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The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis

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Many authors have proposed a fasting endurance hypothesis (FEH) that posits a fitness advantage to larger mammals relative to smaller ones in environments in which food supplies fluctuate seasonally. A central argument of the FEH is that large mammals will not starve to death as quickly as smaller sized ones when deprived of food because of fundamental allometric differences in their metabolic rate and energy storage patterns. We suggest, however, that the FEH is overly simplistic and applies strictly only when the temporal pattern of resource variability and the organism's response to this variability are independent of body size: relationships that are unlikely. Biogeographic models based on the assumptions implicit in the FEH, that large mammal species are better able to withstand periods of seasonal food shortage, do not consider fully other important allometries. Although larger mammals appear to have an advantage in terms of mass-specific metabolic rates and ease of fat store transport, smaller mammals may be better able to exploit torpor, hibernation, food caching, and microhabitat climatic differences. Thus, viable strategies for surviving in seasonally food-limited environments are potentially available to mammals of all body sizes and no body size is favoured clearly in seasonal environments or under enforced seasonal fasting. We suggest further that intraspecific inferences regarding Bergmann's rule, stemming from consideration of the FEH, are based on an interpretation of the increase in fat stores with body size within species that is tautologous. We support our argument with data on fat stores in free-ranging polar bears (Ursus maritimus), a species that displays considerable variation in body fat stores.

Many authors have proposed that large body size affords a fitness advantage to mammals living in environments where food supplies fluctuate seasonally (Lindstedt and Boyce 1985, Zeveloff and Boyce 1988, Millar and Hickling 1990). Their arguments are based on the empirical observation that, both among and

within mammal species, body fat stores appear to increase with body mass more rapidly than do metabolic expenditures. Consequently, "all other factors being equal" (Millar and Hickling 1990: 8), larger mammals should survive longer without food (Calder 1984, Lindstedt and Boyce 1985, Millar and Hickling 1990). Although this fasting endurance hypothesis (FEH) provides no causal explanation for the different allometric scalings of metabolic rates and fat stores, it forms the basis of a number of recent biogeographical inferences regarding body size trends across mammalian faunas (Zeveloff and Boyce 1988) and clinal variation in body size within mammal species (Lindstedt and Boyce 1985, Millar and Hickling 1990). We suggest, however, that the seemingly compelling observation at the heart of the FEH, that smaller mammals should starve to death more quickly than larger ones, is lacking in meaningful ecological context. In addition to body-fat stores, many other environmental, physiological, and life history variables related to the ability of mammals to survive in seasonal environments vary allometrically with body size (Sauer and Slade 1987). Hence, all factors relevant to the FEH are not equal generally. The purpose of our paper is to evaluate critically, in light of these other factors, the ecological and biogeographical implications of the FEH.

Both within and among species, the FEH has been applied to questions regarding observed body size patterns. Variation in body size and other factors that influence the ability of mammals to survive in seasonal environments, however, is potentially much greater among than within species. Accordingly, we treat the inter- and intra-specific cases separately.

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The fasting endurance hypothesis: interspecific case

Lindstedt and Boyce (1985) noted that among mammal species the proportion of body mass allocated to fat stores appears to scale with a mass exponent well in excess of the generally accepted 0.75 scaling for metabolic rate (Calder 1984), implying that the length of fast that could be supported by fat stores will increase with body mass. Lindstedt and Boyce (1985) concluded, therefore, that the ability of mammal species to cope with annually recurring food shortages, and hence their ability to inhabit seasonal environments, should increase with body size (also see Brodie 1975).

The conclusion that, when deprived of food, a small mammal will starve to death before a larger one follows directly from the different allometric scaling of metabolic rate and body fat stores with body size. The corollary that larger species must have an advantage in environments where food supplies fluctuate seasonally, however, is more problematic. For example, in its strongest form the FEH predicts that an elephant-sized mammal will have a selective advantage over a mouse-sized mammal in a seasonal environment. Clearly, such an extrapolation solely from the original observation regarding starvation time and body size is unjustified and would ignore consideration of several rudimentary ecological principles: the most important being that the environments perceived by very large and very small mammals, as well as their behavioural and physiological responses to those environments, differ markedly. That this must be the case generally is supported by the most compelling of empirical evidence: the wide diversity of small mammals found in seasonal environments. If small mammals do have shorter fasting endurance, their presence in large numbers in seasonal environments implies not their inherent inferiority but, as noted above, that the modes of foraging and the foods exploited by mammals in seasonal environments must vary with body size such that long periods of starvation combined with normal metabolic demands become less likely as body size decreases. However, any such variation in the functional availability of food with body mass or the efficacy of adaptations to this variation violate the assumptions of the FEH, implicit in its application across mammal species, that environmental variation and adaptation are mass independent. We conclude, therefore, that fasting endurance does not impose a general constraint on the body size-structure of mammalian faunas.

