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# METABOLISM OF WEASELS: THE COST OF BEING LONG AND THIN<sup>1</sup>

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**Abstract.** Metabolism of cold stressed weasels is 50–100 per cent greater than that of normally shaped mammals of the same weight. This can be attributed to their greater surface area, shorter fur, and inability to attain a spherical resting posture. In evolving an elongate shape which enables them to enter confined spaces in search of prey, weasels have sacrificed energetic efficiency. Increased ability to obtain prey, made possible by elongate shape and sexual dimorphism in body size, apparently more than compensates for the energetic cost of being long and thin. The information on weasels indicates that body surface area is an important determinant of heat loss in small homeotherms and suggests that energetic efficiency has played a significant role in the evolution of body shape and size.

Mammals and birds devote a large share of their total energy expenditure to maintaining a constant body temperature, and they exhibit many morphological, physiological, and behavioral adaptations for the efficient acquisition and expenditure of energy. Since most of the energy lost by homeotherms is dissipated from the body surfaces as heat, both the amount of surface and the quality of its insulation should be subject to rigorous selection. As early as 1847, Bergmann recognized the importance of relative surface area in the heat conservation of homeotherms. More recently Hart (1956), Scholander (1955), Hammel (1955), and Scholander et al. (1950) have emphasized the importance of insulative materials of birds and mammals (e.g., feathers, fur, and blubber). It has been difficult to evaluate the significance of body surface area in the energetics and evolution of homeotherms because most birds and mammals have roughly similar body proportions.

Some homeotherms have unusual shapes. For example, a number of carnivorous mammals have evolved elongate body shapes which permit them to enter burrows and other confined spaces in search of prey. Weasels and some of their relatives presumably have significantly more surface area than standard-shaped mammals of the same weight. If surface area is an important determinant of heat loss, then the elongate shape of weasels was evolved despite the presumed disadvantages in energy expenditure.

The purpose of the present study was to compare some metabolic characteristics of longtail weasels (*Mustela frenata*) with those of normally shaped mammals. We have measured oxygen consumption and estimated the extent to which it is influenced by body surface area, pelage insulation, and postural

changes. Weasels show great sexual dimorphism in body size which enabled us to obtain a two-fold range of body weights within a single species. This permitted a detailed comparison with a group of standard-shaped mammals of the same size, woodrats (genus *Neotoma*), for which comparable data were already available (Brown and Lee 1969).

## MATERIALS AND METHODS

Twelve longtail weasels were used in the present study. They were trapped at elevations between 2,250 and 3,000 m in the Snake Range of eastern Nevada (White Pine County) during September, 1969, and transported to Los Angeles. They were maintained in large cages in a windowless room where the temperature averaged 23°C and the photoperiod was adjusted to follow the seasonal changes at the latitudes of capture. The weasels were provided with drinking water and fed canned dog food, raw meat, vitamins, and bone meal. They remained healthy during the course of the experiments.

All physiological measurements were made between mid-October and mid-December, 1969, when the weasels were in fresh pelage. Metabolism of post-absorptive animals was measured during the day when the weasels tended to be inactive. Oxygen consumption was determined using open flow respirometric techniques with a Beckman G-2 oxygen analyzer. Dry, CO<sub>2</sub>-free air was circulated at 1,500 cc/min through 6-liter lucite chambers in which the animals were confined for 3-hour periods at each ambient temperature ( $T_A$ ). The  $T_A$  was maintained within  $\pm 0.5^\circ\text{C}$  by a constant temperature cabinet. Oxygen consumption, corrected to STP, was calculated from the lowest rates maintained for a half-hour period. Body temperatures ( $T_B$ ) were taken rectally with a thermistor-telethermometer at the end of each metabolic determination. Six measurements of evaporative water loss were made to estimate the contribution of evaporation to total heat loss; in these cases the animal was placed in the lucite chamber on a wire

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mesh platform suspended over mineral oil (which caught urine and feces). The water evaporated was trapped in U-tubes filled with Drierite, and the amount was determined by weighing.

