suggest that their heart rates are actually substantially lower than those recorded in the same species trained to fly behind a truck (Butler and Woakes, 1980). This might suggest that flight during migration is much cheaper than that reported in other studies. However, there are several alternative explanations for the low heart rate, and at present it is not possible to extrapolate the energy demands of migrating geese from the heart rates of geese flow in different situations (Butler et al., 1998). Indeed, by making assumptions about oxygen extraction efficiency and stroke volume, and combining these with the observed heart rate, Butler et al. (1998) estimated that the oxygen consumption during flight was 302 ml min⁻¹ at the start and 215 ml min⁻¹ at the end of the flight. These values are equivalent to approximately 21 and 18 times the resting oxygen consumption at the same stages respectively. Since some birds flew for between 60% and 80% of the time on migration, this would imply sustained expenditure of between 13 and 15 times resting metabolic rate over the entire 2.5–4-day trip, very similar to the levels expended by a human running for an entire day.

Although mammals weighing around 100 kg (such as humans) and birds can perhaps sustian maximum energy expenditures of around 12–15 × RMR, it would appear that smaller terrestrial mammals do not have the same capabilities. Taylor (1981) summarized the data across all species of the maximum
J.R. SPEAKMAN reported levels of oxygen consumption, and found that maximum oxygen consumption ($V_{O_2} \text{max}$) scaled with body mass with the relationship:

$$V_{O_2} \text{max} (\text{ml O}_2 \text{ min}^{-1}) = 0.43M_b(g)^{0.81}$$

whereas the standard or resting metabolic rate scales with the relationship:

$$V_{O_2} (\text{SMR}) (\text{ml O}_2 \text{ min}^{-1}) = 0.063M_b(g)^{0.75}$$

(after Kleiber, 1975) where $M_b$ is body mass. Because the exponents of these relationships are slightly different, the curves describing these trends diverge slightly as mass increases. This means the $V_{O_2} \text{max}$ as a multiple of resting metabolic rate also increases as animals get bigger. This effect can be illustrated by considering predicted levels of oxygen consumption for a 70-kg and for a 70-g animal. For the 70-kg animal the ratio is 13.3x (close to the value predicted for a human based on running speeds). However, the predicted ratio for a 70-g animal is only 8.8x. This lower ratio for small terrestrial mammals is reinforced by the review of McMillan and Hinds (1992), who compared the maximum oxygen consumption of rodents during exercise with the resting oxygen consumption. Their results are plotted in Figure 2. In this sample of animals the maximum oxygen consumption induced by exercise followed a curve that was parallel to the resting metabolic rate curve, leading to a fixed ratio between the two of about 7x. This lends support to the idea that, for terrestrial small mammals, the maximum daily energy expenditure may be more constrained at the upper margin than the expenditure of either larger mammals or birds (and presumably bats).

History does not record what Yiannis Kourous did on 3 March 1997, the day after his record-breaking 24-h run. It is a pretty safe bet, however, that he did not immediately set out on a repeat of his performance. Similarly, migrating birds cannot migrate over expanses of open ocean endlessly. They must prepare for the trips by depositing energy stores which they utilize during the flight (Marsh, 1983; Biebach, 1998; Butler et al., 1998; Jenni and Jenni-Eierman, 1998), and perhaps must recuperate once they arrive at their destination. The performances of 24-h record-breaking distance runners and transoceanic migrants are consequently not sustainable feats, since the energy expenditure over the periods when the heavy exercise occurs cannot be sustained indefinitely.

There has been considerable interest in the levels of the maximum average daily rates of energy expenditure that animals can maintain for indefinite periods. In practice this means the maximum expenditure that animals can engage in over protracted periods, whilst still performing all the activities essential for longer-term survival (for example, sleeping sufficiently to avoid prolonged sleep deprivation). Moreover they must intake sufficient food that the energy expenditure is covered completely, i.e. the animal is not relying on depletion of stored energy reserves to support the high rates of expenditure. When animals perform at this level, it is generally called the maximum sustainable metabolic rate (Peterson et al., 1990; Hammond and Diamond, 1997).

The reasons why ecologists are interested in this maximum sustainable level of energy expenditure is that it forms an interesting upper boundary on the sum total of activities in which an animal can engage. Because all activities require energy, the summed requirements of the activities that an animal performs must fit within the envelope of the total sustainable energy requirements (apart from interesting multiple uses of resources such as using the heat generated from activity to pay the costs of thermoregulation; e.g. Paladino and King, 1984; Webster and Weathers, 1990; Zebra and Walsberg, 1992). If we knew what the sustainable limits were, this would provide a powerful tool for predicting the limitations on animal performance.

For example, imagine that we know a given animal species is capable of expending a maximum sustainable energy expenditure of 40 kJ each day. If

Fig. 2. Maximum oxygen consumption of small rodents in relation to resting (standard) metabolic rate (SMR). Mammals stressed by cold temperatures (and mixtures of helium and oxygen); $\triangle$, mammals stressed by exercise. Reversed symbols ($O$, $\blacktriangle$) reflect the corresponding standard metabolic rate. The levels for exercise exceed those for cold exposure and indicate a maximum expenditure of around 7-8x RMR. From McMillan and Hinds (1992).
the animal is an endotherm, we also know that its energy requirements increase in relation to decreases in ambient temperature. If each drop in temperature by 1°C below the thermoneutral zone increased daily energy demands by 1 kJ, and the basal requirement was 10 kJ, then we would know that the species in question could not survive for protracted periods in areas with ambient temperatures more than 30°C below its lower critical temperature. Imagine the same animal requires 5 kJ per day to raise an offspring. In warm regions the spare capacity to expend energy beyond that committed to thermoregulation might allow animals to raise up to four offspring, but in cold conditions the animals may be able to raise only two, and in some regions there may be no spare capacity for reproduction at all, although survival might be possible. The notion of a sustainable maximum energy expenditure therefore provides an attractive framework for understanding many aspects of animal ecology, such as geographical distributions and breeding ranges (Root, 1988; Bozinovic and Rosenmann, 1989). Most of life history theory is founded on the assumption that energy resources are limited and animals must therefore trade-off their use of these resources (Gadgil and Bossert, 1970; Pianka and Parker, 1975; Steams, 1976; 1983; 1993; Calow, 1979; Townsend and Calow, 1981).

Part of the problem in sustaining their energy expenditures at 12–15x basal metabolic rate (BMR) for transoceanic migrant birds, and perhaps also for ultra-long distance runners, is the fact that while they are engaged in their high rates of energy expenditure they are unable to feed, and perhaps also to sleep properly. This is particularly the case for the birds, because over the open ocean, at the high altitudes at which they migrate, there is no food available. Runners also need to stop to consume adequate amounts of food and to sleep. Consequently, in both examples, the high rates of expenditure over 24 h cannot be sustained indefinitely, because over the long term the expenditure cannot be balanced by sufficient energy intake.

Ultra-long distance runners compete in events that normally last for up to 6 days, although there are some exceptional events that last for over 20 days and cover up to 3100 km (for example, the Sri Cinnmoy event in the USA). The relationship between speed and distance for these events follows a different slope, indicating further limits on the performance capabilities as the duration of events increases (Figure 1, line D). This is mostly related to a decrease in the proportion of the period that athletes are able to remain actively running, as opposed to a decline in the running speed. The 6-day world distance record is also held by Yiannis Kouross. Between 2 and 8 July 1984 he covered 1022 km in New York. Note this is an average of 170 km per day, which is only 58% of the 24-h record distance set by the same man. Assuming that he was running for 60% of each day and had an expenditure during this time of 14.2x RMR (above) and that during the rest of the time he expended energy at only 2x RMR, over this more prolonged period his expenditure was probably down to around 9x RMR. For humans this is probably the maximum possible metabolic rate that can be sustained over a protracted (possibly indefinite) period.

Some birds do fly almost continuously and feed when they are flying, for example several species of swifts (Apodidae), terns (Sternidae) and the albatrosses (Diomedeidae). It is even suggested that swifts sleep and copulate on the wing (Lack, 1954) and from fledging to their first breeding attempts, 2 years later, they may never land, covering approximately 500 000 km in continuous flight. It is interesting that all these bird species have extreme adaptations of their wing morphology (Greenwalt, 1962; Norberg, 1990). The wings have very high aspect ratios, which means they are very long and thin. Theoretical aerodynamic modelling suggests that this form of wing shape minimizes the energy costs of flying (Pennycuick, 1969; 1989; Rayner, 1979; Norberg, 1990), but has some disadvantages; for example, manoeuvrability is reduced and it is difficult to fly slowly (Norberg, 1986, 1990), hence the birds have difficulty taking off from flat surfaces.

Direct measurements of the energy costs of flight, in these animals, have been measured. They confirm the predictions of the aerodynamic models as the costs are between about 2x and 5x BMR (e.g. Utter and LeFebvre, 1973; Hails, 1979; Bryant and Westerterp, 1982; Flint and Nagy, 1984; Westerterp and Bryant, 1984; Costa and Prince, 1987; Bevan et al., 1999a; Adams et al., 1986), compared with 13–18x BMR for most other birds (Tucker 1966; Masman and Klaasen, 1987; Rothe et al., 1987) and bats (Speakman and Racey, 1991; Winter, 1998; Winter and von Helversen, 1998; Winter et al., 1998). There are no continuously flying birds with wing shapes that would require continuous energy expenditure at the much higher levels. This observation suggests that there is some other limiting factor on the rates at which birds can expend energy, apart from the physiological aspects of substrate utilization by actively metabolizing tissues. If another limit existed, for example at around 5x BMR, this would constrain the types of animals that fly continuously to be only those with flight morphologies permitting such cheap flight.

There are two different types of hypothesis that aim to explain the nature of the limitations on sustainable daily energy expenditure. These might be termed the extrinsic and intrinsic hypotheses.

C. The Extrinsic Limitation Hypothesis

The extrinsic limitation hypothesis suggests that the dominant limitation on the expenditure of most wild animals is the availability of their food supply from the environment. Animals must forage for energy, and must therefore expend energy in its acquisition. If food is widely scattered, and the energy spent finding it is significant, the net energy return when foraging may be relatively small. Animals may be limited in their total energy demands, therefore, by the duration of time they can devote to searching for and ingesting food (Weiner,
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In richer habitats, where the net gain when foraging is higher, or where the time available for foraging is greater, the maximum sustainable energy demands would be predicted to be higher if this hypothesis were correct.

The extrinsic limitation hypothesis is intuitively attractive, and formed a fundamental assumption underpinning much of the development of optimal foraging ideas in the late 1960s and 1970s. Optimal foraging theory, in its classical form, was based on the premise that animals should be selected to maximize their net intake of energy during the periods that they spend foraging (Emlen, 1966; McArthur and Pianka, 1966; Schoener, 1971; Charnov, 1976; Krebs, 1978). This would likely be important to animals if either energy supply in the environment were limiting or, alternatively, if there were a selective advantage in minimizing the time spent foraging to meet their energy demands (Schoener, 1971). The former of these fundamental assumptions of the theory is equivalent to the extrinsic limitation hypothesis.

There are some data that are consistent with the extrinsic limitation hypothesis. For example, it is widely observed that clutch sizes of small birds get larger as one moves from the tropics to the temperate and arctic regions (Skutch, 1949). One interpretation of this trend is that energy supply is lower in the tropics, and increases as one moves further north during the summer, because day length is longer, thereby increasing the time available for foraging. Longer periods of input of solar radiation may also lead to greater environmental productivity in temperate and arctic regions when compared with tropical areas during the summertime. The greater amounts of energy available to animals in temperate and arctic regions may therefore allow them to raise more offspring, the energy costs of which rise in relation to the number being raised (e.g. Bryant and Westerterp, 1983; Kenagy et al., 1989).

There can be no doubt that, as summer turns into winter in the temperate and arctic regions, the extrinsic supply of energy becomes a potent limitation on the energy expenditure of many small endothermic animals. There are three fundamentally different ways that animals can respond to the decline in food supply during the winter. The first response is literally to flee the problem by migrating away from these regions to more equable climates. To migrate from temperate and arctic regions to tropical or subtropical areas, animals need to travel long distances. Typically migrations need to be at least 1500 to 2500 km to avoid successfully the extrinsic limitations that winter imposes. These distances pose strict limitations on the types of animals that can use this strategy. Studies of short-tailed field voles (Microtus agrestis) in captivity suggest that the absolute maximum distance that voles can travel during the night-time, when they are active, is about 15 km (Redman, P. and J.R. Speakman, unpublished data). If voles were to migrate 2500 km it would take them over 300 days to travel this distance and return for the breeding season the following year (Speakman and Rowland, 1999; see also similar arguments in McNeil Alexander, 1998, 1999). In contrast, small birds can fly at speeds of 15 m s\(^{-1}\) for protracted periods, and with tail winds may achieve ground speeds of 25 m s\(^{-1}\). At these speeds they could cover approximately 300-300 km each day (Hedenstrom and Alerstam, 1998) and migrate 2500 km in less than a fortnight. Migration over land is a feasible strategy only for small animals that can fly. It is used by approximately 30% of temperate and arctic birds (Baker, 1978) and several species of bats (Davis and Hitchcock, 1965; Strelkov, 1969) but is unknown, for example, in rodents.

The second strategy for coping with the decline in the extrinsic supply of energy is to flee physiologically, by using hibernation. Hibernation involves regulating body temperature at a considerably reduced level (Hock, 1951) and suppressing metabolic rates (Geiser, 1988; Heldmaier et al., 1993; Geiser and Ruf, 1995) so that energy demands are massively reduced to match more closely the reduced extrinsic availability of food supply (Kenagy, 1987). Even this may be insufficient and the animals usually also store considerable deposits of fat to supplement the available extrinsic energy supply during this period (Krzanowski, 1961; W.W. Baker et al., 1968; Kunz et al., 1998b; Speakman and Rowland, 1999). Hibernation is a strategy adopted by many small mammals to survive the winter months.

The third approach to surviving the winter is to remain endothermic but to reduce energy requirements by behavioural or morphological adaptations rather than physiological modifications. For example, in several species there is a breakdown in territoriality and animals become sociable and gregarious, allowing them to conserve energy by huddling together in shared nests (Vogt and Lynch, 1982; Karasov, 1983). Many species build well insulated nests during winter (Casey, 1981); they may also increase the insulation of their pelage to reduce heat loss (Hart and Heroux, 1953; Chappell, 1980); and often they also reduce their body masses to reduce total energy requirements (Iverson and Turner, 1974; Heldmaier, 1989). In some species, such as shrews, this may include reductions not only in body mass but also skeletal remodelling and shrinkage (Pucek, 1970; Pasanen, 1971; Merritt, 1986).

Even after adopting these different approaches, many animals also find it necessary to supplement the winter energy supply by caching food in autumn so that they can use it over the winter (Lyman, 1954). In addition, many small endothermic animals need to feed all day in winter to meet their energy requirements (Gibb, 1957) and often suffer their greatest seasonal mortality rate when the weather conditions deteriorate and they are unable to meet energy requirements from the available extrinsic energy supply (Chitty, 1952; Berry, 1968). The behavioural, morphological and physiological responses of temperate and arctic animals, in combination with the fact that starvation in winter is a common cause of death, strongly suggest that extrinsic supply of energy is the dominant factor limiting energy expenditure in many (most?) small endothermic mammals in the temperate and arctic regions during the winter months.
In summer, and in tropical regions, however, the limitations are less apparent and there is considerable evidence to suggest that if limitations do apply they are unlikely to be extrinsic. For example, many food supplementation studies have been performed in summer in temperate and arctic regions. The responses of animals to this supplementation do not indicate that energy supply before supplementation was limiting. For example, if food supply was limiting we might expect that animals would respond to supplementation by increases in reproductive output, increased home range areas and increased activity. Normally, however, reproductive output remains unchanged by supplementation, and home ranges and activity commonly decline rather than increase (e.g. Akbar and Gorman, 1993a,b; Cucco and Malacarne, 1997; Monadjem and Perrin, 1998). This suggests that energy demands are limited by some other factor, and the animals use the supplemented energy to meet these demands more rapidly than they would do if feeding from the unmanipulated environment.

Further evidence that animals are capable of harvesting more energy from the environment than they routinely do, in summer, comes from elegant manipulations where animals are experimentally tricked into gathering more food from the environment than they routinely collect. Masman et al., 1989, for example, manipulated kestrels (Falco tinnunculus), rearing young by waiting until the parents had delivered a prey item to the offspring, and stealing the food item from the chicks via a trapdoor cunningly placed in the back of the nest. This activity meant the chicks did not become satiated, and kept begging their parents for more and more food. In these conditions the adult kestrels continued foraging far longer than they normally would, and managed to harvest about three times more food from the environment than they would have otherwise. These data strongly suggest that, at least during the summer, there is far more energy out there than animals are capable of using (but also see Wiehn and Korpimaki, 1997). Limitations on energy demands would appear to be more intrinsically set than extrinsically determined.

D. The Intrinsic Limitation Hypotheses

If energy expenditure is not limited by the external supply of energy, it must be limited by some intrinsic aspect of the animal itself. The potential limiting processes can be appreciated by considering the whole process from energy ingestion to final energy utilization (Figure 3). Apart from a few compounds such as nectar, the foods that animals eat are generally complex macromolecules, which must be digested in the alimentary tract and broken down into more simple compounds which are absorbed across the gut lining. Further processing of these absorbed compounds occurs in the liver, and waste products of the digestive process are eliminated by the kidneys. The first potential limitation may be the process of ingestion. It has been often suggested that this may impose a limit; for example, McNab (1980, p.106) stated that the '...rate of energy expenditure may be limited by the rate of acquisition', and it is frequently observed that animals reach an asymptote in their food intake as a function of prey density. Early studies inferred that the asymptote was a consequence of animals reaching a capacity for intake linked to handling times (Holling, 1959). However, studies in the 1980s showed that the asymptote actually occurs long before animals are spending all their time handling prey, and the asymptote reflects a complex interaction of prey density and diet choice (Sutherland, 1982). Nevertheless the process of ingestion does impose a theoretical potential limit on expenditure. A parallel, potentially limiting, process may be the capability to acquire oxygen at a sufficient rate to
oxidize the ingested foodstuffs (Pasquis et al., 1970). Once the food has been ingested, the second potential limiting process is the rate at which it can be digested by the alimentary tract and processed by the liver.

Processed food may be utilized for respiration immediately, or it may be stored for later use. In general only a small proportion of the food processed by the liver is utilized at this site. The primary end-products of digestion—amino acids, triglycerides, fatty acids and simple sugars—must all be transported around the body to storage depots or to sites of utilization, such as muscles and other organs. The distribution of the processed products of digestion from the alimentary system to storage depots and utilization sites is performed by the circulatory system. This may represent another limiting process on the total energy expenditure of animals.

The chemical energy in substrates derived from ingestion is released during systematic oxidation of the substances and the ultimate formation of water and CO$_2$. The released energy is trapped by conversion of ADP and phosphate to ATP. The generation of ATP may depend on the availability of substrates (Wang, 1978; Weber, 1992) and activities of enzymes that control the TCA and the cytochrome system. Alternatively the system may be limited by the capability of the circulatory system to transport oxygen to the cells in sufficient quantity (Karas et al., 1987). ATP is the energetic currency of cellular reactions, and ultimately conversion of ATP back to ADP and phosphate underpins almost all the energy-consuming processes that animals engage in. A notable exception is the generation of heat in brown adipose tissue, where the coupling of energy release to generation of ATP is deliberately disrupted to generate heat directly. The efficiency of ATP generation may act as another limitation on sustainable energy expenditure (Wang, 1978), as might the capacity of different processes to utilize ATP once it has been formed.

There are six basic processes, therefore, that might serve as intrinsic limits on sustainable energy demand. The first is the process of ingestion of the food and acquisition of the oxygen to oxidize it. The second process is digestion of the food and generation of metabolic substrates. The third is the process of distribution of metabolic substrates and oxygen around the body. Fourth is the efficiency of conversion of metabolic substrates to ATP during oxidative metabolism, and fifth is the capability of tissues to utilize ATP at major sites of energy expenditure, such as the major organs and muscles. Finally, a limit may exist in the capacity to dispose of waste products generated by the whole process.

Previous treatments of the potential areas where intrinsic limitations might occur have generally recognized only two processes or systems that might serve as limitations on sustained energy expenditure: the process of energy assimilation and the process of energy utilization. Definitions of these have been rather informal, and energy assimilation has been taken to include not only the processes of absorption by the gut, transformation by the liver and excretion by the kidneys, but also the distributional and storage processes involving the heart and circulatory systems. Energy utilization has been taken to include all the processes involved in conversion of substrates to ATP, and the subsequent utilization of ATP to generate work and heat. Separating the complex processes in Figure 3 into two broad categories certainly simplifies the conceptual understanding of where limits might apply in this system. However, as is often the case, such simplicity, although conceptually appealing, may obscure the reality of where intrinsic limitations apply.