It could still be argued that the FEH applies among subsets of species that do experience comparable seasonal food shortages and, within these, that smaller species would be disadvantaged or eliminated because of their inability to sustain a long-term fast. Even here, however, an examination of the relationship between body size and energy storage strategies indicates that smaller mammals are not necessarily at a disadvantage.

Body size and strategies of energy storage

Fat storage

If we assume that metabolic expenditures of mammals scale with body size (M) according to the allometric expression aM^b, where b ranges from 0.5–0.75 (Nagy 1987) and a is a constant, then the caloric value of the energy store required to support a fast of duration T, equivalent to the metabolic expenditures over that period, will be $aM^b \cdot T$. Since $b < 1$, the relative size of energy store required declines as M increases. Thus, relative to their mass, smaller-bodied mammals require a calorically larger store than larger mammals to support a fast of given duration. To illustrate, a mammal with a lean body mass (LBM) of 10 g requires a lipid store, relative to its LBM, from 18–300 times larger than that of a 10^6 g (LBM) mammal to support a fast of similar duration (Appendix A). Clearly, the smaller mammal would be less able to store and transport its proportionally larger fat store because of the higher fitness costs of fat transport: a reduced ability to escape from predators; reduced foraging efficiency; and increased stress on the locomotory apparatus.

Concluding, however, that the efficacy of fasting endurance increases in lock-step with body size is not entirely correct. In particular, some mammals are able to decrease metabolic expenditures during fasting through torpor or hibernation (Wang and Wolowyk 1988). This has three important effects. First, reductions in metabolic rate while fasting decrease the foraging time required to obtain the fat stores necessary to sustain a fast in direct proportion to the decrease in metabolic rate. Second, because it reduces the size of the required fat store, torpor also reduces the cost of transporting fat prior to fasting. Finally, torpor eliminates transport costs during a fast. Notably, the latter two effects become more pronounced as body mass decreases. For example, our hypothetical 10 g and 10^6 g mammals would have equivalent fasting endurance, under normal metabolic demands, with fat stores equivalent to 50% and 2.8% of their LBM, respectively (Appendix B). A 50% decrease in metabolic rate during fasting would result in a 50% reduction for both in the amount of fat required to support the fast. In terms of total body mass (TBM = fat + LBM), however, the result would be a decrease of 25% and 1.4%, respectively; a much greater absolute reduction for the small mammal in the fitness costs associated with fat transport prior to fasting.

If only the smaller mammal in our example were to reduce its metabolic rate, the reduction required to give it a fasting endurance equivalent to that of a larger mammal of similar body composition (% fat) would be described by the relationship $\delta = \gamma^{1-b}$ (Appendix C), where δ is the proportionate reduction in the metabolic rate of the small mammal and γ is the mass ratio of the two mammals (small/large). Thus our representative mammals would have equivalent fasting endurance (for

b = 0.75) with the same % fat if the smaller mammal reduced its metabolic rate during fasting by 94%. Such values are not unusual in deep hibernating small mammals where reductions in metabolic rate may approach 98% (Hochachka and Somero 1984).

Although the energy savings associated with a seasonal reduction in metabolic rate appear to apply to mammals of all sizes equally, allometric constraints may limit the use of both torpor and deep hibernation to smaller mammals (Morrison 1960). Smaller mammals clearly gain more energetically from short term reductions in metabolic rate (torpor) because they can more rapidly decrease and increase their body temperature. In addition, smaller mammals are better able than larger ones to hide while in torpor and hence have a lower vulnerability to predation then.