Data on body size and metabolism of woodrats (*Neotoma*) were already available from a previous study (Brown and Lee 1969). These data were obtained from 10 populations representing 4 species: *N. cinerea*, *N. albigula*, *N. fuscipes*, and *N. lepida*. Metabolism of these woodrats was measured using techniques virtually identical to those employed for the measurements on weasels. It was necessary to obtain data on surface area, pelage length, and postural configurations of woodrats during the present study. Individuals of *N. fuscipes* and *N. lepida* from the mountains of Southern California were used for these measurements. It was necessary to use both species in order to obtain a two-fold variation in weight comparable to that in weasels.

Relative surface areas of weasels and woodrats were estimated from the skins of freshly killed animals. The carcasses were skinned with minimal stretching and the fresh skin was tacked, fully spread but unstretched, over a piece of paper. The outline of the skin was traced and the area encompassed was measured with a planimeter. The relative surface estimated in this manner did not include the surfaces of the tail, feet, and ears.

In order to determine how changes in posture affect body surface area in weasels and woodrats, we placed individual animals in a 10 gallon aquarium which had been fitted with an overhead mirror fixed at an angle of 45 degrees. This permitted us to photograph simultaneously the lateral and dorsal views of the resting postures assumed by cold stressed ( $T_A = 5^\circ$ ) animals.

The insulative values of the pelts of weasels and woodrats were estimated by measuring the length of the mid-dorsal underfur on dried skins of animals of known weight. Scholander *et al.* (1950) and Hart (1956) have shown that the insulation provided by the pelt can be estimated by length of underfur.

## RESULTS

Metabolic rates of adult male weasels (wt,  $297 \pm 36$  g; all measures of statistical variability are  $\pm$  one standard deviation) were greater than those of adult females (wt,  $153 \pm 3$  g) at all  $T_A$  (Fig. 1). At  $32^\circ$ , which was within the thermoneutral zone, the metabolic rates of resting, postabsorptive weasels approximated those predicted for mammals of comparable size (Fig. 1, dotted lines). Standard metabolic rates were  $1.36 \pm 0.20$  and  $0.84 \pm 0.12$  kcal/hr for 4 males and 4 females respectively. Metabolism was inversely related to  $T_A$  below  $35^\circ$ . Mean  $T_B$  was  $39.0^\circ\text{C}$  and did not vary with  $T_A$ .

We shall define the metabolic coefficient,  $C$ , by the equation

$$M = C (T_B - T_A)$$

where  $M$  is the metabolic rate in  $\text{cc O}_2 (\text{g} \cdot \text{hr})^{-1}$ ,  $T_B$  is the rectal temperature and  $T_A$  is the dry bulb temperature. The units of the metabolic coefficient are  $\text{cc O}_2 (\text{g} \cdot \text{hr} \cdot ^\circ\text{C})^{-1}$ . The minimal metabolic coefficient (maximum insulation) was estimated by using the values of oxygen consumption and  $T_B$  obtained at a  $T_A$  of  $5^\circ\text{C}$ . The metabolic coefficient in weasels is inversely related to body weight as it is in

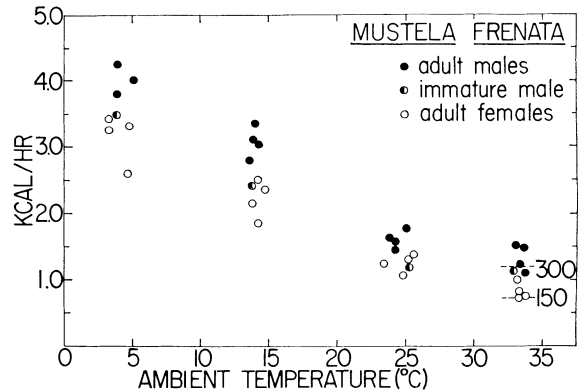


FIG. 1. The relation between metabolic rate and ambient temperature for nine resting, postabsorptive weasels. Metabolic rates were determined from oxygen consumption rates; it was assumed that .0048 kcal are produced per cc of  $\text{O}_2$  consumed. The dashed lines indicate the standard metabolic rates predicted for mammals weighing 150 and 300 g by Kleiber's (1961) equation relating standard metabolism to body weight.

