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The impact of locomotor energetics on mammalian foraging

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The ecological impact of energy expended on an activity stems from its effect on foraging requirements. For locomotion, the effect of moving each additional unit distance probably depends on the proportional increase in energy expenditure. Other common measures of the cost of locomotion do not reflect the impact of energy expenditure on foraging requirements. In terrestrial mammals, both the effect of body mass and the unit cost itself are very small: moving one kilometre requires less than 2% of all other energy expenditures combined. Total locomotor energy expenditure ranges from ½% of daily metabolism for a 10 g mammal to 6% for an elephant. Potential sources of bias in the estimation of these costs include systematic bias in estimates of distance traversed and extra energy required for non-linear locomotion. Because larger mammals can readily locomote at greater speeds, the primary locomotor advantage of large size may not be conservation of energy but of time, which can mean greater safety and more or better food.

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Introduction

Among mammals, variables contributing to a reduced reproductive rate tend to increase as body size increases, including gestation length, weaning age, age at sexual maturity, and interbirth interval (Clutton-Brock & Harvey, 1983). Overall, annual natality in placental mammals scales as $M^{-0.33}$, where M is body mass (Western, 1979). This decline in reproductive rate implies that there must be compensating changes in size-related variables that increase survivorship. Indeed, mammalian life expectancy scales as $M^{0.35}$ (Calder, 1983). Thus the product of natality and life expectancy, which approximates lifetime reproduction, is, as expected, essentially size-independent, a result confirmed by direct regression of lifetime production of offspring against body mass (Fleming, 1975; Eisenberg, 1981).

What factors contribute to the greater life expectancy of larger mammals? One possibility is this. In the literature on animal size and energetics (e.g. Schmidt-Nielsen, 1972; Bourlière, 1975; Taylor 1977*b*), it has been stated repeatedly that the energy-cost of locomotion is less per unit

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distance for larger mammals, giving them the advantages of foraging over a larger distance at the same cost, or covering the same distance for less. For energy-limited animals, the resulting increase in net energy could result in a potential increase in life expectancy and, thereby, in fitness.

Does locomotion have a smaller impact on the energy requirements of large mammals than of small ones? The answer, as we shall see, depends on how one interprets the energy requirements of an activity.

In what follows, three questions will be considered. First, from an ecological and evolutionary viewpoint, how should the energy requirement of locomotion be evaluated in comparing mammals of various sizes? Secondly, why is it that if one uses a measure of locomotor energy requirements that reflects the impact of locomotor energy on foraging requirements and estimates those requirements from the best available data, unbelievably low values result? Finally, might there be some other significance to the allometric relationships between locomotion and body size in mammals?

The energy impact of locomotion

Whatever the activity of an animal, food is, with very few exceptions, the source of energy. Consequently, greater energy expenditures must be met by correspondingly greater intake in food energy (or possibly, a decrease in energy allocated to other activities). This means that from an ecological viewpoint, the impact of any change in the activities of an animal is the imposed change in its dietary requirements and consequently in its foraging. That is true for phylogenetic as well as ontogenetic changes in activity. Beyond that, the sizes of living mammals (and thus their total metabolic expenditures) span several orders of magnitude, and so, for comparative purposes—that is, in order to obtain values of equivalent effect across species—the impact on foraging of energy expended on an activity depends not on the absolute amount of food energy expended on that activity per day but on that amount relative to total metabolism (or total non-locomotor metabolism). In short, when we ask whether locomotion is less costly in energy for large mammals than for small, we are asking about the relationship between body size and the proportion of metabolism that is expended on locomotion: we are asking about *relative* costs, not absolute.

Alternative measures of energy costs

Several other measures of the effect of body mass on the energy cost of locomotion have been used. For example, the energy required per unit body mass to move a given distance decreases with increasing body mass, and that is true not only for running mammals but also for flying birds and swimming fishes (Schmidt-Nielsen, 1972). 'The significance of the relationship,' says Schmidt-Nielsen (1979: 194), 'is that, for a running mammal, it is metabolically relatively less expensive, and thus an advantage to be of large body size.' Similarly, Taylor (1977*b*) says that '. . . large animals can move about in their environment . . . at a lower cost per unit mass of animal. So, on energetic grounds, there are some advantages to being large . . .' By this criterion, the energy cost of locomotion can be expressed in J kg^{-1} km^{-1} units. It has been referred to by Taylor (1980) as the *incremental cost of transport*.

