



Seasonal changes in heat transfer in the small mammal *Calomys musculus* (Rodentia, Muridae). The role of the skin

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Received 8 August 2001; accepted 8 August 2002

Abstract

1. Cooling coefficients of cylinders covered with *Calomys musculus* skins were significantly different between seasons ($F_{5,75} = 12.36, p < 0.001$). Winter and spring skins had significantly lower cooling coefficients than summer and fall skins. Cooling coefficients of naked skins were not different between seasons
2. Cooling coefficients were significantly different between hair treatments ($F_{2,75} = 673.98, p < 0.001$). Fluffed hair skins had lower cooling coefficients than skins with hair laying naturally and naked skins.
3. Body masses of animals were significantly different between seasons ($F_{5,27} = 5.39, P < 0.001$).

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Keywords: Seasonal changes; Cooling coefficients; Pelage; Insulation; *Calomys musculus*

1. Introduction

Animals exchange matter and energy with the environment permanently. The rate of energy flow between an animal and its surroundings is determined by environmental factors and animal-dependent variables like metabolic rate; evaporative water loss rate; thermal conductance of fat, fur or feathers; absorptivity to radiation; size and shape of the body and body orientation (Porter and Gates, 1969).

Two physiological mechanisms act together in order to maintain a high and constant body temperature in homeotherms: (a) metabolic heat production and (b) insulation to retard heat loss (Webb et al., 1990). A simple linear relationship, derived from Fourier's law of heat and Newton's law of cooling (McNab, 1983), may be used to characterize the relationship between heat

production and the difference between body and air temperature of a mammal. When the heat loss rate and heat production rate are equal and the animal is at an air temperature below the thermoneutral zone, this relationship may be formulated as follows (Kleiber, 1961; Hart, 1963):

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

where the metabolic rate or rate of heat loss (M) is directly proportional to the whole-body thermal conductance (C), and to the difference between the body (T_b) and air (T_a) temperatures. Thermal conductance is "a measure of the ease with which heat enters or leaves a body" (McNab, 1980) or "a measure of the ease of heat transfer from the body" (Bradley and Deavers, 1980). In spite of the apparent simplicity of this definition, this overall thermal conductance includes the effects of convection, thermal radiation, evaporation, fur or feather layer conductance and surface tissue conductance (Bakken et al., 1985). Each one of these processes may be more or less important, depending on animal

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traits and physical characteristics of the environment (McNab, 1980; Porter and Gates, 1969; Birkebak, 1966). Thickness and nature of the insulating layer and surface area are important factors that determine the amount of heat exchanged between a body and the environment. The effectiveness of fur and plumage as insulating layers is determined by the presence of a “dead layer” of air that minimizes the convective heat transfer (Birkebak, 1966; Morrison and Tietz, 1957).

Animals living in thermally stressful environments often exhibit morphological, physiological and/or behavioral adjustments to regulate the rates of energy exchange. For instance, an increase in the thickness of the insulating layer by piloerection or a reduction of the body surface area by adopting a curled posture may reduce heat loss. Over the long-term (i.e., over the lifetime of the animal) morphological changes, variations in body size and shape may occur (Morrison and Tietz, 1957; Chappell, 1980; Reynolds, 1993). When animals are exposed to long-lasting seasonal low temperatures, changes in fur properties provide an efficient way to increase the insulation without increasing energy expenditure, because denser and longer pelage reduces both: conductive and convective heat loss (Harris et al., 1985). Seasonal changes in density, thickness and length of hair fibers that result in changes in thermal conductance, have long been recognized as important adjustments to seasonal variations in climatic conditions in homeotherms, principally in mammals from arctic and subarctic climates (Scholander et al., 1950; Hart and Heroux, 1953; Hart, 1956; Reynolds, 1993). Although the insulation provided by the pelt is not the most dynamic thermal physiological variable, it is a major determinant of metabolic rate and thermoregulatory capacity (Gordon, 1982).

