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# Fasting endurance and the evolution of mammalian body size

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## Introduction

The idea that the need for energy reserves may have been important in the evolution of different body sizes can be traced to Lindsey (1966) who recognized that 'the energy reserves may last longer in large rather than in small animals' and suggested that this may be one possible reason for large body sizes among northern poikilotherms. Several subsequent investigators drew similar conclusions based on studies of other taxonomic groups. A number of environmental correlates of body size among mammalian carnivores suggested that 'homeostatic needs' might set a lower limit to body size at higher latitudes (Rosenzweig, 1968). Body size in whales is inversely correlated with the length of the feeding season and suggests that large size reflects the need for energy reserves during the fasting period (Brodie, 1975). Large body size has also been recognized as important in enhancing the survival of terrestrial vertebrates during periods of resource shortage in strongly seasonal environments (Boyce, 1979; Murphy, 1985; Zeveloff & Boyce, 1988). Quantitative models of energy reserves and fasting endurance in relation to body size have been developed (Morrison, 1960; Calder, 1974, 1984; Searcy, 1980; Peters, 1983; Lindstedt & Boyce, 1985). Similar arguments have been used to explain size dimorphism between the sexes (Downhower, 1976; Ralls, 1976; but see Shine, 1988).

Despite this diverse support over many years, energy reserves and fasting endurance are not commonly incorporated into models considering the evolution of mammalian body size. Most studies still rely on traditional comparisons of insular faunas (e.g. Angerbjorn, 1986) and geographic clines (e.g. Langvatn & Albon, 1986) to identify indirect correlates of body size, or, at best, consider fasting endurance to be one alternative among many (e.g. Clutton-Brock & Harvey, 1983).

There are several reasons why fasting endurance has not been incorporated into models considering the evolution of body size. First, the assumption that fasting endurance is related to size has not been adequately tested (Clutton-Brock & Harvey, 1983; Langvatn & Albon, 1986). Second, large animals require more food than small animals; it is difficult to visualize how food shortages can favour a larger size. Third, the hypothesis as currently stated accounts only for increases in body size. Finally, the relationship between the fasting endurance hypothesis and others involving competition, food particle size and food quality are not clear. The purpose of this paper is to reconsider the evidence relating body size and fasting endurance, to consider the evolution of both large and small sizes, and to consider the relationship between fasting endurance and other environmental correlates of body size.

## Body size and fasting endurance

Quantification of the relationship between size and fasting endurance is difficult. Direct measures of fasting endurance by depriving animals of different size of food is clearly unacceptable, for good reasons. Two indirect approaches that consider physiological scaling can achieve the same end.

A first approximation of fasting endurance may be derived from the fact that metabolic requirements do not scale isometrically with body mass. Rather, homeostasis requires an amount of energy that varies approximately as the 0·75 power of mass. Relating to this, metabolic intensity (energy requirements per unit of mass) varies approximately as the −0·25 power of mass, while biological time (life-span, generation time, circadian rhythms) scales approximately as the 0·25 power of mass (Daan & Aschoff, 1982; Peters, 1983;

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Calder, 1984). Ecologically, this means that small animals must feed more frequently than large animals in order to maintain homeostasis. This consequence of physiological scaling is reflected in the fact that small mammals exhibit more activity bouts per day than large ones. Shrews have more than 10 activity periods per day (Calder, 1984; p. 235), voles and mice have five to six activity bouts per day (Harland & Millar, 1980; Madison, 1985), ungulates often exhibit two activity bouts per day (e.g., Bowyer, 1981; Eberhardt, Hanson & Caldwell, 1984), and large whales maintain homeostasis by having essentially an annual feeding bout (Brodie, 1975). Thus, homeostasis requires that large mammals consume more food, but at less frequent intervals, than small mammals.