The ability to exploit longer term reductions in metabolic rate through use of deep hibernation also decreases with body size because of constraints associated with reproduction. In eutherian mammals, gestation period increases generally with adult body size (Martin and MacLarnon 1985). At high latitudes, gestation in mammals of large body size occurs during the winter, the period when deep hibernation would be most advantageous. Concurrent deep hibernation and active gestation is not possible, however, because normal foetal development cannot be maintained (Ramsay and Dunbrack 1986). Smaller mammals, on the other hand, are able to exploit deep hibernation because their relatively short gestations allow them to forgo foetal development during hibernation yet still complete a normal reproductive cycle during the period of resource abundance (Oxberry 1979). Because the delay in reproductive timing resulting from deep hibernation decreases with decreasing body size, the net fitness benefits of hibernation appear to increase as body size decreases. Notably, the largest mammal known to undertake deep hibernation has a body mass of approximately 7.5 kg (Lyman 1982).

External food stores

Small mammals are also better able than large ones to take advantage of food caching, a strategy of energy storage analogous in many ways to fat deposition. The available energy content of a cache, sufficient to meet maintenance costs for some period of fasting, must increase with body mass as does metabolic rate. Smaller mammals, therefore, require a larger cache relative to their body mass than do larger mammals to survive any given period of food shortage. Food caching differs from fat storage, however, in that the fitness costs associated with long-term transport of body fat stores do not apply. Instead, the primary constraints associated with food caching for mammals of all sizes are related to storage rather than transport. Effective storage requires a secure and dry storage site as well as food of high energy density that is resistant to spoilage (Smith and Reichman 1984). The rapid spoilage to which animal carcasses are prone, the relatively low quality of the foods exploited by large herbivores (Demment and Van Soest 1985), and the difficulties of obtaining secure storage sites of sufficient size may explain, in part, why the use of external food stores is restricted largely to small granivorous mammals (Smith and Reichman 1984).

Microclimate exploitation

During harsh climatic conditions smaller mammals have an additional advantage over larger ones; namely better access to microclimatic refugia such as burrows, dens, nests, and subnivean lairs. Use of these refugia can offset partly the relatively higher maintenance costs of smaller mammals by reducing the energy costs of thermoregulation and hence the rate at which energy stores are depleted (Reichman and Smith 1990).

In summary, the use of fat stores to meet energy demands during periodic food shortages appears available to mammals of all body sizes, albeit by use of differing physiological and behavioural stratagems. Although the ability to transport body fat sufficient to support a fast under normal metabolic demands increases with body size, small mammals are able to compensate by a greater capacity to reduce metabolic rate while fasting. Reduction in metabolic expenditures reduces the size of fat stores required and has the additional advantage of decreasing the foraging time required to obtain energy stores. Although the strategies of energy storage outlined above may differ in their body-size scaling of costs and benefits, energetically equivalent, although not identical, strategies for surviving enforced periods of resource shortage appear to be available to small as well as large mammals. Consequently, it is not evident that any body size should be favoured when there is a requirement for long or short-term fasting. However, the greater ability of smaller mammals to exploit torpor, deep hibernation, and the accompanying reduction in the foraging time required to obtain their energy stores, may make the complete dependence on body fat stores (fasting) during predictable periods of resource shortage increasingly feasible as body size decreases.

In light of the arguments presented, we suggest that the empirical trend noted by Lindstedt and Boyce (1985) should not be interpreted as evidence of size-dependence in the ability of mammal species to survive in seasonal environments. Instead we contend that the FEH, in concentrating on an allometric trend in fat stores, ignores other important body size allometries relevant to living in seasonal environments. We believe that the trend noted by Lindstedt and Boyce (1985) is best interpreted as a predictable consequence of the increasing efficacy of fat storage, with no accompanying torpor or deep hibernation, and the decreasing ability to exploit other equivalent strategies such as torpor, deep hibernation, food caching, and microclimate, with increasing body size.

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Despite our suggestion that the efficacy of torpor, deep hibernation, and food caching decreases with body mass, however, we do not conclude that smaller mammals are favoured over larger in seasonal environments. Indeed, the diversity of body size found within all mammal faunas implies the existence of a corresponding range of effective strategies, each with different size-dependent costs and benefits, for living in seasonally variable environments. We contend that biogeographic inferences regarding the size-structure of mammalian faunas that ignore the size-dependence of strategies to cope with seasonal variability are deficient necessarily.