This cost is similar to the *net cost of transport*, which can be defined as the metabolic power per unit mass during locomotion minus metabolic power per unit mass during rest, all divided by velocity (Taylor, 1977*a*). Equivalently, at any specified speed, the net cost is the energy expended during locomotion in excess of resting metabolism per unit mass of animal and distance travelled (Alexander, 1982). It too has units of J kg^{-1} km^{-1}. It would be identical to Taylor's incremental cost of transport if, in the regression of metabolic power against speed, the y-intercept (metabolic power at an extrapolated zero velocity) were equal to resting metabolic power, but it is in fact greater, by a factor of 1·7 (Taylor, 1977*a*) or 1·2 (Paladino & King, 1979) in quadrupeds. The extra energy is thought by some (Taylor, 1977*a*), but not others (Paladino & King, 1979), to represent the energy required to maintain an upright posture. In terrestrial mammals, the incremental and net cost of transport are independent of speed (Taylor, Schmidt-Nielsen & Raab, 1970; Taylor, Heglund & Maloiy, 1982), but this is not true for flying birds or swimming fish for which velocity-specific values are required (Taylor, 1980).

Alternatively, one might measure the energetic cost of locomotion inversely in terms of efficiency: the ratio of work accomplished to work expended. If work expended is measured as metabolic energy expended on locomotion and work accomplished is measured in terms of the gravitational and kinetic potential energy of repeatedly elevating the centre of mass of the body and moving its parts, assuming no elastic storage, then large mammals are more efficient than small ones (Taylor, 1980).

However, from an ecological standpoint, none of these measures is a satisfactory indicator of the impact of locomotion on energy requirements. A moving animal moves not just a kilogram of body mass, it moves its entire body, whatever that weighs, and must pay the energy cost of doing so. Energy expended in moving the whole body over a unit distance goes up with body mass, not down, approximately in proportion to body mass to the 0·7 power, as indicated below. Since the energy of locomotion comes entirely from food, however indirectly, energy expended in locomotion ultimately must be supplied by feeding, and its impact on the organism will depend on its effects on the intake and allocation of food energy.

I know of only two other published statements about the problem of measuring energy expenditure on a mass-specific basis: in an article on Bergmann's Rule, McNab (1971) points out that large mammals lose more heat than small ones, not (as usually claimed) less. 'Here,' he writes, 'is a classical case of the confusion that often exists between the total rate of metabolism and the weight-specific rate. Although weight-specific expressions are often convenient, it is important to realize that an animal does not live on a per gram basis, but lives rather as an intact individual.' Garland (1983), in an article that takes up this line of argument, based his *ecological cost of transport* on total metabolism. Similarly for efficiency: the greater efficiency of large mammals does not mean that larger mammals work less hard than smaller ones. On the contrary: in each stride, large mammals elevate body parts of greater mass over greater vertical distances, and in total they expend more energy per kilometre, not less.

Neither increased locomotor efficiency nor reduced mass-specific costs of transport have any intrinsic selective value. That is the fallacy of big machines. A large automobile might be more efficient by engineering criteria but it still requires more fuel per kilometre than a small one, as well as being more expensive to purchase. Over a given distance, expending less energy per unit body mass or per unit of work accomplished, as large mammals do, is not energetically advantageous if, in the evolution of larger size, the energy required for basal metabolism and for other activities increases more than does the energy cost of moving the whole body that distance. The impact of energetics on the evolution of body size depends on all of the energy costs and benefits that a change in body size entails.

