

SEASONAL ADJUSTMENT OF SOLAR HEAT GAIN IN A DESERT MAMMAL BY ALTERING COAT PROPERTIES INDEPENDENTLY OF SURFACE COLORATION

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Summary

Physical theory predicts that animals with fur or feather coats can adjust solar heat gain independently of surface coloration or environmental factors by altering coat structure or hair optical properties. This hypothesis is tested by examining seasonal changes in the solar heat load transferred to the skin by the pelage of a desert-dwelling mammal, the rock squirrel (*Spermophilus variegatus*). Although coat colour remains constant, solar heat gain at low wind speeds is about 20% greater in winter coats than in summer coats. This change is in an apparently adaptive direction and is predicted to have a major effect on the animal's heat balance in nature. The determinants of these alterations in solar heat gain are explored using an empirically validated biophysical model and are found to result from changes in hair optics and coat structure. These results suggest the existence of a previously unknown mode of long-term thermoregulation that allows adjustment of solar heat gain without affecting the animal's external appearance.

Introduction

The evolution of animal coloration is presumably coerced by sets of selective pressures relating either to visual signalling or to radiative heat gain. A common view is that coat colour, as manifested by surface reflectivity to short-wave radiation, is a prime determinant of solar heat gain (e.g. darker surfaces increase solar heat gain) and that there is a consistent linkage between radiative heat gain and animal coloration (Hamilton, 1973). The degree to which solar heat gain and animal coloration may be independently modified therefore has substantial importance for understanding the costs, benefits and evolutionary limits upon patterns of animal coloration. In the following analysis, we describe a mechanism by which a diurnal desert mammal, the rock squirrel (*Spermophilus variegatus* Erxleben), substantially modifies solar heat gain independently of environmental factors and surface coloration.

Solar heat gain in animals with fur or feather coats is a complex function of environmental properties such as wind speed and intensity of solar radiation, as

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well as a suite of animal properties that are often subtle. The latter include hair optical properties and coat structure (Kovarik, 1964; Hutchinson & Brown, 1969; Øritsland, 1970, 1971; Øritsland & Ronald, 1978; Cena & Monteith, 1975a; Walsberg *et al.* 1978; Walsberg, 1983, 1988a,b). An example of the possible importance of such complex effects is the reduction of solar heat gain by optimization of coat structure in rock squirrels, diurnal rodents inhabiting rocky canyons and slopes in Mexico and the western United States, including the Sonoran Desert (Hall, 1983). The pelage of *S. variegatus* consists of two well-defined layers that contrast in their structure and optics: a dense inner coat dominated by fine, dark hairs, and a sparse outer coat dominated by coarse, light hairs that produces the animal's cryptic appearance (greyish-brown in this population). During the summer months, the ratio of inner to outer coat depths characteristic of rock squirrels in the Sonoran Desert is very near that theoretically predicted to minimize radiative heat gain (Walsberg, 1988b). This population therefore illustrates a mechanism by which solar heat gain may be adjusted without affecting coat insulation and surface coloration.

Selection may favour adaptive adjustments of solar heat gain independently of surface coloration, either between populations occupying contrasting environments or within populations exposed to seasonal changes in the thermal environment. There is marked seasonality in the Sonoran Desert. During the midday period, in which these diurnal ground-dwelling squirrels are most active, air temperatures near (5 cm above) the soil surface are typically 20–30°C in the winter and 40–55°C in the summer (G. E. Walsberg, unpublished data), with clear skies and intense radiation in both summer and winter.

We tested for the existence of adaptive adjustment of solar heat gain by comparing the radiative heat loading characteristics of winter and summer rock squirrel coats. We quantified the radiative heat load transferred to the skin, as well as the optics, structure and thermal insulation of the inner and outer coats. Walsberg's model (1988b) was then used to explore the role of coat properties in determining observed changes in solar heat gain. Finally, we estimated the consequences of observed adjustments in coat structure upon net heat flow between the animal and the environment.

List of symbols

(All radiation relationships refer to total solar radiation)

α	absorptivity of individual hairs.
α_c	absorptivity of coat.
β	backward scattering coefficient ('reflectivity') of individual hairs.
β_c	reflectivity of coat.
β_s	reflectivity of skin.
ΔT_e	temperature gradient from outer coat surface to environment (K).
ΔT_c	temperature gradient from skin to outer coat surface (K).
ΔT_{ic}	temperature gradient across inner coat layer (K).
ΔT_{oc}	temperature gradient across outer coat layer (K).