Seasonal insulative changes have been proposed as of limited value in small mammals from arctic and North temperate zones. Hart (1956) concludes that “small mammals, which have the greatest metabolic response to temperature changes, have only limited possibilities for seasonal insulative change” and “unless these species entirely escape exposure to winter cold, seasonal acclimatization must largely lie in their ability to change heat production”.

In the present study we test seasonal changes in the heat transfer through the fur in a small South American mammal dwelling in a moderate climate with wide seasonal variations, the corn mouse, *Calomys musculus* (Rodentia, Muridae). *C. musculus* is a good model to study the problem because (1) it has a widespread distribution, including regions with harsh and mild as well as dry and wet winters and (2) this rodent has been considered a poor endotherm with a low basal metabolic rate and small body size (Bozinovic and Rosenmann, 1988; McNab, 1983), making it a good candidate to show some kind of insulative adjustments to survive

during the cold seasons. To our knowledge, this is the first study evaluating seasonally the thermoregulatory role of the fur in a neotropical sigmodontine rodent.

2. Materials and methods

Corn mice were captured monthly between March of 1989 and April of 1990 in Donovan (33°20'S, 66°21'E), San Luis, Argentina. Sherman traps baited with rolled oats were used. Traps were distributed in a 1.5 ha area and checked for captures every day early in the morning. Captured animals were weighed, sexed and transported to the laboratory. Instantaneous air temperature ($\pm 0.1^\circ\text{C}$; at 07:30 AM), maximum and minimum air temperatures ($\pm 0.1^\circ\text{C}$; in a period of 24 h) and relative humidity ($\pm 1\%$; at 07:30 AM) were registered daily at the trapping site while the capture grid was active (6–7 days every month).

After transport to the laboratory, animals were measured for morphometrics and euthanized using ethyl ether (Sigma, St. Louis, MO, USA) overdose, not later than 12 h after capture. Skins were carefully removed from carcasses by making a lateral cut along one side of the body, approximately between abdominal and dorsal pelage. After removal, skins were carefully cleaned of adhering fat and tissues, avoiding stretching. Carcasses were frozen and stored at -20°C for use in other studies in the laboratory.

Freshly excised skins were wrapped around solid aluminum cylinders (Bozinovic et al., 1987), sewn up and left to dry for at least 72 h in a Drierite desiccator. Cylinders had square ends (also covered with fur) and were all the same size (22.68 cm²).

A platinum thermo-resistance connected to a multiple digital thermometer (IEA, Técnica Seis, Rosario, Santa Fe, Argentina) was inserted in the geometrical center of each cylinder to register core temperature (T_c). Cylinders were heated in a culture oven up to a T_c of 40°C and then placed in a thermoregulated chamber at an air temperature (T_a) of $0 \pm 0.5^\circ\text{C}$. Core and air temperature were automatically computed every minute for 30 min.

The cooling procedure was performed for each wrapped cylinder on three hair conditions: (a) hair lying naturally, with approximately the same angle and depth of intact animals, (b) fluffed hair, simulating maximum piloerection, and (c) naked skin, without hair. Fluffed hair was achieved by blowing the fur against the hair insertion. Naked skins were obtained using a commercial depilatory agent (Emal Diamant, Email Diamant S.A., Capital Federal, Argentina). Naked skins were rinsed with water to remove the depilatory agent and hair left, and then allowed to dry before performing the heating-cooling procedure (Turner and Schroter, 1985).

The rate of heat loss of these cylinders wrapped with skins may be determined using the equation (Morrison

and Tietz, 1957):

$$C(\text{J cm}^{-2} \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}) = b(\text{min}^{-1}) c(\text{J cm}^{-2} \text{ } ^\circ\text{C}^{-1})60, \quad (2)$$

where b is the slope of the cooling curve $\ln(T_c - T_a)$ versus time (min^{-1}) and c is the heat specific capacity of aluminum. Since c is a constant and aluminum cylinders were all the same size, the only source of variation was the quality of furs. Thus, we compared cooling coefficients (b) of cylinders wrapped with furs between seasons to estimate variations in heat exchange properties of the skins per surface area.

