
THE ENERGETICS OF ENDOTHERMS¹

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ABSTRACT

The energy expenditure of endotherms is influenced by body size, climate, and food habits. Body size is the most important factor determining basal rates of metabolism and thermal conductances. The interaction of these two parameters produces a temperature differential between an endotherm and its environment at the lower limit of thermoneutrality that normally increases with body weight. Greater basal rates of metabolism than expected from weight are found in temperate and arctic species; low basal rates are found in desert species. Low basal rates are also found in species that have a periodic food supply, in species that harvest food in an indiscriminate manner, or in species that use food of low available energy content. Geographic limitations in the distribution of endotherms and the use of such evasatory tactics as torpor or migration may also be responses to a limited energy availability. Thermal conductances are low in temperate and arctic species, but high in tropical endotherms. Thus, the temperature differentials maintained by endotherms tend to vary with both climate and food habits. The weight-independent variations in metabolism and conductance permit an endotherm to compensate for a small body size, making temperature differentials independent of body weight. High intensity species compensate for a small size by an increase in the basal rate of metabolism beyond that expected from the standard weight-metabolism curve; low intensity species compensate for a small size by a decrease in thermal conductance. It therefore appears that the energy expenditure of endotherms is sensitive to their economic roles and to the physical conditions they face.

Organisms require energy for their maintenance and, if they are to persist, energy income must balance expenditure. This requirement places restraints on organisms, because the parameters that set the cost of maintenance are different from those that determine energy availability. Ultimately, energy expenditure

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and complexity of maintenance are determined by the availability of energy in the environment. The environmental limitations to energy expenditure are striking in the most expensive homeostatic mechanism, endothermic temperature regulation. Endothermy is found in most mammals and birds, in a few fish, and intermittently in at least one reptile and certain insects.

Many laboratory measurements of the energetics of mammals and birds have been made in the belief that the measurements reflect differential responses in the field. It is gratifying to see that when the energetic equivalent of behavior is multiplied by the time period over which the behavior occurs in the field, the resulting estimate of the total energy budget is similar to that measured in the field with D_2O^{18} (Utter and LeFebvre, 1973). Nevertheless, it is important to realize that the energy expenditure of animals in the laboratory is not equal to that in the field. This paper will attempt to examine how the energy expenditure of endotherms varies as a function of the ecologically important variables of body size, climate, and food habits.

ENDOTHERMIC ENERGETICS

For an endotherm to maintain a constant body temperature (T_b), heat production (M) must equal heat loss:

$$(1) \quad M = C(T_b - T_a) + LE$$

where C is the "dry" thermal conductance, T_a ambient temperature, L latent heat of vaporization, and E amount of water lost by evaporation. (Thermal conductance might be more appropriately called the coefficient of heat transfer, or thermal coefficient.) Since it is often difficult to measure heat production by oxygen consumption, and evaporative water loss simultaneously (Lasiewski, *et al.*, 1966), a "wet" thermal conductance, C' , can be defined for convenience:

$$(2) \quad M = C'(T_b - T_a)$$

This simplification is acceptable only at moderate to low temperatures, where evaporative heat loss is a small fraction of total heat loss. The lower limit of

TABLE 1
Equations used to describe the relation of basal rate of metabolism and thermal conductance to body weight in mammals and birds¹