The idea that capacity for energy assimilation (in its broadest sense) imposes a limit on sustainable energy expenditure has been termed the 'central limitation hypothesis' (Gross et al., 1985; Karasov and Diamond, 1985; Weiner, 1987, 1989, 1992; Peterson et al., 1990). It is termed 'central' because the process is common to and independent of all the various methods by which energy might be expended. Central limitation imposes the same limits on sustained energy expenditure whether the animal is stressed by decreases in ambient temperature, increases in physical activity, reproduction or combinations of stressors. A direct prediction of the central limits model, therefore, is uniformity in the observed maximal rates of sustained energy expenditure. In contrast, the idea that energy expenditure is limited at the sites of energy utilization has been generally called the 'peripheral limits hypothesis'. In contrast to the central limitation idea, it predicts that limitations imposed by different processes need not necessarily be the same. On the face of it, therefore, a suitable test of the contrasting hypotheses might be to push a group of animals to their limits of sustainable energy expenditure in several different ways, and to compare the sustained limits.

1. Comparisons of Sustainable Energy Expenditure under Different Stressing Factors

Several attempts have been made to compare the sustainable metabolic rates of animals under different stressors to establish whether their maximum sustainable capacities are equivalent. McMillan and Hinds (1992), for example, compiled data on maximum oxygen consumption of rodents not only during exercise but also during cold exposure (Figure 2). They found that rodents routinely did not expend energy at the same high levels during cold exposure as they managed to achieve during exercise. However, these were not sustainable rates, because, as we have discovered, animals generally are unable to exercise continuously. However, they may be able to thermoregulate continuously, and this difference might bring the sustainable rates of expenditure much more closely in line.

Direct measurements of maximal 24-h energy expenditures, under different stressors, in small mammals are more sparse than measurements of short-duration maximal rates, and researchers have relied on using lactation as an
alternative to exercise, presumably because of difficulties in getting animals to exercise for prolonged periods (but see also Perrigo, 1987). Comparative data are presented in Table 1. In these cases the maximum for each species is expressed as a multiple of the resting metabolic rate measured at thermoneutral. These are generally termed sustained metabolic scopes (Peterson et al., 1990).

Across these five comparisons, the maximum sustainable scope during lactation exceeds the maximum during cold exposure (paired t = 8.16, 4 d.f., P = 0.0012). This would appear to support the peripheral limitation hypothesis, because the central limitation hypothesis would predict these maxima to be equal. There are, however, several problems with these comparisons.

First, food intake has been very widely employed as a measure of sustainable energy expenditure. This is because over protracted periods, for animals in mass balance, the ingested food is mostly oxidized. However, there will be a discrepancy to true levels of expenditure because some of the food will not be assimilated. Because assimilation rates are generally high, however, food intake does provide a convenient approximate measure of long-term expenditure. This assumption, however, of the approximate equivalence of intake and expenditure, breaks down when considering lactation as a stressor. During lactation animals take in energy but not all of their intake is oxidized and appears as energy expenditure. This is because a substantial proportion of energy ingested is converted into milk and re EXPORTED. Inevitably, then, the energy expenditure during lactation will be lower than the peak energy intake estimated from food intake. Few studies have quantified the extent to which these two measures differ. Scantlebury et al. (submitted) measured the food intake, milk production and energy expenditure of lactating dogs (miniature schnauzers and labradors). They found that the peak energy demands in lactation, expressed from food intake, averaged 5.0x and 6.5x RMR for the two breeds respectively. However, actual energy expenditures were considerably lower at only 2.4x and 2.9x RMR respectively. Clearly, then, the measurements of lactational food intake are not closely linked to the true levels of energy expenditure. This means that, although the levels of food intake are generally higher during lactation than during prolonged cold exposure (Table 1), the levels of actual expenditure may not be.

The central limitation model predicts that expenditure will be limited by central processing capacity. The key question is whether maximal food intake is a valid measure of central processing capacity. Although animals may eat more food in lactation, and must absorb this across the gut walls, there may also be a single system which controls the distribution of this energy for expenditure. Hence, although the levels of food intake may differ, if the levels of expenditure do not then we cannot rule out the possibility that there is a central control mechanism involved (see Figure 3 for different levels of control).

The second problem is that all these comparisons involve animals measured under laboratory conditions. In this situation it is possible to question whether the animal comprehends the basis of the experiment, and complies by expending energy at its maximal possible rate. We do not fully understand the motivations of animals when they are kept in captivity, and therefore this may undermine attempts to measure maximal rates of performance. Finally, even if we were to measure accurately the levels of expenditure in both situations and they proved to be the same (or at least not significantly different), this would not necessarily support the central processing model because the expenditures might be limited peripherally, yet by chance have equal values.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum sustainable metabolic scope</th>
<th>Lactation</th>
<th>Cold</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acomys cahirinus</td>
<td>6.9</td>
<td>4.0</td>
<td>Koteja et al. (1994)</td>
<td></td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
<td>4.35</td>
<td>5.0</td>
<td>Koteja (1996)a,b</td>
<td></td>
</tr>
<tr>
<td>M. musculus</td>
<td>7.7</td>
<td></td>
<td>Stebbins (1977)</td>
<td></td>
</tr>
<tr>
<td>Microtus agrestis</td>
<td>6.0</td>
<td></td>
<td>Millar (1979)</td>
<td></td>
</tr>
<tr>
<td>Phodopus sungorus</td>
<td>4.3</td>
<td>2.7</td>
<td>Hammond and Diamond (1992), Konarzowski and Diamond (1994)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Speakman and McQueen et al. (1996)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M.S. Johnson and J.R. Speakman (unpublished data), Migula (1969), McDevitt and Speakman (1994a)</td>
<td></td>
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<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Phodopus sungorus</td>
<td>3.4</td>
<td>3.1*</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Weiner (1987)</td>
<td></td>
</tr>
</tbody>
</table>

In all cases the maximum daily expenditure is calculated from the food intake and the resting metabolic rate (RMR) is quantified from the oxygen consumption. Maximum sustainable metabolic scope is the maximum expenditure/RMR.

*Refers to animals after a period of thermal acclimation to low temperatures.

### E. Experimental Studies of the Limitation Hypotheses

Perhaps the best set of experimental studies that have been performed to examine the nature of limitations on the sustained energy expenditure of small mammals are those by Kim Hammond and Jared Diamond (and colleagues) using the lactating Swiss Webster mouse as a model system. Swiss Webster mice normally eat about 4 g of food each day. During lactation, however, their food intake increases enormously to around 18–20 g per day, almost equalling their own body mass. If the mice are given five pups to raise, they eat only about 11 g, but for litters of 8 and 11 offspring the food intake is higher. Food
intake, however, does not rise in direct proportion to the number of offspring, so the intake for litters of 8 and 11 is actually fixed at the 18–20-g level. In consequence, there is less food available to support the production of milk and therefore there is an inverse relationship between the size of the litter and the size of the individual offspring in that litter. Bigger litters contain smaller offspring, presumably because they are getting less milk per pup. This trade-off in litter and offspring size is not a specific feature of Swiss Webster mice and is observed in other strains of mice and many other species of small rodent during lactation (see examples in Stearns, 1993). Findings from the study of these mice are therefore likely to be more generally applicable.

Because food intake in these mice reached an asymptote as litter size increased, Hammond and colleagues reasoned that this might represent a central limit on the system, ultimately controlling the production of milk. To test this idea they attempted to manipulate the system in different ways to see whether they could force the mice to increase their food intake. First, they added pups to the litters so that they were abnormally large (Hammond et al., 1992). The mice responded by producing even smaller individuals, and did not increase their food intake. Second, the mice were placed in cages where the female had to climb up a wire funnel to get to the food. This was not designed to make her work harder for the food, but rather prevented the young pups from gaining access to it. Consequently, when the pups came to the day 18 of lactation, at which point they normally start to eat solids and thus demands on the female start to decline, they were unable to, and instead of declining the demands on the females continued to increase until 24 days postpartum (Hammond et al., 1992). Nevertheless, the females continued to eat only 18–20 g of food, strongly suggesting that there was a central limit operating in the system which was involved in food intake. These observations are also consistent with earlier work performed by Perrigo (1987), who forced mice to work for their food. When mice were forced to work to get food, they had to expend more energy in its acquisition. They could respond in theory to this increased demand by increasing their food intake. However, they did not do this. Instead they kept eating the same amount of food. This meant they had less to allocate to the process of lactation and in response to this reduction in energy available for lactation, they actually killed some of their offspring, to reduce the litter size to a level compatible with the resources that were being allocated.

Taken together, the data from Hammond, Diamond and colleagues, and Perrigo, strongly suggest that there is a central limit controlling the maximum sustainable energy expenditure. Measurements of the resting metabolic rate of the Swiss Webster mice indicated that when they were working at this maximum limit they were ingesting energy at about 7.2× RMR. This appeared to be the maximum rate at which they could take in resources. Hammond et al. (1994) performed yet another manipulation to test this idea of centrally mediated sustainable limit during lactation. In the same laboratory they had previously shown (Konarzewski and Diamond, 1994) that during cold exposure the mice also increase their food intake to meet the increased thermoregulatory requirements. How would mice respond when faced with these cold demands during lactation? If the central limit idea was correct, the mice would face exactly the same dilemma that had been faced by the mice studied by Perrigo (1987). They would have fewer resources available to support lactation and consequently they would have only two options: kill some of the offspring to sustain their weaning size (as Perrigo's mice had done), or reduce the average size of the offspring (as Hammond and Diamond's mice had previously done during manipulations).

Against all the flow of the data, the response of the mice was completely unexpected. They increased their food intake to cover the extra demands of being in the cold. Instead of eating 18–20 g they upped their intake to about 23 g each day, which is 10–25% higher than it had been. This is really a remarkable result. Remember that previous manipulations had all failed to get the mice to eat more food. In Perrigo's experiment the mice had actually been prepared to kill their babies rather than eat more. Yet, in the cold, the mice demonstrated that they were capable of eating more food. The impact of this experiment was enormous because it forced a whole rethink of what was actually going on in the model system. Hammond et al. (1996) reasoned that all the previous manipulations had involved not only trying to get the mouse to eat more, but also attempting to get her to produce more milk (although this was not the case in the Perrigo (1987) experiment). By giving her more offspring to raise, or delaying weaning, the manipulations aimed to increase milk demands and thereby increase food consumption. Perhaps, then, the limit was not actually at the central level of processing the food, but at the peripheral level of milk production. Mice had been unable to produce more milk, and therefore had responded by producing smaller offspring, and there was no point in increasing food intake because the extra energy could not be channeled into raised milk production.

Hammond et al. (1996) performed a further experiment to test this idea. This involved surgically removing mammary tissue. They reasoned that, if the milk production capacity of the tissue was already at a maximal level, removing mammary tissue would necessarily reduce milk production. The mice would be unable to respond by cranking up production in the remaining tissue, and there would be several knock-on consequences: litters would grow less and the mother would eat less food in response to the lower demand. However, if the limit acted centrally, the mice would increase milk production in the remaining tissue, milk production would continue to sustain the offspring who would have unafflicted growth, and food intake would also be unaffected. The experiment was slightly more complex than this, as it involved manipulations of the ratio of offspring to teat number, but the
bottom line was that the results supported the peripheral limitation model rather than the central limitation model. The mammary tissue remaining after surgery appeared unable to respond to replace the production of tissue that had been removed.

Similar work has been performed more recently by Rogowitz and McClure (1995) and Rogowitz (1996, 1998), who have demonstrated directly that milk production appears to be the limiting stage in lactation of a different species, the cotton rat (Sigmodon hispidus). These data further support the suggestion that sustainable energy demands are set at the peripheral rather than the central level.

F. The Central Limitation Hypothesis and Links between FMR and RMR

One of the major ideas that had led to the suggestion that animals were controlled by a central limit was the observed linkage between resting metabolic rate and sustainable metabolic rate (King, 1974; Drent and Daan, 1980; Weiner, 1987, 1989, 1992). The idea that this link is connected with the central limitation theory stems from observations that different tissues in vitro respire at different rates. In particular, fat tissue and muscle tissue have relatively low metabolic rates but organs such as the alimentary tract, the liver and kidneys have very high rates, as does neuronal tissue and the brain (e.g. Field et al., 1939; Krebs, 1950; Martin and Fuhrman, 1955; Scott and Evans, 1992). This information was combined with data showing that when animals have increased energy requirements (such as following cold exposure or during lactation) they respond to the increased demands by growing these tissues. Kennedy et al. (1958), for example, documented growth of the liver, and Jolicoeur et al. (1980) reported changes in the size of the pancreas during lactation, and similar changes in the alimentary tract were reported by Fell et al. (1963) and by Cripps and Williams (1975). This phenotypic flexibility in organ size in relation to demand is a very general phenomenon, for which there are many demonstrations (e.g. Myrcha, 1964; Drozdz, 1967; Gębczaski and Gębcznski, 1971; Gross et al., 1985; Green and Millar, 1987; Bozinovic et al., 1990; Hammond, 1993; Nagy and Negus, 1993; Konarzewski and Diamond, 1994; Derting and Noakes, 1995; Derting and Austin, 1998).

If animals grow their alimentary tract and processing machinery (notably the liver) when they have high energy demands, it follows that in parallel with greater levels of food intake there will be an increase in resting metabolic rate (Szarski, 1983; Else and Hulbert, 1985; Karasov and Diamond, 1985; Weiner, 1987, 1992), because these organs have high metabolic rates. Indeed, several studies have demonstrated that interspecific and within-species (interstrain) variation in resting metabolic rate is linked to differences in the relative organ sizes. Animals with higher metabolic rates generally also have larger hearts, kidneys, livers and alimentary tracts (e.g. Daan et al., 1989, 1990a; Konarzewski and Diamond, 1995). Given these studies, it was suggested that a limit on sustainable metabolic rate exists at around 7x RMR, which reflects the link between RMR and the central processing machinery (Weiner, 1987, 1992; Daan et al., 1990a; Peterson et al., 1990). Maximum achievable metabolic rates were therefore viewed as limited by the sizes (or activities) of the central processing system at around seven times the prevailing resting rate of metabolism.

These linkages can be illustrated by considering a study from my own group, on lactation performance in a different strain of mice to that studied by Hammond et al.: the MFI strain (Speakman and McQueenie, 1996). When these mice are virgins they consume about 4.5 g of food daily. Their RMRs at rest and in thermoneutral average 1.0 ml O₂ min⁻¹ and their energy expenditure for RMR is thus about one-third of the daily energy expenditure (DEE) expressed as food intake. The ratio of DEE to RMR is thus about 3.1. During lactation, the food intake increases dramatically. During the last 6 days of lactation the mice eat, on average, 23 g each day. The precise amount depends on the litter size, but for litters above 10 offspring the females all eat 23 g per day. If RMR had remained at the level reported before mating, the mice would be taking in food at about 12 times their resting expenditure. This is well beyond the suggested alimentary limit at around 7x RMR. The animals achieve this because during pregnancy and lactation they grow their guts and their livers to accommodate the increased food intake. A lactating MFI mouse actually grows its small intestine by about 12 cm compared with the length before breeding, and the gut wall thickens and becomes more folded. In addition the liver increases from a wet mass of around 1.0 g to over 0.5 g. Because of these changes in the organ structures, the lactating MFI mouse also has an increased resting metabolic rate, averaging 2.1 ml O₂ min⁻¹. This brings the ratio of food intake to resting metabolic rate down to about 5.9x RMR, which is within the supposed limit of around 7x RMR, supporting the general model.

On the other hand, there are several studies that do not support the model of linkages between food intake, RMR and variation in the alimentary tract. For example, we have studied the process of thermal acclimation in the short-tailed field vole (Microtus agrestis). During cold exposure small mammals experience increases in their energy demands and food intakes, at the same time as having changes in their resting metabolic rates (Adolph, 1950; Adolph and Lawrow, 1951; Hart, 1953a,b; Krog et al., 1954; Depocas et al., 1957; Chaffee and Roberts, 1971; Rosenmann et al., 1975; Feist and Rosenmann, 1976; Klaus et. al., 1988; Heldmaier, 1989). One interpretation of the pattern of change is that the energy demands increase above the sustainable capacity of the alimentary tract, and that in response the tract grows, leading to an increase in RMR. Detailed studies, however, in M. agrestis reveal that this is
not the case (McDevitt and Speakman, 1994a). Before cold exposure the voles have a food intake that averages about 1.3 times their basal rate of expenditure. During chronic cold exposure (5°C) the animals respond by increasing their food intake immediately to about twice the non-breeding level, but this still averages only 2.8x RMR. Exposure to colder temperatures direct from the warm is fatal (McDevitt and Speakman, 1994b), indicating that the voles reach a critical limit in their capacities at around this temperature. These seem unlikely, however, to be mediated centrally, given the low multiple of RMR involved. Over the following 15 days the RMR slowly increases, following, rather than preceding or occurring in parallel with, the change in food intake. This change in RMR appears to be linked most closely to variation in the brown adipose tissue, rather than alterations in gut length and mass or the liver mass (McDevitt and Speakman, 1994a,b). These interactions suggest that during cold exposure these rodents are peripherally rather than centrally limited.

G. Interspecific Reviews of the Link Between DEE and RMR

Several previous reviews have addressed the nature of the linkage between RMR and DEE, summarizing data collected across species (Drent and Daan, 1980; Bryant, 1990; Peterson et al., 1990; Bryant and Tatner, 1991; Koteja, 1991; Daan, 1990b; Degen and Kam, 1995; Ricklefs et al., 1996; Hammond and Diamond, 1997). These reviews stemmed from the suggestions in the 1970s (King, 1974) that DEE and RMR might somehow be linked. The study by Drent and Daan (1980) explicitly suggested that there was a limit on DEE of small birds set at around 4x RMR. Subsequently, as more data accumulated, the 4x RMR limit was breached on several occasions. Bryant and Tatner (1991) and Bryant (1990) reviewed the bird literature again, and concluded there was no evidence favouring a rigid 4.0x RMR limit as it was breached in over 10% of studies. Peterson et al. (1990) reviewed data from both mammals and birds, and concluded that the limit sits at a higher level of around 7x BMR. This was more consistent with the data reviewed by Bryant and Tatner (1991), and would also prove to be close to the limits observed later in laboratory experiments on mice pushed to their lactation limits (see Hammond papers reviewed above).

To an extent, RMR and DEE will be correlated because both are dependent on body mass. Koteja (1991) examined the links between sustainable energy expenditures and resting metabolic rates in birds and mammals, and removed the covariable effects of body mass to establish how close the links where in the absence of this shared variation. He found that in both birds and mammals there was a link even after the shared variation due to mass had been removed. Subdividing these groups, however, revealed some groups where there was no significant effect, for example in marsupials and in passerines and seabirds.
Supporting this viewpoint, several studies have suggested that there are links between interspecific variations in RMR (or BMR) and life history parameters such as litter size and intrinsic rates of population increase (Henneman, 1983; Padley, 1985; Haim, 1987; McNab, 1987a,b; Koteja and Weiner, 1993). However, other studies have disputed such claims (Hayssen, 1984; Harvey et al., 1991), and attempts to find links at the intraspecific level have been similarly disappointing (Derting and McClure, 1989; Hayes et al., 1992a). The wider implications of the possible link between RMR and sustainable metabolic rate are consequently still quite confused.

H. Summary and Aims

The overall picture that emerges from this analysis is that intrinsic limitations on sustainable energy demands are probably set in the peripheral systems (Figure 3). The energetically demanding absorption system (gut and liver) as well as the elimination system (kidneys) respond to match these requirements, thus generating a link between RMR and FMR. In this paper I will address two particular questions concerning sustainable energy requirements. First, what are the dominant factors that influence the levels of energy expenditure of free-living small mammals? Second, what is the nature of the linkage between RMR and SusMR?

Measurements of energy expenditure have been made on a very wide range of animals including insects, reptiles, birds, and both small and large mammals. The scope of this study has been restricted to small endothermic mammals weighing less than 4 kg. The reasons for this restricted data set are 2-fold. Smaller animals tend to have relatively high metabolic rates (per gram of metabolizing tissue; e.g. Pearson, 1947; Lasiewski, 1963; Chai et al., 1998) and this is particularly so for small endotherms, which regulate their body temperatures by generating heat internally. If limits on rates of energy expenditure are important, this is likely to be the case for this group of animals more than for any other. The second reason is that there are some methodological complexities involved in comparing the daily energy expenditures of large and small animals, which will be explored further in the Methods section. These methodological difficulties mean that it is desirable to compare energy demands for a restricted size class of animals either exceeding or lower than a threshold of around 4 kg. Most data collected to date are for animals below this threshold, and consequently it was decided to review the data from below the threshold rather than those from above it.

