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## Life with fur and without: experimental field energetics and survival of naked meadow voles

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**Abstract** Hair is considered to be a basic mammalian feature that provides protection and insulation, promoting energy conservation and survival. To quantify the functional significance of mammalian pelage, we tested the short-term experimental effects of fur removal in a natural population of the California vole, *Microtus californicus*, in winter. The daily energy expenditure (DEE) of seven voles was directly measured in the field using stable isotopes, first with the animals in their natural condition and then again after experimental removal of pelage by shaving. The initial mean $\pm$ SD DEE of 96.0 $\pm$ 23.1 kJ/day increased by only about 10%, to 106.3 $\pm$ 21.4 kJ/day, following shaving. The voles showed a body mass loss of 5%, about half of which was due to fur removal. Comparing slightly larger samples of all animals whose local survival could be documented, we found 100% survival over the 5 initial days of the experimental manipulation in 16 control animals and nine shaved animals; over the following 3 weeks the survival of shaved mice did not differ significantly from that of controls. We were surprised that the average increase in energy expenditure of voles without fur was so modest, though the range of individual values was great, and likewise we were surprised that shaved voles survived as well as they did. *M. californicus* survives naturally in winter under conditions of social aggregation that include huddling together of individuals in nests; this situation probably provided our experimentally shaved voles an opportunity to minimize the energetic disadvantages of pelage loss. They may also have employed a variety of compensatory physiological and behavioral responses, including reduction in activity time and food intake, and perhaps a related small decline in body mass.

Our limited sample sizes made it difficult to detect subtle differences that may have been biologically significant in the system we studied. Nonetheless, we can reaffirm that fur has an insulative value that promotes energy economy and survival. However, we also conclude that mammalian physiology and behavior are sufficiently complex and flexible that a variety of responses can be deployed to promote survival under unusual circumstances such as those of our experimental test.

**Key words** Energetics · Thermoregulation · Fur · Insulation · Survival · *Microtus*

### Introduction

Hair is one of the basic structural features of mammals. It probably evolved as a body-covering concurrently with the evolution of endothermy. The furry coat functions not only as insulation but also as mechanical protection. Under most conditions involving terrestrial mammals, insulation provided by fur conserves the body heat and constant temperature that are produced by regulated energy metabolism. This conservation of energy by fur should reduce the energy expenditure budget and food requirements. Fur can also shield day-active mammals from excessive heat load from solar radiation.

The role of fur as an insulator seems so fundamentally obvious that few attempts have been made, particularly in the field, to confirm and quantify its value for thermal energetics and survival. A laboratory study of the harvest mouse, *Reithrodontomys megalotis*, showed an increase of oxygen consumption in mice whose fur was experimentally removed by shaving (Pearson 1960a). In three species of small mammals, increases in depth of fur and minimizing body surface area by postural adjustment were shown to decrease thermal conductance (Morrison and Tietz 1957). Fur of white-footed mice, *Peromyscus leucopus*, was shown to be denser in winter and this led to increased survival in acute laboratory exposures to cold in the absence of food (Sealander 1951). Lemmings,

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*Dicrostonyx groenlandicus*, also showed denser fur and corresponding lower heat loss in winter (Reynolds 1993). We report here an experimental field investigation that assessed both the energetic significance and survival value of fur in a small rodent. We studied the California vole, *Microtus californicus* (about 40 g body mass), which is active in its above-ground runways on a daily basis throughout the entire year (Pearson 1960b) and maintains tight control over its warm body temperature (Wunder 1985). Our study design consisted of measuring rates of daily energy expenditure (DEE) in individuals before and after shaving their fur, and then assessing local survival in the population.

## Materials and methods

We studied a population of voles inhabiting areas of dense grass and weed-cover mixed with sparse shrubs in the hills east of Berkeley near Orinda, Contra Costa County, California. We worked only with non-reproductive adults, which we encountered during the winter season of our study in January through early March 1990. We used 100 Sherman live traps set out at intervals of 5–10 m and baited with oats. *M. californicus* is active above ground at all hours of the day and night, but especially during the day at this season (Pearson 1960b). By beginning to trap at 0630 hours PST and checking traps at 2-h intervals, we minimized the duration of confinement in traps, and we generally ceased trapping by early afternoon. We examined and weighed animals at each capture, and all were identified numerically. A final round of trapping was conducted on 5–7 March, continuously day and night, to assess the longer-term local survival (recapture within our area of trapping) of all the previously marked voles.