Another way of assessing the cost of locomotion is this. In most terrestrial vertebrates, mass-specific metabolic power (J s^{-1} kg^{-1}) increases as a linear function of speed over a wide range of speeds (Taylor, Schmidt-Nielsen & Raab, 1970; Taylor, Heglund & Maloiy, 1982). Among mammals, the only known exceptions, according to Taylor & Heglund (1982) are human walking (Margaria, 1938), kangaroo hopping (Dawson & Taylor, 1973) and lion running (Chassin, Taylor, Heglund & Seeherman, 1976). That is, for a given animal, the increment in energy to move an extra kilometre is independent of the speed at which the distance is traversed. This increment in energy expenditure per kilometre varies with body mass and, as indicated below, is approximately 10700 $M^{0 \cdot 684}$ J km^{-1}. By this cost criterion, locomotion is considerably more expensive for larger animals, not less, and the cost measured in this way reflects the additional energy per kilometre that must be supplied by food. Yet even this criterion of cost does not adequately reflect the impact of locomotor energy on foraging requirements. Although larger mammals expend more energy walking a kilometre than do smaller ones, they also expend more energy altogether, and their diets must be of correspondingly higher total energy content. The impact of locomotion on foraging requirements cannot be determined from the absolute energy increment that results from it. An additional energy requirement that an elephant could easily satisfy in a few minutes of foraging might represent a month's worth of labour to a mouse. Thus the ecological effect of body size on the energy expended in moving a given distance depends on the relationship between size and the *relative* increase in non-locomotor energy per unit distance.

Unit expenditure

If we take one kilometre per day to be the unit of locomotion, the relative energy expended per unit of locomotion, expressed as a percentage, is:

$$U = \frac{100\,(\text{energy increment per km})\,(1\text{ km per day})}{(\text{total daily metabolism}) - (\text{energy increment per km})\,(\text{km moved per day})} \qquad (1)$$

or in dimensional terms:

$$U = \frac{100\,(J'/\text{km}\,(1\text{ km/d})}{J/\text{d} - (J'/\text{km})\,(\text{km/d})}$$

where J′ represents locomotor energy and J represents total daily metabolism. I make the assumption, usually implicit in the literature on allometry, that we are dealing with independent random variables, so that the mean of their products equals the product of their means.

An alternative measure of unit cost would involve dividing by total daily metabolism instead of by non-locomotor metabolism. The use of non-locomotor metabolism as the denominator stems from the fact that locomotor energy depends on how far animals actually walk, and is not the same fraction of total metabolism in all species. It thus avoids the problem, mentioned by Garland (1983), that for animals that walk farther, total metabolism may, as a consequence, be higher. As will be seen, the choice of denominators makes little difference in the numerical values.

Estimated mean values for the variables in equation (1) as a function of body size in terrestrial, non-carnivorous mammals were obtained as follows. Energy increment per unit distance = 10700 $M^{0 \cdot 684}$ J′ km^{-1}, regardless of speed (from 10·7 $M^{-0 \cdot 316}$ J′ m^{-1} kg^{-1} in Taylor, Heglund & Maloiy (1982) multiplied by M). (Here and elsewhere in this paper, M = body mass in kilograms and d = day. All other abbreviations are standard SI units.) Total energy expended per day = 8×10^5 $M^{0 \cdot 71}$ J d^{-1}(Garland, 1983). Distance moved per day = 0·875 $M^{0 \cdot 22}$ km

d^{-1} (Garland (1983), for non-carnivorous, terrestrial mammals). Substituting these values into equation (1) and simplifying, we get:

$$\hat{U} = 1{\cdot}34\,(M^{0{\cdot}026} - 0{\cdot}0117\,M^{0{\cdot}22})^{-1} \tag{2}$$

where $\hat{U}$ designates an estimate of U.

Within the size range of terrestrial mammals (up to 10^4 kg), this estimate of U is a decreasing function of body mass M. That is, moving an additional unit distance will result in a greater percent increment in the non-locomotor metabolism of a small mammal than of a large one. By this criterion, locomotion per unit distance is cheaper for larger mammals. However, the size effect is very small and, as will be shown below, may be in the opposite direction if other recently published parameter estimates are used. More illuminating are the numerical values of U with increasing size. Energy expended on locomotion by mammals ranging in size from 10 g to 10,000 kg ranges, respectively, from a mere 1·51% to 1·13% of the value of non-locomotor energy. (If total energy, not just non-locomotor energy, had been used as the base for comparison, the values would have been even smaller but only slightly different). That is, energy expended on locomotion per unit distance, measured relative to the total of all other energy expenditures, apparently has changed very little with body mass in mammals and is, in any case, very small. If these figures are reliable, conservation of energy per unit distance is not an explanation for evolution of large body size in animals.