The aim of this review is 3-fold. First, I hope to produce a quantitative description of the factors that influence energy demands, which might subsequently be used as a predictive model for scientists involved with modelling energy flows in populations and communities. Second, such a predictive model will be beneficial to other researchers examining aspects of mammalian ecophysiology, by providing a comparative reference point to the levels of demand that might be expected in different circumstances. Significant deviations from these expectations may then indicate that given study animals are performing interesting things with their energy budgets that are worthy of further investigation at different levels (e.g. behavioural, physiological, biochemical and molecular studies). Finally, I intend to investigate more closely the idea of a link between sustainable field metabolic rate and resting metabolic rate. In the Methods section I propose to review the methods available for measurement of energy expenditure, in particular the method of indirect calorimetry and the field techniques of time and energy budgeting and doubly labelled water.

III. METHODS

This section reviews the alternative approaches available for the measurement of daily energy expenditure (DEE) by animals. This review sets the scene for later comparisons of daily energy demands to resting and basal energy expenditure, as well as highlighting the methodological complexities of measuring daily energy demands. This section, therefore, also explains the inclusion criteria of estimates of DEE for the present study.

A. Measuring Energy Expenditure by Indirect Calorimetry

The standard method for quantifying the energy requirements of animals is indirect calorimetry. Indirect calorimetry is based on the fact that animals consume oxygen from the air to oxidize organic compounds, thus releasing the chemical energy stored in the bonds of those chemicals for use by the animal. The exact relationship between consumed oxygen and energy expenditure depends on the organic substrate being utilized. When animals oxidize carbohydrate, the amount of energy released per millilitre of oxygen consumed is about 20.9 kJ. When an animal metabolizes fat, the energy released per millilitres of oxygen consumed is lower, at around 19.66 kJ. Exact conversion values vary slightly depending on the substrate being utilized, but on average the difference between the lowest and highest conversion values is about 6%. Different substrates result in the generation of different amounts of the primary end-product of oxidation, carbon dioxide. The ratio of O₂ consumption to CO₂ production (called the respiratory quotient, or RQ) gives an indication of the substrate utilization. If the RQ is known, the conversion of O₂ consumption to energy expenditure generally involves relatively minor errors (< 0.5%; Gessaman and Nagy, 1988). However, when RQ is unknown an error of varying magnitude can be introduced to the conversion from O₂ consumption.

In theory, measurements of CO₂ production alone can also be used to estimate energy expenditure. Measurements of O₂ consumption, however, are
preferred. This is because there is much greater variability in the amount of energy released per millilitre of \( \text{CO}_2 \) produced, than per millilitre of \( \text{O}_2 \) consumed. For example, when an animal mobilizes carbohydrate (RQ = 1.0), the energy equivalent of 1 ml \( \text{CO}_2 \) produced is 20.9 kJ. However, when fats are being mobilized, the energy equivalent of 1 ml \( \text{CO}_2 \) is 28.1 kJ. The difference between the lowest and highest conversion values for \( \text{CO}_2 \) is therefore about 34%, compared with a 6% difference for \( \text{O}_2 \) consumption. Because the error in conversion from \( \text{CO}_2 \) production to energy (in the absence of information about RQ) is potentially much greater than the conversion from \( \text{O}_2 \) consumption to energy, measurements of \( \text{O}_2 \) consumption rather than \( \text{CO}_2 \) production dominate the literature.

Measurements made by indirect calorimetry generally involve confining the subject animal inside a chamber through which a flow is passing. Oxygen consumption is evaluated by measuring the flow rate and the \( \text{O}_2 \) content of the gasses entering and exiting the chamber. A full discussion of the theory behind this method is presented in Appendix A. The major advantage of using indirect calorimetry to estimate the metabolic rates of animals is its accuracy and precision. The major disadvantage is that the animal needs to be confined in a chamber for the measurement to be made.

### B. Basal and Resting Energy Expenditure

It was recognized very early in the study of animal metabolism that many factors affect metabolic rate. Lavoisier and Sequin, for example, at the end of the eighteenth century had already established that \( \text{O}_2 \) consumption depended on the size of the subjects, whether they were active or not, and whether or not they had recently eaten a meal. In comparing the energy requirements of different species, therefore, it was desirable to define a set of conditions that would be equivalent across all animals. Kleiber (1932, 1961) and Brody (1945) were instrumental in establishing a set of standard conditions for the measurement of animal metabolism that would allow broad comparisons across species. In particular, it was thought desirable to remove the effects of any environmental factors that might increase metabolism to produce a comparable estimate across species of the lowest level of metabolic rate. These conditions, as enumerated by Kleiber (1961), were that the animal should be, ‘Mature animals in the post-absorptive state and measured in a range of metabolically indifferent environmental temperatures at rest, or at least without abnormal activity’ (Kleiber, 1961, p. 204). Because this was considered to be a minimal estimate of metabolism, measurements conforming to these criteria were defined by Kleiber (1932, 1961) as ‘basal metabolic rate’ (BMR). A similar definition was used by Brody (1945) for minimal metabolism, which differed from the Kleiber definition only in that the animals were not required to be post-absorptive. This was called ‘resting metabolic rate’ (RMR). Although it was originally defined as a measurement almost identical to BMR, but lacking the requirement that the animals be post-absorptive, subsequently RMR has been used to describe the metabolism of any animal that is inactive, whether it is inside the thermoneutral zone or not. This has led to some confusion, therefore, about how restrictive the term RMR actually is. To avoid any ambiguity in this chapter, I have used two terms: RMRt, to reflect resting metabolism without any control of temperature, and RMR, to reflect the use of RMR in the original sense defined by Brody (1945) as measured inside the thermoneutral zone.

As more and more animals have been measured, it has become increasingly obvious that the criteria for measurement of basal metabolism are most useful for the small set of animals that Kleiber had measurements for at the time the criteria were established. All of these animals are strict thermoregulators and maintain their body temperatures within very tight limits. A major factor, however, that influences the metabolic rate of an animal is its body temperature. Because Kleiber did not incorporate this effect into the definition, it is not a requirement that an animal be maintaining its body temperature at euthermic levels. Most animals have a circadian rhythm in body temperature and in parallel maintain a rhythm of metabolic rate (Aschoff and Phol, 1971). Yet time of day is also not part of the Kleiber criteria.

Kleiber (1961) did recognize that when the animals in his group were reproducing, or growing, their demands increased and thus the measurement of basal metabolic rate was compromised. However, an important factor he did not consider was the effect of seasonal changes on BMR. This is probably because the domesticated animals in his sample were routinely maintained in constant environments throughout the year and experienced minimal seasonal fluctuations in day length and ambient temperature. In contrast, wild animals experience large shifts in ambient temperatures and photoperiod if they live in temperate or arctic regions, and large fluctuations in rainfall if they inhabit the tropics. These large seasonal changes in environmental conditions also result in large seasonal differences in BMR as animals become seasonally acclimatized. Season of measurement is also not a factor that Kleiber required to be controlled in his definition of BMR.

Several problems also arise because in some animals the criteria are mutually exclusive. In soricid shrews, the response to food deprivation is generally to increase activity to seek out food (Hanski, 1985). The requirements, therefore, that the animals be post-absorptive and inactive are therefore almost impossible to attain in these species (McDevitt and Andrews, 1997), although some researchers claim that all that is required is patience (McNab, 1997). There are, however, some much clearer incompatibilities in the criteria than evidenced by shrews. In many temperate zone insectivorous bats, starving the animals to ensure that they are post-absorptive often forces them to abandon temperature regulation compared with animals that are fed as
normal (Kurta, 1991). The animals that are fed and regulating their body temperatures at euthermic levels yield a measurement that is closest to the spirit of measuring a broadly comparable minimal metabolic rate. However, this measure would not conform to the Kleiber criteria because the animals might not be post-absorptive. On the other hand, the animals starved overnight would definitely be post-absorptive and therefore would meet the Kleiber criteria although the low metabolic rate would occur only because the animals had abandoned thermoregulation at euthermic levels. In ruminants there is the problem that the rumen contents are also actively metabolizing. This will add to the observed heat production. Should this be included in the measurement of basal metabolism, or should the rumen be emptied before the measurement is made?

It has been suggested that these are abnormal exceptions and that the Kleiber criteria form a broad basis for comparison across the vast majority of species (McNab, 1997). However, this is an optimistic view of basal metabolism as a unifying measurement. There are several other factors that influence the measurement of BMR, which are universal across all animals but not controlled in the Kleiber definition. These are the duration for which an animal is measured and the time period over which the minimal metabolic rate is defined. Many small rodents, for example, exhibit a stress response to handling and have high metabolic rates immediately after they have been placed into a respirometry chamber. Hayes et al. (1992b) found in wood mice (Apodemus sylvaticus) that extending the length of time a measurement was made from 1 to 3 h could reduce the minimal metabolic rate by 10%. The minimum duration for which animals should be measured does not feature in the Kleiber definition.

Given the arbitrary nature of the Kleiber criteria, there is a clear need to apply some common sense in deciding whether a measurement is acceptable as a measurement of BMR or not. Gallivan (1992), for example, has suggested that all previous estimates of Cetacea could not be included as BMR measurements because previous measurements in the animals (e.g. Kasting et al., 1989; Innes and Lavigne, 1991) were not completely inactive, or were inactive but the measurements were very short. (This is further complicated by the fact that Kleiber did not specify complete inactivity in his definition—"...inactive or nearly so"). As has been pointed out, rejecting these measures is probably not justified on this basis, because making Cetacea completely inactive for prolonged periods is probably unachievable (Speakman et al., 1993). Sometimes, getting close to the Kleiber criteria is as close as we are ever going to get, so rejecting such data does not really advance our understanding very much. Including them does not necessarily imply a complete relaxation of the Kleiber criteria to include anything (McNab, 1997).

Despite these apparent methodological problems with measurement of BMR, estimates of it have proliferated in the literature since its first definition. Ignoring the fact that some (much?) of the variability between measurements may reflect methodological differences between studies, many attempts have been made to understand the observed interspecific variability that is evident in this trait. Some authors have suggested that environmental factors such as latitude (Ellis, 1984), climate (McNab and Morrison, 1963; Hulbert and Dawson, 1974) and diet (McNab, 1980, 1983, 1986a, 1986b, 1987a, 1988) are the most important factors. Others have emphasized the linkage of variation in BMR to variation in the morphology of the animals (Daan et al., 1989, 1991; Konarzewski and Diamond, 1995), but others have suggested that the variation is mostly linked to differences in phylogeny (Hayssen and Lacy, 1985; Bennett and Harvey, 1987; Elgar and Harvey, 1987; Harvey and Elgar, 1987; Harvey and Pagel, 1991). This argument, however, has been confused because of some misclassifications of diet and because some measurements of BMR probably did not conform to the Kleiber criteria as they were measured below thermoneutral in the species included in reviews favouring phylogenetic effects (McNab, 1987b). In this context an important but seldom referenced set of data are those collected by Stephenson and Racey (Stephenson and Racey, 1993a, 1993b, 1994, 1995; Racey and Stephenson, 1996) concerning the resting energy requirements of the Tenrecidae. This group of insectivorans, isolated in Madagascar, shows remarkable convergence in many metabolic traits with rodents and insectivores occupying equivalent niches in mainland Africa.

C. Time and Energy Budget Estimates of Daily Energy Expenditure

Most animals living in their natural environment expend energy above the basal requirement almost all the time. By observing an animal over a 24-h period it would be possible to classify its behaviour into several distinct classes. The time and energy budget method for estimating the DEE suggests that an estimate of total daily demands can be derived by multiplying the time spent in each activity by the energy costs of that activity (McNab, 1963; Schartz and Zimmerman 1977; Weathers and Nagy, 1980, 1984; Buttemer et al., 1986; Goldstein, 1988). For example, imagine an animal that spends its time either flying or resting. The daily time budget might consist of 5 h of flight and 19 h of rest. If the cost of flight was 1 W and the cost of rest was 1 W (1 J s⁻¹), the accumulated cost would be:

\[
(5 \times 3.6 \times 10) + (19 \times 3.6 \times 1) = 248.4 \text{ kJ}
\]

In most circumstances determining a simple behavioural time budget for an animal is not difficult. The problem arises when one attempts to convert the simple time budget into an energy budget. This is because assigning a cost to a particular activity is complicated by the fact that the costs are not constant for
a given behaviour but depend on several other factors. Take for example the energy cost of resting (RMR). The cost of resting depends on a wide range of external factors that relate to the thermoregulatory demands being placed on the animal: ambient temperature, wind speed, solar radiative input, whether it is raining or not, the presence of an insulating nest and the time of day. In addition, even under a set of completely fixed external conditions, the cost of resting also depends on several attributes of the individual animal: its body mass, body condition, whether it is digesting food or not, what the composition of that food was, whether it is growing or not, what ambient conditions it had previously encountered and whether it is reproducing or not.

It might be relatively simple, therefore, to establish that an animal has spent 12 h each day at rest. However, assigning a single energy cost to that behaviour would be impossible, because the factors that can potentially affect resting energy expenditure would be unlikely to remain constant over such a long period of time. To construct an accurate time and energy budget, one would need to subdivide the time spent at rest into the time spent resting in each of the potential situations that might affect the energy expenditure. Only in this way could a realistic energy cost be assigned to the time budget.

The second problem is that, even if it was possible to construct a detailed time budget, such that the time spent in each situation that might affect energy demands was quantified, one would need to know the actual energy demands associated with each unique combination of factors. For a single behaviour (like rest) there are at least five external factors, some of which are continuously variable traits (like ambient temperature), and at least five internal factors (again, several of which are continuously variable) that can affect energy demands. The potential numbers of combinations of these factors, for even a single behaviour, means that establishing energy costs for all potential conditions would take an incredible amount of time to establish. Once one adds the fact that animals routinely perform a complete repertoire of behaviours, the task facing the constructor of an accurate time and energy budget is truly gargantuan.

One development that has provided some hope that time and energy budgeting might be feasible is the use of copper taxidermy mounts to quantify the complex thermal environment of an animal. The theory behind the use of these models is elegant. There are a potentially diverse range of factors that influence thermoregulatory requirements. Quantifying the effects of such a large array of factors on energy expenditure would be time consuming and complex. However, if the different factors could be reduced to a single dimension, one would need only to quantify the metabolic response of the animal to that single dimension and record in the field the effects of the diverse environmental factors on this single trait. The single dimension is called the standard operative temperature. Standard operative temperatures are measured using a heated copper model of the animal in question covered by skins from live specimens. Imagine that such a model has been constructed. If it was placed into an incubator at a known air temperature, the electrical energy required to heat the model would be related to the air temperature and the setting of the thermostat inside the model. If the thermostat was set at the body temperature routinely maintained by the animal, the electrical energy required to heat the model would reflect the thermal load placed on an animal at any given temperature. It would be possible to place a live animal into the incubator as well and to measure its metabolic rate in relation to incubator temperature by indirect calorimetry.

The clever part is subsequently to take the heated model out into the environment. Here the model is exposed to a multitude of factors that affect its thermal load: air temperature, ground temperature, sunshine intensity, wind speed, rain, etc. By measuring the electrical energy required to heat the animal in any given circumstance, one can estimate the equivalent incubator temperature for any environmental situation. Complex multidimensional changes in the environmental conditions can all be reduced to their effect on the electrical energy required to heat the model. The multidimensional nature of heat loading is thus reduced to a single dimension (the standard operative temperature). The energy expenditure of a real animal can be estimated knowing the relationship between real animal metabolic rate and incubator temperature. This approach greatly simplifies the construction of time and energy budgets, and its development owes much to the work of George Bakken of the University of Indiana (Bakken and Gates, 1975; Bakken, 1976, 1980, 1992). The method has been criticized recently because of inconsistencies in the responses shown by different models (Walsberg and Wolf, 1996). However, at least part of the problem is in the method used to express error (Larcheolle, 1998) and lack of standardization of the models, which can remove much of the intermodel variability.

Although the use of heated models may provide a useful method of condensing the environmental variability into a single dimension that is equivalent to thermoregulatory demands, there is still the problem of quantifying the energy demands connected with activity. Added to this complexity is the fact that many studies have suggested that the costs associated with thermoregulation and activity are not simply additive. This is because animals appear able to utilize heat generated by activity to supply their thermoregulatory requirements (Paladino and King, 1984; Webster and Weathers, 1990; Zebra and Walsberg, 1992; Chai et al., 1998). Consequently there is a saving to the animal when compared with the predicted additive costs. Although thermal substitution is probably the best known, and best quantified example of lack of additivity in energy budgetting, there are other less obvious cases, for example the utilization by bats of the same muscles to generate the forces necessary for them to fly, and the respiratory burst necessary for them to echolocate. Consequently, although the costs of echolocation vocalizations for
a stationary but are very high (Speakman et al., 1989), when a bat is flying these costs disappear (Speakman and Racey, 1991).

Even taking the magnitude of the task of quantifying the energy costs of different behaviors into account, and evaluating whether these costs are additive to the thermoregulatory requirement, there are further logistical obstacles that impair the ability to measure energy expenditure in some circumstances. These are limits imposed by the difficulties of mimicking accurately the situation for which one requires an energy cost, inside a respirometry chamber. It seems probable that there are many situations in which animals routinely find themselves for which we are unlikely ever to derive a realistic energy cost estimate for indirect calorimetry, for example the energy cost of a bird flying in rain. Finally, assuming everything could be measured, each term of a time and energy budget is measured with an error. Travis (1982) has shown that these errors in individual components of the budget can accumulate to produce very wide confidence limits in the eventual estimates of daily energy demands.

D. Direct Measurements of Free-living Energy Expenditure

1. Heart Rate Method

When an animal consumes oxygen it must transport that oxygen from outside its body to the sites where it is being consumed. This involves the ventilatory system to move \(O_2\) from the atmosphere into the blood, and the circulatory system to transport the oxygenated blood to the sites of its utilization. In the ventilatory system, the delivery of \(O_2\) into the blood is a function of the ventilation rate and the tidal volume, as well as the partial pressure of \(O_2\) in the air, relative to the loading characteristics of the respiratory pigment(s) involved. In the circulatory system \(O_2\) delivery to tissues is governed by heart rate, stroke volume and the extent to which \(O_2\) is off-loaded from the blood at the tissues where it is being utilized. Animals may respond to changes in demand by varying different parameters of the supply lines. For example, during activity an increase in \(O_2\) demand at the muscles could be met by an increase in ventilation rate and tidal volume to drive more \(O_2\) into the blood, combined with an increase in heart rate and \(O_2\) extraction efficiency to deliver it to the sites of utilization. If the dominant mode of response involved a single parameter, such as ventilation rate or heart rate, then monitoring of this parameter would provide a method of continuously measuring the animal’s metabolism without the need to restrict it in a respirometer. Ventilation rate and heart rate provide the most convenient parameters in this respect, because the electrical signals involved in muscle contraction are relatively easily picked up by appropriately located electrodes, and the resultant electromyographic or electrocardiographic signal can be monitored to measure ventilation and heart rates.

The potential of this approach is enormous because it provides not only a direct field estimate of metabolic rate over protracted periods, enabling an estimate of sustainable metabolism to be derived, but also enables subdivision of the total costs into its components. There are, however, several methodological complexities that need to be surmounted when applying the method. The first problem is that externally mounted electrodes (even if the animal will tolerate their presence) seldom produce signals of sufficient clarity for use. Ideally, then, the whole package, consisting of the electrodes and a unit to transmit or store the information, should be mounted internally. The current minimum size of such packages means that this method is restricted to animals weighing more than 100 g. Moreover, the method is consequently much more invasive than the alternative approaches detailed below. In at least some areas of the world performing such invasive work on wild animals might involve legislative problems.

A second potential problem is that several studies have highlighted the individual nature of the relationships between heart rate and \(O_2\) consumption (Morhardt and Morhardt, 1971; Bevan et al., 1994; Boyd et al., 1995). To generate precise estimates of \(O_2\) consumption, therefore, it is necessary to generate a relationship for each individual animal involved in the experiment. This requires a further period of holding the study animal to establish such a relationship, which may be inappropriate if the animal is performing behaviors in the field where a period spent in the laboratory would be disruptive, such as caring for offspring. Finally, the link between heart rate and \(O_2\) consumption may vary according to the source of energy demands placed on the animal. In response to low-level activity, for example, an animal may cover the increased \(O_2\) requirements completely by changing heart rate, yet during cold exposure increases in \(O_2\) extraction efficiency and stroke volume may make additional contributions. Even during exercise there may be a limit in the manner of response by heart rate alone. At low levels increased \(O_2\) demands appear to be met by changes in heart rate alone, but at high levels changes in \(O_2\) extraction efficiency become important (Grubb, 1982; Jones et al., 1989; Butler, 1991) and stroke volume remains unaffected.

