ENERGETICS: THE BEHAVIORAL AND ECOLOGICAL CONSEQUENCES OF BODY SIZE

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SYNOPSIS

The significance of body size for animal energetics is demonstrated by the seasonal behavior of the monarch butterfly and the fin whale. Both species in summer live in environments that are unacceptably harsh in winter; consequently, the butterfly and whale migrate in winter to hospitable environments at lower latitudes, which nevertheless are characterized by limited food supplies. As a result, both species in winter principally rely on stored lipids as their source of energy. The difference between the butterfly and whale in the time period over which starvation is tolerated can be accounted for by their differences in body mass and in their level of energy expenditure. The huge difference in body size between butterflies and whales does not necessarily mean that the solutions to environmentally imposed problems are different.

The one most important characteristic of animals is, above all, body size. It influences everything from the means of temperature regulation, type and amount of food consumed, and rate of locomotion to longevity, potential predators, and rate of reproduction. Size may be measured in many ways, including body length, wing spread, body volume, and body mass. Body mass is preferentially used as a measure of size in physiological studies because most functions depend on the amount of material reacting with the environment. For example, the rate of energy expenditure in animals normally is compared to their masses, and such a comparison has shown (Figure 1) that an individual's rate of metabolism (i.e., the total rate) generally increases with body mass raised (approximately) to the 3/4 power (i.e., $m^{0.75}$). This pattern occurs both in ectotherms, i.e., in animals that have body temperatures determined by ambient conditions, and in endotherms, animals that have temperatures that are determined mainly by high rates of chemical heat production (Hemmingsen 1960). It is somewhat disconcerting to note, however, that no adequate explanation for the $m^{0.75}$ proportionality has ever been given.

At any particular body size, endotherms have rates of metabolism that are about 9 times those of ectotherms, assuming that endotherms have a body temperature of about 39°C and that ectotherms have a temperature of about 20°C, although endotherms can reduce energy expenditure somewhat by having an effective insulation. When body temperature in ectotherms is lower than 10°C, the metabolism-mass curve, although parallel to the endotherm and 20°C curves, is lower still (Figure 1): at 10°C rate of metabolism is only about 4% of that expected in endotherms. Another way of stating that total rates of metabolism are proportional to $m^{0.75}$ is to note that mass-specific rates of metabolism are proportional to $m^{-0.25}$, which

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Fig 1. Logarithm of the standard rate of metabolism (cm³O₂/h) plotted as a function of the logarithm of body mass (g) for mammals (Kleiber 1932) and for ectotherms at 20 and 10°C (McNab 1983). The boundary curve was reported by McNab (1988). The shaded area below the boundary curve indicates endotherms that enter daily torpor. The data on Indian pythons were reported by Hutchison et al. (1966) and Van Mierop and Barnard (1978).
simply means that small animals have higher rates of metabolism per gram than large animals. As convenient as mass-specific units are, the ecologically relevant rates of energy expenditure are the total rates, because they describe the rate at which energy is used by an individual and the rate at which food must be harvested in the environment.

The only animals that had been considered to be endothermic, until recently, were birds and mammals. All animals other than these vertebrates were thought to be ectothermic. Within the last 20 years, however, many other animals have been shown to be endothermic to some degree. Among large vertebrates, some sharks and tunas are known to be endothermic (Barrett and Hester 1964, Carey and Teal 1969a,b), as are female pythons while incubating their eggs (Hutchison et al. 1966, Van Mierop and Barnard 1978); the leatherback turtle (Dermochelys) may also be endothermic (Fraise et al. 1972). Among small animals, various insects, including some moths, hymenopterans, dragonflies, and beetles, are endothermic, at least during periods of activity (Heinrich 1974, May 1979). Periodic endothermy is of special interest because it is also found in mammals and birds that weigh less than 10 g, such as small mice and insectivorous bats, and all hummingbirds. In other words, the existence of continuous endothermy, itself, depends on body size.

At a small mass, animals, independent of taxonomy, can variously be continuously endothermic, discontinuously (periodically) endothermic, or completely ectothermic, depending on the level at which energy is expended (McNab 1983): rate of metabolism must be high to insure effective endothermy, ectothermy (as stated) is associated with low rates of metabolism, and discontinuous endothermy is characterized by intermediate rates (Figure 1). The transition between ectothermy, at one extreme, and continuous endothermy, at the other, also varies with body mass: compared to the standard mammalian relation, small animals must have high rates of metabolism to remain continuously endothermic, but animals weighing more than 70 g may have a low rate of metabolism without sacrificing continuous endothermy. These observations mean that another relationship between total rate of metabolism and body mass can be described, and it defines the boundary between continuous and periodic endothermy. This relationship, the so-called boundary curve for endothermy, is proportional to $m^{0.33}$ (Figure 1); it is derived empirically from measurements on rate of metabolism in relation to body mass in those species of mammals, birds, fish, and snakes in which there is continuous endothermy.