τ	forward scattering coefficient ('transmissivity') of individual hairs.
τ_c	transmissivity of entire coat.
τ_{ic}	transmissivity of inner coat.
τ_{oc}	transmissivity of outer coat.
τ_s	transmissivity of skin.
τ_{s+c}	transmissivity of skin and entire coat.
τ_{s+ic}	transmissivity of skin and inner coat.
η	$[(1-\tau)^2 - \beta^2]^{1/2}$.
d	hair diameter (m).
I	radiation interception function, 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 ($1200 J m^{-3} K^{-1}$).
l_c	coat thickness (m).
l_h	hair length (m).
n	hair density per unit skin area (m^{-2}).
Q	net heat flux across skin and fur ($W m^{-2}$).
$Q(z)$	heat generated by radiation absorption at level z ($W m^{-2}$).
Q_s	heat load on animal's skin from solar radiation ($W m^{-2}$).
r_e	external resistance to convective and radiative heat transfer ($s m^{-1}$).
r_c	coat thermal resistance ($s m^{-1}$).
r_{ic}	thermal resistance of the inner coat layer ($s m^{-1}$).
r_{oc}	thermal resistance of the outer coat layer ($s m^{-1}$).
r_z	thermal resistance from skin to level of ray absorption in coat ($s m^{-1}$).
S_i	solar irradiance at the coat surface ($W m^{-2}$).
S^-	flux of solar radiation going towards the skin ($W m^{-2}$).
S^+	flux of solar radiation going away from the skin ($W m^{-2}$).
T_a	air temperature (K).
T_s	skin temperature (K).
u	wind speed ($m s^{-1}$).
z	depth within coat (m).

Materials and methods

Collection and preparation of samples

Nine adult rock squirrels were collected during December and January in the Sonoran Desert, in Maricopa Co., Arizona. An approximately 20 cm² 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 temperature-controlled plate with a 0.25 cm² heat flux transducer embedded in its upper surface. Construction, calibration and method of signal measurement for this

device were previously described by Walsberg (1988a,b). Skin temperature was maintained near 40°C. Temperature of the skin surface and the upper fur surface was sensed using two sets of three thermocouples (0.05 mm diameter, copper/constantan) connected in parallel, with connecting wires of equal length. A single 0.01 mm diameter thermocouple was placed at the inner coat/outer coat boundary with the aid of a precision vertical translator. 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 near 20°C and skin temperature near 40°C. Wall temperature in the room was within 1°C of air temperature. Thermal resistances were calculated as:

$$r = k\Delta T/Q, \quad (1)$$

where r is either r_c , r_{ic} , r_{oc} or r_e and ΔT is, as appropriate, either ΔT_c , ΔT_{ic} , ΔT_{oc} or ΔT_e .

Solar heat gain was determined from measurements of heat flow at the skin and calculated as (net heat flux with solar radiation) minus (net heat flux without solar radiation). Consistent with the theoretical model described below, this value 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). Irradiance perpendicular to the beam was measured at the level of the coat using an Oriel Corporation model 7080 pyroelectric radiometer and maintained at $1000 \pm 5 \text{ W m}^{-2}$.

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 anterior to posterior portions of the sample. This mimics the condition experienced by an animal oriented with its head directed into the 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

Total reflectivity of the coat and skin to simulated solar radiation were measured using the techniques of Walsberg (1988a,b). 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 simulated solar radiation was measured using the method of Walsberg (1988a,b) and was determined 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. The transmissivity of the fur layers was calculated by recognizing that the 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:

$$\tau_{ic} = \tau_{s+ic} / \tau_s \quad (2)$$

and

$$\tau_{oc} = \tau_{s+c} / \tau_{s+ic} \quad (3)$$

In addition to total solar reflectivity (β_c), coat colour was quantified by measuring spectral reflectivity in the wavelength range typically visible to vertebrates (400–700 nm). For such measurements, samples were mounted behind a 12 mm port facing the interior of a 60 mm diameter integrating sphere coated with Kodak total reflectance paint^M (primary ingredient = barium sulphate). A 10 mm diameter beam of light from a tungsten/halogen lamp was directed through a port onto the sample, with the beam held perpendicular to the sample. Reflected light left the integrating sphere through a port set at 90° from either the sample port or the light entry port. Reflected light was then passed into an Oriel model 77250 grating monochromator, through which selected wavelengths were transmitted to an Oriel model 7070 photomultiplier detection system. A plate coated with 2 mm of Kodak total reflectance paint^M, which has a reflectance ranging from 0.98 to 0.99 over the waveband of 400–700 nm, was used as a standard. Reflectivity was measured at 20 nm intervals.

