SEASONALITY, FASTING ENDURANCE, AND BODY SIZE IN MAMMALS

It has been argued that environmental seasonality selects for larger body size among homeotherms (Brodie 1975; Downhower 1976; Boyce 1979). Indeed, strong correlations between body size and seasonality have been shown both within species of mammals (Brodie 1975; Boyce 1978) and among mammal faunas (Zeveloff 1982). Because of high mortality during the season of resource shortage, surviving individuals enjoy low competition and abundant resources during the growth season. Selection then favors rapid growth and attainment of large size because of enhanced survivorship (Lindsey 1966; Peters 1983; Calder 1984) and, in some taxa, increased fecundity (Sadleir 1969; Boyce 1981). Large individuals experience higher survival rates during the period of resource shortage because they metabolize somatic stores at a lower weight-specific rate. Thus, seasonality may produce two consequences to body-size evolution: (1) reduced density-dependent competition because of seasonal high mortality, known as Ashmole's hypothesis (Ashmole 1963; Ricklefs 1980) and (2) increased fasting endurance for individuals of large size (Lindsey 1966; Calder 1974).

In this note we analyze data that substantiate the significance of large body size for enhancing fasting endurance, responding to the challenge of Clutton-Brock and Harvey (1983), who claim that further knowledge of "food reserves" is necessary to evaluate the seasonality hypothesis. There are now sufficient data to predict fasting endurance in mammals by dividing energy reserves by their rate of use (after Stahl 1962). The result, the scaling of fasting endurance, favors large body size. This relationship will, of course, be of primary significance in seasonal environments where organisms must endure occasional periods of fasting.

ANALYSIS AND RESULTS

Energy stores.—Mammals store energy primarily in the form of adipose tissue, which is both dense in energy and easily accessible. Hence, when food intake is limited, metabolism shifts "to almost pure reliance on lipid catabolism" (Allen 1976, p. 642). Although structural proteins constitute a final "desperation" energy source, body fat may be justifiably equated with usable energy stores. Pitts and Bullard (1968) measured total fat stores as a function of body size in a variety of mammals from North and South America. Their sample was "seasonally heterogeneous"; thus, though seasonal fluctuations in body fat will add variance to their sample, their sample is not biased toward large- or small-massed mammals. Expressing body size as the weight of the skinned, eviscerated, fat-free carcass, they reported that fat varies in proportion to body size with an exponent greater than unity. As a consequence, the magnitude of stored fat becomes a greater fraction of body mass as size increases among mammals. Calder (1984)

reexamined their data, regressing the mass of body fat (M_f, kg) in eutherian terrestrial mammals only against total body mass (M_b, kg), and found the same pattern:

$$M_f = 0.075\ M_b^{1.19}, \qquad (R^2 = 0.97,\ N = 54). \tag{1}$$

The 95% confidence interval of the slope extends from 1.13 to 1.25. Fat may also be expressed in terms of stored energy (E, kJ), since fat contains 39.3 $kJ{\cdot}g^{-1}$ (Schmidt-Nielsen 1979):

$$E = 2948\ M_b^{1.19}. \tag{2}$$

Energy use.—Basal metabolic rate (energy use per unit time, $\dot{E}_{\text{basal}}$, $kJ{\cdot}day^{-1}$) scales roughly as $M_b^{0.75}$ (Kleiber 1961):

$$\dot{E}_{\text{basal}} = 317\ M_b^{0.75}, \tag{3}$$

as does maximal metabolic rate (Taylor et al. 1981).

Survival time.—In an energy survival crisis, an animal's metabolic requirements are typically near or even below basal (Westerterp 1978; Harlow 1981). Thus, survival time (t_s, days), or fasting endurance, may be estimated by dividing usable energy stores (eq.[2]) by minimal survival requirements (eq.[3]):

$$t_s = E/\dot{E}_{\text{basal}} = 2948\ M_b^{1.19}/317\ M_b^{0.75} = 9.30\ M_b^{0.44}. \tag{4}$$

Temperature and fasting endurance.—Larger mammals have thicker fur and a lower ratio of surface area to body mass. As a result, there are two shifts in thermoregulatory energetics accompanying increased body size: (1) an increased width of an animal's thermoneutral zone (Morrison 1960) and (2) reduced thermal conductance (Herreid and Kessel 1967). The thermoneutral zone is that range of ambient temperatures in which "passive" mechanisms requiring low energy are adequate to maintain body temperature. Below this temperature range, active mechanisms of heat production (e.g., shivering) require much more energy. Thermal conductance (the inverse of insulation) is a measure of the ease of heat loss to the environment. The result of these two body-size-dependent effects is that smaller mammals must expend more energy to stay warm (to maintain a constant, high body temperature) in low ambient temperatures.

