

## THE SIGNIFICANCE OF FUR STRUCTURE FOR SOLAR HEAT GAIN IN THE ROCK SQUIRREL, *SPERMOPHILUS VARIEGATUS*

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### Summary

The coats of birds and mammals typically vary through their depth in structure, insulation and optical qualities. Physical models predict that such variation can substantially affect the solar heat load acquired by an animal. This study quantifies the consequences of complex coat structure for solar heat gain in the rock squirrel (*Spermophilus variegatus* (Erxleben, 1777)), a species normally exposed to intense solar radiation.

This species' pelage consists of two well-defined layers: a dense inner coat of fine, dark hairs, and a sparse outer coat of coarse, light hairs. The optics, structure and thermal insulation of the inner and outer coats are quantified and used to predict rates of radiative heat gain using a physical model. The radiative heat load measured at the skin compares well with model predictions. The validated model is then used to explore the consequences for solar heat gain of varying the relative proportions of the inner and outer coat layers. Results demonstrate that the ratio of inner to outer coat depths occurring in rock squirrels is very near that theoretically predicted to minimize solar heat gain. This indicates that optimization of fur structure may represent an effective means of adjusting solar heat gain independent of coat insulation and surface coloration.

### Introduction

In mammals and birds, fur or feather coats form the critically important outermost barrier between animal and environment. The insulating coat affects thermal balance, including passive heat loss and solar heat gain, and visual characteristics, including social signalling and crypsis. Solar heat gain in these taxa is a function of coat properties, including structure, insulation, short-wave reflectivity, hair or feather optics and skin colour (Walsberg *et al.* 1978; Walsberg, 1983, 1988*a*). Previous analyses of these complex determinants of solar heat gain relied on the simplifying assumption that the coat is uniform throughout its depth (Walsberg *et al.* 1978; Walsberg, 1988*a*). However, birds and mammals commonly possess coats that vary through their depth in optics and structure. A typical

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pattern in mammals is for hairs to vary in colour along their length and for the coat to consist of a fine inner layer and a coarse outer layer. Such complexity in coat structure and optics seems likely to affect both effectiveness of coat insulation and the solar heat load transferred to the skin.

The rock squirrel *Spermophilus variegatus* presents an excellent model system for analysing the effects of complex fur structure. The coat is not uniform throughout its depth, but consists of two well-defined layers: a dense inner coat, dominated by fine, dark hairs, and a sparse outer coat, dominated by coarse, lighter hairs. Though each layer consists largely of one hair type and there is a readily distinguishable boundary between outer and inner coats, coarse guard hairs and thinner, dark hairs occur in both layers. The inner coat includes basal portions of the guard hairs and some finer underfur hairs extend into the outer coat layer. The outer coat produces the animal's mottled, greyish-brown appearance which is cryptic in the arid, rocky canyons and slopes that it typically inhabits in Mexico and the western United States (Hall, 1983).

This analysis first quantifies the optics, structure and thermal insulation of the inner and outer coats of *S. variegatus*. Radiative heat load transferred to the skin is quantified and compared with predictions of a physical model derived from that of Walsberg *et al.* (1978) and Walsberg (1983, 1988a). This experimentally validated model is then used to explore the consequences for solar heat gain of varying the depths of the inner and outer coat layers.

### List of symbols

(All radiation relationships refer to total solar radiation)

$\alpha$	absorptivity of individual hairs
$\beta$	backward scattering coefficient ('reflectivity') of individual hairs
$\beta_c$	reflectivity of coat
$\beta_s$	reflectivity of skin
$\Delta T_c$	temperature gradient from outer coat surface to environment (K)
$\Delta T_c$	temperature gradient from skin to outer coat surface (K)
$\Delta T_{ic}$	temperature gradient across inner coat layer (K)
$\Delta T_{oc}$	temperature gradient across outer coat layer (K)
$\tau$	forward scattering coefficient ('transmissivity') of individual hairs
$\tau_c$	transmissivity of the entire coat
$\tau_{ic}$	transmissivity of the inner coat
$\tau_{oc}$	transmissivity of the outer coat
$\tau_s$	transmissivity of the skin
$\tau_{s+c}$	transmissivity of the skin and entire coat
$\tau_{s+ic}$	transmissivity of the skin and inner coat
$\eta$	$[(1 - \tau)^2 - \beta^2]^{\frac{1}{2}}$
$d$	hair diameter (m)
$I$	probability per unit coat depth that a ray will be intercepted by a hair ( $m^{-1}$ )