Coat structural characteristics

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

$$I = n \tan(\cos^{-1} [l_c/l_h]) \quad (4)$$

The depth of the entire coat, as well as the component inner and outer coat layers, was measured using Vernier calipers. Hair density (n) was determined by trimming the fur 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 narrower hairs dominant in the inner coat. These hair types could be readily distinguished by their sixfold difference in diameter, and were quantified separately. Hair length (l_h) and diameter (d) were measured using a microscope with an ocular micrometer. Hair diameter was taken as the average of 11 measurements made at equally spaced intervals along the length of each hair. Data were collected in each sample for 10 hairs of each 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, as these longest hairs form the outer coat surface. Hair angle to the skin and measured

length of inner coat-type hairs was used to compute the degree to which these hairs penetrated into the outer fur layer.

Hair optical properties

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

Theoretical analyses

Determinants of solar heat gain in a fur coat were analysed using a theoretical framework adapted from Walsberg *et al.* (1978) and previously used by Walsberg (1988b). Fluxes of solar radiation going towards (S^-), and away from (S^+), the skin at a particular level in an animal's coat were given by the following expressions of Cena & Monteith (1975a):

$$S^- = S_i [(1 - \tau - \beta\beta_s)\sinh\eta I_z + \eta\cosh\eta I_z]/X, \quad (5)$$

$$S^+ = S_i [(\beta - \beta_s + \tau\beta_s)\sinh\eta I_z + \eta\beta_s\cosh\eta I_z]/X, \quad (6)$$

where

$$X = (1 - \tau - \beta\beta_s)\sinh\eta I_c + \eta\cosh\eta I_c. \quad (7)$$

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 given by (Walsberg *et al.* 1978):

$$Q(z) = dS/dz = dS^-/dz - dS^+/dz. \quad (8)$$

Heat generated at a particular level in the coat that flows towards the skin is determined by the fraction of the total thermal resistance in the system opposing its loss to the environment (Walsberg *et al.* 1978). 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 z within the coat contributing to the heat load on the skin is (Walsberg *et al.* 1978):

$$Q_s(z) = Q(z)(r_c - r_z)/(r_c + r_e). \quad (9)$$

In addition, heat was generated 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 divided mathematically into 200 segments and equations 5–9 were used to estimate S^- , S^+ ,

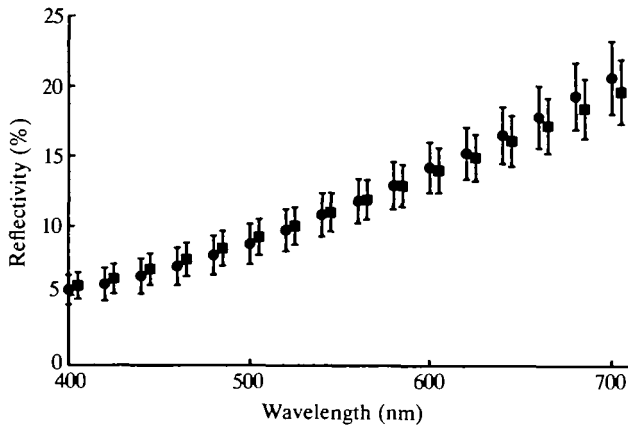


Fig. 1. Spectral reflectivity of rock squirrel coats. Values are means ($\pm 95\%$ confidence limits). $N = 9$ for winter coats (\bullet) and $N = 10$ for summer coats (\blacksquare). Data for summer coats are from samples described in Walsberg (1988b).

$Q(z)$ 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.

Results

Radiative heat gain

It is remarkable that although rock squirrels did not differ seasonally in their appearance, visible coloration (Fig. 1), or total solar reflectivity (Table 1), solar heat load transferred to the skin was substantially greater in winter coats than previously reported for summer coats (Fig. 2). At wind speeds below 2.0 m s^{-1} , heat gain was increased about 20% in winter compared to summer. As in summer coats (Walsberg, 1988b), mean radiative heat gain at the skin beneath winter coats declined from 52 to 38% of short-wave irradiance at the outer coat surface as wind speed increased from 0.5 to 4.0 m s^{-1} and external resistance declined from 54 to 14 s m^{-1} (Figs 2, 3).