Weather data were obtained during our study from a station at the Orinda Filter Plant, located within 5 km of the study site. We measured ground temperatures in the study area with a 25-cm-long glass thermometer that we inserted vertically to a depth of 15 cm.

The general design of our study was to measure DEE of voles living in their natural habitat, then to remove their fur and remeasure DEE. In a preliminary test in early January at a location near the study area, we captured and shaved four animals and immediately released them at the site of capture. We shaved the voles using a battery-powered hair clipper with fine teeth (9 teeth/cm), removing as much fur as possible over the body but not shaving the face and head to avoid perturbing the animal. One of us held the animal gently by the head and tail while the other one operated the electric clipper. Of these four initially shaved animals, we recaptured three over the following 3 weeks. Based on the successful survival of these individuals we proceeded with our study as designed.

We made an additional measurement to determine the total amount of fur covering of adults by examining three additional individuals near the study area. We first shaved each vole, as described above, and carefully retained the fur of each for weighing. We then completely immobilized each of these three voles and shaved them, on the head and all other furred areas, to the point of no remaining hair apparent. We saved and weighed this second batch of hair to determine total hair mass. The average of the initial hair removal 78% ( $n=3$ ) of the total hair subsequently removed. We used this value to estimate the total fur mass of all of the other voles on which we subsequently determined DEE. We also determined maximum hair length of the nine voles that were later shaved for the energy balance analysis. To do this the entire hair sample of each individual was searched for 5 min for ten hairs that appeared to be of maximal length; these were all measured to 0.1 mm. We took the mean length of the ten hairs to give a representative value for each individual.

We captured nine voles for the initial measurement of DEE between 9 and 11 February, using the general protocol of the "doubly labeled water method" (Nagy 1987), with animal handling and

sampling as described by Kenagy et al. (1989). Upon capture each animal was injected intraperitoneally with 0.55 ml of a mixture of oxygen-18 (dose about 3 ml/kg; 97 atom%) and deuterium (dose about 1.5 ml/kg; 99.9 atom%). Each vole was held in its trap for 1 h to allow equilibration, after which a blood sample of about 150  $\mu$ l was obtained from the infraorbital sinus and sealed in glass capillaries for measurement of initial isotope concentration, and the animal was released. These animals were captured a second time 1 or 2 days later and a second blood sample obtained as close to 24 or 48 h as possible from the original sample, typically within 1–2 h of these periods. At this time the animal was reinjected with a new supply of the oxygen-18/deuterium mixture and all fur removed except on the face and head. At the end of 1 h, a new blood sample was obtained and the naked vole released. These individuals were recaptured 1 or 2 days later, bled as before, and released. The DEE of shaved voles was determined on 10–13 February. Voles were weighed at each capture and bleeding, and the mean mass at each of these stages was taken to represent each interval of metabolism determined. The isotope concentrations of the blood samples were measured by isotope ratio mass spectrometry at the Laboratory of Isotope Research at the University of Groningen, The Netherlands. We obtained successful samples for the determination of data for seven individuals in both the furred and shaved condition. We converted ml carbon dioxide production to kJ by multiplying the former by a factor of 21.7 J/ml CO<sub>2</sub>, assuming metabolism associated with a plant diet.

Survival of voles was assessed in the natural population by comparison of nine animals that were shaved on 10–12 February with 16 unshaved animals known to be alive during those same dates. The shaved animals included two individuals on which we did not successfully measure DEE. We conducted overnight and daytime trapping again on 5–7 March to determine the numbers of animals remaining alive in the area of our trapping (local survival) at that time.

Local survival was tested with a 2 $\times$ 2 contingency test, with Fisher exact probabilities. Body mass and energy expenditure were compared between natural and shaved voles using the Wilcoxon matched-pairs ranked sign test. Measured values are expressed as mean $\pm$ SD.

## Results

The hair that we removed from nine voles amounted to 2.0% of body mass, based on an initial mean $\pm$ SD body mass of 43.0 $\pm$ 6.8 g and a hair mass of 0.88 $\pm$ 0.17 g. With a residual hair mass, independently measured in three other voles, amounting to 0.25 $\pm$ 0.06 g we estimated that total body hair mass for all voles was 1.13 $\pm$ 0.22 g, i.e., 2.6% of body mass. Our experimental removal of fur thus amounted to about 78% of total body hair. The longest hairs found for each of the nine voles had a mean length of 13.8 $\pm$ 0.6 mm.