$k$	volumetric specific heat of air at 20°C ( $1200 \text{ J m}^{-3} \text{ K}^{-1}$ )
$l_c$	coat thickness (m)
$l_h$	hair length (m)
$n$	hair density per unit skin area ( $\text{m}^{-2}$ )
$Q$	net heat flux across skin and fur ( $\text{W m}^{-2}$ )
$Q(z)$	heat generated by radiation absorption at level $z$ ( $\text{W m}^{-2}$ )
$Q_s$	heat load on animal's skin from solar radiation ( $\text{W m}^{-2}$ )
$Q_i$	solar irradiance at coat surface ( $\text{W m}^{-2}$ )
$r_e$	external resistance to convective and radiative heat transfer ( $\text{s m}^{-1}$ )
$r_c$	coat thermal resistance ( $\text{s m}^{-1}$ )
$r_{ic}$	thermal resistance of the inner coat layer ( $\text{s m}^{-1}$ )
$r_{oc}$	thermal resistance of the outer coat layer ( $\text{s m}^{-1}$ )
$r_z$	thermal resistance from skin to level of ray absorption in coat ( $\text{s m}^{-1}$ )
$S_i$	solar irradiance at the coat surface ( $\text{W m}^{-2}$ )
$S^-$	flux of solar radiation going towards the skin ( $\text{W m}^{-2}$ )
$S^+$	flux of solar radiation going away from the skin ( $\text{W m}^{-2}$ )
$z$	depth within coat (m)

### Theory

The fate of solar radiation striking a fur coat and the heat that is consequently generated were analysed using a theoretical framework adapted from Walsberg *et al.* (1978). The fluxes of solar radiation going towards ( $S^-$ ), and away from ( $S^+$ ), the skin at a particular level in an animal's coat are given by the following expressions of Cena & Monteith (1975):

$$S^- = S_i[(1 - \tau - \beta\beta_s)\sinh\eta l_z + \eta\cosh\eta l_z]/X, \quad (1)$$

$$S^+ = S_i[(\beta - \beta_s + \tau\beta_s)\sinh\eta l_z + \eta\beta_s\cosh\eta l_z]/X, \quad (2)$$

where

$$X = (1 - \tau - \beta\beta_s)\sinh\eta l_c + \eta\cosh\eta l_c. \quad (3)$$

The heat generated by radiation absorbed at a particular depth in the coat,  $Q(z)$ , equals the change in the total radiant flux density going from  $z$  to  $z + dz$ . This change in flux density is (Walsberg *et al.* 1978):

$$Q(z) = dS/dz = (dS^-/dz) - (dS^+/dz). \quad (4)$$

Heat generated at a particular level in the coat that flows towards, and acts as a heat load on, the skin is determined by the fraction of the total thermal resistance in the system that opposes its loss to the environment (Walsberg *et al.* 1978). The total thermal resistance is the sum of the coat's insulation and the resistance to heat flow between the outer coat surface and the environment. The fraction of the thermal resistance opposing heat loss from the level of ray absorption to the

environment is  $(r_c - r_z)/(r_c + r_e)$ . Therefore, the heat generated at a level within the coat,  $z$ , that contributes to the heat load on the skin is (Walsberg *et al.* 1978):

$$Q_s(z) = Q(z)(r_c - r_z)/(r_c + r_e) . \quad (5)$$

Added to this heat load generated within the coat is that produced by solar radiation penetrating to the skin. Of this radiant flux, the fraction  $1 - \beta_s$  acts as a heat load on the skin (Walsberg *et al.* 1978).

This model was applied using numerical integration; the coat was mathematically divided into 200 segments and equations 1–5 were used to estimate  $S^-$ ,  $S^+$ ,  $Q(z)$  and mean  $r_z$  in each increment. Values for  $Q_s(z)$  were summed and added to the estimated heat generated at the skin level to obtain the total heat load at the skin produced by solar radiation ( $Q_s$ ). The coat was assumed to consist of two internally uniform compartments representing the inner and outer layers. Each increment within a layer was assumed to contain equal fractions of that layer's total insulation and coat elements determining radiation interception.

## Materials and methods

### *Collection and preparation of samples*

Ten adult rock squirrels were collected between 13 May and 15 June in the Sonoran Desert, approximately 60 km south of Apache Junction, Maricopa Co., Arizona. A 25 cm<sup>2</sup> square section of skin and attached fur was removed from the mid-dorsal region of each animal and dried in a flat position with the coat normally depressed.

### *Measurement of heat flow and thermal resistances*

Pelage preparations were mounted on the upper surface of a heat flux transducer/temperature-controlled plate apparatus (Walsberg, 1988a). The temperature-controlled plate maintained skin temperature at  $40 \pm 0.2^\circ\text{C}$  and a 0.5 cm  $\times$  0.5 cm heat flux transducer (Tanner, 1963) was embedded in its upper surface. Signal output from the transducer was measured with a Fluke 8840a microvoltmeter. The transducer was calibrated by the method of Idso (1971). Temperatures of the skin surface, the upper fur surface and the boundary between the inner and outer coat layers were sensed using 0.05 mm diameter copper–constantan thermocouples. Temperatures of the skin and upper fur surface were measured using sets of three thermocouples distributed over the area and connected in parallel, with connecting wires of equal length. A single thermocouple was placed at the inner coat/outer coat boundary. Thermocouple output was measured with a Fluke 8840a microvoltmeter and referred to a distilled-water ice-bath.