A more direct estimate of fasting endurance can be obtained knowing how metabolic requirements and metabolic reserves scale with body mass. Lindstedt & Boyce (1985) assumed that energy reserves were represented by fat content, and found these to vary as the 1·19 power of mass. Since metabolism varies approximately as the 0·75 power of mass, fasting endurance varies as the 0·44 power of mass. Unfortunately, this and other models of fasting endurance (Calder, 1974; Searcy, 1980) rely on exponents derived from interspecific comparisons of metabolism and fat in relation to body size. Exponents to body size tend to be different for wide ranges of species than for closely related species (Tuomi, 1980; Clutton-Brock & Harvey, 1984; Millar, 1984), and exponents derived from intraspecific comparisons tend to be different from those derived from interspecific comparisons (Thonney *et al.*, 1976; Wilkie, 1977; Poczopko, 1979; Heusner, 1982). Because evolved changes in body size require selection among individuals (rather than among species), intraspecific patterns of metabolism and fat deposition provide the most appropriate estimates of fasting endurance. This fact was recognized by Lindstedt & Boyce (1985) who suggested that intraspecific patterns should be more pronounced than those among species.

We know of no published records documenting both metabolism and fat deposition in relation to body size in any population. However, our data on food ingestion and fat deposition (Table 1) can be used to estimate the exponent for fasting endurance, assuming that food ingestion reflects metabolic requirement. All data were originally collected for other reasons, and were subsampled to provide comparable estimates of both food ingestion and fat content. All samples consisted of adult males and non-breeding females; young animals and pregnant or lactating females were not included. In all cases, food ingestion was measured as consumption of laboratory rat chow by captive animals over several days, expressed in grams per day. Live weight (total body weight) was the average of all weights recorded while consumption was measured. Total body fat was determined by drying kill-trapped animals to constant weight and conducting petroleum-ether extractions on 1–2 g subsamples of homogenized dry material (Kerr, Ankney & Millar, 1982; Dobush, Ankney & Krementz, 1985). Weight of these animals was recorded as total body weight at capture. These procedures violate the assumption of independence in regression models, because total body weight includes fat, but were necessary to keep body weight comparable between samples. Six sets of paired data, involving five species, are presented in Table 1 (1–6). These indicate that the exponents relating energy reserves to body mass were always greater than those relating food ingestion to body mass. Fasting endurance ranged from the 0·20 to the 1·10 power of mass. Analyses of covariance of total fat in relation to body mass among seven samples (Table 1, 1–7) indicated a common exponent of 1·45 ± 0·23 SE. Analyses of covariance of ingestion in relation to body mass among 14 samples (Table 1, 1–6 and 8–15) indicated a common exponent of 1·05 ± 0·19 SE. A comparison of the common exponents indicated that fasting endurance varied as the 0·40 power of mass. This exponent is similar to the exponent of 0·44 among species (Lindstedt & Boyce, 1985). Body size exponents for both energy reserves and requirements are higher within species than among species, but fasting endurance is consistent. Lindstedt & Boyce's (1985) prediction that intraspecific patterns of fasting endurance should be more pronounced than interspecific patterns is not supported by these data. Nevertheless, fasting endurance is positively related to body mass within all species.

## Responses to decreasing food

No organism has a uniformly available food source. Shortages occur due to seasonal changes in the abundance and quality of primary production, natural fluctuations in the spatial and temporal availability of food species, or periodic inclement conditions which preclude foraging. In some cases, periods of negative energy balance are imposed by the habits of the organisms themselves. Migration, the need to attend young in a nest, or the use of patchily distributed foods can all

**Table 1.** Exponents relating fat content (reserves), food ingestion (requirements), and fasting endurance to body size within population of mammals.