Of the nine voles shaved and followed through the second series of energy expenditure measurements between 10–12 February, all were captured alive again within 1 or 2 days after shaving. Thus the initial survival rate for shaved voles during the DEE measurements was 100% (Table 1). Of these nine, three were recaptured 3 weeks later (Table 1). These final survivors showed considerable regrowth of fur. The patches of skin that had been growing new fur (molting) at the time of shaving were now covered with fur of almost full length; adjacent patches of skin were still naked. The result was a covering that must have provided considerable insulation. We compared survival of 16 naturally furred voles that had been marked before 12 February; 10 of these remained

**Table 1** Local survival of voles on a short-term basis (9–12 February) and long-term (after 3 weeks, 5–7 March) in relation to fur condition: natural (control) vs. shaved. 2x2 contingency test, with Fisher exact  $P=0.226$ , indicates no significant difference in survival in the long term

	Short-term		Survival (%)	Long-term		Survival (%)
	Alive	Dead or missing		Alive	Dead or missing	
Natural	16	0	100%	10	6	63%
Shaved	9	0	100%	3	6	33%

**Table 2** Mean daily energy expenditure (DEE) and body mass in seven voles, measured initially (9–11 February) and after removal of fur (10–13 February) in their natural environment. Values are means $\pm$ SD. Comparison of individuals under natural and shaved conditions is made by the Wilcoxon matched-pairs ranked-sign test

	Natural	Shaved	Test
Body mass (g)	43.3 $\pm$ 7.8	41.3 $\pm$ 7.6	$P=0.02$
DEE (kJ/day)	96.0 $\pm$ 23.1	106.3 $\pm$ 21.4	$P=0.31$

**Table 3** Individual values of DEE (kJ/day), for seven voles measured initially (9–11 February) and after removal of fur (10–13 February), with percentage change in response to the experimental manipulation. Means $\pm$ SD are shown in Table 2

Natural (before)	Shaved (after)	Change
66	94	43%
96	137	42%
87	119	38%
69	79	14%
112	126	12%
121	101	-17%
121	89	-26%

alive after 3 weeks (Table 1). Although the local short-term survival rates of 33% (shaved) and 63% (control) did not differ significantly (Table 1), their difference in magnitude suggests a trend that might have become significant had samples been larger. Nonetheless, it was surprising that shaved voles survived as well as they did, beginning with an initial, short-term survival rate of 100%.

During the period of DEE measurement on natural and shaved individuals, the February winter weather conditions remained consistent, without precipitation and with generally clear skies both day and night. Nighttime minimum temperatures fell each night to the same range of 1–2°C; and daytime maxima rose to 14–17°C. A series of 26 soil temperatures taken at a depth of 15 cm in the soil around the study area between 7 and 13 February at various times of day between 0600 and 1730 hours all fell between 6°C and 9°C. Weather was generally similar over the following 3 weeks, except for two rainy spells, during 15–17 February and 1–4 March.

All seven voles had a lower body mass (mean reduction of 5%), during the interval of metabolic measurement when shaved than previously while furred (Table 2).

Of the 2.0-g mean decrease, however, nearly half was due to the experimental removal of fur, and if that was discounted, the additional change of mass was insignificant ( $P>0.05$ ). Thus, removing the fur did not cause an additional significant loss of mass related to energetic stress of fur loss, despite the near-freezing nighttime air temperatures. When we handled the recaptured, shaved individuals upon removing them from the cold aluminum traps in which they had been captured, they were conspicuously warm to the touch. This emphasizes that they were not resorting to hypothermia to conserve energy.

The mean DEE of all seven shaved voles was about 10% higher than that of the same individuals when naturally furred, but this was not statistically significant (Table 2). The lack of statistical significance resulted from the enormous variability in the data recorded for individuals, both when furred and shaved, and between these two stages. The individual whole-animal values of DEE (Table 3) showed changes following shaving that ranged from 43% to -26%, while the variation among the animals within each of the two stages showed a range of nearly twofold from minimum to maximum. Although the resulting mean energy impact of fur loss was low, it is possible to highlight the potential increase in DEE by examining the data only for the five individuals that increased DEE following shaving (Table 3). For these individuals, the increase was 29%, rising significantly from 86.1 $\pm$ 19.3 kJ/day to 110.9 $\pm$ 24.0 kJ/day (Wilcoxon test,  $P=0.04$ ). It is noteworthy that the two animals that decreased DEE after being shaved showed the highest DEE of all the animals beforehand (Table 3). These two individuals must have encountered behavioral or ecological challenges during the “pre-shaved” DEE measurements that had energetic consequences greater than those of fur loss; indeed their DEE while they still had fur was also higher than that of all of the shaved individuals except two. One of these two former individuals also had the highest mass-specific DEE of all individuals under each of the two measurement conditions.