Closely conforming to measured values for radiative heat gain in winter coats were those predicted using mean data presented in Tables 1 and 2, and the two-compartment model based on equations 5–9 (Fig. 2). Mean errors ranged from 0 to 5.4% over the range of wind speeds used. Similarly small errors have been found in previous tests of this model and data for summer coats (Walsberg, 1988b).

Thermal resistances, coat structure and optics

Unexpectedly, thermal resistance of winter coats was 42–50% lower than the

Table 1. *Coat properties of rock squirrels*

	Outer coat		Inner coat	
	Winter	Summer	Winter	Summer
β_c	0.26 (0.023)	0.25 (0.010)	0.19 (0.009)	0.18 (0.006)
τ	0.53 (0.038)	< 0.85 (0.027)	0.85 (0.038)	> 0.77 (0.028)
α	0.31 (0.022)	> 0.09 (0.003)	0.12 (0.005)	< 0.15 (0.005)
β	0.16 (0.011)	> 0.07 (0.002)	0.03 (0.001)	< 0.08 (0.003)
l_c (cm)	0.06 (0.029)	< 0.14 (0.017)	0.234 (0.033)	0.240 (0.015)
I (cm^{-1})	38.0 (1.92)	> 31.4 (0.97)	54.2 (2.46)	> 42.5 (0.73)
r_c (s m^{-1})*	5.0 (1.3)	< 15.6 (1.16)	30.5 (3.8)	< 48.1 (3.3)

Values are means (95 % confidence limit), with $N = 9$ for winter coats and $N = 10$ for summer coats.

Data for summer coats are from Walsberg (1988b).

Statistically significant differences between winter and summer coats are indicated by < or > (ANOVA, $P < 0.05$).

See text for an explanation of symbols.

* Measured at $u = 1.0 \text{ m s}^{-1}$.

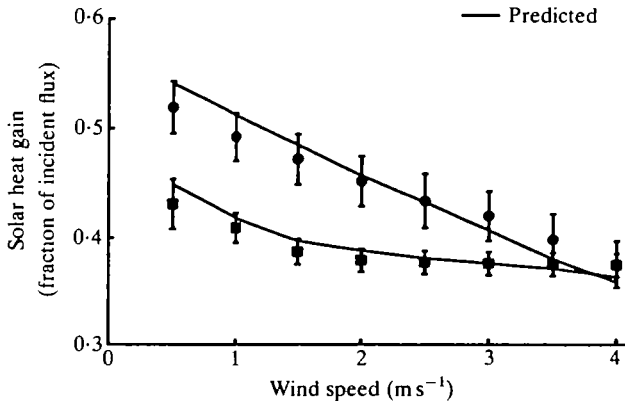


Fig. 2. Measured and theoretically predicted rates of radiative heat gain in winter (●) and summer (■) coats as a function of wind speed. Heat gain from simulated solar radiation to the skin is expressed as a fraction of radiant energy incident on the outer coat surface. Measured values are mean (± 95 % confidence limits), $N = 10$ for summer coats and $N = 9$ for winter coats. Lines connect theoretically predicted values. Data for summer coats are from Walsberg (1988b). Measured values for summer and winter coats differ significantly at all wind speeds $\leq 3 \text{ m s}^{-1}$ (ANOVA, $P < 0.05$). Measured values at 4 m s^{-1} were too similar to plot separately.

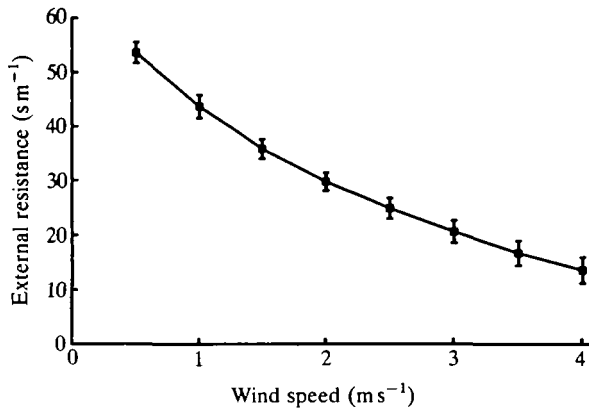


Fig. 3. Thermal resistance between outer coat surface and environment (r_e) as a function of wind speed. Values are means ($\pm 95\%$ confidence limits), $N = 9$.