| Species | Source | Sample | Reserves | | | Requirements | | | Fasting endurance exponent |
|---|---|---|---|---|---|---|---|---|---|
| | | | $N$ | $r$ | $b \pm SE$ | $N$ | $r$ | $b \pm SE$ | |
| 1. *Neotoma cinerea* (Ord, 1815) | Alberta | Summer | 57 | 0·61*** | 1·45 ± 0·25 | 13 | 0·76** | 1·21 ± 0·31 | 0·24 |
| 2. *Neotoma cinerea* (Ord, 1815) | Alberta | Winter | 61 | 0·65** | 1·54 ± 0·24 | 8 | 0·76* | 1·01 ± 0·35 | 0·53 |
| 3. *Microtus pennsylvanicus* (Ord, 1815) | Alberta | Summer, montane | 16 | 0·49* | 1·24 ± 0·59 | 53 | 0·78*** | 0·77 ± 0·09 | 0·47 |
| 4. *Peromyscus leucopus* (Rafinesque, 1818) | Ontario | Summer | 75 | 0·23* | 0·65 ± 0·33 | 41 | 0·53*** | 0·39 ± 0·10 | 0·26 |
| 5. *Peromyscus maniculatus* (Wagner, 1845) | NWT | Summer | 48 | 0·56*** | 2·35 ± 0·51 | 18 | 0·61** | 1·25 ± 0·40 | 1·10 |
| 6. *Clethrionomys gapperi* (Vigors, 1830) | Alberta | Summer, montane | 39 | 0·39** | 1·09 ± 0·42 | 69 | 0·74*** | 0·89 ± 0·10 | 0·20 |
| 7. *Blarina brevicauda* (Say, 1823) | Ontario | Summer | 26 | 0·65*** | 1·88 ± 0·45 | | | | |
| 8. *Peromyscus maniculatus* (Wagner, 1845) | Alberta | Summer | | | | 40 | 0·62*** | 0·86 ± 0·18 | |
| 9. *Peromyscus maniculatus* (Wagner, 1845) | Manitoba | Summer | | | | 42 | 0·49*** | 0·77 ± 0·22 | |
| 10. *Peromyscus maniculatus* (Wagner, 1845) | Alberta | F$_1$ colony | | | | 49 | 0·46*** | 0·61 ± 0·17 | |
| 11. *Peromyscus maniculatus* (Wagner, 1845) | Alberta | F$_{11}$ colony | | | | 56 | 0·45*** | 1·05 ± 0·28 | |
| 12. *Clethrionomys gapperi* (Vigors, 1830) | Alberta | Summer, subalpine | | | | 38 | 0·85*** | 0·80 ± 0·08 | |
| 13. *Clethrionomys gapperi* (Vigors, 1830) | Manitoba | Summer | | | | 21 | 0·70*** | 0·87 ± 0·21 | |
| 14. *Microtus pennsylvanicus* (Ord, 1815) | Alberta | Summer, subalpine | | | | 43 | 0·68*** | 0·47 ± 0·07 | |
| 15. *Microtus pennsylvanicus* (Ord, 1815) | Manitoba | Summer | | | | 36 | 0·74*** | 0·90 ± 0·14 | |

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

result in intrinsically imposed food shortages.

There are several potential responses to food shortages. Reduced metabolic rates through torpor or hibernation have evolved in a wide variety of mammals, primarily in response to predictable seasonal energy imbalances. However, even with reduced metabolism, mammals are limited by energy in the amount of time they can spend in torpor or hibernation. In addition, reduced metabolism does not appear to be a viable option during the breeding season. At that time, enhanced metabolism appears to be advantageous (Thompson & Nicoll, 1986).