Wunder (1975) has attempted to quantify the combined effects of body size and ambient temperature on mammalian energetics. He successfully incorporated allometric equations from a variety of sources to predict the metabolic cost of thermoregulation. We have converted units and expanded Wunder's model to form a single equation that predicts an animal's total rate of energy use ($\dot{E}_{\text{total}}$, $kJ{\cdot}day^{-1}$) as a function of body mass (M_b, kg), body temperature (T_b, ° C), and ambient temperature (T_a, ° C):

$$\dot{E}_{\text{total}} = \dot{E}_{\text{basal}} + (\dot{E}_t + |\dot{E}_t|)/2, \tag{5}$$

where the energetic cost for thermoregulation ($\dot{E}_t$, $kJ{\cdot}day^{-1}$) is

$$\dot{E}_t = (16\ M_b^{0.5}){\cdot}(T_b - T_a - 22.5\ M_b^{0.25}). \tag{6}$$
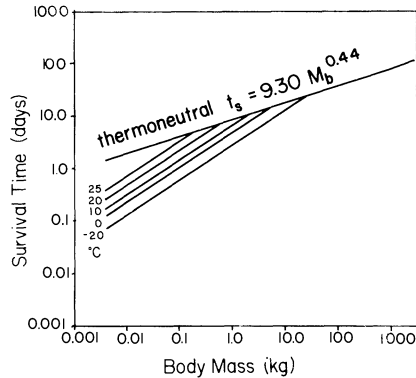
FIG. 1.—Fasting endurance (or survival time), t_s, as a function of body size for mammals. Top line represents survival time at thermoneutral ambient temperature, where $t_s = 9.30$ $M_b^{0.44}$. Steeper lines represent survival times at elevated metabolism induced by cold.

Fasting-endurance allometry (eq. [4]) can now be readily modified to reflect the size-dependent consequences of low ambient temperature. By dividing equation (3) by equation (5) we can predict fasting endurance (survival time) as a function of body mass and ambient temperature in mammals. If we make the assumption that T_b is equal to 38° C in all mammals (Schmidt-Nielsen 1984), then

$$t_s = 2948 \ M_b^{1.19}/[317 \ M_b^{0.75} + (\dot{E}_t + |\dot{E}_t|)/2], \tag{7}$$

where $\dot{E}_t$ may be simplified to

$$\dot{E}_t = (16 \ M_b^{0.5}) \cdot (38 - 22.5 \ M_b^{0.25} - T_a). \tag{8}$$

When we solve equation (7), fasting endurance is seen in figure 1 to be a dependent variable of both ambient temperature and, especially, body mass in all terrestrial mammals.

DISCUSSION

A large proportion of the variation in life history characters can be attributed to variation in body size among mammals (Western 1979; Millar and Zammuto 1983; Stearns 1983); birds (Western and Ssemakula 1982); reptiles (Stearns 1984); and invertebrates (Bell 1983). The apparent bond linking life history characters to body size may be a direct and inevitable consequence of size-constraining physical relations (McMahon 1973) and/or physiological time scales (Lindstedt and Calder 1981) among animals. Alternatively, both body size and other life history traits may be shaped independently by the same set of environmental conditions (Stearns 1984). In either case, a consideration of factors shaping the evolution of body size is critical to any explanation of variation in life histories.