The fasting endurance hypothesis: intraspecific case

Lindstedt and Boyce (1985) suggested that the relationship between body fat and body mass observed among mammal species might also apply within species, and, if this were the case, that larger conspecifics would then enjoy a selective advantage which should increase with the requirement for fasting endurance. They therefore concluded that "... fasting-endurance allometry contributes to Bergmann's Rule ..." (p. 876; see also Calder 1984). One of the best known of the biogeographic patterns that have been attributed to endothermic faunas, Bergmann's rule describes the tendency, within some species, for adult body size to increase with latitude (Mayr 1963). Although the generality of this pattern has been questioned (McNab 1971, Geist 1987), Lindstedt and Boyce (1985) argued that a positive relationship between body size and lipid-based fasting endurance could lead to a relationship similar to Bergmann's rule if seasonal variability in food supply, and hence the requirement for fasting endurance, increased with latitude. To explore their hypothesis we examine the likelihood that size-dependent constraints on fat storage are expressed within mammal species.

If the efficacy of fat storage is strongly size-dependent within a species, a causal relationship between body size and the ability to store or transport body fats is necessary. Although the allometry of metabolism dictates that smaller individuals can only achieve a fasting endurance equivalent to that of a larger individual if they have a relatively heavier fat store, for the intraspecific case the argument is misleading because the allometric effects are weak.

To illustrate, assuming that metabolic rate scales within species as approximately $LBM^{0.75}$, then a mammal with fat stores equivalent to 10% of its LBM would have the same fasting endurance as a conspecific with a 10% smaller LBM and a fat store equivalent to 10.3% of its LBM (Appendix D). Even a conspecific smaller by 50% would only have to increase its fat stores to the equivalent of 11.9% of its LBM to maintain the same fasting endurance. For any fixed period of fasting,

therefore, the required allometric increases in relative fat stores with decreasing body size would be very small (< 1%) over the adult size ranges found in most mammal populations. Because differences in % body fat in the order of 1% are well within the intraspecific range of variability typically found at any single adult LBM (Pond 1978) we suggest, therefore, that the relative increase in body fat stores required to maintain fasting endurance with decreasing LBM would be unlikely to cause undue mechanical stress or impair escape from predators for smaller conspecifics.

We now examine how the cost of transporting fat may vary with body size within species. For interspecific comparisons, the cost of locomotion (energy/distance) for terrestrial mammals has been shown to scale as $TBM^{0.7}$ (Garland 1983), so that the actual cost of transporting a fixed mass of fat per unit distance decreases with body size. However, since daily movement distances also scale allometrically as $TBM^{0.25}$ (Garland 1983), the total daily cost of transport per unit mass of fat scales as $TBM^{0.95}$. Based on the confidence intervals given in Garland (1983) this exponent is not significantly different from unity, implying that the daily cost of transporting a unit mass of fat is more or less independent of body size. The time between the acquisition and subsequent use of a fat store should also be independent of body size for individuals experiencing the same temporal pattern of environmental seasonality. Hence, the energy cost of transport ([cost/day]·[days transported]) should add a constant proportion, across all body sizes, to the total energy investment (energy stores plus transport costs) represented by a store of fat.

If the inter- and intraspecific cases are comparable, then the cost of transporting fat (energy/[time·g fat]) is independent of body size, and the total cost to an individual of transporting fat is directly proportional to the mass of those fat stores. Since for any fixed fasting endurance, fat stores should scale as the metabolic rate (e.g. $LBM^{0.75}$), the direct proportionality of transport costs to fat mass implies that total individual transport costs will also scale as does the metabolic rate (e.g. $LBM^{0.75}$). Consequently, since the transport costs for fat stores and metabolic rate scale identically, transport costs will represent a similar portion of an individuals energy budget regardless of its body size. That is, there should be no effect of body size on the relative energy cost of transporting fat sufficient for some fixed period of fasting. We conclude that there is no evidence of a size-dependence in the relative costs associated with either the storage or transport of fat that would prevent smaller conspecifics from achieving a fasting endurance equivalent to that of larger conspecifics.