	units	equation	source
A. Basal Rate of Metabolism			
mammals:	kcal/day	$M_b = 70W^{+0.75}$	Kleiber, 1961
	ccO ₂ /g·hr*	$M_b/W = 3.4W^{-0.25}$	
birds:			
non-passerines	kcal/day	$M_b = 78.3W^{+0.728}$	Lasiewski and Dawson, 1967
	ccO ₂ /g·hr*	$M_b/W = 4.6W^{-0.28}$	
	kcal/day	$M_b = 73.5W^{+0.734}$	Aschoff and Pohl, 1970
	ccO ₂ /g·hr*	$M_b/W = 4.0W^{-0.27}$	
passerines	kcal/day	$M_b = 129W^{+0.724}$	Lasiewski and Dawson, 1967
	ccO ₂ /g·hr*	$M_b/W = 7.5W^{-0.28}$	
	kcal/day	$M_b = 114.8W^{+0.726}$	Aschoff and Pohl, 1970
	ccO ₂ /g·hr*	$M_b/W = 6.6W^{-0.27}$	
B. Thermal Conductance			
mammals:	ccO ₂ /g·hr°C	$C'/W = 1.0W^{-0.50}$	McNab and Morrison, 1963
	kcal/day°C*	$C' = 3.6W^{+0.50}$	
	ccO ₂ /g·hr°C	$C'/W = 1.0W^{-0.51}$	Herreid and Kessel, 1967
	kcal/day°C*	$C' = 3.4W^{+0.49}$	
birds:	ccO ₂ /g·hr°C	$C'/W = 0.85W^{-0.51}$	Lasiewski <i>et al.</i> , 1967
	kcal/day°C*	$C' = 2.9W^{+0.49}$	

¹Where there is a conversion between gaseous exchange and energetics, 4.8 cal/ccO₂ were assumed; note that for the equations M' is in grams when metabolism is in ccO₂ and in kilograms when metabolism is in kilocalories.

*Converted units.

thermoneutrality (T_l) is the lowest temperature at which the basal rate of metabolism (M_b) may be measured; therefore,

$$(3) \quad M_b = C'(T_b - T_l)$$

That is, the temperature differential at T_l , ΔT_l , is equal to M_b/C' .

Both M_b and C' are functions of body weight, and the best estimates for mammals and birds are found in table 1. Although new data may shift the mean functions somewhat, it is clear that the power of weight for M_b differs from that for C' in both mammals and birds. Consequently, ΔT_l is also a function of weight. In mammals:

$$(4) \quad \Delta T_l = M_b/C' = 3.4 W^{+0.25}$$

In non-passerine birds, the mean ΔT_l is approximately 38% higher than for mammals of the same weight, and for passerines it is about 128% higher than for mammals. The large temperature differentials in birds result from higher rates of metabolism and lower thermal conductances (McNab, 1966a, 1970). In all cases, however, ΔT_l increases with an increase in body weight.

All species do not conform to the mean weight functions of M_b and C' . This observation may be incorporated into a factor F , defined as the ratio of the temperature differential observed at the lower limit of thermoneutrality to the value expected from body weight in equation 4. Therefore:

$$(5) \quad \Delta T_l = 3.4 FW^{+0.25}$$

Graphically, F represents the slope of the curve when ΔT_l is plotted against $3.4 W^{+0.25}$; it may be high if the basal rate is high or if thermal conductance is low. Variation in basal rate and thermal conductance depends upon body size, climate, and food habits.

BODY SIZE

Body size, measured by body weight, is the most important determinant of the energy expenditure of endotherms; total basal expenditures are proportional to the $\frac{3}{4}$ power of body weight. Various explanations for this relation have been made (Hemmingsen, 1960). For example, the similarity of 0.75 to 0.67 has led to the suggestion that total heat production is proportional to total surface area because heat is lost via the surface. This correlation has doubtful significance, because ectotherms show a similar relationship. Whatever the explanation for this relation, it appears that the $\frac{3}{4}$ power rule has wide applicability. It is profitable, in determining the influence of body size on energetics, to examine endotherms at the extremes of body size. However, with little data on metabolism and thermal conductance of large endotherms, it is necessary to concentrate on small body size.