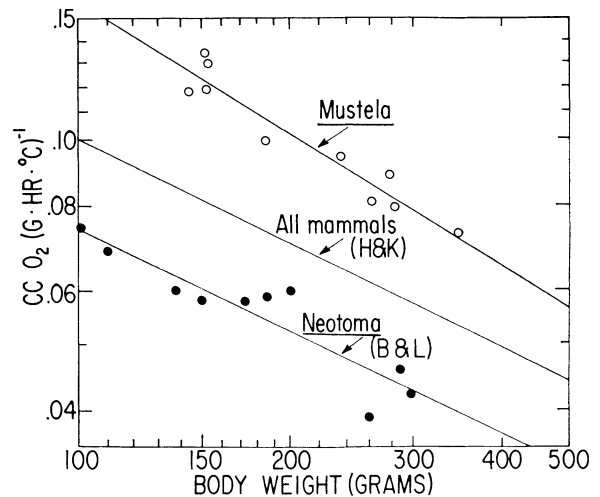


FIG. 2. The relation between the metabolic coefficient and body weight in weasels (present study), woodrats (Brown and Lee 1969), and a variety of small and medium-sized mammals (Herreid and Kessel 1967). Least squares regression lines have been fitted to the data for weasels and woodrats and the equations describing the lines are given in the text.

woodrats and other mammals (Fig. 2). The regression equations relating the metabolic coefficient ( $C$ ) to body weight ( $W$ ) for weasels ( $\log C = 0.486 - 0.64 \log W$ ), woodrats ( $\log C = -0.169 - 0.49 \log W$ ), and a variety of small mammals (Herreid and Kessel, 1967;  $\log C = 0.014 - 0.51 \log W$ ) have similar slopes, but weasels lost about twice as much heat as comparably sized woodrats and approximately 50 per cent more than predicted by the Herreid and Kessel equation. In weasels, evaporative heat loss accounts for only 14 per cent of the minimal ( $T_A = 5^\circ\text{C}$ ) metabolic coefficient.

Relative body surfaces of weasels are about 15 per cent greater than those of woodrats measured in the same way (Fig. 3). The regression equations relating body surface area ( $A$ , in  $\text{cm}^2$ ) to body weight ( $W$ , in grams) are  $A = 6.04 W^{0.73}$  for weasels and  $A = 7.26 W^{0.66}$  for woodrats. Because our measurements do not include the surfaces of the tail, feet and ears, the above equations have similar slopes to the empirical equation for standard-shaped mammals but give lower surface areas (Fig. 3).

When active, weasels have more body surface than normally-shaped mammals of the same weight. Significantly, even when weasels are minimizing their heat loss at low ambient temperatures, they are unable to achieve the nearly spherical shape assumed by woodrats and most small mammals in the cold (Fig. 4). Cold stressed weasels coil their elongate bodies into a flattened disc, a shape with considerably more surface than a sphere of the same mass.

Estimated by the length of underfur, the pelage

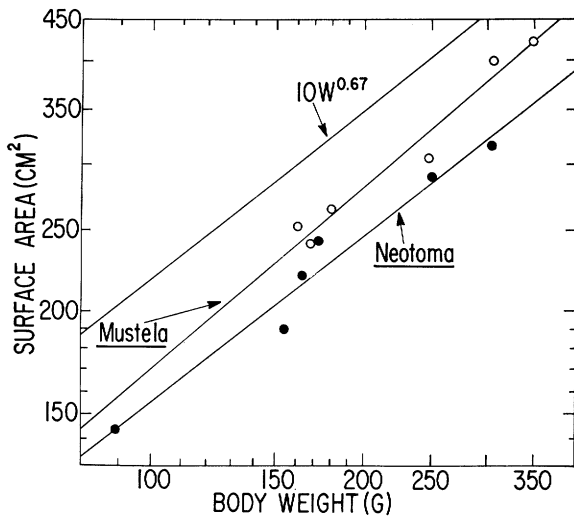


FIG. 3. The relation between body surface area and body weight for weasels (unshaded circles) and woodrats (shaded circles). Least squares regression lines have been fitted to the data. The values of surface area indicated do not include the surfaces of the tail, feet and ears and hence are less than those predicted by the equation (top line) relating total surface area to weight in mammals.