Consequently, the purported rapid increases in fat stores with body size within species should be treated with caution. Certainly, there is substantial variation in fat stores within many mammal populations (Pond 1978, 1987). In reference to this relationship, Lindstedt and Boyce (1985) predict that there should be a pro-
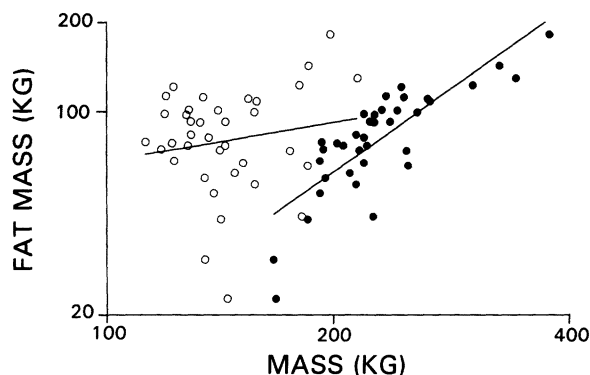
Fig. 1. The relationship between body fat stores and body mass in adult (> 3 yr) female polar bears sampled from south-western Hudson Bay, Canada. Body mass is expressed as either lean body mass (LBM; open circles) or total body mass (TBM = LBM + FAT; closed circles). There was a significant relationship between body fat and TBM (FAT = 0.1 TBM$^{1.25}$; $r^2 = 0.61$) but none between body fat and LBM (FAT = 11.2 LBM$^{0.43}$; $r^2 = 0.08$).

nounced positive relationship between body mass and the proportion of this mass allocated to lipid stores within species because "Within a species, body fat is the most variable constituent of body mass (Pond 1978), and the difference" [in body mass] "is attributable to differences in the mass of body fat" (p. 876). Their argument, however, is tautological. Such data do not indicate a relationship between body size and body fat but rather a relationship between body fat and body fat (i.e., heavier individuals are fatter). Biogeographic patterns in body size, such as that described by Bergmann's Rule, presumably refer to indicators of body size that exclude body fat, such as lean mass or measurements of skeletal dimensions.

To illustrate the problem we present data on the relationship between body fat and both TBM and LBM in free-ranging adult female polar bears (Ursus maritimus) from south-western Hudson Bay, Canada (Pond et al. 1992). Polar bears are a particularly appropriate species for illuminating our argument because of their wide range in adult body size and their use of body fat stores to support long term seasonal fasts (Pond and Ramsay 1992). When these data are analysed in terms of TBM there is a significant positive relationship between fat mass and TBM with a body mass exponent of 1.25. When fat mass is regressed against LBM, however, the mass exponent does not differ significantly from 0 (Fig. 1); the significant relationship between body fat and TBM is simply an artifact of the statistical procedure.

Millar and Hickling (1990) made an argument similar to that used by Lindstedt and Boyce (1985) and supported their contention that the relative size of fat stores increases with adult body size, within mammal species, with data from rodents reared on laboratory diets. Although their data indicate that, averaged across the

species tested, body fat stores increased with body mass as $W^{1.45}$, their measure of body mass was once again total body mass rather than lean body mass. As we note, such data reveal only that fatter individuals are heavier, but are not relevant to the relationship between lean body mass and body fat, and hence to the scaling of fasting endurance with LBM.

We conclude that there is no compelling evidence of a relationship between body mass, fat storage, and the ability to inhabit seasonal environments. Mammal species have evolved numerous adaptations to seasonal environments and fat storage is only one of these. We suggest that more insight into questions regarding the body size allometry of adaptations to environmental conditions, and hence between body size and life history, will be gained by a comparative approach which examines the allometric basis of a spectrum of equivalent, but different, strategies (Reiss 1989).

Appendix A

The fasting endurance (T) of a mammal with a fat store of mass X can be expressed as

$$T = \frac{K \cdot X}{a \cdot LBM^b} \tag{A1}$$

where K is a proportionality constant that converts fat mass into metabolic energy. The size of the fat store required to support a fast of duration T is obtained by rearranging eq. (A1) as

$$X = \frac{T \cdot a \cdot LBM^b}{K}.$$

Expressed as a proportion of LBM (mass specific fat store) this is

$$\frac{X}{LBM} = \frac{T \cdot a \cdot LBM^{b-1}}{K}.$$

The mass specific fat store required to support a fast of duration T will be therefore

$$\frac{T \cdot a \cdot 10^{b-1}}{K} \tag{A2}$$

for a 10 g mammal and

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$$\frac{T \cdot a \cdot 10^{6b-6}}{K} \qquad (A3)$$

for a 10^6 g mammal. Dividing expression (A2) by expression (A3) and setting $b = 0.75$ gives the ratio of the mass specific fat stores of the 10 g and 10^6 g mammals as

$$\frac{T \cdot a \cdot 10^{-0.25}}{K} \bigg/ \frac{T \cdot a \cdot 10^{-1.5}}{K}$$

which reduces to $10^{1.25}$ ($= 17.8$). The larger value of 300 approximates the result obtained by setting $b = 0.5$.