Thermal resistances were measured in the absence of short-wave radiation by quantifying heat flux across the fur sample as a function of the skin-to-environment temperature gradient. Air temperature was held at  $20 \pm 0.5^\circ\text{C}$  and

skin temperature at  $40 \pm 0.2^\circ\text{C}$ . Wall temperature in the room was within  $1^\circ\text{C}$  of air temperature. Total coat resistance was calculated as:

$$r_c = k\Delta T_c / Q, \quad (6)$$

where  $k$  is a constant taken by convention to equal the volumetric specific heat of air at  $20^\circ\text{C}$  (Monteith, 1975),  $Q$  is net heat flow across the sample, and  $\Delta T_c$  is the skin-to-outer fur surface temperature gradient. Thermal resistance of the inner coat was computed as:

$$r_{ic} = k\Delta T_{ic} / Q, \quad (7)$$

where  $\Delta T_{ic}$  is the temperature gradient from the skin to the inner coat/outer coat boundary. Thermal resistance of the outer coat was calculated as:

$$r_{oc} = k\Delta T_{oc} / Q, \quad (8)$$

where  $\Delta T_{oc}$  is the temperature gradient from the inner coat/outer coat boundary to the upper fur surface. Thermal resistance from the coat surface to the environment was calculated as:

$$r_e = k\Delta T_e, \quad (9)$$

where  $\Delta T_e$  is the fur surface-to-air temperature gradient.

Solar heat gain was determined from measurements of heat flow at the skin and calculated as (net heat flux with solar radiation) – (net heat flux without solar radiation). Consistent with the model generated using equations 1–5, this value thus equals the portion of the heat generated by insolation that functions as a heat load on the skin.

#### *Environmental simulation and measurement*

Simulated solar radiation was generated by a Kratos Analytical Corporation SS1000X solar simulator (see Walsberg, 1988a, for description). Irradiance perpendicular to the beam was measured at the level of the coat using an Oriol Corporation model 7080 pyroelectric radiometer and maintained at  $1000 \pm 5 \text{ W m}^{-2}$ .

Air temperature was held at  $20 \pm 0.5^\circ\text{C}$  during all measurements. Laminar wind flow was produced by an open-throat wind tunnel with turbulence intensity less than 0.5% (Walsberg, 1988a). Air flowed parallel to the skin, from the anterior to posterior portions of the sample. This mimics the condition experienced by an animal oriented with its head directed into a wind. Wind speeds were measured with a Thermonetics HWA-101 thermoanemometer mounted 2 cm above the sample surface. The anemometer was calibrated using the method of Walsberg (1988a).

#### *Reflectivity, absorptivity and transmissivity of coat and skin*

Coat and skin reflectivity were measured by mounting the sample behind a 12 mm port facing the interior of a 60 mm diameter integrating sphere coated with

Kodak Total Reflectance Paint™ (primary ingredient barium sulphate). A 10 mm diameter beam of light from the solar simulator was directed through a port onto the sample, with the beam held perpendicular to the sample. The sensor was an Oriel model 7080 pyroelectric radiometer mounted on a port set at 90° to either the sample port or the light-entry port. A plate coated with 2 mm of Kodak Total Reflectance Paint™, which has a reflectance ranging from 0.96 to 0.99 over the waveband of 300–1300 nm (average reflectance = 0.98), was used as a standard. Initially, reflectivity of the outer coat surface was measured, then the outer coat was trimmed off and the reflectivity of the inner coat layer measured. Skin reflectivity was similarly measured after all hair had been trimmed from samples.

Transmissivity to solar radiation was measured using an apparatus similar to that used for reflectivity measurements except for modification of sample placement and form of the integrating sphere. This integrating sphere had only two ports, one for transmission of light to the sensor and one for entry of light. The sample was mounted over the latter port and simulated solar radiation perpendicular to the plane of the sample was directed onto it. Transmissivity was measured separately for the intact skin/fur preparation, the skin/inner coat preparation with the outer coat removed, and for the skin with all hair removed. Transmissivity of the fur layers was calculated by recognizing that transmission of the intact skin/fur preparation is the product of the separate transmission values of the skin, the inner coat and the outer coat, and that the transmission of the skin/inner coat preparation is the product of the separate values for the skin and inner coat. Thus:

$$\tau_{ic} = \tau_{s+ic} / \tau_s \quad (10)$$

and

$$\tau_{oc} = \tau_{s+c} / \tau_{s+ic} \quad (11)$$

Transmission of light as a function of coat depth was measured using a 0.2 mm diameter, 4 cm long quartz fibre to receive and transmit radiation to a pyroelectric radiometer. The entire apparatus was mounted on a precision vertical translator that allowed placement of the probe's tip to within 1 μm. The tip of the quartz fibre was moved vertically through the coat by passing it through a 0.5 mm diameter hole in the skin and upwards to the outer coat surface. Measurements were made at 21 equally spaced intervals from the outer coat surface to the skin.