Values of $T_c - T_a$ were log transformed and the regression versus time fitted using the least-squared means routine in SYSTAT 5 (Wilkinson, 1992), over a range $T_c - T_a$ between $37.81 \pm 0.83^\circ\text{C}$ and $7.16 \pm 1.99^\circ\text{C}$.

Cooling coefficients were compared between seasons (summer, fall, winter and spring 1989, and summer and fall 1990) and hair treatments using two-way ANOVA. Body mass (Mb) was included in the analysis as a covariate. Tukey's honest significant difference test was used for a posteriori multiple comparison. Reported values are mean ± 1 standard error of the mean. Percent comparisons were performed with arcsine transformed values.

3. Results

Regression coefficients of cooling curves ($\ln(T_c - T_a)$ versus time (min^{-1})) of aluminum cylinders wrapped with *C. musculus* skins were all highly significant ($r^2 = 0.99$; $p < 0.001$). Non-linearities in the log plot that would indicate internal temperature gradients or other problems were not apparent.

Body mass of captured rodents was significantly different between seasons ($F_{5,27} = 5.39$, $p < 0.001$). Body mass of winter (1989) animals was significantly lower than body mass of summer and fall animals ($p < 0.05$), (Table 1).

Cooling coefficients of cylinders covered with *C. musculus* skins were significantly different between seasons ($F_{5,75} = 12.36$, $p < 0.001$) and between hair treatments (hair lying naturally, fluffed hair and naked skins) ($F_{2,75} = 673.98$, $p < 0.001$) (Fig. 1). The interaction between hair conditions and season was also significant ($F_{10,75} = 2.67$, $p < 0.05$). Body mass was not a significant covariate for cooling coefficients ($F_{1,75} = 2.14$, $p = 0.14$).

Aluminum cylinders covered with winter and spring skins, measured under conditions of hair lying naturally and fluffed hair, had significantly lower cooling coefficients than cylinders covered with skins from animals collected in summer and fall, (all p 's < 0.05). There were not significant differences between seasons in cooling coefficients of naked skins. (Fig. 1). Maximum reductions of cooling coefficients were observed between

summer and winter 1989 for hair laying naturally (16.1%) and fluffed hairs (15.7%).

Fluffing hair (in skins from both summers, winter and spring) significantly reduced heat transfer, compared to naturally laying hair (all p 's < 0.05). This treatment resulted in a heat transfer reduction between 7.61% (winter 1989) and 10.79% (fall 1989). This percent reduction (arcsine transformed values) on cooling coefficients was not significantly different between seasons ($F_{5,27} = 0.394$, $p = 0.849$). Cooling coefficients of naked skins were significantly higher than cooling coefficients for the other two treatments in all seasons (all p 's < 0.001). The percent increase in heat transfer (arcsine transformed values) due to the absence of hair was significantly different between seasons ($F_{5,22} = 5.94$, $p = 0.001$). Winter and spring 1989 estimates (31.03%

Table 1
Body mass of animals used in this study

Year	Season	Body mass (g)
1989	Summer, $n = 4$	21.59 ± 2.45
	Fall, $n = 4$	14.91 ± 2.45
	Winter, $n = 5$	9.76 ± 2.19
	Spring, $n = 8$	16.65 ± 1.73
1990	Summer, $n = 9$	21.89 ± 1.63
	Fall, $n = 3$	22.62 ± 2.82