Appendix B

Let the total body fat stores of the 10 g mammal equal 50% of its LBM. Its fasting endurance is then obtained from eq. (A1)

$$T = \frac{K \cdot 0.5 \cdot LBM}{a \cdot LBM^b}$$

or

$$\frac{0.5 \cdot K}{a \cdot 10^{b-1}}.$$

A 10^6 g mammal with a fat store of X would have equivalent fasting endurance if

$$\frac{K \cdot X}{a \cdot 10^{6b}} = \frac{0.5 \cdot K}{a \cdot 10^{b-1}}.$$

Setting $b = 0.75$ and solving for X gives

$$X = (0.5 \cdot 10^{-1.25}) \cdot 10^6$$

or

$$X = 0.028 \cdot 10^6.$$

Thus, the required fat store is 2.8% of the LBM of 10^6 g.

Appendix C

The fasting endurance of a mammal is given by A1. The ratio of the fasting endurance of two mammals differing in LBM will be therefore

$$\frac{K \cdot X_1}{a \cdot LBM_1^b} \bigg/ \frac{K \cdot X_2}{a \cdot LBM_2^b} \qquad (C1)$$

where the subscripts 1 and 2 correspond to the two body

masses. If these two mammals have identical body composition (% fat) then

$$\frac{X_1}{LBM_1} = \frac{X_2}{LBM_2}$$

or

$$X_2 = X_1 \frac{LBM_2}{LBM_1}. \qquad (C2)$$

Substituting this value of X_2 into expression (C1) gives

$$\frac{K \cdot X_1}{a \cdot LBM_1^b} \bigg/ \frac{K \cdot X_1 \dfrac{LBM_2}{LBM_1}}{a \cdot LBM_2^b}$$

which simplifies to

$$\frac{a \cdot LBM_2^b}{a \cdot LBM_1^b} \bigg/ \frac{LBM_2}{LBM_1} \qquad (C3)$$

or

$$\left(\frac{LBM_2}{LBM_1}\right)^{b-1}$$

If $b < 1$ and $LBM_1 < LBM_2$ then clearly

$$\left(\frac{LBM_2}{LBM_1}\right)^{b-1} < 1$$

or equivalently from (C3)

$$\frac{a \cdot LBM_2^b}{a \cdot LBM_1^b} \bigg/ \frac{LBM_2}{LBM_1} = \delta \qquad (C4)$$

where $\delta < 1$. Dividing both sides of (C4) by δ gives

$$\frac{a \cdot LMB_2^b}{(\delta \cdot a \cdot LBM_1^b)} \bigg/ \frac{LBM_2}{LBM_1} = 1. \qquad (C5)$$

Eq. (C5) can be interpreted as the ratio of the fasting endurance of the two mammals when the metabolic rate of the smaller mammal ($a \cdot LBM_1^b$) has been reduced by a

factor δ. But, since this ratio equals 1, the large and small mammals will now have equal fasting endurance. Substituting

$$\gamma = \frac{LBM_1}{LBM_2}$$

into eq. (C5) gives

$$\frac{\gamma^{-b}}{\delta}/\gamma^{-1} = 1$$

or

$$\delta = \gamma^{1-b}. \tag{C6}$$

Eq. (C6) expresses the proportional reduction in the metabolic rate of the smaller mammal required for these two mammals of different LBM, but identical body composition, to have equal fasting endurance.

Appendix D

The fasting endurance of a mammal with a fat store equal to 10% of its LBM is from (A1)

$$\frac{K \cdot 0.1 \cdot LBM}{a \cdot LBM^{0.75}}. \tag{D1}$$

A second conspecific with a 10% smaller LBM and fat stores of mass X would have a fasting endurance of

$$\frac{K \cdot X}{a(0.9 \cdot LBM)^{0.75}}. \tag{D2}$$

These conspecifics will have equal fasting endurance if (D1) = (D2) or if

$$X = (0.9)^{0.75}(0.1)\,LBM. \tag{D3}$$

The mass of this fat store as a proportion of the second conspecific's lean body mass is obtained by dividing both sides of equation (D3) by (0.9 LBM)

$$\frac{X}{0.9\,LBM} = (0.9)^{-0.25}(0.1) = 0.103$$

Consequently, when the conspecifics have equal fasting endurance, the fat store of the second conspecific is equal to 10.3% of its lean body mass.

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