#### *Coat structural characteristics*

The coat interception function (I) was calculated using equation 15 of Cena & Monteith (1975):

$$I = n \tan[\cos^{-1}(l_c/l_h)] \quad (12)$$

Required data were collected using a 1 cm<sup>2</sup> section of skin and fur that had been removed from the centre of each sample. The depths of the entire coat and the component inner and outer coat layers were measured using a microscope with an ocular micrometer. Hair density (n) was determined by trimming the hair to within

0.2 mm of the skin and counting the remaining stumps using a microscope with an ocular grid micrometer. Coats consisted of guard hairs and the much narrower hairs dominant in the inner coat. These hair types could be readily distinguished by their five-fold difference in diameter, and were quantified separately. Hair length ( $l_h$ ) and diameter ( $d$ ) were also measured using a microscope with an ocular micrometer. Hair diameter was taken as the average of 10 measurements made at equally spaced intervals along the length of each hair. Data were collected in each sample for 40 of each hair type. The interception function was calculated separately for the fine and coarse hairs and summed to yield the value for the entire coat, the inner coat and the outer coat. Hair angle to the skin was computed from the ratio of total coat depth to guard hair length. These longest hairs form the outer coat surface. Hair angle to the skin and measured length of inner coat-type hairs were used to compute the degree to which these hairs penetrated into the outer fur layer.

#### *Hair optical properties*

Cena & Monteith (1975) described the relationship between optical properties of individual hairs and readily measured coat properties (reflectivity, transmissivity, depth and interception function). Using Walsberg's (1988a) method, these relationships were used to compute the unique set of hair optical properties necessary to produce the measured reflectivity and transmissivity of coats with the depth and interception function characteristic of individual samples. This was done separately for the inner and outer coats.

### **Results and discussion**

#### *Coat structure, optics and insulation*

The inner coat of rock squirrels typically comprises 63 % of total coat depth and 76 % of total coat insulation (Table 1). Thermal resistance of the inner layer is 80 % greater per unit depth than that of the outer layer (calculated from mean data in Table 1). Increased effectiveness of insulation in the inner coat is associated with a higher value for the radiation interception function ( $I$ ), which is on average 35 % greater in the inner coat than in the coarse and more sparse outer coat. Such increased interception of long-wave radiation tends to retard heat flow through the coat (Cena & Monteith, 1975; Walsberg, 1988b).

Outer coat reflectivity is significantly greater than inner coat reflectivity (Table 1). This is associated with lower absorptivity and higher fractional forward scattering by individual hairs in the outer coat compared with the inner coat (Table 1). These optical properties of individual hairs combined with the inner coat's higher interception function markedly decrease transmission of light through the inner coat compared with the outer coat. This is manifested by an abrupt decline in downward radiation in the region near the boundary between the outer and inner coats, suggesting that this boundary is a major site of radiation absorption and heat generation (Fig. 1).

Table 1. *Coat and hair properties of rock squirrels*

	Inner coat	Outer coat
$\beta_c$	0.18 (0.010)	0.25 (0.015)
$\tau_c$	0.05 (0.0084)	0.62 (0.053)
$\beta_s$	0.18 (0.016)	0.18 (0.016)
$\alpha$	0.15 (0.0088)	0.09 (0.0047)
$\beta$	0.08 (0.0047)	0.07 (0.0036)
$\tau$	0.77 (0.045)	0.85 (0.044)
$I$ ( $\text{cm}^{-1}$ )	42.5 (1.16)	31.4 (1.51)
$l_c$ (cm)	0.24 (0.024)	0.14 (0.027)
$r_c$ ( $\text{s m}^{-1}$ )*	48.1 (5.29)	15.6 (1.87)

\* Measured at a wind velocity of  $1 \text{ ms}^{-1}$ .

Values are means (s.d.), with  $N = 10$  in all cases.

All values differ significantly between the outer and inner coats (ANOVA;  $P < 0.05$ ), except those for  $\beta_s$  and  $\beta$ .

See text for explanation of symbols.