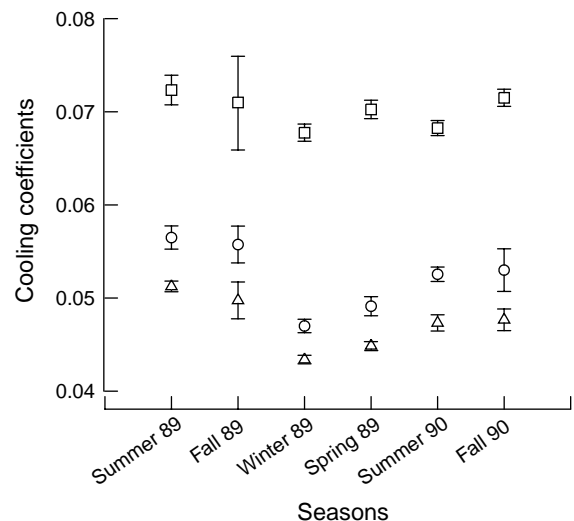


Fig. 1. Cooling coefficients of aluminum cylinders covered with *C. musculus* skins in the six seasons studied. (○) hair lying naturally; (△) fluffed hair; (□) naked skin. Number of skins tested on each condition (hair lying naturally, fluffed hair, and naked skin respectively): Summer 89: 4, 4 and 4; Fall 89: 4, 4 and 3; Winter 89: 5, 5 and 4; Spring 89: 8, 8 and 7; Summer 90: 9, 9 and 8; Fall 90: 3, 3 and 2.

and 29.87%, respectively) were significantly higher than summer 1989 (21.19%) and spring (23.55%) (Fig. 2).

4. Discussion

4.1. Seasonal variation in heat transfer of skins

We estimated a winter reduction of 16.1% in the heat loss rate of *C. musculus* skins. This value is similar to insulation changes reported in previous studies. Hart and Heroux (1953) reported a winter increase in insulation of 21.1% in *Peromyscus maniculatus* from Ottawa, Canada. Hart (1956) found a winter increase in insulation between 12% and 52% in arctic mammals in

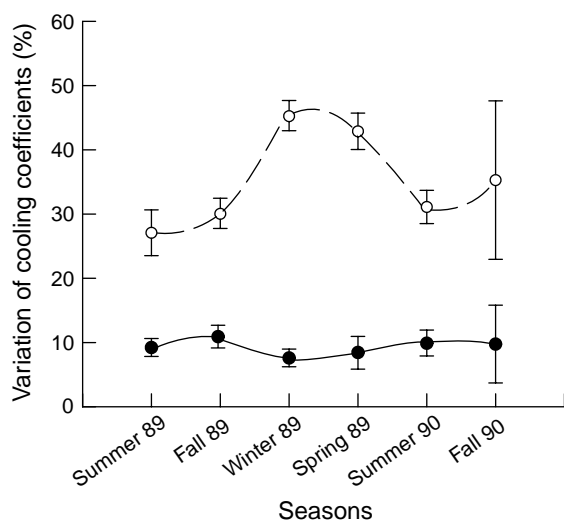


Fig. 2. Percent variation in cooling coefficients of aluminum cylinders covered with *C. musculus* skins between the different hair conditions. (●) percent variation between fluffed hair and hair lying naturally. (○) percent variation between hair lying naturally and naked skin.

a wide range of body masses. Reynolds (1993) determined a rise of 18% in the heat loss of summer pelts of lemmings.

4.2. Seasonal environment

Seasonal changes in fur insulation have been reported in mammals under seasonal climatic fluctuations similar to those *C. musculus* is exposed. Harris et al. (1985) detected a 48.9% decrease in heat transfer of winter pelage of black tailed jack rabbits from northwestern Utah (USA), where the mean monthly temperatures vary from -7°C in January to 23°C in July and lows of -25°C and highs of 35°C are not uncommon. Héroux et al. (1959) determined an increase of 25% in winter insulation in white rats exposed to a seasonal temperature range of 31°C in outdoor enclosures.