Perhaps because of these potential problems and technical difficulties, relatively few studies have utilized techniques based on this theoretical outline. For example, Weatherly et al. (1982) used the opercular movements of fish (= ventilation rates) to evaluate their metabolic rates, but no studies have attempted to link ventilation rates to \(O_2\) consumption in free-living mammals and birds. Probably the most development has occurred in the use of heart rate to estimate metabolism. This has been used extensively to evaluate the metabolic rates of fish (Priede and Tytler, 1977; Priede, 1983; Armstrong, 1986; Lucas and Armstrong, 1991) and birds (Gessaman, 1980; Stephenson et al., 1986; Bevan et al., 1994, 1995a,b,c, 1997), but has been applied only infrequently to free-living mammals.
Although I have detailed above some of the problems of using heart rate to monitor O$_2$ consumption, it is important to note that several validation studies have been performed using heart rate monitoring at the same time as the doubly labelled water method (detailed below, and on which most of this paper is based), and comparing both of these to standard indirect calorimetry (Nolet et al., 1992; Bevan et al., 1994, 1995c; Boyd et al., 1995; Hawkins et al., submitted). In all these studies, the predicted DEE by heart rate was at least as accurate as that derived by the doubly labelled water method, and in many cases individual estimates were better matched to the estimates by indirect calorimetry. This is perhaps in part because the use of heart rate involves prediction of O$_2$ consumption, while the doubly labelled water method involves prediction of CO$_2$ production, and conversion of the latter to energy expenditure is potentially less accurate. The improved accuracy when using the heart rate approach occurs in addition to the wealth of data furnished on temporal partitioning of the costs. There is no doubt that, where it has proved possible to apply this method, the insights generated into the components of field metabolism have been spectacular (Bevan et al., 1995a; Butler et al., 1998).

2. Isotope Elimination Methods

Although there are several methods based on the elimination rates of various isotopes (e.g. Baker et al., 1968; Chew, 1971; Baker and Dunaway, 1975; McLean and Speakman, 1995; Peters et al., 1995) which appear to provide reliable estimates of food intake for free-living animals, none of these methods, with the possible exception of $^{23}$Na elimination (e.g. Green 1978; Green and Dunsmore, 1978a,b; Green and Eberhard, 1979; Green et al., 1984; Tedman and Green, 1987; Gales, 1989), has been applied to sufficient animals to provide a large enough database for comparative analysis. The only method that has been used sufficiently for this purpose is the doubly labelled water (DLW) technique. The method was invented by Lifson and colleagues in the 1950s (Lifson et al., 1955) and a complete history of the development of the method can be found in Speakman (1997a, 1998).

3. Theory of Using Doubly Labelled Water

I have elaborated in detail elsewhere the theoretical basis of the technique (Speakman, 1997a). Other treatments can be found in Lifson and McClintock (1966), Nagy (1980), Speakman and Racey (1988), Tatner and Bryant, (1989) and Bryant (1989). Briefly, the method depends on the fact that isotopes of primarily by the flow of water and CO$_2$ leaving the body. In contrast, an isotopic label of hydrogen will leave the body primarily only as water. If both isotopic labels are introduced at the same time (hence doubly labelled) the difference in their respective elimination will reflect the CO$_2$ production and thus indirectly the energy expenditure (see above). It is perhaps important to reiterate at this point that conversion of CO$_2$ production to energy expenditure is less accurate than the conversion using O$_2$ consumption. The problem of converting DLW derived estimates of CO$_2$ production to energy expenditure, in the absence of a known RQ, may therefore limit its accuracy.

After an isotopic label has been injected into an animal, the time course of its enrichment follows a complex path reflecting several different processes (Figure 4). Before injection the isotopic enrichment is at some background level. For heavy oxygen ($^{18}$O) the background level of the isotope in most living systems is around 2000 ppm and for heavy hydrogen ($^2$H) it is around 150 ppm. After injection, the enrichment in the blood rises very rapidly as the pool of isotope at the injection site diffuses into the bloodstream. Over time, isotopes

![Graph showing hypothetical time course for variation in isotope enrichment of a small mammal](https://via.placeholder.com/150)
will be eliminated from the system in water and (for oxygen) expired CO₂. At some point a dynamic equilibrium will occur where the rate at which isotopes flood into the system from the injection site exactly equals the rate of elimination. The result is a stable isotope enrichment in the blood which is generally called the plateau phase. The enrichment may home in on the plateau from above or below depending on the method of isotope administration. The plateau may also last a variable time depending on the dynamics of the system. Eventually, however, when all the isotope has flooded into the system the enrichment starts to decline because only the elimination process dominates it. The elimination follows a negative exponential. At first lots of isotope is removed because its enrichment in the body water and eliminated products is high. However, as the enrichment declines, the amount lost in each volume of water and CO₂ also declines, and the rate of decline becomes progressively slower and slower, until the enrichment reaches the background level again.

If the difference between the isotope enrichment in the body and the background enrichment is converted to logarithms, the curved exponential becomes linear, and the gradient of this linear relationship allows us to characterize the rates of isotope elimination from the system. The gradient is generally called \( k_o \) or \( k_d \), for the oxygen and hydrogen isotope respectively. One other thing is needed to convert these elimination rates into actual flows of materials carrying the isotopes, and that is the dilution volumes in which the isotopes are distributed (generally called \( N_o \) and \( N_d \) respectively for oxygen and hydrogen). In general, the flow of material carrying oxygen is approximated as \( k_o \cdot N_o \), and the flow of material carrying hydrogen is approximated as \( k_d \cdot N_d \).

There has been considerable debate in the literature, however, about the ideal manner in which \( k_o \), \( k_d \), \( N_o \), and \( N_d \) should be combined to estimate the CO₂ production of an animal. One of the alternatives concerns the use of both \( N_o \) and \( N_d \) in the equation, or whether \( N_o \) should be used alone. These have been respectively termed the two-pool and single-pool methods. The difference between these models in the estimated CO₂ production depends on several factors but the most important is the ratio of \( k_o \) to \( k_d \). When this ratio approaches unity, the models produce widely divergent estimates of CO₂ production. For most animals, however, the difference is likely to be between 5% and 25%. The choice of pool model is consequently not trivial. Validation studies in recent years are strongly pointing towards both methods being appropriate, but in animals of different body sizes (reviewed in Speakman, 1997a). Moreover, there are good theoretical grounds for expecting this to be the case (Speakman, 1987).

The exact point at which the different models become appropriate has not yet been determined precisely. However, it appears that for animals weighing in excess of 4-5 kg the two-pool model is likely to be most appropriate, whereas smaller animals should be measured using the single-pool model. Unfortunately most studies of animals, independent of their size, have utilized the single-pool model. This generally leads to an overestimate of the metabolic energy expenditure of larger animals. This would not be too serious a problem if it were not for the fact that it is generally impossible to recalculate the CO₂ production estimates using the two-pool model because the data necessary to make these recalculations are generally not quoted in the papers. This is a potentially important problem, which might compromise reviews of energy expenditure that utilize data from animals drawn from across the boundary, which delimits single-pool and two-pool determinations. Unfortunately this encompasses almost all the reviews of DEE based on the DLW technique that have been published to date.

E. Summary and Data Inclusion Criteria for the Present Review

In conclusion, the measurement of energy expenditure by free-living animals is difficult. The time and energy budget method provides an estimate of expenditure. However, in general, even if the time and energy budget methods employed are thorough, and include detailed quantification of the effects of thermal and activity regimes on energy demands, combined with detailed time budgets, the complexity of interactions in energy demands makes the resultant estimates prone to considerable error (Travis, 1982).

In contrast to the time and energy budget approach, the heart rate telemetry and isotope elimination methods provide more direct estimates of daily energy demands which take into account the wide diversity of potential interactions in the individual elements that go to make up the total expenditure. Heart rate estimates have been applied to too few animals yet to make a substantive review possible. For the doubly labelled water isotope elimination method, validation studies suggest that the resultant estimates have a mean individual error of around 12-15%. Individual estimates, therefore, may be unreliable. However, group mean estimates of CO₂ production are generally very accurate (1-3% in error). What one sacrifices with the isotope approaches is a detailed breakdown of the component costs, which contribute towards the total cost. In theory, at least, this is provided by the time and energy budget method, but the reliability of the subdivision of the budget is open to considerable speculation, given the poor conformation of the totals to simultaneous DLW estimates. Only the heart rate method may allow a detailed component breakdown as well as a reliable overall estimate to be derived.

Although several isotope methods are available, only one (the DLW method) has been used on sufficient species to provide a comparative database for investigation. Previous reviews of this database have generally covered the complete body mass range. However, the general use of the single pool DLW model for studies of larger animals makes inclusion of larger animals suspect.

In view of these facts, the present study concerns a review of all DLW measurements made on free-living mammals weighing up to 4 kg. The
database searched for included information on all studies published between 1970, when the first measurements were published for a free-living wild mammal (Mullen, 1970), and June 1998. Many studies involve groups of animals measured in different conditions, for example in different seasons or at different stages of their annual cycles. In all cases I have taken the mean energy expenditures for homogeneous groups of animals and have not pooled the data across all conditions for any particular species. This is because it is apparent that energy demands fluctuate with many different factors and pooling data together masks these effects. However, this does raise problems of independence in the data, since some species provide several data points to the analysis. I have treated this problem differently and explicitly at different points throughout the paper. In addition to estimates of energy expenditure, the papers were scoured for information on the following for each group that provided an energy expenditure estimate: body mass of the animals, ambient temperature, latitude of the study site, altitude of the study site, diet of the group, sex and reproductive status of the animals.

IV. RESULTS

A. Overview of the Database

I found a total of 69 papers containing data on small mammal field metabolic rates measured using the doubly labelled water technique that had been published between 1970 and 1998. I added to these studies an unpublished study from my own research group. The published and unpublished studies together included a total of 184 measurements of homogeneous groups of adult mammals in different situations (e.g. seasonal, altitudinal or reproductive classes) on a total of 74 different species (Appendix B). I excluded from the review estimates that had been made on immature or juvenile mammals that were still growing. Each ‘measurement’ includes between 1 and 20 individual estimates of energy expenditure across a group of individual animals (median 8 per measurement). The total number of individuals contributing to the database is uncertain. In some studies the same individuals contributed repeated measurements, but, while this is mentioned, the authors did not quantify it precisely. Moreover, it is possible (probable) that in some cases the same individual measurements contributed to multiple papers by the same authors. In the database I have treated these as independent measurements, which they may not be. Thus, for example, Berteaux and colleagues published three papers in 1996 and 1997 on the meadow vole (Microtus pennsylvanicus). These papers address different biological aspects of the species and each includes a different sample size, different mean values for body mass and metabolic rate. These probably represent different subsets of a single data set. The extent of overlap between papers, however, is impossible to ascertain from the published information. The same is true of the two papers by Salsbury and Armitage (1994, 1995) on yellow-bellied marmots (Marmota flaviventris) which also include different means and sample sizes but probably refer to subsets of the same group of animals. Despite these problems, the total number of individuals contributing to the 184 measurements is probably in excess of 1000.

There are currently 20 recognized orders of extant mammals (Novacek, 1992). Of these orders, however, five contain no representatives that weigh less than 4 kg (the cetaceans, sireniens, proboscids, perissodactyls and tubulidentates). Of the remaining 15 orders, data were available for representatives of eight of them. At present we are still lacking any information on the daily energy requirements of small (<4 kg) representatives of the monotremes, dermopterans, tupids, artiodactyls, pholidotids, macroscelids, hyracoids and primates. I am aware that measurements for small representatives of at least three of these groups were in progress in late 1998, and early 1999.

The presently available data set was dominated by measurements made on rodents, which accounted for almost half the total (n = 89 measurements on 32 species). The second largest order represented in the data was the marsupials with a total of 68 measurements on 24 species. Five other orders contributed smaller numbers (Chiroptera, n = 11 measures of nine species; Insectivora, n = 6 measures of five species; Lagomorpha, n = 2 measurements of a single species: Edentata, n = 3 measures of a single species; and Carnivora, n = 5 measurements of three species). To an extent this bias reflects the large diversity of small rodents. However, this is not the entire reason. The bats, for example, comprise almost 1000 species, all of which weigh less than 4 kg (Altringham, 1996), yet we have data on daily energy expenditures for only nine of them (less than 1% of the total). The lagomorphs are similarly grossly under-represented in the available data. Despite rodents being well represented, there are still some large groups of rodents for which we have no data on free-living energy demands (e.g. the hystricomorphs).

The latitudinal distribution of available measurements (Figure 5) shows a large peak around 30°-40°N, with 71 of the 184 measurements in this 10° latitude band. This is in part a consequence of the intensive research efforts of three researchers (Ken Nagy at the University of California at Los Angeles in the USA, Allan Degen at Side Boquer in Israel, and Brian Green at CSIRO in Australia). Between them, these three research workers with their collaborators and students have made 127 (nearly 70%) of the 184 published measurements. Since these researchers all live around 35°N or S and have studied their local faunas extensively, this accounts for the large number of measurements made at this latitude. As two of these workers (Nagy and Degen) have specialized in desert ecology, the data at these latitudes pertains mostly to desert living mammals, in particular desert-living rodents. We have comparatively few data for mammals that inhabit the tropical and temperate forests, and almost no data (n = 5 measurements for two species) for the arctic.
Fig. 5. Latitudinal distribution of measurements of field metabolic rate included in the database. There was a very strong bias around 35°N and S.

Geographically the data originate mostly from the North America (n = 86), Eurasia (n = 22) and Australia (n = 67). Relatively few data are available for South America (n = 3) and all these refer to measurements made north of the Amazon. Similarly, sparse data are available for Africa (n = 6 including Madagascar). This geographical bias may reflect, at least partly, the high financial costs of applying the DLW methodology. We still have no measurements of the energy demands of small mammals living in mainland Asia (including all of Russia and China) and the Indian subcontinent.

Temporally the pace at which measurements are being added to this database is increasing. In the 1970s data were accumulating at about two measurements each year. This doubled during the 1980s. The first serious attempt to summarize the available information was made by Nagy (1987), who included 19 measurements from 13 species of small mammal in a more wide-ranging review, which also took into account field energy expenditures of larger mammals and birds. Koteja (1991) included 24 species of mammal weighing less than 4 kg in his review of field energy demands, and Karasov (1992) included 17 species of mammal in his review of links between FMR and RMR. The pace of data collection, however, seems unlikely to be sustained with trends for science funding increasingly being dominated by molecular work at the expense of whole-animal physiology. The patterns of data accumulation are currently very biased in favour of rodents, and in particular North American and Eurasian representatives of this group. These biases should be borne in mind when evaluating the data. As information continues to accumulate for different groups of mammals living in more diverse habitats and geographical regions, our views about the habitual levels of energy demand and the relative importance of factors influencing them may change, certainly in minor ways and perhaps radically. Because of the inherent limitations in the available information it is probably the case that this review can serve only to summarize the extent of our current ignorance rather than document the degree of our insight.

B. Factors Influencing Daily Energy Expenditure

1. Body Mass

Including all the data pooled across all animals in all conditions, ignoring any potential problems of pseudoreplication and lack of independence of the data, the dominant factor influencing the field metabolic rates of small mammals was body mass. There was a linear relationship between loge body mass and loge field metabolic rate (Figure 6) which explained 85.9% of the variation in field metabolism. The least squares fit equation was:

\[
\log_{e} \text{FMR (kJ day}^{-1}\text{)} = 2.022 + 0.627 \log_{e} \text{body mass (g)}
\]

\((F = 1111.8, 1,182 \text{ d.f., } P < 0.001)\). The gradient of this relationship was significantly shallower than the expected gradient for basal metabolism based on the Kleiber relationship (0.75; \(t = -6.55, P < 0.001\)), and was also significantly
shallower than the value 0.67 ($t = 2.29, P < 0.05$) which is expected from the surface law. Inspection of these data (Figure 6), however, reveals a potential bias because the largest mammal represented is the three-toed sloth ($Bradypus tridactylus$; Nagy and Montgomery, 1980), which has a particularly low metabolic rate for its body mass, and among the smallest mammals represented is the common shrew ($Sorex arenicus$; Poppi et al., 1994), which has a very high metabolic rate for its mass. Because of the large leverage on gradients exerted by data at the extremes, this unfortunate coincidence will tend to make the observed gradient including all the data shallower. Excluding these two sets of measurements ($n = 5$ measurements in total) yields the following equation:

$$\log_e \text{FMR (kJ day}^{-1}) = 1.878 + 0.659 \log_e \text{body mass (g)}$$  \hspace{1cm} (2)

($r^2 = 88.0\%; F = 1302.3, 1,179 \text{ d.f.}, P < 0.0001$). The gradient of this relationship is almost identical to that anticipated by the surface law.

The validity of using least-squares regression to fit the gradient fitted to these data is in some doubt because the body masses of the animals are not measured without error (Riska, 1981; Rayner, 1985; LaBarbera, 1989). The reduced major axis (RMA) fit gradient fitted to the uncensored data set (including shrew and sloth) was 0.676, which did not differ significantly from 0.66 but was still significantly different to the Kleiber value of 0.75. In the censored data set (excluding shrew and sloth data), the RMA gradient was 0.702, which was marginally significantly greater than the surface law prediction ($t = 1.98, P < 0.05 > 0.01$) but substantially lower than the 0.75 prediction.

Using the censored data set the least-squares fitted curve predicts energy expenditures for average 10, 100, 1000 and 4000-g small mammals of 29.9, 136.8, 625.9 and 1564 kJ per day. The RMA curve predicts field metabolic rates of 27.8, 135.5, 630.2 and 1577.8 kJ per day respectively. The logged relationships tend to minimize the perceived extent of differences to these mean values. The 95% predictive intervals for these mean predictions at any given body mass spans an approximate 4-fold range. This can be illustrated by considering the 95% predictive interval at each of the above mean masses. At 10 g the range is 14.0–63.7, at 100 g it is 64.4–290.5, at 1000 g it is 293.2–1336.2 and at 4000 g it is 727.3–3363 kJ per day. It is apparent from these ranges that the top of the 95% predictive interval is approximately equal to the bottom of the interval for a body mass 10 times greater. It is literally true, therefore, that there are some small mammals that have absolute metabolic rates equal to those of other mammals 10 times their own body mass, and this is true in the data set that excludes the most extreme examples of the sloth and the shrew. These two species make the most remarkable comparison. The shrew weighs only 9 g and has a metabolic rate of about 100 kJ per day (Poppi et al., 1994), while the sloth weighs over 200 times more but expends energy only five times faster (489 kJ per day; Nagy and Montgomery, 1980).

Although body mass explains almost 90% of the variability in metabolic rates of small mammals included in the data set, these ranges clarify that the predictive value of the relationship between mass and field metabolic rate for any particular species is minimal. This is apart from the inherent biases in the
selection of species that has already been highlighted. Using the predictive equation, the expected values for all the available measurements can be generated, and the difference between these values and the actual values calculated. Given the nature of least-squares regression, these deviations sum to the average error that would occur if the predictive equation were utilized to predict field metabolic rates. On average, predicted metabolic rates would be in error by 124% using this approach. This is an optimistic estimate because the same data used to derive the gradient are also used to evaluate the errors.

In the preceding analysis I included each ‘measurement’ as an independent datum. This follows the procedure adopted by Nagy (1987) in his review of field metabolic rates. Such an approach has been strongly criticized because it includes multiple measurements for some species (up to 16 in the case of the kangaroo rat Dipodomys merriami). The multiple appearance of data for some species might be regarded as pseudoreplication. For example, Green (1997) states: ‘The regression analyses (by Nagy, 1987) are flawed due to the multiple representation of some species’. In response to this type of criticism, Nagy (1994) reanalysed and updated his analysis using only a single datum for each species. However, this is open to a different criticism because the condensing of data obscures much of the variability between species which can be attributed to the different environmental conditions during their measurement: some mammals are measured in winter, for example, and others in summer. Hence Green (1997) states: ‘Another review by Nagy...does not use multiple data for any species. However, the mean FMR value derived for some species is derived from different seasons and cohorts’. This is a clear case of being damned if you do and damned if you don’t. Whatever approach you take with these data, somebody will take offence at it.

I have taken two approaches to the problem. The first is to emulate the approach taken by Nagy (1994) and to condense the data for each species into a single datum reflecting the average body mass and average field metabolic rate across all the ‘measurements’ available for that species. As pointed out by Green (1997), these species data are not directly equivalent because some represent averages across several seasons and conditions, whereas others represent measurements for only single seasons or particular groups (e.g. males). Pooling the data in this manner yields a total of 74 species’ data points. In this more restricted sample there was still a very dominant effect of body mass on metabolic rate (Figure 6b). Including all the data the least-squares fit regression:

\[
\log_{e} \text{FMR} = 2.062 + 0.621 \log_{e} \text{body mass (g)}
\]

explained 86.4% of the variation in FMR \((F = 450.9, 1.72 \text{ d.f., } P < 0.001)\). Excluding the data for the shrew and sloth (above), which exert high leverage on the gradient, results in the equation:

\[
\log_{e} \text{FMR} = 1.929 + 0.650 \log_{e} \text{body mass (g)}
\]

\((r^2 = 88.8% ; F = 523.5, 1.70 \text{ d.f., } P < 0.001)\). These equations, their \(r^2\) and probability values are almost identical to those derived for the entire data set. In practice, therefore, although inflation of degrees of freedom is a valid critique of the analysis which includes multiple data for each species, the problems of lack of independence of the data and pseudo-replication appear to have only minor effects on the fitted equations for the effect of body mass on FMR.