Total expenditure

The distance moved per day by placental mammals scales in proportion to body mass to the 0·22 power and energy expended per unit distance scales in proportion to body mass to the 0·68 power (references above). Thus their product, energy expended per day on locomotion, goes up as $M^{0{\cdot}90}$, that is, it increases with size more rapidly than total metabolism but less rapidly than body mass. For a mammal of any given size, the relative amount of non-locomotor energy per day that is devoted to locomotion, expressed as a percentage, can readily be calculated:

$$T = \frac{100\,(\text{energy increment per km})\,(\text{km moved per day})}{(\text{total daily metabolism}) - (\text{energy increment per km})\,(\text{km moved per day}).} \tag{3}$$

We note, however, that the product on the right of the denominator—energy expended on locomotion—is about two orders of magnitude smaller than total metabolism, and so for all practical purposes can be ignored. If we do so, T becomes equivalent to Garland's (1983) *ecological cost of transport*. Using the estimates for variables that were given above, an estimate $\hat{T}$ of T can be obtained:

$$\hat{T} = \frac{100\,(10700\,M^{0{\cdot}684})\,(0{\cdot}875\,M^{0{\cdot}22})}{8 \times 10^5\,M^{0{\cdot}71}} = 1{\cdot}17\,M^{0{\cdot}194}. \tag{4}$$

Garland (1983), using a slightly different value for the incremental cost of locomotion, got an estimate of $1{\cdot}17\,M^{0{\cdot}21}$ for non-carnivorous mammals.

For a mammal of 100 kg, its daily trek of 2·4 km accounts for only 2·9% of its daily energy expenditure, according to equation (4). For a 10 g shrew, the results are even more extreme: locomotion accounts for a mere 0·5% of total energy expenditure, and even an elephant spends only about 6% of its energy on locomotion. That is, except for very large mammals, energy spent on locomotion seems to be a negligible fraction of total metabolism.

The small but positive exponent of $\hat{T}$ suggests that, during the evolution of larger body size in various mammalian groups, energy expended on locomotion has increased slightly more rapidly than total metabolism. However, as shown above, relative energy expended per unit distance, U, is nearly independent of body mass, and so cannot account for the fact that large mammals expend a larger proportion of metabolism on locomotion. As Garland (1983) has pointed out, the positive exponent of T results primarily from the positive scaling of day-journey length to body mass, and he has argued that this positive scaling is primarily a reflection of the allometric scaling of foraging requirements. Because highly nutritious foods make up only a small fraction of the biomass in any community, most large herbivorous mammals must feed on food of low quality (Jarman & Sinclair, 1979). That, in turn, means they must move farther to satisfy nutritional requirements, but how much farther? Although the scaling of food availability as a function of mammalian body size is as yet unknown for any community, the positive scaling of T suggests that large mammals must expend a greater proportion of their metabolism on locomotion in order to satisfy their nutritional needs. If so, then foraging requirements are both a cause and a consequence of size-related differences in the proportion of metabolism devoted to locomotion.

Accuracy of estimates

How reliable are these values? Neither the total locomotor expenditure T nor the unit expenditure U can be measured directly. However, we can check their plausibility either by checking the estimated values of the variables or by looking at the implications of these measures.

First, consider the estimates. Energy expended per kilometre has been regressed against body size in several recent studies. Recalculated to standard SI metric units, J km^{-1}, the values in the three most comprehensive compilations are:

Estimate 1: 10,700 $M^{0.684}$ for mammals and birds (Taylor, Heglund & Maloiy, 1982),
Estimate 2: 11,300 $M^{0.72}$ for mammals and birds (Fedak & Seeherman, 1979), and
Estimate 3: 11,100 $M^{0.68}$ for mammals and birds (Paladino & King, 1979).

If the other variable values that I used are nearly correct, then there is no appreciable difference in the percentage of energy expended per unit distance when calculated from any of these estimates. For a 10 g mammal, estimates of the cost of moving one kilometre per day (probably too far for most mammals of that size) ranged from 1·42% to 1·60% of non-locomotor energy; for a 10,000 kg elephant, the values ranged from 1·13% to 1·56%. With Estimate 2, contrary to the others, relative energy expenditure per unit distance, calculated via equation (1), increases with body mass, but the scale effect is negligible, as it is with the other two estimates. In calculating the results given above, I used the most recent value, Estimate 1.