An alternative response to predictable food shortages or periods of unpredictable food availability involves energy storage in the form of exogenous food caches or endogenous lipid reserves. Food caching is found in many taxonomic groups of mammals, although most caching behaviour is opportunistic (Formozov, 1966; Smith & Reichman, 1984; Sherry, 1985). Opportunistic food storage may be a response to increased food availability, rather than a response to potential food shortages. Because food caches are subject to decomposition, consistent caching of foods for long-term use appears to be most common among granivores and omnivores with access to seeds, such as heteromyids, sciurids, and cricetids (e.g. Smith 1968; Fleming & Brown, 1975; Barry, 1976; Stapanian & Smith, 1978; Wrazen & Wrazen, 1982; Sanchez & Reichman, 1987; Tannenbaum, 1987) or species with access to protected storage sites, such as pikas, woodrats and beavers (e.g. Millar & Zwickel, 1972; Slough, 1978; Fulk & Khokhar, 1980). Even among species with preservable foods, food hoarding is not always advantageous (Andersson & Krebs, 1978). Only 10 groups of mammals exhibit consistent, long-term food storage (Smith & Reichman, 1984).

Fat deposition appears to represent the most common form of energy storage among mammals (Pond, 1978, 1981; Young, 1976). Numerous studies have shown the deposition of fat reserves prior to predictable periods of high energy demand (e.g. Randolph *et al.*, 1977; Fedak & Anderson, 1982; Tyler, 1987; Verme, 1988) or periods of environmental uncertainty (e.g. Gyug & Millar, 1980). Such energy reserves are ultimately limited, however, by the ability of the animal to maintain and carry the reserves. Hibernators may carry as much as 50% of their total body mass as fat (Morrison, 1960) (although 35% may be a more realistic limit; Tyler, 1987), while large non-hibernators generally carry considerably less (Tyler, 1987). At some level, the metabolic costs of maintaining fat reserves, or the risks associated with carrying them, exceed the benefits accrued by them (Pond, 1981).

Given the constraints on metabolic reductions and the extent of exogenous and endogenous food reserves, populations are likely to encounter periods when energy shortages lead to potential starvation. If all other factors are equal (cf. Clutton-Brock & Albon, 1985) the smallest individuals will deplete their energy reserves first. These weak individuals will be most susceptible to predation or will succumb to starvation first, resulting in directional selection for a larger size. This larger size, however, will be ultimately favoured only if the losses incurred during fasting can be recouped later, and the greater average demands of a large body size can be met. Alternatively, a smaller body size will be favoured if foods are generally in short supply, but never unavailable. A smaller body size can only be favoured when there is no need for fasting endurance.

Various interactions among body size, fasting endurance and quantity of food available are schematically presented in Fig. 1. Scenario a would result in no directional selection on body size. The reduced food availability in period 2 will not result in an energy imbalance for smaller-than-average individuals. Larger-than-average individuals will be in negative energy balance during period 2, but have sufficient fasting endurance to survive this period, and can recoup their losses during subsequent periods. Scenario b would favour large-bodied individuals. Smaller-than-average individuals have insufficient reserves to survive period 2; larger-than-average individuals have sufficient reserves to survive period 2, and can recoup their losses during subsequent periods. Scenario c would favour smaller-than-average individuals. Larger-than-average individuals cannot meet their metabolic requirements after period 1, while the metabolic requirement of smaller-than-average individuals can always be met. Scenario d presents an untenable situation. Smaller-than-average individuals do not have the fasting endurance to survive period 2. Larger-than-average individuals have sufficient fasting endurance to survive period 2, but cannot recoup their losses in subsequent periods. These sorts of interactions can occur in any environment in which the quantity or quality of food available varies temporally or spatially.