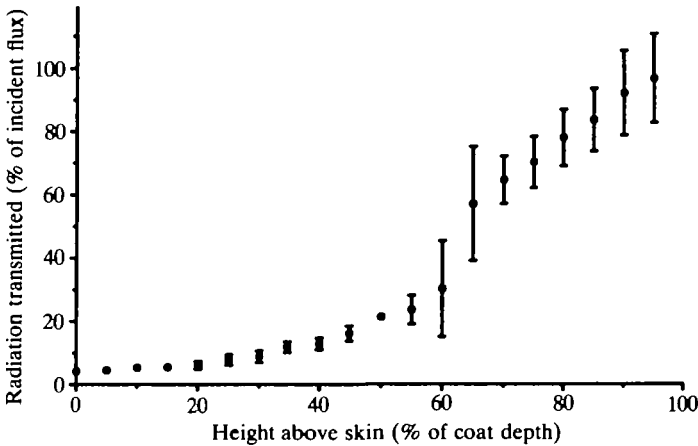


Fig. 1. Percentage transmission of simulated solar radiation as a function of depth within fur. Values are mean  $\pm$  2 s.d.,  $N = 10$ . Standard errors for data collected in the lower 20% of coat depth are too small to plot separately from mean values (i.e.  $2 \times \text{s.e.} = 0.9\text{--}1.2\%$ ).

#### *Thermal resistances and radiative heat gain*

The relationship between wind speed and the thermal resistance from the coat surface to the external environment ( $r_c$ ) is presented in Fig. 2. Note that this relationship is specific for conditions of measurement (e.g. turbulence intensity) and cannot be transferred uncritically to other situations.

Over the range of wind speeds used, coat thermal resistance ( $r_c$ ) averaged  $63.7 \text{ s m}^{-1}$  (Fig. 2). Least-squares regression reveals no significant relationship



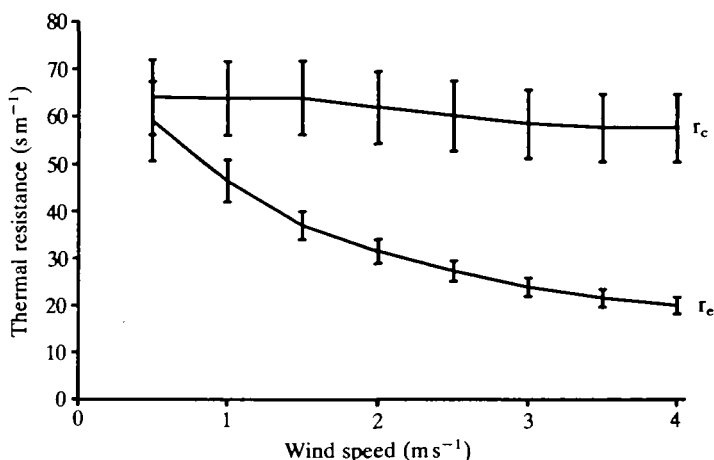


Fig. 2. Total coat thermal resistance ( $r_c$ ) and thermal resistance between outer coat surface and environment ( $r_e$ ) as a function of wind speed. Values are mean  $\pm$  2 s.d.,  $N = 10$ .

between  $r_c$  and wind speed (analysis of variance, ANOVA,  $P > 0.05$ ) and mean values decline only 10% as wind speed is increased from 0.5 to 4.0 m s<sup>-1</sup>.

Average radiative heat gain at the level of the skin ranged from 38.4 to 44.1% of short-wave irradiance at the outer coat surface (Fig. 3). Though average heat gain declined as wind speed was increased from 0.5 to 4.0 m s<sup>-1</sup>, no significant regression exists between wind speed and radiative heat gain (ANOVA;  $P > 0.05$ ).

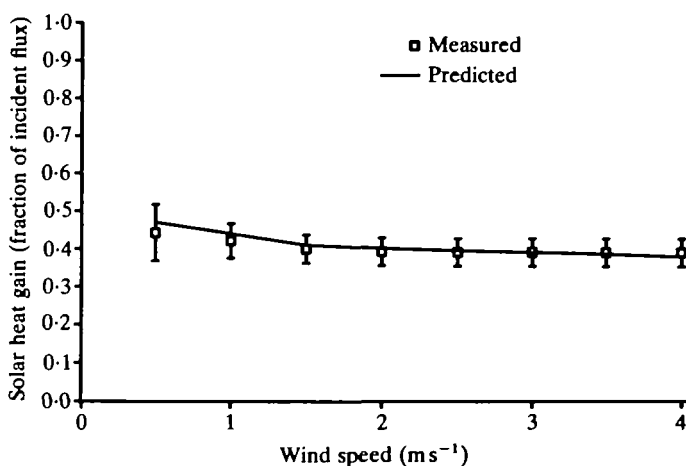


Fig. 3. Measured and theoretically predicted rates of heat gain from simulated solar radiation as a function of wind speed. Solar heat gain to the skin is expressed as a fraction of solar energy incident on the outer coat surface. Measured values are mean  $\pm$  2 s.d.,  $N = 10$ . The line connects theoretically predicted values.