There is, however, a further problem with using species averages as independent data in the relationship between FMR and body mass, which has not been considered previously in the majority of allometric summaries of FMR in mammals published to date (Nagy, 1987, 1994; Koteja, 1991; Bryant, 1997; Green, 1997; Hammond and Diamond, 1997; Speakman, 1997b). This problem is the potential lack of independence between species because of their shared evolutionary history (Felsenstein, 1985; Harvey and Pagel, 1991; Garland et al., 1992). Two closely related species may be both large and have high field metabolic rates. In the preceding analyses, these two species would contribute two independent data to the analyses. However, the body masses and metabolic rates of these species might not reflect an independent effect of mass on metabolism, but might occur because of the shared evolutionary history of the two species which has resulted in both of them having the same character traits for metabolism and body mass.

For example, in the database there are several closely related pairs of species. The two spiny mice, Acomys russatus and A. cahirinus, and the two shrew tenrecs, Microgale talazaci and M. dobsoni, are examples of such pairs. Within each pair the component species have shared the vast majority of their evolutionary history and have diverged from each other only recently. In both cases the species within the pairs have very similar values for body mass and field metabolic rate. For A. russatus and A. cahirinus the body masses are 38.3 and 45 g respectively and the metabolic rates are 51.8 and 47.6 kJ day\(^{-1}\). However, for M. dobsoni and M. talazaci the values for mass are 42.6 and 42.8 g respectively and the estimated metabolic rates are 77.1 and 66.5 kJ day\(^{-1}\). The masses of the mice and shrew tenrecs are also similar, but the metabolic rates of the shrew tenrecs are much higher (by over 40%). The problem is whether these are really four independent data, or whether the sample size is inflated by the inclusion of such recently diverged species as independent points. Most researchers agree that these closely related species should not be regarded as truly independent data because of this shared evolutionary history (Felsenstein, 1985).

Several methods have been derived in the past decade to overcome this problem. The most popular of these methods is the calculation of phylogenetically independent contrasts for the respective character traits and seeking
relationships between these phylogenetically independent data (e.g. Harvey and Pagel, 1988, 1991; Garland et al., 1992). As far as I am aware, the only study that has performed such an analysis on the context of the field metabolic rates of small mammals is the study of Ricklefs et al. (1996) which involved 32 species (see also analysis by Nagy et al., 1999). Unfortunately, this previous analysis is slightly compromised by two mistakes in the phylogenetic tree (p. 1059) used to derive the independent contrasts. First, the bat Macrotus californicus is misspelt (Microtus californicus) and, perhaps as a result of this misspelling, is misclassified among the microtine rodents (genus Microtus). The node connecting this bat to the microtines (node z5) exerts a large influence in the regression of the residuals (Ricklefs et al., 1996, Figure 3) and probably has further knock-on effects in the phylogeny. A second potential problem is the geomyids in their phylogeny are linked more closely to the sciurids than to the muroids, yet several authorities suggest the geomyids should be placed among the muroidomorphs (e.g. Eisenberg, 1981). The fact that removing the effect of phylogeny in their analysis had no impact might thus in part reflect the erroneous phylogeny used to test the hypothesis, since the contrasts methods depend on a ‘known and correct phylogeny’ (Harvey and Pagel, 1991).

These misclassifications may, however, be less important than it may first appear, if only because the phylogeny of the mammals as a whole has been a matter of considerable debate. Over the past 15 years disputes have occurred over the positioning of several major groups. For example, there has been a protracted debate over the Chiroptera, with many authorities claiming that this is a monophyletic group (Simmons and Geisler, 1998; Baker et al., 1991), but others claiming that the megachiropterans should be placed among the muroidomorphs (e.g. Eisenberg, 1981). The fact that removing the effect of phylogeny in their analysis had no impact might thus in part reflect the erroneous phylogeny used to test the hypothesis, since the contrasts methods depend on a ‘known and correct phylogeny’ (Harvey and Pagel, 1991).

There was a significant positive relationship between the log of the standardized phylogenetically independent contrast of field metabolic rate and the log of the standardized independent contrast for body mass (Figure 7). The figure shows several outlying points at the lower end of the plot. These were the contrast between the two Microgale species (node i1), between Peromyscus crinitus and the other two Peromyscus species (node r26), between the two Mus species (node r17), and between Hemibeldideus lemuroides and the two Pseudochirus species (node m15). In all these four cases the situation was the same. The branch length was short and the contrast in mass was very small, but there was a larger difference in the field metabolic rates. This effect might be expected to occur occasionally under the Brownian motion model of evolution on which the contrast calculation is founded, since early in the diversification of the traits there may be periods when by chance...
one of the traits drifts back to the starting value while the other trait does not. Perhaps a certain degree of divergence is necessary before the contrasts are sufficient to detect associations between the traits. There was no indication of any problem with the nodes around *Ammospermophilus* and *Thomomys bottae* which Ricklefs et al. (1996) eliminated as outliers in a similar analysis. This is perhaps because I associated the geomyids with the muroids, rather than the sciurids (see above).

Even including these four outliers, there was a significant relationship between body mass and field metabolic rate. In the least-squares fit regression, body mass contrast explained 52.4% of the variation in the field metabolic rate contrast. The equation was:

\[
\log_{e} \text{FMR contrast} = -0.07 + 0.588 \log_{e} \text{body mass contrast} \quad (5)
\]

\(F = 78.01, 1,71\) d.f., \(P < 0.001\). Excluding the four data where mass change was negligible at the node resulted in an improved \(r^2\) and a different equation:

\[
\log_{e} \text{FMR contrast} = -0.09 + 0.76 \log_{e} \text{body mass contrast} \quad (6)
\]

\(F = 125.6, 1,68\) d.f., \(P < 0.001; r^2 = 65.3\%\). Because the explained variation was much lower than the regressions involving the tip data, the variation around these fitted gradients was much greater. Including all the data, the gradient did not differ from the expectation based on the surface law (\(t = 1.08, P > 0.05\)) but did marginally reach significance at the 5% level for difference to the expectation from Kleiber (\(t = 2.42, P = 0.045\)). The gradient fitted excluding the outliers did not differ from either prediction. The significant relationship in the phylogenetically independent contrasts of FMR and mass indicates that the link between field metabolic rate and body mass is not a phylogenetic artefact of using species as the sampling unit.

Although in one sense repeated measurements for a given species (and even species points) are not independent, in all the cases included in the database the measurements are separated because they differ with respect to some presumed variable which is likely to affect energy expenditure. In a real sense each individual datum represents an independent set of conditions where species is one of only a number of multivariate predictors for FMR. The problem of multiple representations of each species is only a problem therefore to the extent that the data are not fully balanced with respect to all the predictor variables. Compressing the data so that each species appears once (and calculating the phylogenetically independent contrasts) removes the independence problem but introduces a second problem, as highlighted by Green (1997), that the data are not equivalent. A third problem, however, is that all the within-species variability, reflecting the effects of variables apart from body mass, is completely lost. My second approach to the problem is to leave all the individual measurements included in the analysis as 'independent' data (without phylogenetic correction), and attempt to explain the resultant residual variability in FMR as a function of these other factors.

2. Ambient Temperature

Ambient temperature measurements were available, or inferred from location and time (Oliver and Fairchild, 1984) for 160 of the 184 FMR measurements. Body mass and temperature were unrelated predictor variables (\(r^2 = 0.5\%\)). There was a strong negative relationship between the residual FMR (from the least-squares regression on mass) and the ambient temperature (\(T_A\)) (Figure 8).

The least-squares fitted regression:

\[
\log_{e} \text{residual FMR} = 0.429 - 0.0258 T_A \quad (\text{°C})
\]

explained 32.6% of the residual variation (\(F = 76.2, 1,158\) d.f., \(P < 0.001\)). Examination of the plot reveals three data at very low temperatures, which
make the temperature data negatively skewed. These data could have a strong
leverage on the regression and hence I removed them to explore their effect on
the relationship between residual FMR and temperature. The effect of these
three points, however, was minor, resulting in an elevated intercept and
gradient but unaltered \( r^2 \) and \( F \) value \((r^2 \text{ excluding the data } = 34.5\% \text{ and the}
equation was } y = 0.506 - 0.0297x; F = 81.6, P < 0.001).\)

Including all the data and entering both temperature and body mass as inde­
dependent predictors resulted in the following equation:

\[
\log_{10} \text{FMR (kJ day}^{-1} = 2.382 + 0.644 \log_{10} \text{ body mass (g)} - 0.0261 T_A (\text{°C}) \tag{8}
\]

\((F = 695.4, 2,157 \text{ d.f.}, P < 0.001, r^2 = 0.899).\) Excluding shrew and sloth data
results in a slightly different equation where the effect of mass is more
pronounced and the effect of temperature slightly diminished, and the \( r^2 \)
improved:

\[
\log_{10} \text{FMR (kJ day}^{-1} = 2.22 + 0.670 \log_{10} \text{ body mass (g)} - 0.0236 T_A (\text{°C}) \tag{9}
\]

\((F = 790.8, 2,152 \text{ d.f.}, P < 0.001; r^2 = 0.912).\)

Although the effect of ambient temperature on residual FMR in small
mammals is very marked, understanding the reasons for this relationship is
less clear. On one hand it may seem intuitively obvious that endothermic
animals require greater heat production to sustain their high body tempera­
tures as ambient temperature declines. All other factors being equal, one
would expect decreases in ambient temperature to require increased energy
expenditure. Indeed this effect has been demonstrated many times by indirect
calorimetric studies of many species of small mammal in the laboratory. In
the field, however, all other factors are not equal, and animals respond the
changes in their immediate ambient temperature in a variety of different ways
amenable to temperature effects. For example, during winter when it gets colder, animals may respond to the decreased temperature
by building better insulated nests (Casey, 1981) and reducing their aggressive
behaviours to allow huddling together as a mechanism to conserve heat loss
(Contreras, 1984; Karasov, 1983). Temperatures within nests of huddling
animals are consequently substantially higher than the reported ambient
temperature, and the summed thermal environment experienced by the
animals may differ substantially from that expected from ambient tempera­
ture alone. A rather simplistic interpretation that this observation represents
the expected thermoregulatory effect of decreased ambient temperature on
metabolism is consequently not warranted. This is particularly the case
because attempts to establish such an effect in other data on field metabolic
rate, pertaining to the endothermic birds, have failed to demonstrate the same
relationship (Bryant, 1997).

For two species there were multiple measurements covering a wide range
of ambient temperature conditions. These were the pocket mouse \((Perognathus formosus)\) (Mullen, 1970; Mullen and Chew, 1973) and the
kangaroo rat \((Dipodomys merriam)\) (Mullen, 1970; Nagy and Gruchacz,
1994). Pooling data across studies in both these cases, there were strong
effects of the temperature of the measurement site at the time of the
measurement and the FMR \((\text{kJ day}^{-1})\) (Figure 9). The effect of temperature
across species was consequently evident in at least two species where suffi­
cient repeated measurements were available to examine the effect.

The extent of the effect of temperature on FMR can be compared for these
two species to the effects of ambient temperature on RMR, since \(Dipodomys
merriam\) and a closely related species of \(Perognathus\) \((Perognathus califor­
nicus)\) have been studied in the laboratory using standard indirect calorimetry.
The effects of temperature on RMR in both cases were greater than the
observed effects on FMR (Hart, 1971). In both species RMR increased
approximately 4-fold between the lower critical temperature and 0°C,
compared with the 2-fold increase observed in FMR (Figure 9). This suggests
that in both cases the mammals effected mechanisms when exposed to the cold
that ameliorated the effects of the cold exposure. In both species, however,
these mechanisms were insufficient to remove the effect of temperature on
FMR completely.

\[
\begin{align*}
\text{Ambient temperature (°C)} & \quad \text{Residual field metabolic rate (FMR)} \\
0 & \quad 2 \quad 1 \quad 0.5 \quad 0 \quad -0.5 \quad -1 \quad -1.5 \quad -2 \\
\text{Fig. 8. Residual field metabolic rate (FMR) after taking account of the effect of body}
\text{mass plotted against the ambient temperature (°C) at the study site. All data were}
\text{included (n = 162 measurements across 60 species).}
\end{align*}
\]
3. Season

For many species data were available for more than one season. Generally only two seasons of data were available (summer and winter), although in some species data were available almost monthly (e.g. pocket mouse and kangaroo rat; see above). I examined these seasonal effects in three ways. First, I compared the ratio of the summer FMR to the winter FMR. Since body mass may differ between summer and winter mammals, and indeed this has been suggested to be a mechanism used by mammals to ameliorate the impact of reduced winter temperatures, I also calculated the residual logged FMRs in summer and winter, and took the difference between these values. Finally, on average one would expect winter temperatures to be lower than summer temperatures, and thus on average the metabolic rate in winter should exceed that observed in summer if the temperature impact on residual FMR is a consequence of summed seasonal effects across several species. Accordingly, I made a third comparison using the residuals to the multiple regression predictions of logged FMR using both mass and temperature as predictors. This was feasible only where temperature data for winter and summer were also available in addition to the FMR and mass data (Table 2).

In total, data were available for 16 species that had been measured at single sites in both winter and summer (including the kangaroo rat and pocket mouse; see above). Several species had also been measured in spring and autumn but there were too few for any formal analysis. There was no significant difference in the mean body mass across species between summer and winter (paired \( t = 0.56, 15 \text{ d.f.}, P > 0.58 \)). In four species the difference between summer and winter masses was less than 10%. In five species the winter mass was greater than 10% higher than the summer mass, and in the remaining seven species the reverse was the case, with the summer mass being more than 10% greater than the mass in winter. In all cases the winter was 10–20°C cooler than in the summer at the same site. Given this large temperature difference and the significant effects of temperature on FMR across all the pooled data (Figure 8), one might a priori expect that, in spite of the confounding effects of body mass variation between seasons, FMR would on average be greater in winter than in summer. However, there was also no significant difference between the mean FMR in summer and in winter (paired \( t = -0.67, 15 \text{ d.f.}, P = 0.51 \)). In some species the metabolic rates were almost identical, despite there being large differences in body mass; for example, for the pocket gopher *Thommys bottae* the summer mass was 10% lower than the winter mass, but the respective values for summer and winter FMR were 126.6 and 127.7 kJ day\(^{-1}\). In direct contrast, in the ground squirrel (*Ammospemophilus leucurus*) the body masses in summer and winter were almost identical (97.5 and 96.1 g respectively) yet the FMR differed by over 50%, with the summer FMR averaging 130.6 kJ per day but the winter FMR averaging only 82.6 kJ per day. In total, in seven of the species summer and winter FMR differed by less than 10%. In five species the summer rate exceeded the winter rate by more than 10%, and in four species the winter FMR exceeded the summer FMR by more than 10%.

When body mass effects were removed from the calculated FMR there was also no significant difference between summer and winter measurements for the same species at single sites (paired \( t = -0.5, 15 \text{ d.f.}, P = 0.62 \)). This suggests that, on average, mass changes between summer and winter did not
There was a significant effect of latitude on the residual FMR (accounting for body mass) (Figure 10). The least-squares fit regression:

$$\text{Residual FMR} = -0.0696 \times \text{latitude (°N or °S)}$$

explained 22% of the variation in the residual FMR. The effect was accounted for mostly because there was a strong

4. **Latitude**

This difference indicates that during winter small mammals generally activate their thermoregulatory mechanisms which reduce the impact of the lower winter temperatures. These mechanisms are not generally based on reductions in body mass between summer and winter. Rather, they reflect other factors that reduce the difference between the mammal's summer metabolic rate and the lower metabolic rate expected when the mammal is at rest. These mechanisms include an increase in social gregariness to enable huddling behavior, an increase in surface insulation, an increase in nest-building activity to increase external insulation when the mammals are out of the nest, and efficient use of favorable microclimates when the mammals are resting (e.g., Hayward, 1963; Chappell, 1980; Casey, 1983). The present analysis shows that these mechanisms are an important aspect of the energy expenditure budgeting in wild small mammals.

The residual FMR is defined as the FMR accounting for both body mass and ambient temperature (rFMR). This definition is used in the following analysis of the relationship between seasons and species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Mass (g)</th>
<th>FMR (W kg⁻¹)</th>
<th>rFMR (W kg⁻¹)</th>
<th>rFMRt (W kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ammospermophilus leucurus</td>
<td>W</td>
<td>96.1</td>
<td>82.6</td>
<td>-0.47</td>
<td>0.303</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>97.5</td>
<td>130.6</td>
<td>-0.02</td>
<td>-0.380</td>
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<tr>
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<td>13.6</td>
<td>64.9</td>
<td>0.497</td>
<td>-0.217</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>48.1</td>
<td>66.1</td>
<td>0.418</td>
<td>-0.375</td>
</tr>
<tr>
<td>Thomomys bottae</td>
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<td>108.2</td>
<td>227.7</td>
<td>-0.116</td>
<td>-0.204</td>
</tr>
<tr>
<td>Psammomys obesus</td>
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<td>126.6</td>
<td>-0.07</td>
<td>0.024</td>
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<tr>
<td></td>
<td>W</td>
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<td>184.5</td>
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<td>Valpes cona</td>
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<td>640</td>
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<td>Sorex arenens</td>
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<tr>
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<td>104.8</td>
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<td>1950</td>
<td>1488</td>
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<td>S</td>
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<td>455</td>
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</table>

Measurements refer to species measured at single sites in winter (W) and summer (S). For references refer to Appendix B.
Figure 10. Residual field metabolic rate (FMR) after accounting for the effect of body mass as a function of latitude of the study site. All data were included (n = 165 measurements on 70 species).

A relationship (r² = 40.3%) between the latitude of the study site and the ambient temperature (Figure 11a) described by the relationship:

\[ \text{Temperature (°C)} = 37.5 - 0.573 \text{ latitude (°N or °S)} \]  \hspace{1cm} (11)

However, temperature did not explain all of the latitude effect on FMR since there was also a weak but significant effect of latitude on the residual FMR when both mass and temperature effects were taken into account (Figure 11b). The least-squares fit regression:

\[ \text{Residual FMR} = -0.185 + 0.0051 \text{ latitude (°N or °S)} \]  \hspace{1cm} (12)

explained 4.1% of the variation in residual FMR (F = 4.2, P = 0.043). When body mass, ambient temperature and latitude were all entered as independent predictors of FMR, all three variables emerged as significant predictors. The best fit equation was:

\[ \log_{10} \text{FMR (kJ day⁻¹)} = 1.896 + 0.686 \text{ body mass (g)} - 0.0199 T_a (°C) + 0.0091 \text{ latitude (°N or °S)} \]  \hspace{1cm} (13)

which explained 90.3% of the variation in FMR (F = 482.8, 3,156 d.f., P < 0.001).

Figure 11. (a) Relationship between ambient temperature and latitude for all the study sites and measurements. (b) Residual field metabolic rate (FMR) after accounting for the effects of both body mass and temperature plotted against latitude of the study site (all measurements included). The majority of the effect of latitude (Figure 10) was because of the effect of temperature on FMR (Figure 8) and the covariation of temperature and latitude (a), although there was a slight independent effect of latitude that was significant.
Together with the previous section on seasonal effects, this analysis suggests that the dominant cause of the temperature effect in the data set was the consequences of differences in ambient temperatures between study sites across the globe, rather than seasonal temperature effects at given sites. The reason why field metabolic rates were also independently affected by changes in latitude remains uncertain. However, the magnitude of the latitude effect is quite large. If one moves from the equator to 60°N, for example, the predicted latitude effect would amount to 0.546 log units. Over the same latitude change, the ambient temperature would be expected to fall by on average 34°C (equation (11)) and thus the temperature effect over the same range would amount to 0.676 log units.

To assess the predictive usefulness of equation (13), I adopted the same procedures used to assess the predictive power of the allometric equation using body mass alone (equation (1)). This previous analysis had suggested that, although mass explained 85.8% of the variation in FMR, on average predictions differed from actual values by 124%, making the predictive usefulness of the equation minimal. In contrast, when I used the equation employing body mass, ambient temperature and latitude as predictors to derive an estimate of the logged FMR, the mean deviation of the prediction to the actual data averaged only 21.3% (SD 15.4%, minimum 0, maximum 191%). Although the maximum deviation (for the Namibian golden mole Eremitalpa namibensis) was large, this prediction was a clear outlier. For the remainder, only six data were more discrepant than 50% from the actual values, and all these deviated by less than 60%. The deviant data included two bat species (Macrotus californicus and Plecotus auritus) which had significantly lower metabolism than predicted, and two data for the common shrew (Sorex araneus) which were much higher than predicted.