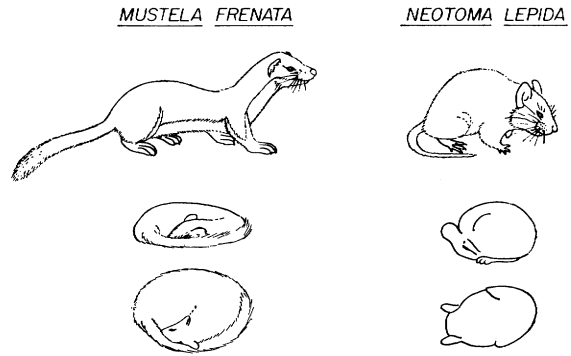


FIG. 4. Postures assumed by normally active and resting, cold stressed weasels and woodrats. The drawings show (from top) normally active animals and lateral and vertical views of individuals resting at  $5^\circ\text{C}$ .

insulation of weasels is less than half that of woodrats. The underfur of six weasels (wt,  $235 \pm 79$  g) averaged  $5.3 \pm 0.5$  mm in length, whereas that of 10 woodrats (wt,  $221 \pm 107$  g) averaged  $13.9 \text{ mm} \pm 2.8$  mm. There was no correlation between length of underfur and body weight in either weasels or woodrats. Despite the highly significant difference in pelage length between weasels and woodrats, values for pelage weight (per  $\text{cm}^2$ ) overlapped greatly and were not statistically different.

DISCUSSION

*Thermal and Energetic Consequences of Being Long and Thin*

Weasels differ from woodrats and other standard-shaped mammals of similar weight in several parameters which affect heat exchange (Table 1). Weasels pay a high energetic price for being long and thin. Although their standard metabolic rates are similar to those predicted for standard-shaped mammals of the same weight (Fig. 1), even moderately cold stressed weasels lose heat at a much greater rate than normally shaped mammals. Since most weasels inhabit temperate or arctic habitats, they must spend more energy maintaining body temperature than many other mammals of their size. The minimal metabolic coefficients of weasels are approximately twice those of woodrats (Table 1). The higher heat loss in weasels can be attributed largely to their greater surface area, shorter pelage, and their inability to achieve a spherical resting posture.

One might ask why weasels have not compensated for their large surface areas by evolving better insulating pelts. If they could do this, they could be long and thin and still lose no more heat than standard-shaped mammals. Scholander (1955) has shown on theoretical grounds that it is more efficient to alter heat loss by changing the thickness of the insulation

TABLE 1. Comparisons of variables affecting energy exchange in weasels and woodrats<sup>a</sup>

	Body Weight g	Surface Area cm <sup>2</sup>	Metabolic Coefficient ccO <sub>2</sub> (g. hr. °C) <sup>-1</sup>	Pelage Length mm	Standard Metabolism kcal/hr	Posture When Cold-stressed
Weasels	150	339	0.122	} 5.3	0.84	disc
	300	379	0.079			1.36
Woodrats	150	203	0.060	} 13.9	0.53 <sup>b</sup>	sphere
	300	322	0.043			1.12 <sup>b</sup>
Difference with reference to woodrats	150	113%	203%	} 38%	158%	
	300	118%	184%			121%

<sup>a</sup>Values were obtained by extrapolating the data of the present study and those of Brown and Lee (1969) to body weights of 150 and 300 g.  
<sup>b</sup>There is no systematic relationship between body size and standard metabolism in woodrats, so we have given the values for populations with mean body weights of 150.6 and 299.0 g.

than by changing surface area. On the other hand, Scholander *et al.* (1950), and Hart (1956) have shown that the insulative value of fur is correlated with length, and pelage length in turn is correlated with body size in mammals weighing less than several kilograms. Apparently for most mammals there is an optimal pelage length which is dependent on body size and which represents a compromise between energetic and other kinds of selective pressures. The fact that weasels have significantly shorter fur than similar sized woodrats suggests that the optimal pelage length is related more to the diameter of the mammal, or to the length of its legs, than to its weight and/or that selection for the ability to enter burrows has led to the evolution of shorter pelage despite its thermoregulatory disadvantages.

Weasels appear to have sacrificed energetic efficiency for predatory ability. In many other homeotherms selection for energetic efficiency has had an important influence on the evolution of body shape and, indirectly, body size (because relative surface area varies inversely with mass). Thus, most small mammals and birds have relatively compact shapes (especially those inhabiting cold climates), and in many groups of animals, body size varies inversely with environmental temperature (Bergmann's rule: Bergmann 1847, Scholander 1955, 1956, Mayr 1956, Brown and Lee 1969, James 1970).