*Comparison with model predictions of radiative heat gain*

Closely conforming to measured values for radiative heat gain are values predicted using mean data presented in Table 1 and the two-compartment model based on equations 1–5 (Fig. 3). Mean errors range from 0 to 6.3% over wind speeds of 0.5 to 4.0  $\text{m s}^{-1}$ . Mean absolute error over all wind speeds equals 2.6%. These results confirm the adequacy of this model, versions of which have previously been validated (Walsberg *et al.* 1978; Walsberg, 1988a).

*Consequences for radiative heat gain of coat structure*

Validation of the theoretical model provides confidence in simulations of this fur system to explore the consequences of varying coat structure. Simulations consisted of using mean measured values for coat properties (Table 1) and equations 1–5 to estimate coat reflectivity and solar heat gain under conditions in which the insulation characteristic of rock squirrels is produced by various combinations of inner and outer coat depths. For the sake of brevity, only simulations computed using mean values for  $r_c$  ( $63.7 \text{ s m}^{-1}$ ) and  $r_e$  ( $46.4 \text{ s m}^{-1}$ ) characteristic of  $1 \text{ m s}^{-1}$  wind speed are presented. These values were chosen because relatively low wind speeds are typical of this species' habitat in Arizona and because variance in data collected at this wind speed is substantially lower than that for a wind speed of  $0.5 \text{ m s}^{-1}$  (Figs 3, 4). Thus, inner and outer coat depths were computed as ranging in complementary fashions from 0 to 100% of total coat depths required to produce  $r_c = 63.7 \text{ s m}^{-1}$ .

Such simulations indicate that coat reflectivity, an index of coat colour, is nearly constant over the range in which inner fur comprises 0–95% of total coat depth (Fig. 4). Only when outer fur constitutes less than about 5% of total coat depth does coat reflectivity substantially decline towards the value of the darker inner coat. Thus, effects upon radiative heat gain in coats whose total depth consists of between 0 and 95% inner fur will be essentially independent of surface coloration.

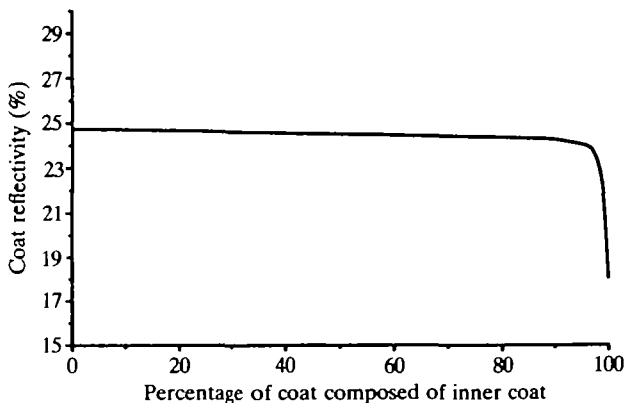


Fig. 4. Theoretically predicted relationship for *Spermophilus variegatus* between bulk coat reflectivity ( $\beta_c$ ) and fraction of coat depth composed of inner fur. Calculated assuming that total coat depth is that required to produce  $r_c = 63.7 \text{ s m}^{-1}$ .

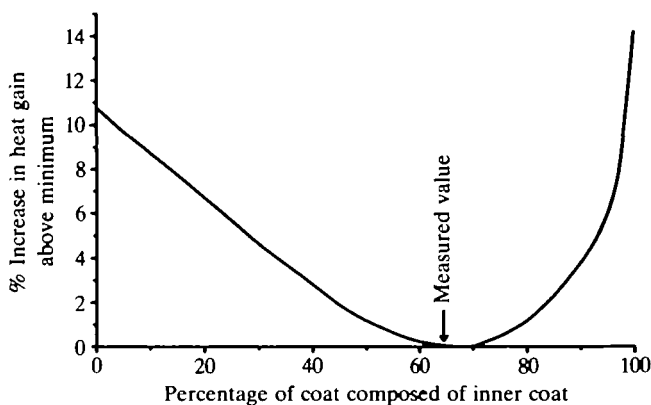


Fig. 5. Theoretically predicted relationship for *Spermophilus variegatus* between solar heat gain and fraction of coat depth composed of the inner fur. Values are percentage increase in heat gain above the minimum possible, calculated assuming that total coat depth is that required to produce  $r_c = 63.7 \text{ sm}^{-1}$ . Also shown is value for inner fur depth actually occurring in *Spermophilus variegatus*.