On average equation (13) provided an assessment of the expected energy demands of a free-living small mammal that is about five times more accurate (21% average error of prediction compared with 124% average error) than a prediction based on body mass alone (equation (1)). Given the imprecision involved in conversion of CO₂ production to energy expenditure when RQ is unknown, this may be as good as it is possible to get with the current methodology. Although this may at first sight appear an impressive improvement, it is important to be aware of the limitations of this prediction. Most importantly, the error assessment is conservative because the same data used to derive the model were also used to test it (this was also the case for the mass). Even using the same data to test the model, some poorly sampled groups (the Insectivora and Chiroptera) produced discrepant values, and in one case this was enormous. The prediction is consequently most likely to yield useful estimates of field metabolic rate when applied to predictions for rodents and marsupials, which provided the bulk of data for its construction. Nevertheless, in the absence of real data pertaining to a particular species, this approach is probably the best predictive method we have for evaluating the field energy expenditure of a small mammal. As such, this might prove useful in the production of models of bioenergetic flows in ecosystem studies and may also provide a predictive benchmark against which future estimates of metabolism can be judged.

5. Altitude

Ambient temperature varies with altitude as well as latitude, but altitude is also accompanied by changes in barometric pressure and therefore the partial pressure of oxygen, and by changes in other climatic variables such as wind as well as altered productivity. This might be expected to have interesting effects on the energetics of animals living at different altitudes. To date, however, only one study has explicitly examined the effects of altitude on field metabolic rates (Hayes, 1989a,b). In this previous study of Deer mice (Peromyscus maniculatus) it was found that the animals living at high altitudes (3800 m) were slightly heavier (18.4 versus 17.6 g) but had a considerably raised FMR compared with mice from lower altitudes (1230 m). At high altitude they had an FMR of 64.8 kJ per day compared with only 48.6 kJ per day at low altitude. This difference in FMR is much greater than would be anticipated by the slight difference in body mass. Indeed, this is confirmed by the fact that the residual FMR accounting for body mass effects derived in the present comparative framework was also much greater at the high altitude site (residual FMR at high altitude was 0.375, and at low altitude 0.013).

A question remains, however, over why the FMR was so greatly increased at high altitude. Dawson and Hulbert (1970), Kinnear and Shield (1975), and Hayes (1989a,b) suggested two potential factors that could be important. First, behaviour might differ between low- and high-altitude sites, combined with differences in the costs of foraging in the two different habitats. Alternatively, the difference might reflect the much lower ambient temperatures reported at the higher altitude. The present comparative analysis allows an assessment of this problem in the framework of the analysis of the temperature effects detailed above. If the effect of altitude were only a consequence of temperature differences between the two sites, we would not anticipate a large difference in the residual FMR for these two sites, once the effects of mass and temperature had been taken into account. Alternatively, if differences in behaviour were solely, or additionally, important, we might expect a much greater difference in the residuals for these two sites. The residual FMR accounting for body mass and temperature effects was 0.166 and 0.155, indicating that the ‘altitude’ effect on FMR can be fully accounted for by the differences in temperature between the two sites.

With the exception of the studies by Salsbury and Armitage (1995) of high-altitude marmots, and by Green and Crowley (1989) of Antechinus living...
under snow, the altitudes of study sites were not detailed in any of the other papers reviewed, suggesting they were mostly at lower elevations. Further discussion of altitude effects is therefore not possible in the present context.

6. Diet

Mammals seldom feed exclusively on single prey types. Classifying dietary habits of mammals is therefore complicated because there are multidimensional spectra along which diets are selected. For example, many mammals feed on insects combined with other prey such as fruits. Yet other mammals are exclusively insectivorous. The situation is further complicated by the fact that mammals change their diets seasonally and different populations of the same species may feed on radically different diets in different parts of their ranges; for example, the woodmouse Apodemus sylvaticus feeds on grains in woodlands (Gorman and Akbar, 1993) but on sand dunes it takes mostly insects (Zubaid and Gorman, 1991). Populations feeding on these very different diets can be found only tens of kilometres apart (Corp et al., 1997a). With this in mind, only very broad dietary classification was possible for the species under study. I reviewed the literature to classify the dietary habits of the mammals that had been studied by DLW techniques. Occasionally this information was present in the papers in which FMR measurements were detailed (e.g. Nagy and Gruchacz, 1994) and the dietary data refer to the particular study population. However, more often than not the information had to be gleaned from general texts concerning feeding behaviour. I classified the diets and foraging strategies of the mammals into one of seven different classes:

1. Leaves of trees: arboreal folivory
2. Grass: grazing
3. Seeds/grains or nuts: granivory
4. Fungus:
5. Insects (either alone or combined with other prey but with insects dominating): insectivory
6. Other vertebrates: carnivory
7. Exudates/nectar/fruit: nectarivory/frugivory

These seven dietary categories are ranked in the approximate order of the energy content of the food source, combined with the ease of its digestibility. Hence the least energy-rich food was foliage. It is well established that foliage is a poor energy source because the energy is trapped among indigestible components, and the leaves additionally contain many toxic secondary compounds designed to prevent feeding behaviour and retard digestive efficiency. At the other end of the scale are fruits and nectar, which are specifically designed to be energy rich (but protein poor) sources of food. One might argue over the locations of individual classes in this hierarchy. However, overall, I think most researchers would agree (give or take individual classes) that this order reflects the ranked availability of energy in dietary foodstuffs exploited by small mammals.

There was a very strong association between the residual FMR (accounting for the effects of body mass, ambient temperature and latitude) and the dietary class (Figure 12) ($F = 6.83, 6,150$ d.f., $P < 0.001$, analysis of variance (ANOVA)). Approximately 21% of the residual variation in FMR (from equation (13)) was associated with differences in dietary class between the different groups. The most striking pattern in the dietary data (including all the individual data points) was the positive link between the subjective assessment of energy availability from the diet and the field metabolic rate. Since most mammals (70 of 74) had constant dietary assignments, in part this result may reflect the multiple representation of the same species within the data set. I therefore calculated the average residual FMR for each species, and also the average dietary assignment, rounding this to the nearest integer where necessary. When each species appeared only once in the data there was no evidence of a significant link between FMR and diet ($F = 1.65, 6.57$ d.f., $P = 0.15$, ANOVA). The absence of an effect of diet in these data contrasts with the suggestions of McNab (1980, 1983, 1986a) that animal energy expenditure (notably BMR) is strongly influenced by the diet. It has been suggested that the link between BMR and diet occurs because animals feeding on foods with high availability of energy can afford to be extravagant in their use of energy, whereas those feeding on low-quality food must be frugal—hence a link between energy availability from food and BMR. It has often been inferred that a link between FMR and diet underpins this link between BMR and diet. In the current data set there was no evidence to support this suggestion.

The effects of diet on metabolism suggested by McNab (1980, 1983, 1986a) have been criticized because of the failure to take into account the phylogenetic lack of independence of the different species as sampling units (Bennett and Harvey, 1987; Harvey et al., 1991).

7. Phylogeny

To assess the impact of taxonomy on the residual FMR (after accounting for the effects of body mass, temperature and latitude), I coded each species according to the order of its classification: 1, Rodentia; 2, Marsupialia; 3, Chiroptera; 4, Carnivora; 5, Insectivora; 6, Edentata; and 7, Lagomorpha. There was no significant effect of phylogeny on the residual FMR ($F = 1.83, 6.57$ d.f., $P = 0.11$, ANOVA).

The patterns of variation in FMR described here appear to deviate significantly from the patterns of variation that have been suggested previously for BMR, in particular the absence of an effect of diet (even in the data uncorrected for
RMR is not a fixed species-specific trait, but varies with many factors including season and the population under study (e.g. Corp et al., 1997b). Where measurements were made for populations that were not also the populations measured by DLW, it would be inappropriate to apply the same RMR measurement across all the multiple measurements of FMR. The question arises, however, of which measurement the RMR should be applied to, when values were not generated from the same study. To overcome this problem I decided that independent of whether the data had been gathered in the same study or not, I would use only a single mean for each species (pooling data from the multiple situations where this was necessary). I therefore compared the mean estimated RMR for each species with the other traits averaged for the particular species in question.

There was a strong relationship between the measured RMR and body mass (Figure 13). The least-squares fitted regression:

$$\log_{10} RMR (kJ \text{ day}^{-1}) = 0.835 + 0.642 \log_{10} \text{body mass (g)} \quad (14)$$

explained 90.2% of the variation in RMR ($F = 554.02, 1,60$ d.f., $P < 0.001$). The gradient of this relationship was not significantly different to the expectation from the surface law (0.66), but was much lower than the gradient derived for BMR by Kleiber ($0.75; r = 4.0, P < 0.01$). As with the measurements of FMR,
however, the gradient of this relationship was possibly affected by the presence of the three-toed sloth as the largest representative, and the common shrew among the smallest. Omitting these data gave the following equation:

\[
\log_{e} RMR (kJ \text{ day}^{-1}) = 0.7056 + 0.668 \log_{e} \text{body mass (g)}
\]  

which explained 92.3% of the variation in RMR. This revised gradient was not significantly different to the expectation from the surface law (0.66) but was still significantly lower than the expectation based on the Kleiber curve (0.75; \( t = 3.28, P < 0.01 \)). Use of RMA regression produced increased gradients, as would be expected. Using all the data, the RMA regression gradient was 0.675, and using the truncated set excluding sloth and shrew data gave 0.695 as the gradient.

There was a significant negative relationship between the residuals of the relationship between RMR and body mass and the latitude of the sites Where the animals were collected (Figure 14). The least-squares fitted regression explained 7.1% of the variation in the residual RMR (\( F = 4.56, 1,57 \text{ d.f.}, P = 0.04 \)). Ambient temperature of the sites, averaged across the FMR measurements made at those sites, was not significantly related to the RMR. However, this probably reflects the heterogeneous nature of the data for FMR, with some sites including measurements made across all seasons, but others reflecting...
explained 53.3% of the variation in the log, RMR contrast ($F = 66.3, 1.58$ d.f., $P < 0.001$). The gradient of this curve was not significantly different to the surface law expectation ($t = 1.41, P > 0.05$), but was significantly lower than the Kleiber expectation ($t = 2.55, P < 0.05$). As with FMR, the outliers at the lower end of the plot reflect situations where mass (or metabolism) hardly changed over a short branch, linking closely related groups. (The exact number of outliers with low mass change was different for RMR because of missing data.) Removing these three outliers improved the $r^2$ value (to 59.6%) and lowered the gradient of the relationship (0.546), but did not alter the significance of the comparisons to the surface law and Kleiber expectations.

Once the effects of mass and latitude had been removed, there was no evidence in this sample of a link between RMR and diet (classes detailed above: $F = 1.42, P > 0.05$, ANOVA) or between RMR and phylogeny (classes also detailed above: $F = 1.95, P > 0.05$, ANOVA). This absence of any further effects on RMR was unexpected in the light of previous demonstrations that RMR may be linked to diet (McNab, 1980, 1983, 1986a) and the established effects of phylogeny on RMR, for example the lower RMR of marsupials (Dawson and Hulbert, 1970; McNab, 1978). The absence of an effect of diet in the present data seems unlikely to be because of insufficient variation in the diets of the mammals included in the database. Although diet may be linked to RMR when a wider comparison is used, in small mammals the evidence appears at best equivocal, even before any assessment of phylogenetic independence of the data is considered (see Bennett and Harvey, 1987). The evidence of an effect of phylogeny in the data was probably because several orders (edenates, carnivora and lagomorphs) were represented by only single species. If these single representatives were removed there was an effect of phylogeny in the remaining four orders ($F = 2.95, 1.55$ d.f., $P = 0.04$, ANOVA). However, the pattern of these effects was not exactly what might have been predicted. The bats had lower than average RMRs for their masses and sites of origin, and the insectivores had higher RMRs, but the RMRs of the marsupials were in line with expectations and did not differ from the values for rodents.

Although previous studies of marsupials have clearly indicated that they have reduced resting metabolic rates compared with eutherians, this effect appears to be dependent on the sample of mammals measured (Lovegrove, 1996). In particular, the small Dasyurid marsupials tend to have higher rates than the expected from their masses (Green, 1997), and this group comprised a major proportion of the marsupial species included in the present study.

The pattern of variation in RMR in these data paralleled very closely in several respects the variation in FMR. The gradients of the mass effect were almost identical and changed in similar ways when the data were either truncated or a different model was used to estimate the regression parameters. Moreover, there was a significant positive effect of latitude on RMR, which was similar to the same effect reported in FMR. In addition, there were no profound effects of either diet or phylogeny on the two traits.

Given the large amount of the total variation in both traits that was dependent on differences in body mass between species, and ambient temperature, it was not surprising that there was a strong relationship between FMR and RMR (Figure 16), using the data for averages across FMR and RMR for each species. The least-squares fitted regression:

$$\log_{10} \text{FMR (kJ day}^{-1}) = 1.472 + 0.911 \log_{10} \text{RMR (kJ day}^{-1})$$ (18)

explained 91.0% of the variation in FMR ($F = 603.9, 1.60$ d.f., $P < 0.001$). The gradient of this relationship was slightly, but significantly, lower than 1.0 ($t = 2.4, P < 0.05$). The reduced major axis gradient was 0.959, and did not differ significantly from a value of 1.0. A gradient of exactly 1.0 would imply a fixed ratio between the RMR and FMR across body mass. In agreement with the gradient being almost equal to 1.0, examination of the actual ratios of FMR
to RMR, as a function of body mass, reveals no such effect of mass on the ratio (Figure 17) \( F = 0.45, P > 0.9; r^2 = 0.01 \), particularly because one of the largest mammals in the sample (yellow-bellied marmot; Salisbury and Armitage, 1994) also had one of the highest ratios.

Across all measurements the distribution of ratios was positively skewed (Figure 18). The modal class was centred on a ratio of 2.5 (range 2.25–2.75). The median was 3.1 and the mean was 3.4 (SD 1.35, SE 0.171, \( n = 62 \) species points). The lowest ratio was 1.62 (greater glider, *Petauroides volans*; Foley et al., 1990) and the highest was 7.63 (fat-tailed dunnart, *Sminthopsis crassicaudatus*; Nagy et al., 1988). Although this appears to be a wide range of ratios between FMR and RMR, the range needs to be examined in the context of the total variation in FMR and RMR. Across all body masses there was a greater than 200-fold range in the FMR and a greater than 100-fold range in RMR. Consequently, if RMR and FMR were not closely linked, the variation in the FMR : RMR ratio would be enormous. The likely range in the absence of any link between RMR and FMR can be simulated by randomizing locations of one of the traits (FMR) and recalculating the ratios using this randomized variable where the link of RMR to FMR is broken. When this procedure is performed, the average ratio FMR : RMR turns out to be 11.7 (SD 24.4, median 3.9) and the range stretches from 0.12 to 155.5. In combination with the plot in Figure 16, this illustrates that RMR and FMR are strongly linked in this sample of small mammals.

There are two reasons why this linkage may reflect only an artefact of the manner in which the analysis has been performed. The first concerns an interpretation of the nature of RMR. There are several ways of considering RMR (Hammond and Konarzewski, 1996). One interpretation is that the
metabolic processes constituting RMR are undertaken perpetually. Thus, when an mammal does things other than rest, it layers on top of the RMR a series of additional metabolic events. RMR, however, is sustained under­neath these other processes—the so-called 'partitioned pathways model' (Ricklefs et al., 1996). A second interpretation is that the processes of RMR are simply speeded up when an animal performs activity—the so-called 'shared pathways model' (Ricklefs et al., 1996). A third alternative interpretation is that RMR exists only when the animal is at rest, and that when it performs some other activity the metabolic processes constituting RMR do not persist—a 'replacement pathways model'. Since establishing exactly what metabolic processes contribute to RMR has proved elusive, direct testing of these ideas is difficult and, by definition, the alternatives cannot be separated simply by measuring energy expenditure, because the source of this expenditure cannot be partitioned. If the shared pathways and replacement pathways models are correct, it would be appropriate to establish a link between FMR and RMR simply by correlating them together. However, if the partitioned pathways model is correct, there is a potential problem because RMR constitutes a major component of the total FMR. Even if the additional activity and thermoregulation were constant, there would still be a link between RMR and FMR because FMR would equal RMR plus a constant. In effect, one would be correlating RMR against itself. For most wild mammals, however, RMR is a state seldom reached. Consequently, although in the shared pathways and alternative pathways models RMR may also potentially contribute to FMR for the short periods that animals spend in the RMR state, more normally it would not.

To evaluate whether RMR is correlated to FMR, even if the partitioned model is correct, it is necessary to examine whether RMR correlates not with FMR alone but with FMR-RMR (Ricklefs et al., 1996; Speakman, 1997b). There was a significant correlation between RMR and FMR-RMR in the present data set (Figure 19). The least-squares fitted regression:

\[
\log_{e} (\text{FMR-RMR}) = 1.222 + 0.863 \log_{e} (\text{RMR})
\]

explained 80.0% of the variation in RMR-FMR. Thus, RMR appears to be linked to FMR even if the partitioned model is correct, and the link is not an artefact of RMR being included within the FMR measurement.

A second cause of the link may be the shared variation in both FMR and RMR that is explained by other factors. I have already shown that both FMR and RMR are closely correlated not only with body mass, but also with temperature and latitude (for FMR) and latitude (RMR) (equations (13) and (16)). This shared variation might precipitate the relationships between RMR and FMR. I examined this possibility in three stages: first, by removing the shared effects of body mass using equations (1) and (14) (as has been performed in several previous analyses; e.g. Koteja, 1991; Ricklefs et al., 1996; Speakman, 1997b); second, by correlating the residuals derived from the phylogenetically independent comparisons, equations (5) and (17) (as performed by Ricklefs et al., 1996); and third, by removing the effects of body mass, temperature and latitude on both traits using equations (13) and (16) (which, as far as I am aware, has not been performed previously). In all three cases I examined whether there was still a relationship between the residual RMR and the residual FMR.

When the effects of body mass on both traits were removed, there was a significant relationship between residual FMR and residual RMR (Figure 20a) which explained 35.6% of the variation in residual FMR. The least-squares fitted regression equation was:

\[
\text{Residual FMR} = 0.0184 + 0.66 \text{ residual RMR}
\]

\[(F = 33.6, 1.60 \text{ d.f.}, P < 0.001)\]. Examination of this plot reveals two very clear outliers at either end of the plot (common shrew at the upper end and Namibian desert golden mole at the lower end) which could exert undue leverage on the relationship. Removing these outliers reduced the explained variability to 12.2%, but the relationship still remained highly significant.
mass (Figures 7 and 15). There was a significant positive relationship between the residual FMR contrast and the residual RMR contrast (Figure 21). The least-squares fitted regression explained 13.3% of the variation in the residual FMR contrast \( (F = 8.91, 1.57 \text{ d.f., } P = 0.004) \). Removing the outliers reduced the \( r^2 \) value to 0.088 but the relationship remained significant \( (P = 0.025) \).

Ricklefs et al. (1996) found that, while there was a strong correlation between the uncorrected residual RMR and residual FMR in birds, this relationship disappeared when the interrelationships of the residual phylogenetically independent contrasts were considered. This was not the case in their analyses of the mammal data, although this could have been because of the errors (pointed out above) in their mammalian phylogeny. The above analysis confirms that the effect of the residuals of phylogenetic contrasts of the small mammals is not a phylogenetic artefact. This does raise the question, however, of why there were contrasting results for the two major groups. Close examination suggests that the absence of a relationship in the residual contrasts of the birds may reflect errors in the derived values of the contrasts. There are, for

\[
\begin{align*}
(F = 7.9, P = 0.007), & \text{ indicating that the link between the traits was not only due to these two outliers.}
\end{align*}
\]

I evaluated residuals to relationships between the logged standardized phylogenetically independent contrasts of FMR and RMR to contrasts of body

Fig. 20. Residual field metabolic rate (FMR) plotted against residual resting metabolic rate (RMR). (a) Both residuals accounting for body mass only; (b) both residuals accounting for the effects of body mass, temperature and latitude.

Fig. 21. Residuals of the standardized phylogenetically independent contrasts of field metabolic rate (FMR) and resting metabolic rate (RMR) on body mass plotted against each other.
example, some wide discrepancies between the plots showing the relationships between the FMR and RMR contrasts and the mass contrasts (Ricklefs et al., 1996, Figure 2, p. 1061), and the plots showing the interrelationships of the residuals (Figure 3, p. 1063). Note, in particular, that in both the plots in Figure 2 of contrasts for FMR and FMR–RMR against the mass contrasts the node L represents the lowest residual value, while in the plots of residuals (Figure 3, p. 1063) it is the highest residual. Several other anomalous positions can be identified (e.g. for nodes V, H and C). Together these errors beg the question of whether the absence of a trend in the residuals of the phylogenetically independent contrasts for the birds is a reliable result.