## Discussion

We were surprised that shaved voles mustered the means to survive. Most of them increased their DEE while existing under nighttime temperatures near freezing, though two individuals actually showed a decrease. The great individual variability in energy expenditure suggests that both the degree and nature of the behavioral and physiological responses themselves were complex and variable. What were the voles doing that allowed them to survive and show only moderate increases in DEE? We can account for the energetic response of voles by comparing their free-living DEE to the basal (minimal) rate and to other expected rates, including maximal rates of expenditure and intake. Our analysis reaffirms the role of fur in providing insulation and energy conservation, but our approach did not document the particular behavior and short-term physiological responses of indi-

**Table 4** Daily energy budgets of *Microtus californicus* (all standardized to body mass=42 g) under various conditions, and factorial increases above basal metabolic rate (BMR).

	Energy expenditure (kJ/day)	Factorial increase
BMR (expected) <sup>a</sup>	27.2	–
SMR at 8°C (expected) <sup>b</sup>	92.7	3.4
DEE (“field conditions”; expected) <sup>c</sup>	69.9	2.6
DEE (winter, with fur; measured) <sup>d</sup>	96.6	3.6
DEE (winter, shaved; measured) <sup>e</sup>	109.2	4.0
DEE (winter, shaved, maximum; measured) <sup>f</sup>	121.3	4.5
Maximum metabolizable intake (expected) <sup>g</sup>	174.8	6.4

<sup>a</sup> Mammalian allometric function of Kleiber (1961):  $BMR=70W^{0.75}$ , where  $W$ =weight (kg). BMR is expressed in kcal/day, converted at 4.188 kJ/kcal

<sup>b</sup> Standard metabolic rate (SMR) of *M. californicus*, adjusted to 8°C ambient temperature, based on conductance given by Bradley (1976; in Wunder 1985). SMR in thermoneutrality=1.55 ml oxygen/g/h; thermal conductance=0.66 cal/g/h/°C, with lower critical temperature=30°C. Energy equivalence of 20.1 J/ml oxygen

<sup>c</sup> Allometric function of Nagy (1987) for daily existence metabolism of mammals under free-living conditions, not involving special energy demands

<sup>d</sup> Present study, value of Table 2, adjusted to 42 g body mass

<sup>e</sup> Present study, value of Table 2, adjusted to 42 g body mass

<sup>f</sup> Present study, based on maximum value of mass-specific DEE of all individuals listed in Table 3, adjusted to 42 g

<sup>g</sup> Allometric function of Kirkwood (1983) for maximum metabolizable energy intake:  $ME_{max}=1713 \text{ kJ/kg}^{0.72}/\text{day}$

viduals that comprised their total response to fur removal. We can nonetheless offer some suggestions as to the nature of the overall response. It is also clear that our limited sample sizes made it difficult to detect subtle differences that may have been biologically significant in the system we studied.

What is the thermal and insulative value of fur with respect to the total energy budget of a vole, and how far towards the limits of physiological survival were the voles pushed? During exposure of a resting vole to an air temperature of 8°C (intermediate between daily maximum and minimum, and also similar to soil temperature at burrow depth) the metabolic rate should be increased to 3.4×basal metabolic rate (BMR); but a general allometric prediction for total 24-h expenditure in the field suggests an increase to only 2.6×BMR (Table 4). On the other hand, our own direct field measurement of *M. californicus* in winter produced a DEE of 3.6×BMR, which increased further upon shaving to a mean level of 4.0×BMR (Table 4). The actual incremental cost of thermostatic heat production in our shaved winter voles, due to nakedness, thus added only about 0.4×BMR to their DEE. Expressed in terms of equivalent changes in air temperature and based on the thermal conductance of voles (Table 4, footnote b), the average increase of 10% in DEE (Table 2) associated with fur removal would be equivalent to existing at a temperature of only 2°C lower, whereas a maximum of 40% increase in DEE (Table 3) would be equivalent to existing under a temperature drop of 8°C. In terms of the possibility of driving total DEE in the field toward maximum limits, this does not seem likely, as the value of 4.0×BMR in our shaved voles approaches but does not meet the top of the range of 4–7×BMR that characterizes the DEE of mammals in the field in maximum observed or peak performances (Drent and Daan 1980; Koteja 1987; Peterson et al. 1990; Ricklefs et al. 1996). Likewise, from the opposite

standpoint of maximal energy intake capacity, estimated as 6.4× BMR for our voles [Table 4, after Kirkwood (1983)], the shaved voles also appear not to have been pushed to the limit of their energetic capacity. As described below, behavioral aspects of vole biology (use of nests, social huddling) have potentially much greater positive impacts on DEE than the negative effects of the small physiological increments that we describe here.