Of course, all of the estimates discussed here are mean values. In addition to the usual statistical questions of their standard errors, which are given in the cited literature, there is an additional problem resulting from the fact that the variables do not correlate perfectly with body size. As Garland (1983) has pointed out, day-journey lengths (his 'daily movement distances') are by far the most variable components in scaling the total cost of locomotion to body size.

Secondly, total daily energy expenditures under free-ranging conditions have been measured for several small mammals but for no very large ones, and the extrapolation upwards may be subject to considerable error. At present, there is much variability in the published regressions of daily energy expenditure against body mass. For 36 species of rodents (3–400 g), French, Grant, Grodziński & Swift (1976) calculated 304 $M^{0.5}$ kJ d^{-1} and that value is close to that obtained by Mace & Harvey (1983) for 19 rodent genera (8·3–252 g), namely 334 $M^{0.53}$ kJ d^{-1}. Garland (1983), using only data from doubly-labelled water studies on eight species of mammals (14 g to 9 kg), calculated 802 $M^{0.66}$ kJ d^{-1}, but argues that this value is inadequate to predict the daily energy expenditure of an elephant. He arbitrarily settled on 800 $M^{0.71}$ kJ d^{-1}, but it is interesting to note that, if one accepts the *y*-intercept value of 800 kJ d^{-1} at a mass of 1 kg, then a mass exponent of 0·75 is needed to predict the elephant metabolism that Garland (1983) quotes from McKay (1973), namely 401664 kJ d^{-1} for a 4000 kg elephant.

The third parameter, mean day-journey length, was obtained by Garland (1983) from a regression of daily distances moved against mammalian body sizes, based on 76 species ranging in size from shrews to elephants. Taken at face value, these data should provide a reliable value. However, I believe that almost all methods now used for estimating day-journey lengths systematically underestimate the true length. An animal's actual route through its home range is more devious than the trajectory of the centre of mass of its group, than a straight line connecting two point samples of its locations, than a straight line connecting the mid-points of quadrats through which the animal moves, or than a plot of its route, particularly on a small-scale map.

An underestimate in distance moved per day would lead to an underestimate in the total energetic cost of locomotion. I do not know of any evaluation of the magnitude of this underestimate, but would not be surprised if the published values are, in most cases, off by a factor of two, three, or even more. The magnitude of the bias probably increases inversely but to an unknown extent with map scale, and thus the values for large mammals will, on average, be farther off than for small ones. I would expect the underestimates to be greater in animals such as arboreal primates that have considerable locomotor fexibility and that move through complex habitats with many obstructions, so that their route is particularly circuitous, both horizontally and vertically. Half the species in Garland's tabulation of mammalian day-journey lengths are primates.

Circuitous pathways may be significant for another reason. In the laboratory, transport energy is measured during linear locomotion, typically on a treadmill. In the wild, appreciable additional energy may be required for repeated changes in speed and direction. The magnitude of this effect is unknown.

Finally, two predictions that can be made on the basis of the values given above are unreasonable. First, the mean daily travel time-budget of mammals (hours per day spent travelling) should equal the mean day-journey length divided by mean travel velocity: $h/d = (km/d)\ (km/h)^{-1}$. Mean day-journey length in non-carnivorous terrestrial mammals is 0·875 $M^{0.22}$ km d^{-1} (Garland, 1983). For mammals, the mean velocity of walking is 0·33 $M^{0.21}$ m/s, according to Peters (1983), based on Buddenbreck's (1934) regression of walking speed in captive mammals on body length combined with mass-length relationships. Note that the size regressions used above for mean day-journey length and walking velocity scale to essentially the same exponent of mass, which implies that the mean daily travel time budget should be essentially independent of size and very nearly 0·74 h. Although I do not know of a compilation of travel time-budgets in mammals, this value is much too low for nearly every mammal with which I am familiar. That is, either mammals walk farther than Garland's regression indicates, or Buddenbreck's regression for walking speeds gives values that are too high for the average velocity at which animals traverse their home ranges, or both. Pennycuick (1979), on the basis of theoretical arguments by Alexander (1977), suggests a different relationship of mean walking speed (V) to mass, namely, $V = 0{\cdot}50\ M^{0.13}$ m/s. However, velocity calculated from Buddenbreck's data ($V = 0{\cdot}33\ M^{0.21}$ m/s) predicts exactly the mean walking speed of wildebeests, 0·98 m/s (Pennycuick, 1975), using, as Pennycuick (1979) does, a body mass of 180 kg.