With a decrease in body weight there is a decrease in ΔT_l (equations 4 and 5). Very small endotherms must either relinquish endothermic regulation (see the section on torpidity) or make adjustments in their energetics. The ideal adjustment would make ΔT_l independent of a decrease in weight by either lowering thermal conductance or raising the basal rate. Factor F must progressively increase with a reduction in weight (fig. 1). An increase in F occurs in small species of neotropical marsupials, termite-eaters, certain rodents, shrews, and weasels (fig. 1) and it probably also occurs in armadillos. Thus, this adjustment occurs in mammals that have a high intensity (high rate of metabolism, e.g. microtine rodents, shrews, and weasels) or a low intensity (termite-eaters and armadillos).

Low-intensity species compensate for a small body weight by a reduction in thermal conductance (fig. 2): *Cyclopes* among termite-eaters and *Marmosa* among marsupials. It seems unlikely that species with low basal rates could adjust ΔT_l by a compensatory increase in M_b (fig. 3-termite-eaters), because factors that set

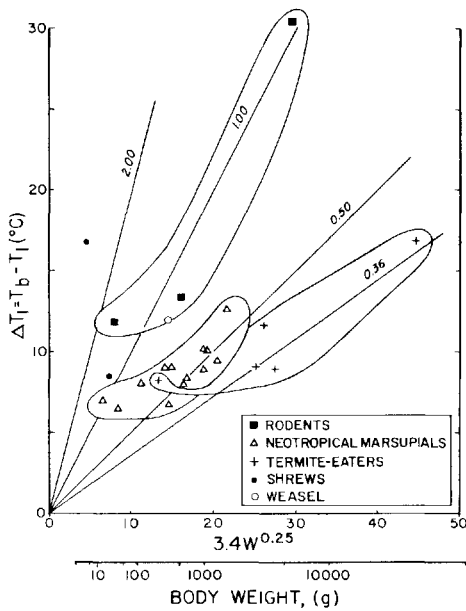


FIGURE 1. Dependence of the temperature differential between a mammal and the environment at the lower limit of thermoneutrality on body weight. Data were taken from Irving, *et al.* (1955), Morrison *et al.* (1959), Packard (1968), Brown and Lasiewski (1972), and personal observations on termite-eaters and the paca.

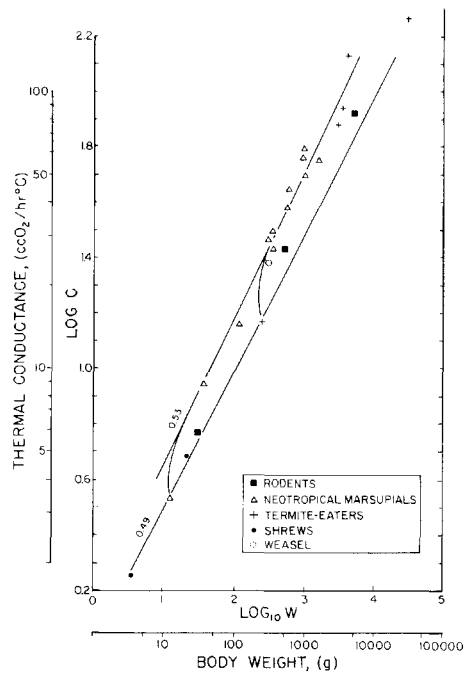


FIGURE 2. Total thermal conductance as a function of body weight. Data taken from the sources cited in Figure 1.

a low basal rate would undoubtedly prevent its increase. It is not surprising that the smallest armadillos, *Burmeisteria* and *Chlamyphorus*, are also the furiest (and presumably have the lowest conductances). This relationship may also occur among heteromyid rodents, which have low rates of heat production.

If a low-intensity species does not compensate for small body size by decreased conductance, the level and preciseness of temperature regulation falls. An extreme example of this failure occurs in the naked mole-rat, *Heterocephalus glaber*, which accentuates the difficulty of thermoregulation by a very high conductance. It is an incompetent endotherm that survives only in a thermally stable environment (McNab, 1966b).