When the effects of both temperature and latitude were removed, as well as body mass, there was still a significant relationship between residual FMR and residual RMR (Figure 20b). However, the significance of the relationship was much reduced ($r^2 = 0.205$) compared with that found when only the effects of body mass were removed. In addition, there were again two outlying points (shrew and mole) which exerted a large influence on the regression. In this instance, removing these outlying data completely removed the significance of the relationship ($r^2 = 0.028; F = 1.4, 1.50$ d.f., $P = 0.242$). This suggests that the existence of a link between FMR and RMR is almost entirely a consequence of the shared variabilty in the two traits that is explained by the effects of body mass, latitude and temperature. No previously published review has accounted for the shared variation, and, as shown above, accounting only for the shared variability due to body mass still leaves a significant relationship, because both residual FMR and RMR depend closely on ambient temperature and latitude.

A question, however, hangs over the validity of removing the outlying data points from the relationship presented in Figure 20. Such outlying data undoubtedly have a disproportionately high leverage in regression analyses, which might be used to justify their removal on statistical grounds. However, another way of looking at this data set is that the total data set represents only 3% of the extant mammal fauna. Both residual FMR and residual RMR were normally distributed, and the data for these two species are exceptional only in the sense that they refer to animals that are apart from the mainstream group which comprise this data set. These are, however, real animals, and there is no reason to doubt the accuracy of the measurements presented for either of them. Although they may be exceptional in the context of this data set, in comparison to the remaining 97% of mammals for which we do not have data they may be very representative. Perhaps these species point to the real underlying relationship between FMR and RMR, which is not exposed when they are omitted. This might occur, for example, simply because the variability in the residual traits is insufficient to detect the trend when they are excluded.

At present, the existence of a link between RMR and FMR appears to be very tenuous and depends only on a few outlying data which may be representative of a wider trend or may not. There are several other species of small mammal that have both high and low residual RMRs. For example, the mustelids have high RMR for their body size (Brown and Lasiewski, 1972; Casey and Casey, 1979) and it would be extremely instructive to know whether they also have high residual FMRs. At the other end of the scale there are several groups with low residual RMR, in particular the tenrecs from Madagascar, for which it would be interesting to establish whether they have similarly low residual FMRs.

A further reason for an artefactual linkage between FMR and RMR is the problem of phylogenetic independence considered above in the context of the effects of body mass on FMR and RMR. Although the correlation of residual FMR and residual RMR accounting for mass is not due to the lack of independence of species as sampling units, it is still possible that a linkage between residual FMR and residual RMR accounting for both mass and temperature/latitude reflects such an effect. In the present context, however, it would be unlikely for the relationship between residual RMR and residual FMR to be a phylogenetic artefact. This is because we already know that the significance of the relationship hinges on data for only two species (one with a high and one with low residual). Removing the effects of both mass and latitude/temperature in the phylogenetically independent contrasts is not possible because of problems of assigning realistic values for the environmental conditions at each of the ancestral nodes of the phylogeny.

B. Sustainable Metabolic Scope

The present estimated ratios of FMR to RMR were all substantially lower than the suggested absolute maximum physiologically possible limit of around 9–12x RMR. The highest ratio in the current data set (7.63) was approximately equal to the maximum sustainable scope of 7x RMR proposed by Hammond and Diamond (1997). However, the overwhelming impression from the observed ratios was that they were all considerably lower than the proposed limits, whether these are set at an absolute maximum of 9–12x RMR (derived in the introduction of the present paper), a limit of around 7x RMR (Peterson et al., 1990; Hammond and Diamond, 1997) or a limit of around 4x RMR (King, 1974; Drent and Daan, 1980). Of the 62 estimates of the ratio, only 12 measurements (19%) exceeded the suggested 4x RMR limit. The average ratio was substantially lower (3.4x RMR), and almost 35% of the ratios were lower than 2.0. These data raise two questions. (1) Why do mammals expend so little energy above their resting requirements? (2) Do the data support the notion of a sustainable metabolic limit?

There are several potential reasons why mammals may routinely expend energy at levels below the putative limits. The first is that by averaging FMR data across all seasons one inevitably pools measurements made in the lowest...
part of the year with data collected in the highest part of the year. Moreover, the data may also be biased because they routinely refer to mammals that are not working at their maximum capacity because it is easier to study mammals using the DLW methods when they are at phases of their annual cycle that are not the energetically most stressful. There is some support for this suggestion, because the period when small mammals are under most energetic stress is during the period of late lactation, yet relatively few of the measurements refer to this phase of the cycle. Perhaps mammals routinely expend energy at levels below their physiological capabilities for most of the year, but sustain resting rates that are appropriate for the period of late lactation (or some other stressful phase) when they would be expending energy at around the supposed physiological limits of either 4x or 7x RMR.

If this were the case, we might expect that by selecting from those species where multiple measurements at different phases of the annual cycle had been made, the maximum ratios for each species would cluster around a mean value much closer to the supposed limits. To test this I performed this selection on the 56 species for which multiple measurements were available. Although the mean ratio across this selected sample was greater than that across all the measurements, it was raised only slightly (from 3.4 to 3.6, and there were still many values where the ratio was lower than 3.0). These data did not cluster around either of the putative maxima. However, this might be because selecting the maxima from the measurements that had been made does not necessarily also include the very highest field metabolic rates because the highest phase of the cycle might not have been sampled.

To test this idea further I selected only those measurements that included mammals in late lactation. This was a much smaller sample of only 15 species, yet the ratio for this supposedly most stressful energetic phase of the annual cycle averaged only 3.4x RMR (SD 1.2, n = 15) and still included mammals that were working at less than 2.5x RMR. This is also an optimistic assessment of the FMR : RMR ratios because the RMR estimates in most of these circumstances do not refer to lactating mammals. As RMR generally increases in lactation, comparing lactating FMR with non-lactating RMR values will overestimate the derived ratio. These two analyses strongly suggest that the low levels of energy expenditure were not a consequence of selecting periods of the annual cycle where the mammals were under the least energetic stress. Moreover, RMR is extremely flexible. It seems improbable that mammals would need to sustain very high basal demands throughout the entire cycle in preparation for only one phase. Indeed, we already know that mammals radically increase their RMR during late lactation (e.g. Speakman and McQueenie, 1996) in response to the high energy demands during this period, and that there is no obvious linkage between pre-breeding RMR and any reproductive parameters (Derting and McClure, 1989; Hayes et al., 1992a), probably because of this flexibility. If mammals were not under maximal stress they could probably reduce their RMR to sustain a working ratio of around 4x or 7x RMR. Clearly, they do not do this routinely.

Why do the mammals not work harder and closer to their putative limits? There are two alternative explanations. The first is that mammals can work harder than they routinely do, up to the supposed limits, but by so doing they would pay a penalty in their life histories. There are several potential penalties that the animals might encounter if they were to increase their energy expenditure. For example, one well established idea concerning the nature of ageing is the free-radical damage hypothesis, first proposed by Harman (1956). This hypothesis suggests that animals age and ultimately die because their bodies are under constant attack by free radicals generated during oxidative phosphorylation.

Mammals could expend more energy but they choose not to because of the potentially negative life history effects that such expenditure might entail. I have suggested elsewhere that this can be envisaged as a curved benefit line that is associated with changes in energy expenditure (Speakman, 1997b). If small mammals expend energy in the field at a level equal to their RMR, they would derive no fitness benefits because they would be unable to do anything apart from rest all day. As expenditure increases, fitness benefits increase because the animal can perform behaviours in addition to resting that enhance its prospects for survival and reproduction. However, increased expenditure brings negative effects as well (in terms of reduced life expectancy), and ultimately these negative effects start to offset the benefits so that the fitness curve reaches a peak at levels well below the physiological maxima at which they are capable of working (Figure 22).

If this model were correct, we might expect that species which have long lives would have greater benefits to derive from staying alive. These animals might therefore have fitness curves that peaked at lower levels than species that are short lived and would have little to lose by expending energy routinely at levels close to their potential maxima. Possible examples include the Dasyurid mice (e.g. Antechinus, Phascogale and Sminthopsis), the males of which have a semelparous reproductive strategy. Males have a period of frenetic reproductive activity followed by death. During this period there would appear to be little benefit to be derived from minimizing expenditure to minimize free-radical damage. Unfortunately estimated energy demands for the two Antechinus species in the data set and the wambenger (Phascogale calura) do not include measurements made of males during their frantic mating period. However, Nagy and Lee (unpublished results, cited in Nagy et al., 1988) found individual 'breeding season' expenditures of 5–10x RMR for the two Antechinus species (stuartii and swainsonii), and the maximum ratio observed in the present review (7.63x RMR) refers to a sample of predominantly male Sminthopsis crassicauda measured in spring (Nagy et al., 1988). Together, these data strongly suggest that these small mammals are
working much closer to their supposed limits at a time when there are immediate benefits associated with such expenditure but no long-term consequences. By implication, the remaining animals may be more prudent in their use of energy because of the trade-offs between current expenditure and future life expectancy.

There is considerable circumstantial evidence to support the idea that increased energy demands may be linked negatively with future survival. For example, in birds there have been many brood manipulation studies in which the number of eggs that birds raise is manipulated by adding to or subtracting from those laid naturally by the female. Where investigators have examined it, there is a link between the energy expenditure of females and their brood size (e.g. Bryant and Westerterp, 1983; Dijkstra et al., 1990), although this has been established in relatively few species. Manipulating a brood size upwards therefore probably experimentally increases energy expenditure of the birds. In 36% of studies reviewed by Stearns (1993) there were negative impacts of brood enlargement on future survival of the parent birds. The remainder did not show any negative effects, but in no case was future survival improved by brood enlargement. Other studies have found the opposite effect of brood reduction (e.g. Daan et al., 1990c). The link is circumstantial, however, because generally effects on energy expenditure are not measured directly. A more direct link of expenditure to survival was established by Bryant (1990), who observed that house martins (Delichon urbica) that died during the 12 months following determination of their energy demands by DLW techniques, had had greater energy demands than those that survived. However, even this link is still correlational and may reflect other covariable factors.

Several experimental manipulations have been made of animals that tend to support the idea that the level of habitual energy demands is governed by a trade-off in their life histories. Schmidt-Hempel and Wolf (1988) observed that bees that foraged for longer had shorter lifespans. To demonstrate the causal nature of this linkage, Wolf and Schmidt-Hempel (1989) forced bees to carry extra weights, so increasing their energy demands during flight, and found that manipulated bees lived shorter lives than unmanipulated bees. Dijkstra et al. (1990) forced kestrels that were feeding their young to work harder and used DLW techniques to confirm that energy demands had been increased (Deerenberg et al., 1995); they found a negative effect on subsequent survival over the winter (Daan et al., 1996). Priede (1977) and Lucas and Priede (1992) manipulated fish by altering the rations they were offered and found that fish fed high rations were more active, leading to greater energy expenditure (inferred), and died faster.

These data indicate that the study animals were capable of working harder in their respective environments, and thus were unlikely to be limited in their expenditure by extrinsic factors, and that they also paid a penalty in subsequent survival for this extra work. As yet, however, no studies have been performed that involve manipulation of free-living energy demands of small mammals, and the mechanisms underpinning the reported trade-offs remain obscure. One area where considerable work on small mammal longevity has been performed is dietary restriction studies. It has been frequently observed that when small mammals are fed food rations below their habitual intake they experience an increase in survival and hence longevity (reviewed in Weindruch and Walford, 1988; Yu, 1994). Because food intake is reduced in dietary restriction, over the long term this must equate reduced energy expenditure. However, the situation is complicated by the fact that dietary-restricted
animals also sustain reduced body masses. In theory, oxidative damage is a phenomenon related to metabolic intensity (metabolism per gram of tissue) rather than whole-animal energy expenditure and, when expressed in this manner, there is no evidence that dietary-restricted animals have reduced metabolic intensity, and some evidence that it may even be increased (Baer et al., 1998). At present, therefore, there is no indication that the increased longevity invariably observed in dietary restriction is mediated via reduced energy expenditure and reduced metabolic intensity, leading to reduced oxidative damage.

To test the idea that small mammals restrict their energy expenditure below the putative intrinsic limitations because of a trade-off with future survival, I made two further analyses. Data for longevity are sparse and generally refer to single individuals maintained in zoos, which may not be representative of larger samples. On a more general level, however, there is a positive correlation between body size and longevity (Peters, 1983; Calder, 1984). On average, we might expect that if animals that live longer have greater benefits to derive from saving themselves there would be a negative relationship between the FMR : RMR ratio and body mass. Although other authors have reported such a linkage (Degen and Kam, 1995), in the present data set there was no evidence to support this prediction (Figure 17: whether bats were included or excluded from the sample; see below). Second, apart from the effects of body mass, some orders of mammals have exceptional longevity. The bats, for example, routinely live five times longer than might be anticipated from their body mass. Because bats have such long lives, we might anticipate they would be prudent in their use of energy above RMR. Refuting this hypothesis there was no significant effect of order on the average ratio (F = 1.18, P = 0.26, ANOVA; a similar result either excluding or including the groups represented by single species). Indeed, the bats averaged the highest ratio from the seven orders represented in the data with an average FMR : RMR ratio of 3.97 (SD = 8). This high ratio is opposite to that predicted from the trade-off model presented above. One explanation for the lack of such an effect is that longevity is linked to lifetime or annual expenditure, which is only poorly reflected in point measurements. This could be particularly the case for bats, many species of which spend winter in hibernation. However, only four of the nine species involved in the sample of bats used here were species from the temperate zone, which hibernate, and there was no difference in the ratio of FMR : RMR between the species that do, and those that do not, hibernate. Apart from the high energy demands in semelparous male marsupial mice, the present data do not provide any evidence in support of the trade-off model.

Why do small mammals not routinely work at 4x, 7x or even 9–12x RMR? An alternative answer to the trade-off solution to this question is that they may be physiologically capable of working at any level up to the uppermost limit of 9–12x RMR, but they are kept from so doing because of the limited supply of energy from the environment (the extrinsic limitation hypothesis).

If this alternative hypothesis is correct, we might anticipate that mammals feeding on rich and abundant food sources would have higher ratios than those feeding on poor food sources. I tested this idea using the dietary categories listed above. The FMR : RMR ratio was significantly associated with the diet (Figure 23; F = 2.85, P < 0.05). The pattern of this effect, however, shows that foods containing more and available energy were associated with higher metabolic rates. Using a dummy variable to code for the dietary energy content there was a significant positive linkage between dietary energy content and the FMR : RMR ratio (r² = 9.3%, P = 0.016). The highest ratios of FMR : RMR are reported for mammals exploiting the most energy dense and available resources (fruit and nectar). In contrast, mammals that exploit the worst energy source (foliage) have the lowest ratios. Phylogenetic order is not a significant factor (F = 0.65, P > 0.05) and hence the effect of diet on the ratio is probably not a phylogenetic artefact. A plausible reason why the ratio is dependent on diet, with higher ratios linked to higher density foods, is that different foods provide different supplies of energy, and thus mammals exploiting different food supplies become extrinsically limited in their potential field energy expenditure at different levels (McNab, 1980, 1983, 1986a).

Of the two ideas explaining the lower than maximal field metabolic rates, these data lean more closely to a suggestion that small mammals may be extrinsically limited in their energy budgets (see also Koskela et al., 1998).

![Image of Figure 23](image-url)
This is not very strong evidence, as the effect of diet only barely managed to reach significance. However, dietary assignments are very crude estimates of food availability, and the fact any relationship at all is found is quite surprising. More refined estimates of energy availability should refine the test of the hypothesis. I think this interpretation is unexpected in the light of manipulative experiments performed on birds and insects which suggest that those animals are working under some form of life-history trade-off. If small mammals are extrinsically limited, this discovery leads naturally to some consideration that the supposed intrinsic limits of 4x RMR (Drent and Daan, 1980) and 7x RMR (Hammond and Diamond, 1997) are perhaps illusory. The supposed limit of 4x RMR is based on identical observations to those summarized here, but based on a much smaller database that was available 20 years ago. In that database (for birds) it was noticed that the maximum values of FMR did not exceed 4x RMR, and this was suggested as a physiological upper limit (Drent and Daan, 1980). There is no other reason to suppose that a 4x RMR limit should apply to mammal energy expenditures apart from the fact that the first measures using DLW methods did not exceed this value. Indeed, the fact that as more data have accumulated the 4x RMR limit has been routinely breached in small mammals and in birds (e.g. Bryant, 1990; Bryant and Tatner, 1991) indicates that it is not a physiological threshold. The 7x limit was derived under very similar circumstances. Hammond and Diamond (1997) and Peterson et al. (1990), for example, accumulated the available data from both laboratory and field studies, and selected from these the values considered to be maxima. The highest of these was around 6–7x RMR, and therefore they increased the supposed limit to 7x RMR. However, there is little evidence to suggest that this is an actual physiological limitation. Summarizing data in this manner becomes a self-fulfilling prophecy. If one selects the maximum observed FMR : RMR ratio across a sufficiently large data set, and suggests that this is a limit, inevitably most following observations will fall below this exceptional value (i.e. will not breach the limit and thus support its existence).

However, data suggestive of higher energy expenditure ratios will be called into question because they are ‘physiologically’ impossible, which may make them more difficult to publish.

The only appropriate physiological limits are those derived independently of the FMR and RMR data. I have suggested here that continuously exercising large mammals, bats, birds and humans would expend energy at around 9–12x RMR, and that for smaller terrestrial mammals the limit might be lower at around 8–9x RMR. This is currently an extrapolation from measurements of active metabolic rate and it requires verification. However, this represents an independent estimate of a potential physiological limitation on energy expenditure. The closest alternative derivations are estimates of uptake capacity across the brush border of the small intestine (Karasov and Diamond, 1985; Hammond et al., 1994) and maximal rates of food intake rate (Kirkwood, 1983). These latter measurements provide an upper boundary for energy uptake to support expenditure. However, the plasticity of the gut is such that any instantaneous measurements of this capacity may reflect only the demands under which the tract is currently being placed. These are not strictly intrinsic limits but reflections of the existing level of demand.

The current data suggest that RMR is probably constrained by a number of different factors. The most important of these are the overall body mass and the ambient temperatures to which it is exposed. This latter effect is presumably related to changes in brown adipose tissue capacity (e.g. Pasanen, 1971; Tarkkonen, 1971; Feist and Rosenmann, 1976; Drent et al., 1977; Bucowiecki et al., 1982; Klaus et al., 1988; Speakman, 1995) and overall tissue thermogenic capacity (see, for example, the suggested links between RMR and the levels of UCP-2 in muscle (Boss et al., 1998a; Bouchard et al., 1997) and the increased expression of UCP-2 during cold exposure (Boss et al., 1998b)), but could also reflect resting activities of other organs such as the heart, kidneys and liver (Daan et al., 1989, 1990a), which may vary with the ambient temperature to which the mammal is exposed. The RMR is set primarily by these two parameters, which in the current data set explain 92% of the variability. There may be other factors infuencing RMR, which would become evident in wider databases (such as perhaps diet; McNab, 1980, 1983, 1986a) but the current data suggest these are probably of minor importance for the sample of small mammals examined here.

Field metabolic rate depends on a number of factors but it is strongly influenced by the demands exerted by the same two factors that dominate RMR: body mass and ambient temperature. This is probably not for exactly the same reasons. Nevertheless, larger body mass and lower temperatures both demand greater field expenditure of energy. Because the direction of these effects on FMR and RMR is the same, there is an apparent linkage between the two, with FMR being about two to three times greater than RMR. Once the effects of body mass and temperature have been removed from both traits, the linkage is virtually eliminated and depends solely on a few outlying data, the significance of which remains to be established. The actual field expenditure, however, depends not only on these demands but also on the supply of energy from the environment. This extrinsic supply of energy depends on the density of the food, its composition and ease of digestibility, and probably also the time available for the animals to collect it. Hence small mammals exploiting rich and abundant foods have raised FMRs because the extrinsic supply of energy allows them to sustain this higher expenditure, whereas those exploiting poor resources have suppressed FMRs. The consequence of this exploiting poor resources have suppressed FMRs. The consequence of this exploitation is a link between the ratio of FMR to RMR and the extrinsic limitation of FMR. This extrinsic limitation of FMR is a link between the ratio of FMR to RMR and the diet of the mammals in question, with low ratios linked to poor-quality diets. At present, there is no evidence for small mammals that favours the hypothesis...
that field energy expenditures are constrained by their implications for future survival, apart from the high-energy expenditures of some semelparous breeding marsupial mice.