C. musculus has a wide geographic distribution in Argentina (Redford and Eisenberg, 1992). The Algarrobo forest where *C. musculus* is found in San Luis is an open formation with shrubs of jarilla (*Larrea divaricata*) and chañar (*Geoffroea decorticans*) (Anderson et al., 1970). Minimum winter and maximum summer average temperatures in our field site (3.9°C and 31.5°C , respectively), computed for the last 25 years, may be considered moderate (Caviedes-Vidal and Bozinovic, 1990); however, the absolute seasonal range in temperature is wide, 52.8°C (Caviedes-Vidal et al., 1987). Based on our own measurements of air temperature during each trapping period in this study, we determined an absolute seasonal range in temperature of 42°C between summer and winter 1989 and of 51°C between winter 1989 and summer 1990 (Table 2). In addition, there is also a wide seasonal variation of the water availability in the study site; rainfalls mostly occur during summer (January rainfall 107.2 mm, June rainfall 3.9 mm) diminishing winter productivity of the habitat (Caviedes-Vidal et al., 1987). Thus, it would not be rare to observe increases of insulation, decreases of body mass (as a way to increase the mass specific metabolic rate)

Table 2
Ambient variables in the field site during the trapping seasons

Season	Air temperature ($^{\circ}\text{C}$)	Humidity (%)	Maximum air temperature ($^{\circ}\text{C}$)		Minimum air temperature ($^{\circ}\text{C}$)	
			Average	Absolute	Average	Absolute
Summer ^a	20.1 ± 1.6	77.7 ± 5.7	31 ± 5.0	35	12 ± 1.3	11
Fall ^a	13.5 ± 2.3	67.2 ± 7.7	32.2 ± 1.9	34	5.4 ± 4.3	0
Winter ^a	8.1 ± 3.0	58.9 ± 15.9	25.7 ± 5.7	33	-1.5 ± 4.4	-7
Spring ^a	17.7 ± 5.2	40.4 ± 22.4	32.3 ± 8.7	46	9.1 ± 5.1	1
Summer ^b	20.2 ± 2.5	71.7 ± 6.6	37.3 ± 3.6	44	15.9 ± 2.4	14
Fall ^b	10.7 ± 6.3	63.7 ± 11.1	28.4 ± 5.0	35	2.9 ± 2.1	1.5

^a 1989.

^b 1990.

and other mechanisms of energy saving in small mammals living in such environment.

4.3. Body size

The greatest absolute seasonal changes in thermal conductance or insulation of pelts have been observed in large animals. In small mammals multiple physical constraints seem to restrict seasonal insulative changes (Hart, 1956; Scholander et al., 1950; Reynolds, 1993). Therefore, small mammals should avoid exposure to winter cold and, their seasonal acclimatization should rely on either the increase in heat production (Hart, 1963) or the decrease in mass specific metabolic rate through a body mass increase (Steudel et al., 1994). Scholander et al. (1950) found that the insulation provided by the fur is substantially increased with an increment of the body mass. As a result, an alternative for winter individuals to increase insulation would be to increase body mass, allowing them to have bigger pelts. This strategy has been observed in collared lemmings that are significantly larger, more insulated and have higher absolute basal metabolic rates in winter (Reynolds, 1993). Another alternative to cope with wide seasonal thermal variations is to reduce body size in winter. This is the case for many microtine rodents measured up to present. They reduce its body mass in response to winter photoperiod, presumably as a strategy to minimize total energy expenditure for maintenance (Wunder, 1985). *C. musculus* is the smallest rodent (20 g) inhabiting the Algarrobo forest and winter animals are significantly smaller than summer animals (Brigada and Caviedes-Vidal, 1987; Mills et al., 1992). Given both, the seasonal characteristics of the physical environment and the low winter productivity in the study site, it is not surprising that *C. musculus* includes in its general pattern of adaptation to winter a reduction of body mass (Table 1) with a decrease in its per animal heat loss rate and a consequently decline in the total energy budget for maintenance. Based on the same scenario, we also predicted a decrease in the heat loss rate on a per surface area basis in winter as an avoidance strategy (Wunder, 1984), that would be reflected in the cooling coefficients we measured. Our results supported this prediction, the small winter individuals had the lowest cooling coefficients values. We regressed the cooling coefficients under the naturally laying hair condition, for summer and fall animals on their respective body mass values (cooling coefficient = $0.60196 (\pm 0.00615) Mb^{-0.036 (\pm 0.034)}$, $r^2 = 0.997$, $F_{2,18} = 2922$, $p < 0.01$). Using this equation, we calculated the cooling coefficient for the average winter body mass (9.76 ± 2.19 g). The obtained value was 15% higher than the actual measure. This deviation from the allometric summer estimates constitutes a line of support to hypothesize the presence of a change in some