The second unreasonable prediction is as follows. In Amboseli National Park, Kenya, an average adult female baboon weighing 11 kg (Altmann, J., 1980) walks 6·10 km per day (Post, 1981) (vs. 1·48 predicted by Garland's regression formula). This travel accounts for 23·9% of the 11 daylight hours during which they are active (Post, 1981), i.e. for 2·63 hours per day (compared with the predicted 0·73 h, above), with an average travel velocity of 2·4 km/h (compared with 1·97 km/h according to Buddenbreck's regression). That is, baboons walk longer, faster, and farther than average for mammals of their size—not a surprise. However, according to equations (1) and (2), this travel adds only 1·35% per km to their non-locomotor energy budget, or is altogether 2% of their total energy budget, and this is unreasonably low, as the following calculations show. For a mammal of 11 kg, basal metabolism (354·24 $M^{0\cdot75}$ kJ/d, Hemmingsen (1960)) requires 2144·78 kJ/d, and total metabolism (800 $M^{0\cdot71}$ kJ/d) requires 4390·14 kJ/d, so that the energy of activity (non-basal metabolism) is 2245·36 kJ/d. Energy expended per day on locomotion (10700 $M^{0\cdot684}$ J/km × 6·10 km/d × 10^{-3}) is 336·53 kJ/d. That is, locomotion occupies 24% of the 11-h active period but accounts for only 15% of non-basal energy. Thus, the remaining 76% of the active period must account for 85% of non-basal energy expenditure. (During the other 13 h, primarily night-time, the animals are usually asleep or dozing and therefore presumably are near basal metabolic rate.) This would require nearly a doubling of the non-basal metabolic rate during the remaining time. That is, these values could be correct only if the energy expended during non-locomotor periods were about as energetic, on average, as running instead of walking. This is surely false: the rest of a female baboon's time-budget during the 11 daylight hours consists of feeding (46%), resting (22%) and socializing (7%) (Post, 1981).

In short, the available data on energetics and locomotion appear to underestimate the fraction of metabolic energy that is expended by mammals on locomotion. I suggest that much of this error is attributable to systematic bias (underestimation) in measurements of day-journey lengths and to unmeasured energy expended in changes in speed and direction. It may also be due in part to an overestimate of total energy expended per day or to an underestimate of the unit cost of locomotion. That is, the estimated *magnitude* of the unit cost of locomotion is too low. What about the *scaling* of the cost to body mass? Two possible sources of error in the mass exponents have been mentioned. As a result of map-scale effects, day-journey underestimates may increase with body size. Secondly, extrapolation from total metabolic rates of small mammals seems to underestimate the energy expended by elephants and presumably other large mammals (Garland, 1983). The first would tend to decrease the mass exponent of U, the second would increase it.

Velocity

If conservation of locomotor energy is not an advantage of large size in mammals, what then? Although the unit cost of locomotion appears to be little affected by body mass in mammals and to be negligibly small in any case, size affects two other components of locomotion: velocity and aerobic scope. Large mammals walk faster than small ones, and as indicated above, mean velocity scales in proportion to $M^{0\cdot21}$. Furthermore, even though the energetic cost per unit distance is independent of speed, small mammals cannot completely compensate for their slow walk by running instead of walking: an upper limit on the rate of sustained activity in a mammal is established by the fastest rate at which it can carry out sustained locomotion aerobically, without accumulating lactic acid (Bennett & Ruben, 1979). Furthermore, other processes, as yet poorly understood, apparently keep it from moving continuously, even at this rate.