In contrast, model simulations indicate that solar heat gain varies markedly with changes in the fractional contributions of the inner and outer coats (Fig. 5). Minimum solar heat gain to the skin occurs when the coat is composed of 67% inner coat and 33% outer coat by depth. Other combinations of inner and outer fur depths yielding equal insulation increase solar heat gain, with maximum elevations of 11% (100% outer coat) or 14% (100% inner coat). This optimal ratio of inner to outer coat depths is remarkably similar to that actually occurring in rock squirrels (63% inner coat, 37% outer coat; Table 1). Thus, the relative fur depths characteristic of this species limit solar heat gain to only 0.2% greater than the theoretical minimum for a coat of equal insulation (Fig. 5). This remarkable similarity of the naturally occurring ratio of fur depths to that theoretically predicted to minimize heat gain is not the result of circularity in simulations; empirically observed values for inner and outer fur depths were not used in simulations. Such data were used only in conjunction with measurements of temperature gradients and total coat resistance to calculate thermal resistance per unit depth for each coat layer.

Minimum solar heating at 67% of inner coat depth results from changing contributions of heat generated in the outer coat, inner coat and skin (Fig. 6). As the fractional contribution to total coat depth of the inner coat is increased, solar heat gain originating in this layer increases and that originating in the outer coat decreases. These changes do not occur at equal rates, however, and the resulting sum varies to yield the pattern observed in Fig. 5. Two factors produce this effect.

First, the outer coat's high transmissivity combined with the inner coat's lower transmissivity produces a peak of radiation absorption near the boundary of the two layers (Figs 1, 7). If the inner layer is very thin, peak absorption occurs deep in

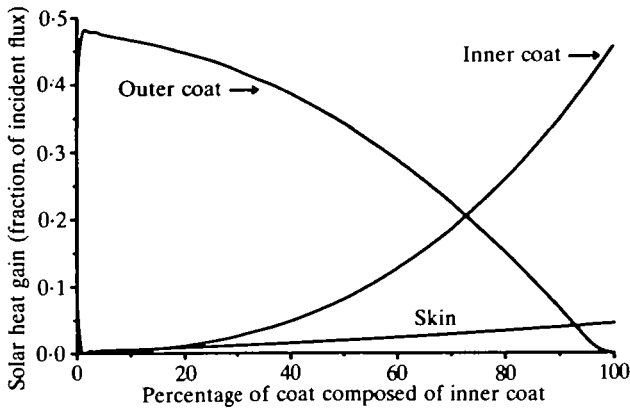


Fig. 6. Contributions of solar heat gain generated in the outer coat, inner coat and skin as functions of the fraction of coat depth composed of inner fur. Values are heat gain at the skin as a fraction of solar irradiance on the outer coat surface, calculated assuming that total coat depth is that required to produce  $r_c = 63.7 \text{ s m}^{-1}$ .

the coat and therefore contributes substantially to the heat load on the skin (Fig. 7A).

Second, the inner coat exhibits both greater insulation per unit depth and a higher radiation interception function than the outer coat (Table 1). Pelages composed largely of inner coat type require a shallower total depth to obtain a given insulation. For example, a coat composed totally of inner fur would be 44 % shallower than one composed entirely of outer fur. The difference between inner and outer coat layers in insulation per unit depth, however, is greater than that in the radiation interception function. Thermal resistance per unit coat depth is 80 % greater in the inner layer than in the outer layer, although the interception function is only 25 % greater in the inner coat (Table 1). Therefore, pelages with higher fractions of inner coat are shallower for a given insulation and exhibit lower values for the interception function summed over coat depth ( $I_c$ ). When the coat is composed largely of inner fur, the decrease in  $I_c$  tends to increase the average depth of radiation penetration into the coat and thus elevate heat gain. Heat generation still peaks near the boundary of the inner and outer layers, but is less confined to this boundary and tends to be distributed more deeply into the coat (Fig. 7C).

When a very large fraction of the coat consists of inner fur, this latter effect is dominant. When a large fraction of the coat consists of outer fur, the effect of moving peak heat generation nearer the skin dominates (Fig. 7A). For inner and outer coat layers characteristic of rock squirrels, the ratio of 67 % inner coat and 33 % outer coat produces the minimum sum of these two effects.

The conclusion that the observed ratio of inner to outer coat depths in *Spermophilus* is very near that theoretically predicted to minimize radiative heat gain is not dependent upon the use of data collected at  $1 \text{ ms}^{-1}$  wind speed.