Mammals characterized by high rates of metabolism, such as mustelids, shrews, and microtine rodents, respond to small body size with a high M_b to maintain ΔT_i independent of weight. If ΔT_i is to remain constant over some weight range and if the principle means of adjustment to a small size is by M_b , then M_b must have the same power of weight as thermal conductance (equation 4). That is, if there is no adaptive change in thermal conductance, the total basal rate of metabolism must be proportional to $W^{+0.50}$ for ΔT to be independent of body weight. In fact, Iverson (1972) on the basal rates of mustelids shows a break in the exponent at about 1 kg, above which it is about 0.78, and below which it is about 0.49

(fig. 3). For shrews, moles, and microtine rodents the power of weight for metabolism below 100 g is about 0.45. A consequence of this relation is that very small shrews have exceedingly high rates of metabolism; e.g., *Sorex cinereus* has a resting rate in thermoneutrality equal to 2.8 times the value expected for a 3.3 g mammal (Morrison *et al.*, 1959). The higher critical weight for mustelids than for shrews and mice may be related to shape (Brown and Lasiewski, 1972). These data question the significance of the power of weight that describes the relation between the basal rate and body weight. It appears that this power may, in fact, be sensitive to biological demands.

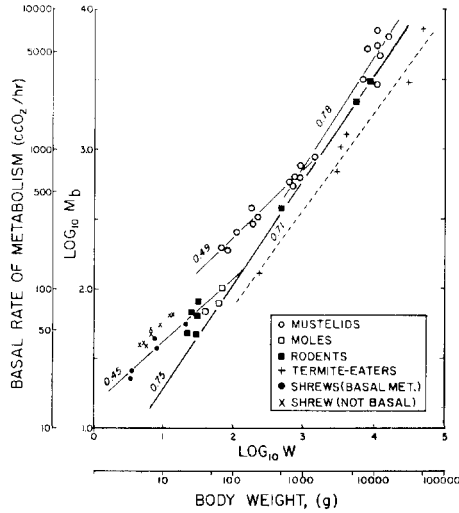


FIGURE 3. Total basal rate of metabolism as a function of body weight. Data from the sources cited in Figure 1 and from Pearson (1947, 1948), Morrison (1948), Gębczyński (1965), and Iverson (1972).

CLIMATE

Climate affects the temperature differential between an animal and the environment and determines the amount and type of food energy available. It may be asked whether climate also has an appreciable influence on either thermal conductance or the basal rate of metabolism. Thermal conductance is low in arctic species of birds and mammals and in temperate species in winter (Scholander *et al.*, 1950a; Hart, 1957). Higher thermal conductances are typical of temperate species in summer and of lowland tropical species throughout the year. These adaptations conserve heat at low environmental temperatures and dissipate heat at high temperatures. Thermal conductance is a function of the surface-to-volume ratio and the surface-specific insulation. Large endotherms living in the tropics potentially face overheating because they have high rates of metabolism and small surface-to-volume ratios. Consequently many are naked, thereby reducing their total insulation.

As a consequence of the importance of both body size and climate on the heat loss of endotherms, it has been suggested that the increase in body size in cold climates observed in some species (often called Bergmann's rule) conserves heat and thereby reduces energy expenditures. This explanation, however, is plagued by its sporadic appearance and the fact that total heat loss increases with size (McNab, 1971). A correlation of a large body size with a cold climate might be related to the larger energy reserves presumably found in larger bodies.

Climate influences the level of the basal rate of metabolism in a manner that is difficult to separate from the effect of food habits. Scholander *et al.* (1950b, c) showed that carnivores living in the cold waters of temperate or arctic regions have higher basal rates than terrestrial carnivores of the same size due to the high specific heat of water. There are few data on the metabolism of terrestrial mammals of given food habits in various climates. In rodents, the basal rate, independent of the influence of body size, is similar in arctic, temperate, and tropical species (fig. 4). However, the cold-temperate varying hare (Hart *et al.*, 1965)