characteristics of the fur (i.e. density or length of hairs) in winter. Since the aluminum cylinders were all of the same size, we did not estimate the effect of a reduction of surface area on the heat transfer of fur. We could not either estimate with our experiment the effect of thinly insulated, shaded or axillary surfaces of the body (Bakken, 1981) that can have a large effect on the overall thermal conductance. Our results support the idea of a seasonal changes in the quality of the pelt that covers the torso of the body and influences the amount of heat transferred.

4.4. Effect of fluffing

Piloerection significantly reduced cooling coefficients of cylinders covered with skins of all seasons except summer 1989 and fall 1990. Fluffing the fur to its maximum extent would decrease heat transfer to a greater extent in winter and spring animals that may have longer and denser furs (Chappell, 1980). During summer and fall this response to cold may be not as important as in winter. The difference between cooling coefficients of furred and naked skins was significantly higher in winter and spring than in summer, which may suggest seasonal changes in the length or density of hairs. However, our observations showed that the percent reduction in cooling coefficients for raising hairs was not different between seasons and was lower in winter animals (Fig. 2). This finding may suggest that changes in other physical properties besides hair length and density, such as, a decrease in the number of highly conductive hair fibers (Webb et al., 1990) or changes in optical properties of individual hairs (Walsberg and Schmidt, 1989) may be responsible for the observed variation in the heat loss rate. Further seasonal studies of density, length and physical properties of skin hairs are needed.

In conclusion, the improved winter insulation of the pelt that covers the torso of the body, possibly determined by changes in physical characteristics and/or in density and length of hairs, is a physiological mechanism that, together with other mechanisms such as torpor bouts and the winter reduction in surface area and body weight, may contribute to a reduction in the animal energy budget. All these mechanisms may favor the existence of *C. musculus* in semidesertic environments with wide seasonal changes in temperature, water availability and productivity.

5. Summary

We evaluated seasonal changes in cooling coefficients of cylinders wrapped with furs of *Calomys musculus* in three hair conditions. Cooling coefficients of cylinders covered with *C. musculus* skins were significantly

different between seasons and between hair conditions (hair lying naturally, fluffed hair and naked skin). Aluminum cylinders covered with winter and spring skins had significantly lower cooling coefficients. Fluffing hair significantly reduced cooling coefficients but the percent reduction in heat transfer as a result of raising hairs was not different between seasons. The values of heat transfer through naked skins were significantly higher than values in the other two conditions in all seasons (all p 's < 0.001). The percent increase in heat transfer due to the absence of hair was significantly different between seasons. The winter decrease in heat transfer of the fur, is a physiological mechanism that favors the existence of *C. musculus* in semidesertic environments with wide seasonal changes in temperature, water availability and productivity.

Acknowledgements

We thank Antonio Mangione and Hugo Nuñez for field assistance; Nator Lopez for building the aluminum cylinders; Konrad Vispo and Kelly Morris for useful suggestions on the manuscript. We dedicate this paper to the memory of Dr. Enrique Caviedes Codelia whose teachings give us support in doing science and in our everyday life. The work was supported by an UNSL grant to Enrique Caviedes Vidal.

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