The attractiveness of the concept of fasting endurance being important to the evolution of body size is related to its generality. Fasting endurance can provide the proximate mechanism
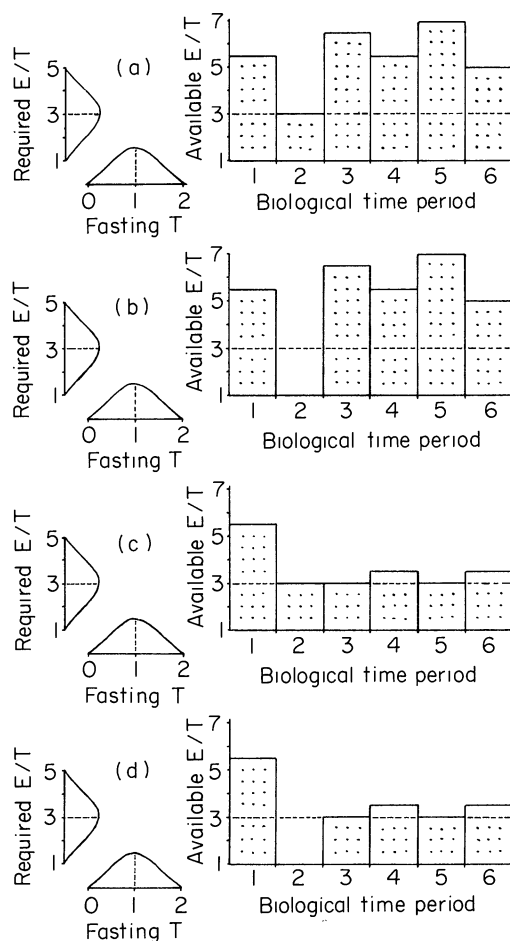
**Fig. 1.** Hypothetical interactions between energy requirements (vertical normal curve) and fasting endurance (horizontal normal curves) for animals of different size, in relation to available food resources (E, energy; T, time). In all cases, an average sized animal has requirements = 3 and fasting time = 1. Requirements and availability are scaled similarly. Fasting time and biological time are also scaled similarly. (a) favours no change in size; (b) favours large body sizes; (c) favours small body sizes; (d) is untenable (see text for further explanation).

whereby nutrient availability dictates both increases and decreases in body size. A wide range of environmental conditions related to latitudinal clines and environmental seasonality can affect the temporal availability of foods. Similarly, the dispersion of foods and the size of food clumps, social behaviour, and the risk of predation can all influence the ability of animals to obtain that which is available. All of these conditions can affect the energy balance of animals; all can therefore affect the need for fasting endurance, and hence body size.

Most nutritional correlates of body size, previously identified as causal factors in the evolution of body size, can be incorporated within the fasting endurance hypothesis. Three examples will suffice.

Langvatn & Albon (1986) found the body weight of Norwegian red deer to increase with latitude. Body weight was also negatively correlated with the length of the vegetative growing season (annual degree days) and positively correlated with quality (protein/fibre ratio) of the forage. They suggest that the higher quality forage at higher latitudes favours enhanced growth and therefore large body sizes. Their argument must assume that enhanced growth and large size are fundamentally beneficial. The alternative argument, that the long non-growing season requires fasting endurance and the high quality forage during the growing season permits the recovery of reserves expended, requires no such fundamental assumption.

Demment (1983), Demment & van Soest (1985) and Demment & Greenwood (1988) observed that interspecific patterns of metabolic rate and food retention time scale less than proportionally with body mass (as the 0·75 and 0·28 power of mass, respectively), gut capacity scales isometrically with body mass, and large herbivores consume foods of higher fibre content than small herbivores. Given these attributes, small mammals have a high ratio of metabolic rate to gut capacity and feed on high quality foods that require a short retention time. Large herbivores have a low ratio of metabolic rate (MR) to gut capacity (GC) and a long retention time is used to digest high fibre diets. Demment & van Soest (1985) consider these physiological constraints to be factors that have shaped the evolution of body size among ruminant and non-ruminant herbivores. Their deliberations were aimed primarily at explaining the dominance of ruminants among medium-sized herbivores, and the distinction between cause and effect was not clear (does body size restrict usable forage quality or does forage quality dictate body size?), but the role of forage quality in the evolution of body size was implied. Animals adapted to high quality diets may evolve small bodies to gain the short retention time necessary to maintain a high MR/GC ratio. Animals adapted to low quality diets may evolve large bodies to gain the large gut capacity (and long retention time) necessary for the fermentation of such diets. .This provides sufficient nutrients to sustain a low metabolic rate (MR) to gut capacity (GC) ratio.