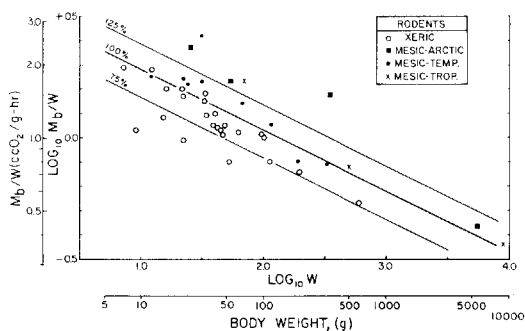


FIGURE 4. Relation of the weight-specific basal rate of metabolism of rodents to body weight and to climate. Data from the literature (see McNab, 1973b) and personal observations on the paca.

has a much higher basal rate of metabolism relative to expectations than warm-temperate lagomorphs, even though they too have high basal rates (Schmidt-Nielsen *et al.*, 1965; Dawson and Schmidt-Nielsen, 1966; Hinds, 1973). One difference between arctic and tropical species is that very low basal rates of metabolism associated with certain food habits are tolerated only in tropical environments. With few exceptions, only high intensity species survive in the arctic.

Many endotherms that live in xeric environments have a food-dependent reduction in the basal rate of metabolism: rodent basal rates are only about 80% of those expected from body weight (fig. 4). For example, the tropical rainforest *Heteromys* has a high basal rate of metabolism, while its desert relatives have low basal rates. Similarly, Dawson and Bennett (1973) have shown that desert pigeons have lower basal rates than pigeons from mesic environments. A low basal rate reduces the evaporative water loss associated with gas exchange (Glenn, 1970), and is most highly developed in species that feed on seeds with a very low water content.

There is little evidence that mammals with other food habits have low basal rates in xeric environments, with the possible exception of Australian dasyurid marsupials (MacMillen and Nelson, 1969; Dawson and Hulbert, 1970). This reduction is not characteristic of marsupials, because opossums from the rainforests of South America have basal rates similar to those of placentals. The low basal rates of dasyurids may be related to life in xeric environments, but unfortunately little is known of the metabolism of desert placental carnivores.

Fossorial mammals live in burrow atmospheres characterized by high humidity, low oxygen tension, and high CO_2 tension. Most fossorial mammals have low basal rates of metabolism and high thermal conductances (McNab, 1966b) and low basal rates may reduce heat storage (MacMillen and Lee, 1970). The most striking evidence for this conclusion is that the naked mole-rat, *Heterocephalus*, has the greatest reduction in M_b and lives at the highest burrow temperatures. Darden (1972) and Baudinette (1972) argued that the low M_b is an adaptation to

gas tensions in the burrow atmosphere. This does not account for the high thermal conductances found in fossorial species.

Clearly climate influences the rate of heat production and thermal conductance, but the extent of its influence is not known.

FOOD HABITS

Food habits would appear *a priori* to be an important factor influencing the rate of energy expenditure (and therefore endothermic temperature regulation), because this energy comes from the food that an endotherm harvests. Tropical bats show the influence of food habits: fruit-, meat-, and nectar-feeding bats have high basal rates, while insectivorous species have low rates (McNab, 1969). Vampires are intermediate. The low basal rates of insectivorous bats were correlated with a seasonal variation in the availability of *flying* insects, even in lowland tropical environments. The other types of food are apparently available throughout the year. This explanation has been partially confirmed by the seasonal fat cycles of bats in the tropics: the cycles are small in some nectarivorous bats and large in certain insectivorous species. Furthermore, most birds that feed on *flying* insects (swifts, goatsuckers) have low basal rates of metabolism (and also have a propensity for torpor), while those species that feed on insect larvae, such as woodpeckers and titmice, normally have high basal rates.