It can be argued that woodrats are not good standards of comparison for weasels, because they have lower metabolic coefficients (Fig. 2) and lower standard metabolic rates (Brown and Lee 1969) than predicted by the empirical equations derived from many mammalian species. For this reason we include comparisons with the empirical equations whenever the data were obtained in a comparable manner (Fig. 1 and 2). However, it is important to realize that comparisons with the empirical relations for mammals are also hazardous because the equations are based on data from a large number of species which include domesticated forms, hibernators, unusually shaped kinds such as bats, and species which are restricted to tropical or subtropical climates. On

the other hand, two species of woodrats (*Neotoma lepida* and *N. cinerea*) occur in the same habitats as the weasels used in this study, and, like the weasels, the woodrats are active throughout the year.

#### Evolution of Body Shape in Weasels

The elongate shape of weasels is apparently a predatory strategy which enables them to enter the hiding places of the rodents which comprise the overwhelming majority of their diet. We have measured the metabolic "cost" of adopting this specialized strategy. Since even moderately cold stressed weasels require significantly more energy than normally-shaped mammals of the same size, in order for natural selection to have favored elongation the long thin shape of weasels must have enabled them to obtain sufficient prey to more than repay its metabolic cost.

There are several characteristics of weasels which seem to be related to the energetic consequences of evolving a long thin shape. These relationships are discussed below and illustrated in the schematic flow chart in Figure 5. Little is known about the biology of wild weasels, so that some of these presumed relationships are admittedly speculative. However, they provide a synthetic view of some aspects of the ecology, behavior and physiology of weasels which hopefully will stimulate discussion and further research.

Elongate body shape and ability to enter burrows have several consequences which increase energy requirements. Decreased pelage length and the increased surface to volume ratio raise the energetic cost of thermoregulation, whereas relatively short legs require that the necessary energy be obtained from a smaller segment of the habitat. The elevated energy requirement, in turn, has additional ecological consequences. First, it selects for the ability to be active at all times of the day, which results in a greater number and variety of prey items which may be encountered. Secondly, it tends to increase the intensity of intraspecific competition for food resources. One strategy which reduces intraspecific competition is the evolution of sexual dimorphism in

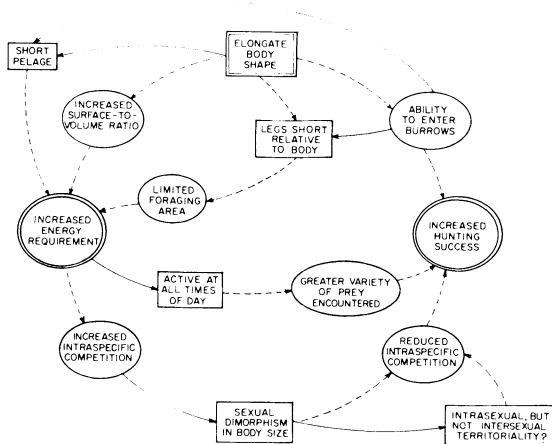


FIG. 5. A schematic representation of factors involved in the evolution of elongate body shape in weasels. The large circles indicate the primary consequences of evolving a long, thin body configuration; the ellipses show secondary consequences; and the rectangles indicate phenotypic characteristics of weasels which are affected by evolution of this body shape. The unbroken lines indicate selective pressures and the dashed lines show causal sequences. Changes will proceed in the direction of the arrows so long as selection favors a more elongate body shape.

resource utilization (Selander 1966). Marked sexual dimorphism in body size is a conspicuous feature of most elongate carnivores. In *Mustela frenata*, males weigh twice as much as females. This sexual dimorphism in size has the apparent advantage of making prey items available to each sex which cannot be obtained by the other; males can capture prey too large and powerful for the females, and females can enter burrows and cavities too small to admit the males. In order for the sexual dimorphism to be maximally advantageous, weasels of each sex should defend hunting areas against members of the same sex, but share them with members of the opposite sex or else pairs should defend a common territory. We know of no available information with which to test this prediction, but Hamilton (1933) has ob-

served both sexes bringing food to the young. Apparently the greater availability of prey made possible by sexual dimorphism helps to compensate for the energetic cost of being long and thin. It is interesting that related carnivores (family Mustelidae) which do not have elongate shapes, such as skunks, badgers, and wolverines, do not have the marked sexual dimorphism in body size characteristic of weasels.

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