We believe that special aspects of the natural history and behavior of voles (*Microtus* spp.) contributed to thermal homeostasis beyond the independent role of the pelage itself, or its absence, in the animals that we measured. Arvicoline (“microtine”) rodents in general and species of *Microtus* in particular form social aggregations, especially in winter, which involve huddling in nests while resting, i.e., not foraging abroad (West and Dublin 1984). This has been documented for *M. californicus* (Pearson 1960b), which occupy underground nests in winter that are shared by 4–5 individuals that also use the same nearby runways for occasional foraging bouts (5–6 min duration), which typically amount to less than 1 h/day spent outside the nest. Thus, the heat balance of the voles that we studied was likely influenced on a regular basis, both in normal and shaved individuals, by the thermal advantages of group huddling and nest occupation for something like 23 h of every day. Laboratory studies of small rodents, including *Microtus* spp., have quantified the energy savings associated with both huddling and nest use (Pearson 1947, 1960a; Wiegert 1961; Hayes et al. 1992). For example, use of nests can reduce metabolism by 20% (Pearson 1960a) and huddling can provide a 23% reduction (Hayes et al. 1992). Such impacts seem to have a greater potential for energy economy in a small rodent than the ability of a fully homeothermic individual to adjust heat flow across its skin and fur by physiological and mechanical means (Porter et al. 1994). Beyond the routine aspects of energy conservation in the daily life of

voles, further responses were possible in the voles whose pelage was removed. Besides increasing the intensity or efficiency of huddling and nest use, they may have, on a short-term basis, simply reduced their total activity and/or decreased food intake, both of which could have closely balanced the energy budget with little or no resultant loss of mass. This complex of behavioral and physiological options for adjustment is likely to have generated much of the variation that we observed among the individual voles we studied.

The hair of rodents is clearly significant in thermal homeostasis, and of four general types of hair (based on length) that have been distinguished (Sokolov 1982), the shortest and densest, the "fur", is most relevant to maintaining body heat. For *Microtus arvalis*, which is similar in size to *M. californicus*, the longest or guard hairs are 12–14 mm in length, the pile hairs are 10–11 mm, the intermediate hairs are 9–10 mm, and the fur is shorter than 9 mm (Sokolov 1982). Our own measurements of guard hairs, approaching 14 mm maximum length in *M. californicus*, indicates a correspondance feature between these two species. Although we did not measure the length of the deep, insulating fur layer on the live animals that we studied, it seems from this comparison that it would generally be less than 9–10 mm in length. Seasonal increases in the density of winter fur, associated with molt, offer evidence of functional adjustments made to enhance the thermoregulatory role of the fur in rodents (Sealander 1951; Morrison and Tietz 1957; Reynolds 1993).

The insulative role of the coat appears to be broadly represented within the class Mammalia, although two orders of large and fully aquatic mammals, the cetaceans and sirenians, lack a covering of body hair. Among small mammals adaptive hairlessness is known only in the naked mole rat, *Heterocephalus glaber*, which lives socially in subterranean burrows of stable and moderate temperature in Africa, huddling in large groups and thus existing thermally as a larger "superorganism" to maintain homeothermy (Yahav and Buffenstein 1991). In fact, naked mole rats, when studied individually in the laboratory, show labile body temperature, closely tracking ambient temperature over the range of 12–37°C, and a decreasing rate of oxygen consumption as air temperature is lowered (Buffenstein and Yahav 1991). Genetically hairless strains of mice (with a simple Mendelian recessive heritability) offer other means for the experimental study of the adaptive significance of fur, and they have been used as a model for investigating basic mammalian thermogenesis (Heldmaier 1974).

Our study evaluates the energetic impact of fur as winter insulation in a free-living rodent, and as such the measurements are quantitatively useful in their own right. However, a further perspective emerges from the attempt to perform an experimental manipulation under natural conditions. The ability of organisms to exploit multiple tactics to enhance survival and energy economy is important, and this results from the complexity and flexibility of their behavior and physiology that allow them to make compensatory adjustments.

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