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**APPENDIX A**

**Measurement of Oxygen Consumption by Indirect Calorimetry**

To measure oxygen consumption animals are usually confined in chambers through which a flow of dry air is passed. The animals consume some of the incoming oxygen and replace it with carbon dioxide. Thus the O2 content of gas in the outflow differs from that in the inflow. Generally the O2 consumption of the animal (Vo2) is estimated by:

Vo2 = (Vflow x CO2 out - Vflow x CO2 in) / F D2
where $V_{in}$ and $V_{out}$ are the volumes of air flowing into and out of the chamber respectively and $p_{O_2in}$ and $p_{O_2out}$ are the proportion of the gas flowing in and out that comprises oxygen. Because the amount of CO$_2$ added to the air by the animal is generally not exactly equal to the O$_2$ it removes, there is a discrepancy in the flow rate entering and leaving the chamber ($V_{in} = V_{out}$). The effect on the flow rate is quite small (usually less than 0.5%) but this has a knock-on effect on the estimated proportional O$_2$ content of the outflow which is more significant (up to 6%). This difference may be further exacerbated if the CO$_2$ is removed from the outflow before measuring the O$_2$ content of the exhaust gas. In respirometry it is unusual for both upstream and downstream flow rates to be determined, and often the inflowing O$_2$ content is also not quantified but assumed to be equal to the atmospheric average (0.2095). The exact calculation of O$_2$ consumption depends on exactly where the flow is measured (i.e. upstream or downstream of the chamber), and the treatment of the gases before measurement of flow and oxygen content (with or without CO$_2$ removed). Several authors (Depocas and Hart, 1957; Hill, 1972; Withers, 1977; Gessaman, 1987) have reviewed the alternative equations for determination of O$_2$ consumption in these different situations.

The system that minimizes the error in the oxygen consumption estimate, if RQ is unknown, is to absorb the CO$_2$ in the excurrent stream and to measure the flow downstream of the CO$_2$ absorber (condition 3; Hill, 1972). Because the CO$_2$ is completely absorbed in this configuration, the measurement is completely independent of the assumed RQ. The worst system for estimating O$_2$ consumption, if the RQ is unknown, is to measure the flow upstream of the chamber and combine this with a measurement of the downstream O$_2$ content without absorbing the CO$_2$. This system effectively assumes an RQ of 1.0 and errors occur if the actual RQ deviates from 1.0. The maximum error occurs if the animal is metabolizing fat (RQ = 0.7) and in this circumstance the error is approximately 6%. However, Koteja (1996c) has shown that, while this latter system may result in erroneous estimates of O$_2$ consumption, when the RQ is lower than 1.0, the error in the estimated O$_2$ content cancels exactly with the error in the conversion of O$_2$ consumption to energy expenditure for the same RQ. Consequently the resultant estimate of energy expenditure with this configuration is independent of the assumed RQ. In contrast the estimated energy expenditure when converting estimates of O$_2$ consumption derived from condition 3 are not independent of RQ. Therefore, the best system configuration for determination of O$_2$ consumption (when RQ is unknown) is not the best system for accurate determination of energy expenditure.

This may be confusing because it has generally been assumed that minimizing error in measurement of O$_2$ consumption will automatically minimize error in estimated energy expenditure. Many workers are familiar with the advice from Hill (1972) and Withers (1977) that measurements of VO$_2$ are best made by absorbing CO$_2$ and measuring flow downstream of the absorber. In my experience (with referees for papers) these researchers tend to respond negatively when presented with studies which use the worst possible protocol for measurement of VO$_2$, on the basis that this minimizes error in the estimated energy expenditure. To clarify why minimizing error in the measurement of O$_2$ consumption does not also minimise the error in the estimated energy expenditure, consider the following example.

In this example we have an animal in a respirometry chamber consuming O$_2$ at a rate of 10 ml min$^{-1}$. The animal is metabolizing carbohydrate and therefore has an RQ of 1.0. The flow rate into the chamber is 1000 ml min$^{-1}$. Because the RQ is 1.0 the flow rate out of the chamber is also 1000 ml min$^{-1}$. The inflowing gas consists of 20.95% O$_2$ and the outflowing gas consists of 19.95% O$_2$. The missing 1% O$_2$ has been replaced by 1% CO$_2$ in the outflow. The energy expenditure of the animal depends on the oxycaloric equivalent for carbohydrate utilization, which is 20.92 J ml$^{-1}$. The energy expenditure is therefore 3.4867 W (= (20.92 x 10)/60). Imagine that half-way through a measurement session the animal switches its metabolic substrate to fat. The RQ changes to 0.7. We will assume that, when the substrate utilization changes, the O$_2$ consumption remains stable at 10 ml min$^{-1}$ and that the energy expenditure of the animal changes. The oxycaloric equivalent for fat and an RQ of 0.7 is 19.66 J ml$^{-1}$. Consequently the energy expenditure falls to (19.66 x 10)/60 = 3.2766 W.

Given this basic system we will evaluate what happens when we make measurements of O$_2$ consumption and energy expenditure using three different standard configurations. First, consider what happens when we have a flowmeter upstream of the chamber metering the dry gas entering the chamber and we measure the O$_2$ content of the dry gas leaving the chamber without absorbing the CO$_2$ before analysis. In this situation, at the start of the experiment, we measure 1000 ml min$^{-1}$ entering the chamber. The gas leaving the chamber each minute has a volume of 1000 ml and an O$_2$ content of 199.5 ml, thus the measured percentage O$_2$ content of the outflow is 19.95%. Assuming the inflow gas content is standard dry atmospheric with an O$_2$ content of 20.95%, the O$_2$ consumption estimated at the start of the experiment is 1000 x (0.2095 - 0.1995) = 10 ml min$^{-1}$. If we assume an RQ of 1.0, the estimated energy expenditure is 3.486 W. Both these estimates (O$_2$ consumption and energy expenditure) are exactly correct. However, consider what happens after the substrate change. Now there is a slight discrepancy between the inflow and outflow. Because the RQ is now 0.7, rather than 1000 ml min$^{-1}$ leaving the chamber there is only 997 ml min$^{-1}$ (i.e. 10 ml O$_2$ is consumed per min but only 7 ml CO$_2$ is put back each minute). The error in the estimated outflow is only 0.03%. The O$_2$ consumption remains constant, thus 3.2775 ml oxygen is in the outflow. However, the analyser measures this as a percentage of the entire flow. Thus the actual measured O$_2$ content of
the outflow is 199.5/997 = 20.01%. The estimated O₂ consumption in this situation thus becomes 1000 \times (0.2095 - 0.2001) = 9.4 ml min⁻¹. Despite the error in the outflow of the chamber being only 0.03%, the resultant error in the estimated O₂ consumption becomes 6%. Consider, however, the estimated energy expenditure during this second part of the experiment. Using the same assumed RQ of 1.0, the energy expenditure estimate is \((9.4 \times 20.92)/60 = 3.2674\) W. This is only 0.03% different from the actual energy expenditure.

In this situation, measuring flow upstream of the chamber and the O₂ content downstream without absorbing the CO₂ and assuming an RQ of 1.0, the estimated O₂ consumption may be in error by up to 6%. The estimated energy expenditure, however, using the same RQ assumption of 1.0 is effectively correct, independent of the true RQ. If the assumption that RQ = 1.0 is replaced with another assumed RQ, the estimated energy expenditure estimate is also compromised. For an assumed RQ = 0.85 the actual expenditure is underestimated by 3% in all conditions, independent of the true RQ, and for an assumed RQ of 0.7 the underestimate in all conditions, irrespective of the real RQ, increases to 6%.

Consider now what happens in this system if we do not measure flow going into the chamber but rather measure the dried outflow. As with the above scenario the O₂ content of the outflow is measured without absorbing the CO₂. At the start of the experiment the outflow meter records 1000 ml min⁻¹ and the O₂ content of the outflowing gas is 19.95%. The estimated O₂ consumption is 1000 \times 0.2095 \times 0.1995 = 10 ml min⁻¹. In the second part of the experiment, however, the outflow metered is lower at 997 ml min⁻¹ and the recorded O₂ content in the outflow is 20.01% (see above for explanation of the changes between the first and second parts of the experiment). Thus the estimated O₂ consumption in the second part of the experiment becomes 997 \times (0.2095 - 0.2001) = 9.37 ml min⁻¹. This is 6.3% lower than the actual O₂ consumption. Using an RQ of 1.0 and an oxycalorific coefficient of 20.92 J ml⁻¹ gives estimated energy expenditures of 3.4866 and 3.2674 W, which have errors of 0% and 0.3% respectively, compared with the true values. Changing the RQ assumption to 0.85 gives a systematic error of 3% in the estimated energy expenditure and, changing it to 0.7 gives a systematic error of 6%.

When measuring O₂ content of the excurrent gas without absorbing CO₂ first, it appears to be marginally better to meter the flow upstream of the chamber rather than downstream. This gives a marginally lower error when estimating O₂ consumption and a very slightly more accurate estimate of the resultant energy expenditure. In practice, however, measurement errors in both flow and O₂ content of the gases makes the difference between the methods negligible. There is, however, a slight difference in the positioning of the flowmeter for the consequences of leaks in the chamber. (Because the chamber must accommodate an entry point for the animal, the chamber seal is the most likely source of leaks in the entire system.) This also depends on the positioning of the air pump that is driving or sucking air through the system. When the pump is upstream, the chamber is under positive pressure. Slight leaks in the seals will lead to air being pushed out of the chamber. When the pump is downstream, there is a slight negative pressure in the system and small leaks in the chamber seals lead to air being sucked into the chamber. Consider what happens with a pump sucking air through the chamber. If the flow into the chamber is measured, small leaks in the chamber seals will lead to errors in the estimated O₂ consumption. This is because the true flow rate coming into the chamber will be greater than that being measured (as a small amount of unmetered air will be sucked in through the seals). The error is basically in direct proportion to the contribution to the total flow made by the leak. If the leak provides 10% of the inflow the estimated O₂ content will be 10% too low. In contrast, if one meters downstream of the chamber (with a sucking pump), a slight leak in the chamber seal will make no difference because the outflow is being monitored and the leak contributes only to the inflow. On the other hand, if the pump is blowing air through the system, air will be lost outwards through leaking seals. In this situation the error is on the outflow, so metering the air into the chamber will be unaffected but metering the outflow will involve an error because some of the outflow has been lost. In general, therefore, meter position (upstream or downstream of the chamber) makes a negligible impact on the accuracy of the measurement (when CO₂ is not absorbed). However, one should always position the meter upstream if an upstream blow through pump is being employed and downstream if a downstream suck through pump is being used since this minimizes any errors that might occur due to a leaky chamber. (In both cases, however, a better solution is to eliminate the leaks, because the above interpretations of the impact of leaks make the assumption that any leaking air is fully mixed with the chamber contents, either before it leaks out, or after it leaks in. In practice this will depend on the exact location of the leak relative to the main inflow and outflow pipes in the system.) In my laboratory we typically use blow-through systems that are metered upstream of the chamber and we do not absorb CO₂ before measurement of O₂ content.

Finally, let us consider what happens in this system if we use the configuration recommended for the most accurate determination of O₂ consumption. In this scenario the dried outflow has its CO₂ removed before the flow being metered and the O₂ content measured. Because 10 ml O₂ in the flow is being consumed and all CO₂ is being absorbed before measurement of the gas flow and O₂ content, the measured flow rate at the start of the experiment is 990 ml min⁻¹. The O₂ content measured is 199.5/990 = 20.15%. Using the equation provided by Withers (1977) for this condition, the measured O₂ consumption is:

\[
V_{O_2} = (990 \times (0.2095 - 0.2015))/(1 - 0.2015) \\
= 9.92 \text{ ml min}^{-1}
\]
The error in this estimate is 0.8% compared with the true $O_2$ consumption of 10 ml min$^{-1}$. When the RQ changes to 0.7, the $CO_2$ in the outflow from the chamber changes and the flow rate at the chamber outflow also changes. However, the different amount of $CO_2$ in the outflow has no impact on this system since all outflowing $CO_2$ is absorbed. Thus, after the change, the measured flow remains the same and the measured $O_2$ consumption remains 9.91 ml min$^{-1}$ compared with the true value of 10 ml min$^{-1}$. This system for measuring $O_2$ consumption is far more robust to changes in RQ compared with the previous two systems. However, consider now what happens when we convert to energy expenditure. If we assume an RQ of 1.0, the initial energy expenditure estimate is 3.4788 W which has an error of 0.8%. However, after the change in the real RQ to 0.7, the estimated expenditure becomes 3.1988 W, which is an error of 6%. In contrast, assuming an RQ of 0.7 throughout reverses the errors. In this situation the initial error is 6% and the final error is only 0.8%. Making an assumption of RQ which is midway between the extremes leads to an error of about 3% in the energy expenditure estimate throughout the experiment (initially 3% lower, then 3% higher).

These examples should clarify that minimizing error in $O_2$ consumption estimates does not lead to the most accurate estimate of energy expenditure. When aiming to measure accurate $O_2$ consumption of animals, one should absorb $CO_2$ downstream of the chamber, and meter the flow of the resultant gas and its $O_2$ content. Oxygen consumption is estimated using equation (4) from Withers (1977). The resultant estimated $O_2$ consumption is independent of the actual RQ and accurate to better than 1%. If an estimate of energy expenditure is subsequently required from these estimates, the error in this derived estimate is minimized by assuming an RQ of around 0.85. Maximum errors in the derived energy expenditure will normally be less than 3%. If, from the outset, the intention is to measure accurate estimates of energy expenditure, one should meter the dry inflow to the chamber (for blow-through systems) or the dry outflow (for suck-through systems) and measure the $O_2$ content of the outflow without absorbing the $CO_2$. Oxygen consumption is estimated as the flow multiplied by the fractional $O_2$ content of the gas and its $O_2$ content change between inflow and outflowing gases. This $O_2$ content estimate may be in error by up to 6%. This should be converted to energy expenditure using an oxycalorific equivalent to an RQ of 1.0. Because of the cancelling errors, the resultant estimate of energy expenditure is independent of the actual RQ and accurate to better than 0.5%.

It is perhaps important to note that, while the errors in the estimates of energy expenditure cancel when using $O_2$ consumption, this is not the case for estimates based on $CO_2$ production. Using the above scenario again as an example, if air flow is measured upstream of the chamber, and $CO_2$ content is measured downstream, at the start of the experiment, when the RQ is 1.0, the $CO_2$ content of the exhaust stream will be 1%. The estimated $CO_2$ production will be 10 ml min$^{-1}$. (This assumes that the inflowing stream has atmospheric $CO_2$ scrubbed from it or all the chamber readings are referred to a pre-measurement baseline.) In the second part of the experiment the $CO_2$ production falls to 7 ml min$^{-1}$ and the total flow falls to 997 ml min$^{-1}$. The measured $CO_2$ content in the outflow is 0.702% and the estimated $CO_2$ production is 7 ml min$^{-1}$. Assuming an RQ of 1.0 gives an estimated energy expenditure of 3.483 W, in the first part of the experiment (correct), but an estimate of 2.87 W in the second part, which is 34% too low. Errors are minimized using an intermediate RQ of 0.85, but the estimated energy expenditure may still be in error by up to 16% (in either direction), compared with an error of less than 0.5% for measurements based on $O_2$ consumption using the same configuration.

These examples clarify that in practice, in most scenarios, whichever method is employed the error in the estimated $O_2$ consumption or energy expenditure is at most 6%, and more normally less than 3%.

**APPENDIX B**

**Raw Data**

The data are listed chronologically by date of publication. The Latin name of the species and common name, author and date of the publications are followed by data for distinct groups of the given species, for example different seasons, sites or sexes. For each group the body mass (g), field metabolic rate (kJ per day), approximate latitude of the study site and ambient temperature (T(°C)) are given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Body mass (g)</th>
<th>Metabolic rate (kJ day$^{-1}$)</th>
<th>Latitude (°)</th>
<th>T(°C)</th>
<th>Reference</th>
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<td>Wallis et al. (1997)</td>
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</tr>
<tr>
<td><em>Marmota flaviscutens</em></td>
<td>Moose possum</td>
<td>28.00</td>
<td>53.00</td>
<td>7.00</td>
<td>Green (1997)</td>
<td></td>
</tr>
<tr>
<td><em>Peromyscus auriferus</em></td>
<td>Pine mouse</td>
<td>51.00</td>
<td>64.00</td>
<td>7.00</td>
<td>Green (1997)</td>
<td></td>
</tr>
<tr>
<td><em>Bettongia gaimardi</em></td>
<td>Bettong</td>
<td>1700.00</td>
<td>892.00</td>
<td>44.00</td>
<td>Johnson et al. (1997)</td>
<td></td>
</tr>
</tbody>
</table>

**Metabolic Rates of Small Mammals**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Body mass (g)</th>
<th>Metabolic rate (kJ day$^{-1}$)</th>
<th>T(ºC)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lagostrophus</em></td>
<td>Rufous hare</td>
<td>1453.00</td>
<td>661.00</td>
<td>23.00</td>
<td>Lundie-Hjelmsen, in Green (1997)</td>
</tr>
<tr>
<td><em>Microtus pennsylvanicus</em></td>
<td>Meadow vole</td>
<td>486.00</td>
<td>366.00</td>
<td>-35.0</td>
<td>Green (1997)</td>
</tr>
<tr>
<td><em>Microtus agrestis</em></td>
<td>Horn-tailed field vole</td>
<td>26.50</td>
<td>72.00</td>
<td>53.00</td>
<td>Meirlo et al. (1997)</td>
</tr>
<tr>
<td><em>Phyllostomus hastatus</em></td>
<td>Spear-nosed bat</td>
<td>87.10</td>
<td>59.70</td>
<td>10.00</td>
<td>Kazn et al. (1998a)</td>
</tr>
<tr>
<td><em>Eremitalpa obesus</em></td>
<td>Desert golden mole</td>
<td>20.70</td>
<td>12.46</td>
<td>22.00</td>
<td>Seymour et al. (1998b)</td>
</tr>
<tr>
<td><em>Apodemus sylvaticus</em></td>
<td>Woodmouse</td>
<td>22.00</td>
<td>58.10</td>
<td>57.00</td>
<td>Cor et al. (1999)</td>
</tr>
<tr>
<td><em>Sycomys ludicrous</em></td>
<td>Common blossom bat</td>
<td>17.40</td>
<td>76.90</td>
<td>29.00</td>
<td>Coburn and Geiser (1999)</td>
</tr>
<tr>
<td><em>Talpa europaea</em></td>
<td>Mole</td>
<td>87.70</td>
<td>173.00</td>
<td>54.00</td>
<td>Fears et al. (unpublished results)</td>
</tr>
</tbody>
</table>

**References**

- Nagy and Gruchacz (1994)
- Berteaux et al. (1995)
- Blackwell et al.
- Bradshaw et al. (1994)
- Berteaux et al. (1996a)
- Cordell et al. (1996b)
- Berteaux et al. (1997)
- Wallis et al. (1997)
- Green (1997)
APPENDIX C
Phylogeny used in the Construction of the Phylogenetically Independent Contrasts

Part 1: Marsupials

Dasyurus viverrinus
Antechinus swainsonii
Antechinus stuartii
Parantechinus apicalis
Phascogale calura
Smirnops crassicaudata
Isoodon obesulus
Isoodon auratus
Macrotis lagotis
Marmosa robinsoni
Petaurus breviceps
Petauroides volans
Pseudochirrus peregrinus
Pseudochirrus herbertensis
Hemibelideus lemuroides
Gymnobelideus leadbeateri
Tarsipes rostratus
Bettongia penicillata
Bettongia gaimardi
Aepyprymnus rufescens
Potorous tridactylus
Setonix brachyurus
Lagochestes hirsutus

key

S = Species  G = Genus  SF = Sub-family
F = Family   O = Order   C = Class

Part 2: Bats

Syconycteris australis
Anoura caudifer
Carollia perspicillata
Phyllostomus hastatus
Macrotus californicus
Myotis lucifugus
Plecotus auritus
Pipistrellus pipistrellus
Eptesicus fuscus

Part 3: Insectivora

Microgale dobsoni
Microgale talazaci
Sorex areneus
Talpa europaea
Eremitalpa namibensis

key
S = Species  G = Genus  SF = Sub-family
F = Family   O = Order   C = Class
Part 4: Rodents and Lagomorphs (Glires)

Marmota flaviventris
Spermophilus parryi
Spermophilus saturatus
Ammospermophilus leucurus
Tamias striatus
Thomomys bottae
Dipodomys merriami
Dipodomys microps
Perognathus formosus
Pseudomys albocinereus
Pseudomys nanus
Zygomys (argunus?)
Pracromys natalensis
Acomys cahirinus
Acomys russatus
Apodemus sylvaticus
Mus musculus
Mus domesticus
Lemmus trimucronatus
Arenivora terrestris
Microtus arvalis
Microtus agrestis
Microtus pennsylvanicus
Clethrionomys glareolus
Clethrionomys rutilus
Peromyscus maniculatus
Peromyscus crinitus
Peromyscus leucopus
Psammomys obesus
Sekateamys calurus
Gerbillus allenbyi
Gerbillus pyramidium
Lepus californicus

key
S = Species  G = Genus  SF = Sub-family
F = Family   O = Order   C = Class

Part 5: Carnivores, Edentates and Higher Nodes

Marsupials
Bagariscus astutus
Insectivora
Bats
Vulpes cana
Vulpes velox

key
S = Species  G = Genus  SF = Sub-family
F = Family   O = Order   C = Class