Large mammals have proportionately greater mass of body fat ($M_f \propto M_b^{1.19}$), coupled with proportionately lower daily energy requirements ($\dot{E} \propto M_b^{0.75}$). The

consequence of the scaling of surface area, insulation, and metabolic energy use is that the maximum time between "refueling" is about 200 times longer in an elephant than in a mouse. This scaling of fasting-endurance time becomes even more pronounced at low ambient temperatures. Large mammals are better insulated and have a broader range of thermoneutrality; thus, the liability of small size is aggravated at low temperatures.

Might this interspecific pattern also hold within a species? If anything, we predict that the intraspecific pattern is even more pronounced (steeper slope). Within a species, body fat is the most variable constituent of body mass (Pond 1978), and the difference in weight between large and small individual adult animals is attributable to differences in the mass of body fat. This difference is most pronounced among hibernators (Morrison 1960).

Survival time and Bergmann's Rule.—Bergmann's Rule describes a biogeographic pattern that body size in homeotherms tends to be largest in the coolest regions of a species' distribution (James 1970). The traditional explanation is that the weight-specific cost of thermoregulation decreases with increasing body size. This hypothesis was challenged by McNab (1971), who noted that, in fact, any increase in body size results in an absolute increase in the cost of thermoregulation.

Searcy (1980) proposed two models of foraging efficiency as a function of body size; in one instance, an increase in survival time after foraging offers a selective advantage to individuals of larger body size, particularly at low temperatures. Although Searcy's focus on foraging profits is irrelevant, he nevertheless identified the importance of survival-time allometry and the amplification of this effect at colder temperatures. Earlier, Lindsey (1966) speculated that large body size may confer increased survival through periods of energy shortage, which may account for Bergmann's Rule even among ectothermic vertebrates. Calder (1974) expanded this hypothesis, showing that fasting endurance ranges between $M_b^{0.40}$ and $M_b^{0.60}$ in birds (but these power coefficients were estimated with very small sample sizes).

We concur with Lindsey (1966) and Calder (1974) that fasting-endurance allometry contributes to Bergmann's Rule, since cooler climates tend also to be more seasonal and are thus more likely to impose a fasting-endurance crisis. This becomes even more important when fasting-endurance crises occur at cold temperatures because the allometric slope of fasting endurance is steeper when individuals are forced to add a metabolic cost of thermoregulation to basal metabolic rate. We also recognize that Bergmann's Rule may be reinforced by a reduction in growing-season competition created by high overwinter mortality and the concomitant availability of food resources for growth and attainment of large size (Ashmole 1963; Boyce 1978, 1979; Ricklefs 1980), or possibly by other factors such as reduced interspecific competition or spatial heterogeneity of food supplies.

Brown and Lee (1969) and James (1970) suggested that Bergmann's Rule may relate not to selection for large size in cold climates but rather to selection against large body size in hot environments. Small mammals may be able to dissipate heat more easily, both behaviorally and physiologically. Intriguing though it may be, we feel this idea deserves closer scrutiny. For instance, large size may actually be

an asset in very high ambient temperatures for a number of reasons. (1) Large size confers high thermal inertia. Camels (*Camelus* spp.) store a great deal of heat during the day (with only a small change in body temperature), and they "dump" that heat at night (Schmidt-Nielsen et al. 1957). (2) Larger mammals have lower rates of weight-specific heat production (Kleiber 1961). And (3) large mammals have a smaller relative surface area for absorbing heat by radiation and convection. These factors favoring large size in hot environments (see Lindstedt 1980), coupled with the geographic distribution of many large mammals (e.g., elephants), lead us to conclude that this is an unlikely explanation for Bergmann's Rule.

Body size has profound effects on all aspects of animals' morphology, physiology, and life history (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Most relevant here, changing body size drastically affects fasting endurance, such that at low ambient temperatures a doubling of body size results in a 60% increase in the fasting endurance of small mammals. We view this fasting-endurance allometry as potentially yielding a strong selective pressure on body size in seasonal environments where animals must survive environmentally imposed fasts. These observations support the hypothesis that Bergmann's Rule reflects adaption to environmental seasonality rather than to cold temperatures (Boyce 1979). In fact, many mammals show geographic variation in body size that correlates strongly with seasonality but is independent of temperature (Hiernaux 1968; Bourlière 1973; Brodie 1975; Boyce 1978, 1979).

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