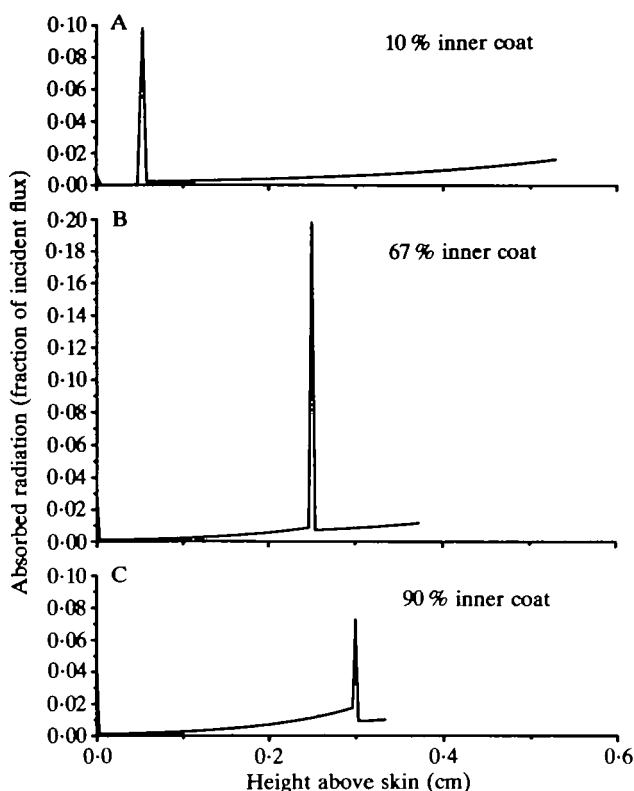


Fig. 7. Theoretically predicted distribution through coat depth of absorption of solar radiation. Values are for three coats with total depth composed of different ratios of inner to outer fur layers: (A) 10 % inner fur, 90 % outer fur; (B) 67 % inner fur, 33 % outer fur; (C) 90 % inner fur, 10 % outer fur. B illustrates the case that minimizes heat gain to the skin. Total coat depth is that required to produce  $r_c = 63.7 \text{ s m}^{-1}$ . Radiation absorption is expressed as a fraction of solar irradiance at the outer coat surface.

Identical simulations, not presented in the interest of succinctness, confirm that the pattern observed in Fig. 5 also occurs at other wind speeds studied.

At a wind speed of  $1 \text{ m s}^{-1}$ , minimum predicted solar heat gain to the skin in *Spermophilus* equals 44 % of energy incident on the outer coat surface. Thus, the total range of variation represented in Fig. 5 equals about 6 % of the energy incident on the coat surface ( $= 0.14 \times 44 \%$ ). Adjustment of coat structure even within this narrow range to minimize the thermal load suggests that natural selection may be very sensitive to variation in solar heat gain in this population. In this species' habitat in Arizona, it is possible that even small fractional changes in radiative heat gain greatly affect the animal's total heat budget. Solar radiation in this region is commonly intense and frequently exceeds  $1000 \text{ W m}^{-2}$  on a plane perpendicular to the solar beam. The basal metabolic heat production (BM) of a mammal with a body mass typical of *Spermophilus variegatus* (0.8 kg) is estimated to equal  $36 \text{ W m}^{-2}$  of skin surface [calculated using the allometric equation of

Kleiber (1961) to estimate basal metabolism and the equation of Morhardt & Gates (1974) to estimate skin surface area]. Thus, a decrease in heat gain equal to 6% of insolation under common conditions ( $60 \text{ W m}^{-2}$ ) may represent heat approximately equal to 1.7BM.

For coats with the structure and optics observed in this species, further reduction of solar heat gain would require increased coat insulation. Such increased insulation would also decrease the rate at which the animal could passively dissipate metabolically generated heat, which is likely to increase thermal stress for a species occupying hot environments. Thus, evolution of maximally beneficial amounts of coat insulation may reflect a coupling of opposing effects on the animal's heat budget of changes in solar heat gain and the ability to dissipate internal heat loads.

This study has demonstrated that optimization of fur structure may represent an effective means of adjusting solar heat gain in a fashion independent of coat insulation and surface coloration, and that coat structure in the species studied is very near that which minimizes radiative heat gain. These conclusions, however, are based only on the consequences of altering the relative proportions of the inner and outer fur layers characteristic of one population. Clearly, these fur layers represent only two out of an unknown set of possible combinations of hair optical properties, coat structures and coat insulations. This suggests that the range through which solar heat gain can be adjusted independent of surface coloration and coat insulation could be substantially larger than that documented.

Finally, it is notable that birds and mammals typically exhibit annual moult cycles that present an opportunity for individuals to adjust insulation and radiative heat gain to seasonal changes in the thermal environment. Specimens for this study were collected during summer months in the Sonoran Desert when reduction of heat gain is likely to benefit diurnal rodents. In contrast, increased solar heat gain may be advantageous in other seasons or other portions of this species' range. This could be achieved, for example, by either increasing or decreasing the fraction of the coat composed of the inner fur layer (Fig. 5). The degree to which natural selection has exploited such opportunities remains to be explored.

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