Unfortunately, there is little direct information on endotherms with other food habits. All placental carnivores studied (arctic fox, red fox, seals, etc.) have high basal rates, but are cold-climate species. The insectivorous-carnivorous mouse *Onychomys torridus* has a higher basal rate of metabolism than desert relatives such as *Peromyscus* (Whitford and Conley, 1971); this difference may be related to a higher water content in the food of *Onychomys*.

Ground squirrels, unlike most browsing or grazing herbivores, have low basal rates. The explanation for their low rates is either that these squirrels are hibernators or that they live in xeric environments. Those ground squirrels that live in the coldest or wettest climates [*Citellus parryi* (Erickson, 1956), *C. lateralis* (Hudson and Deavers, 1973), and *Tamias striatus* (Neal and Lustick, 1974)] tend to have the highest basal rates. Interestingly, desert lagomorphs have high basal rates; they may differ sufficiently in food from ground squirrels to avoid a seasonal deficit either in food or water, thereby avoiding the strategies of low basal rates of metabolism and seasonal torpor typical of ground squirrels.

Seed-eating rodents living in mesic environments, such as tree squirrels, have high, often very high, basal rates of metabolism. Unfortunately, the physiology of tree squirrels that inhabit tropical or seasonally xeric environments is unknown. Fruit-eating tends to be limited as a specialty to tropical regions; it also seems to be correlated in rodents (spiny rat, paca) with high basal rates of metabolism.

From this survey it is apparent that it is difficult to separate the influence of food habits on energetics from that of climate. One major factor tying food habits and climate together in their apparent influence on energetics is that some foods are climatically limited. Thus, most mammals that have low basal rates of metabolism (and consequently have low body temperatures) are limited to the tropics in distribution because they have specialized food habits (*e.g.* termites, fruits, nectar and pollen, etc.) that are permissible only in the tropics. Tropical species may have low basal rates of metabolism if they use foods that 1. are periodically available (*e.g.*, insectivorous bats), 2. are harvested in an indiscriminate manner (*e.g.*, ant- and termite-eaters, armadillos, and hedgehogs), or 3. are of a low available energy content (*e.g.*, sloths, koala, and possibly certain forest primates). Factors 2 and 3 are similar, because "indiscriminate" here means the collecting by large animals of small food particles in such a manner as to ingest much detritus, which reduces the available caloric density of the food. Although many temperate birds and mammals feed on foods that are seasonally available

or have a low caloric density, few *specialize* on these foods without adopting evasive strategies to minimize the cost of endothermy.

EVASION OF THE HIGH COST OF ENDOTHERMY

Endothermy is such an extremely costly process that, even after all of the climatic and seasonal adjustments have been made, it often turns out to be economically unfeasible for such regulation to occur under certain environmental conditions. This high cost may be evaded by limiting distribution, by abandoning endothermy, or by seasonally moving to a more hospitable environment.

Limitations to Distribution. Some endotherms may be limited in their distribution by their inability to balance their energy budgets under certain environmental conditions. Unfortunately, it is very difficult, if not impossible, to determine what limits an animal's distribution. Thus there are no unequivocal examples that demonstrate the importance of energetics in setting the limits of distribution for an endotherm. Obviously, if there is a geographical limitation to a food supply, any predator specializing on that resource will also show a similar limitation.

Some endotherms may be restricted in their distribution to warm environments by a limited capacity to maintain high rates of metabolism. For example, it has been suggested that vampire bats are restricted to the tropics because the daily energy expenditure is fixed by the largest meal that a bat can carry in flight (McNab, 1973a). Brocke (1970) has argued that the northern limits of distribution in the opossum, *Didelphis virginiana*, is set by its maximal rate of metabolism and the size of its energy reserves. These factors may also be important in the armadillo, *Dasypus novemcinctus*. Furthermore, the distribution of geese in winter (LeFebvre and Raveling, 1967) and of ducklings in summer (Koskomies and Lahti, 1964) have been related to their energy expenditures.