This argument requires several assumptions. First, the distinction between cause and effect is not clear; Demment & van Soest (1985) imply that forage quality determines body size, whereas it is

possible that body size has constrained diet selection. Second, these authors assume a close association between diet quality and MR/GC ratios, but do not recognize the possibility that diet quality may influence metabolic rate (McNab, 1980, 1986; but see Elgar & Harvey, 1987), irrespective of GC. Third, the 'constraints' that Demment & van Soest (1985) discuss were based on interspecific scaling patterns. The authors imply that their arguments are applicable within species, but the necessary empirical evidence was not presented. This third objection has been addressed by Belovsky (1987), who showed that foraging models using intraspecific allometric functions could be used to predict differences in diet among individuals of different body size. He also addressed the cause-and-effect question directly, arguing that a consequence of such size dependence in optimal diet would be that any alteration in diet (such as a reduction in dietary overlap through competition among co-existing herbivores) would select for an altered optimal body size.

Finally, it is well established that large-particle feeders tend to consume large prey and that small-particle feeders are restricted to small prey (see McNab, 1971; Clutton-Brock & Harvey, 1983; and references therein). A reasonable interpretation of this is that species feeding on large food particles must be large to handle their food. However, the relationship between predator size and prey size is far from clear (Ralls & Harvey, 1985). For example, grey wolves (*Canis lupus*) weigh up to 55 kg and commonly feed on ungulates < 100 kg (Mech, 1974) while coyotes weigh up to only 18 kg (Bekoff, 1977) and commonly feed on prey >1 kg. There are no structural limits preventing coyotes from handling prey >1 kg. Alternatively, the average kill rates by wolves is only one (per wolf) per 18–45 days, requiring a considerable degree of fasting endurance. This comparison is confounded by the fact that wolves hunt in groups, but it is tempting to suggest the need for fasting endurance may be more important in determining body size of carnivores than the ability to handle large prey.

### Testing the hypothesis

There are a number of predictions that emerge from the fasting endurance hypothesis.

*Prediction I.* Within populations, the larger individuals should survive unpredictable inclement conditions better than small individuals. There appears to be some evidence to support this prediction among birds (Calder, 1974; Boag &

Grant, 1981) and mammals (Guinness, Clutton-Brock & Albon, 1978; Mitchell, 1984; Clutton-Brock, Albon & Guinness, 1987).

*Prediction II.* Within populations, the smaller individuals should survive better than the large individuals when food is in chronically short supply, but predictable over time. Some evidence of the disadvantage of the metabolic demands of a large body size, as suggested by McNab (1971), is available for birds (Price & Grant, 1984), but not mammals.

*Prediction III.* Among closely related species (i.e. with similar physiologies), differences in body size should coincide with differences in available food resources as depicted in Fig. 1. Critical to this test of the hypothesis is an adequate measure of resource abundance. Differences in body size related to seasonality of the environment may be indicative of the need for fasting endurance, but may not reflect actual resources available to individuals at any given time.

*Prediction IV.* Because a change in body size represents only one of several possible responses to patterns of resource availability, one might expect changes in body size only when other options (i.e. hoarding and lipid deposition) are insufficient. If this is true, then species that are large should deposit relatively more fat prior to potentially inclement conditions than those that are small. More precisely, the ratio of average maximum to minimum fat reserves should be greater in a large species than in a small species.

Testing the fasting endurance hypothesis will not be easy because the hypothesis is not amenable to manipulative experimentation. Proper assessment of predictions I and II will require an opportunistic observer who will monitor individuals and their responses to environmental conditions. Proper assessment of predictions III and IV will require the year-round monitoring of several species and their environments. Despite these difficulties, these studies must be conducted if the role of fasting endurance in the evolution of mammalian body size is to be fully understood.

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