Increased walking velocity can be advantageous in two ways. First, for a time-limited animal, increased velocity enables it to cover a given distance in less time. For an animal whose predation risk-rate is higher when foraging or migrating, reduced foraging time means reduced risk of predation.

Increased velocity of walking may also be advantageous in enabling animals to cover greater distances in a given amount of time. An animal's home range is limited to the area that lies within cruising range of the essential resource with the most restricted spatial distribution (Altmann, S. A., 1974). In arid regions, water is often that resource. For example, Pennycuick (1979) has argued that herbivorous mammals, both ruminant and otherwise, cannot deplete their gut contents below a certain point without disrupting their gut flora, so that the cruising range (foraging radius) of a water-dependent herbivore depends on the distance from water that can be traversed before those reserves are exhausted. That distance depends, in turn, on the size of the animal, since large mammals move faster on average than small ones. Thus large water-dependent herbivores can utilize food resources that are too remote from water for small herbivores.

Pennycuick argues that 'the need for a large foraging radius may well be a potent source of selection for large size. If two similar species are using the same water source during a prolonged drought, the one with the larger foraging radius will last longer, other things being equal.' Not necessarily: Pennycuick's rough estimate of the effect of body mass on foraging radius is that radius increases as mass to the 0·40 power. However, basal metabolism, total metabolism, and energy expended per kilometre all increase more rapidly with mass, so that if, with increased body size, food availability increases only as rapidly as the foraging radius, then energy requirements are outstripping energy input. Pennycuick's argument appears to be another example of the fallacy of big machines.

In arid regions, perhaps more important than the size of foraging areas is the ability of larger mammals to get to areas that are more remote from water, and thereby to utilize otherwise untapped food sources. By the end of the dry season on the savannahs of Africa, forage for ungulates is impoverished in the vicinity of permanent water sources.

Let me suggest two other benefits to large mammals of their greater day-journey length. By traversing greater distances per day, large mammals increase the floristic diversity of the foods that they encounter, which is especially important to frugivores (Kortlandt, 1984) and omnivores (Altmann, In prep.), and they are more likely to encounter local concentrations of food, which is important for animals that specialize on spatially heterogeneous foods. Conversely, larger mammals, because they walk farther, may be less susceptible to localized seasonal depletions in available food. I suggest that for this reason, vervet monkeys but not the larger baboons breed seasonally in Amboseli. In short, the locomotor advantage of larger size in mammals may not be a conservation of energy but of time, and that, in turn, can mean greater safety and more or better food.

Concurrently, however, size alters animals' nutrient requirements and the array of foods that are available to them, so that the ability of larger mammals to move farther and faster does not necessarily result in comparable increases in available food, or in improved proficiency at meeting nutritional needs. Distance and time have different size-dependent meanings to animals. A foraging distance that would satisfy a mouse would leave a gazelle hungry.

At present, little information is available about the effects of mammalian size either on nutritional requirements (Peters, 1983) or on the adequacy and reliability of available foods to satisfy those requirements. I suggest that, in many mammalian groups, the latter have increased more rapidly than the former, and that this has been a consequence of the ability of larger mammals to forage over greater distances per day. If so, then increased locomotor velocity has been a factor selecting for large size in mammals.

Summary

According to currently available values on locomotor energetics, locomotor energy expenditure in terrestrial mammals requires less than 2% of the energy expended in total on all other activities, and this value is nearly independent of body size. Total locomotor energy expenditure ranges from $\frac{1}{2}$% of daily metabolism for a 10 g mammal to 6% for an elephant. These estimates probably are not correct. Potential sources of error include systematic bias in estimates of distance traversed per day and extra energy required for non-linear locomotion. Because larger mammals can readily locomote at greater speeds, the primary locomotor advantage of large size may not be conservation of energy but of time, which can mean greater safety and more or better food.

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Postscript (added in proof). Since writing this article, I have learned of another potential source of systematic error in estimating the amount of energy expended on locomotion. Almost all studies of locomotor energetics utilize animals on treadmills, with the tacit assumption that locomotion is unaffected. However, when patterns of locomotion on treadmills and overground were compared, they were different in cats (Wetzel *et al.*, 1975) and humans (Nelson *et al.*, 1972). The energetic consequences of such differences apparently have not been studied in any animal.

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