It is doubtful, however, that the contrary explanation for distribution has validity: high rates of metabolism do not exclude cold-temperate species from warm-temperate or tropical regions. For example, microtine rodents are replaced in the southern United States by tropical sigmodontid rodents; both groups have high basal rates. Nevertheless, microtine and sigmodontid rodents are essentially excluded from desert environments, except along water courses, which may be related to both high rates of metabolism and a poor capacity to produce a concentrated urine. Both factors contribute to high rates of water loss. In this instance it would be most interesting to examine the energetics of the sagebrush vole, *Lagurus curtatus*, the microtine with most xeric distribution in North America.

Torpor. Another method of balancing an energy budget is to enter torpor. Torpor takes various forms depending upon its periodicity and the environmental conditions that are required for entrance into this state (Bartholomew, 1972).

Daily torpor occurs in many insectivorous bats and in a few rodents, frugivorous bats, and insectivorous birds, all of which are characterized by a small size. Torpor occurs most frequently in small species because of the decrease of ΔT_l with weight (equation 5), unless there is a significant compensatory increase in the rate of metabolism. Still smaller endotherms, such as certain moths, hymenoptera, and dragonflies, maintain a large temperature differential only when activity and feeding can occur. The frequency of daily torpor in mice has been shown by Tucker (1966) and Brown and Bartholomew (1969) to depend upon the amount of food available.

Little is known of the ecological aspects of seasonal torpor, except for the study of MacMillen (1965) of estivation in *Peromyscus eremicus*, where both food and water availability regulate entrance into torpor. Although hibernation has been the subject of many detailed physiological studies, there are few investigations of the energetics of hibernation. Energetics would be most interesting to study in species that hibernate in only part of their range. For example, it can be shown

in temperate bats that hibernation (and torpor) is size- and temperature-dependent, the interaction of these two factors dictating daily and seasonal activity and to some extent geographical distribution (McNab, 1974).

Most mammals that enter torpor have low basal rates of metabolism. It appears, however, that entrance into torpor does not require low basal rates, since some rodents that enter torpor have expected or even high basal rates (*e.g.*, *Tamias* [Neal and Lustick, 1974]; *Zapus* [Morrison and Ryser, 1962]; and some *Peromyscus* [Glenn, 1970]). Torpor and low basal rates of metabolism may simply be parallel adaptations to a common problem—the seasonal unavailability of water or food.

Migration. If endotherms are sufficiently mobile, they may respond to periodically harsh environments by migration. Migration permits an animal to occupy two ranges, each of which may be determined by the necessities of a balanced energy budget. Unfortunately, most of the estimates of the geographical limits of a balanced energy budget are obtained in the laboratory either by measurements of gas exchange (*e.g.*, Wallgren, 1954) or by food consumption (*e.g.*, West, 1960; Zimmerman, 1965; Helms, 1968) and are subject to the same problems as with the estimates for non-migrants.

Most birds migrate, and therefore few enter torpor. For that matter, temperate birds do not show a marked correlation of the basal rate of metabolism with food habits (Yarborough, 1971). Rather, the propensity for migration is the main correlate of food habits.

QUESTIONS FOR THE FUTURE

An endotherm obviously has a limited number of degrees of freedom within which its energy expenditure is determined. Influential factors include body size, climate and food habits, but we do not know to what extent these parameters account for the variability in endothermic energetics. For example, what determines body size? What dictates climatic tolerance? How do food habits depend on climate and body size? Why don't endotherms have basal rates of metabolism one half of their actual values and insulation twice as great? Is that possibility limited either by the capacity for insulation or by the necessity for heat dissipation? Furthermore, it may be asked whether there is a taxonomic component to the determination of the level of energy exchange. For example, why do birds have higher basal rates than mammals? Or passerines higher than non-passerines? Or placentals higher than Australian marsupials?

It is clear that we have only the beginnings of an understanding of what factors determine the energetics of endotherms. It is also obvious that energetics offers some of the most promising relations in which to study the strategies of adaptation.

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