At large masses, the resting rate of metabolism of an endotherm may be less than that of an ectotherm. For example, the mean boundary curve intercepts the 20°C ectotherm curve at about 18 kg and the 10°C ectotherm curve at about 180 kg (Figure 1). These observations mean that the distinction between endothermy and ectothermy is not simply related to the level of energy expenditure. Unfortunately, there are few measurements of energetics in vertebrates at masses greater than a few kilograms, so the boundary between these states at large masses is unclear, and needs to be explored, especially in species with an intermediate form of thermal behavior. Nevertheless, the existence of the boundary curve at large masses is shown in the behavior of the Indian python (Python molurus): it raises its rate of metabolism sufficiently to exceed the boundary curve (Figure 1),
but it does not need "mammalian" rates of metabolism to assure effective endothermy (McNab 1983).

The impact of body mass on rate of energy expenditure can be shown by comparing the seasonal energetics of multicellular animals at the two ends of the size spectrum: a monarch butterfly (*Danaus plexippus*), which may weigh only 0.5 g, and a fin whale (*Balaenoptera physalus*), which may weigh up to 50,000,000 g. In spite of this great dissimilarity in mass, these species both migrate to wintering grounds on which they have a restricted food supply and intake. Monarchs winter in coastal California and in the highlands of central Mexico, while fin whales winter in tropical waters. There is evidence that neither the whale (Brodie 1975) nor the monarch (Chaplin and Wells 1982) feed much, or at all, on their wintering grounds. It is of interest here to compare the periods of time that these species live without eating, or at least with a highly restricted food intake, to see to what extent the observed periods can be quantitatively accounted for by comparing energy expenditures, as derived from the differences in their masses.

The amount of time that an animal can live without feeding is proportional to the ratio of the size of the energy store divided by the rate at which the store is consumed (Morrison 1960). If the size of the energy store is proportional to body mass, the time period for starvation would be proportional to \( m^{0.25} = m^{1.00/4} \). For example, if two animals are compared, one the size of a monarch butterfly and the other the size of a fin whale, and if both have rates of metabolism that fall on the same metabolism-mass curve, then the ratio of time periods would be proportional to

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\left( \frac{\text{whale mass}}{\text{monarch mass}} \right)^{0.25} = (10^8)^{0.25} = 100:1.
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Fin whales may not feed (much) for the half-year that they spend in tropical waters, which suggests that an animal the size of a monarch would be expected to tolerate starvation for about 1.8 (= 180/100) days, but only if it conformed in rate of metabolism to the endothermy curve. If, however, a monarch were a continuous endotherm, it would have to follow the boundary curve for endothermy (see Figure 1), which at 0.5 g would raise the resting rate of metabolism by a factor of 8.4. That is, a continuous endotherm the size of a monarch could tolerate 1.8/8.4 = 0.21 days, or about 5 hours, by burning its fat stores. This graphically illustrates why animals the size of an insect cannot afford continuous endothermy. Actually, monarchs are not endothermic; their body temperature equals air temperature, as long as they are not exposed to the sun. In coastal California, monarchs face cool, cloudy weather in winter; mean body temperature is only about 10°C (Chaplin and Wells 1982). Measurements of oxygen consumption indicate that monarchs at 10°C have resting rates that are only about 3% of the value expected from the endothermy curve at 0.5 g. Consequently, the starvation time expected in monarchs is about 1.8/0.03 = 60 days. Chaplin and Wells estimate that monarchs in coastal California, given their fat stores, can tolerate starvation for about 60 days, a close agreement, seeing that here the estimate is derived from an extrapolation of the energetics of whales!

The difference in time period for starvation between monarch butterflies and fin whales, as absurd as this comparison might seem at first glance, can be accounted for by differences in body size, thermal behavior, and level of energy expenditure. In spite of all of these differences, both species
respond to the shortage of food and to seasonally harsh environments—such as cold temperatures in western North America (in the case of monarchs) and cold seas and winter storms (in the case of fin whales)—by the use of a similar response, namely, migration to benign environments, which nevertheless are characterized by a shortage of food and require the use of stored energy resources. Given their fixed energy reserves (dictated as they are by body size), these species reduce their rates of energy expenditure to extend the period over which starvation can be tolerated. In the endothermic fin whale, energy expenditure is reduced by living in warm water, that is, by retreating to the tropics. Time of starvation is extended to great lengths by a large body size, as is required to permit a polar-tropical migration on an annual cycle. Monarchs, being ectothermic, have to walk a thermal tightrope, because they have a reduced control over body temperature: they must avoid freezing temperatures, and must avoid warm temperatures that raise rate of metabolism, thereby reducing starvation time. It therefore is significant that wintering monarchs congregate in coastal California, where the environment in winter is cool and damp, and in the mountains of central Mexico, where monarchs cluster in forests at an elevation of 3100 m. Ambient temperatures encountered in Mexico generally fall between 3 and 12°C (L. Brower, personal communication), temperatures that are strikingly similar to those found in winter in coastal California.

This analysis suggests that many of the obvious differences between butterflies and whales are related to a striking difference in body mass, and when this difference is taken into consideration, a commonality is seen in their biology. Insects, by concentrating at the small end of the size spectrum, tend to be ectothermic, or if they are endothermic, are so only on a periodic basis. But as has been seen in the case of monarch butterflies, a small body size does not mean that the ecological problems faced, or even some of the solutions used, are necessarily different from those of large endotherms.

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