Table 2. *Hair properties of rock squirrels*

	Guard hairs		Fine hairs	
	Winter	Summer	Winter	Summer
n (cm^{-2})	856 (94.0)	> 640 (82.1)	3240 (296)	3450 (332)
d (cm)	0.0086 (0.0015)	0.0089 (0.0022)	0.0015 (0.00012)	0.0013 (0.0011)
l_h (cm)	1.35 (0.0188)	< 1.62 (0.0265)	0.80 (0.063)	< 1.26 (0.085)

Values are means (95% confidence limit), with $N = 9$ for winter coats and $N = 10$ for summer coats.

Data for summer coats are from Walsberg (1988b).

Statistically significant differences between winter and summer coats are indicated by < or > (ANOVA, $P < 0.05$).

See text for an explanation of symbols.

values previously reported for summer coats (Fig. 4). Over the range of wind speeds used, coat thermal resistance (r_c) averaged 33.0 s m^{-1} and declined 23% as wind speed was increased from 0.5 ($r_c = 37.1 \text{ s m}^{-1}$) to 4.0 m s^{-1} ($r_c = 28.7 \text{ s m}^{-1}$) (Fig. 4). The lower thermal resistance of winter coats reflects both a 23% decline in the total depth of winter coats compared with summer coats, and a decreased thermal resistance per unit depth in winter coats (calculated from data in Table 1). The decrease in coat depth was not an artefact of increased fur compression during sample preparation as the ratio of total coat depth to the average length of the guard hairs forming the outer fur boundary was similar in winter (0.22) and summer (0.23).

Outer coat reflectivity was significantly greater than inner coat reflectivity

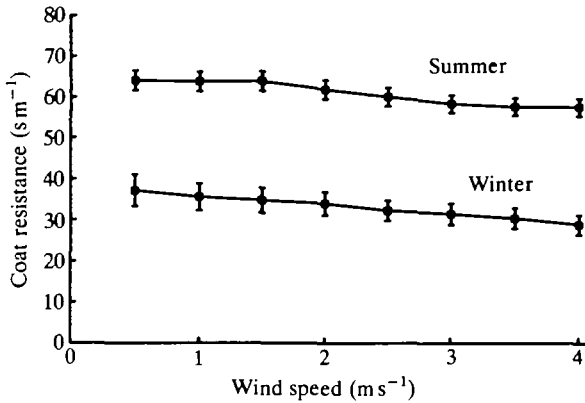


Fig. 4. Coat thermal resistance during winter and summer as a function of wind speed. Data for summer coats are from Walsberg (1988b). Values are mean \pm 95 % confidence limits, $N = 9$ (winter) or $N = 10$ (summer). At each wind speed, values for winter and summer coats are significantly different (ANOVA, $P < 0.05$).

(ANOVA, $P < 0.05$, $N = 9$; Table 1). Hair optical properties differed significantly between inner and outer coats (ANOVA, $P < 0.05$), and between the same coat layer in winter and summer pelages (Table 2). Particularly notable were differences in the inner coat, which forms most of the fur depth. Here, forward scattering (τ) by individual hairs was increased by 10% in winter months compared to summer months, absorptivity (α) was decreased by 20%, and backwards scattering (β) was decreased by 63% (Table 1). These changes occurred without seasonal modification of coat reflectivity (Table 1).

Significant seasonal differences were apparent in coat structure. Due mainly to a 34% increase in density of guard hairs during winter months, the radiation interception function was increased by 21% (outer coat) or 28% (inner coat) in winter compared with summer (Table 1).

Discussion

Significance of seasonal changes in solar heat gain

The increase in radiative heat gain observed in winter coats compared with summer coats is equivalent to that which would be produced by a 20% elevation in the fraction of sunlight absorbed by the animal's coat ($\alpha_c + \tau_c = 1 - \beta_c$), if all other fur properties could be held constant. The quantity $1 - \beta_c$ is about 0.75 in rock squirrels (Table 1). A 20% increase ($1 - \beta_c = 0.90$) would produce a black coat ($\beta_c = 0.10$). Thus, the seasonal difference in solar heat gain is equivalent to that which might be produced by a major change in the animal's appearance, if surface coloration could be changed without affecting other coat properties.

A first approximation of the net effect of the observed changes in solar heat gain and coat insulation upon an animal's total heat balance can be derived by

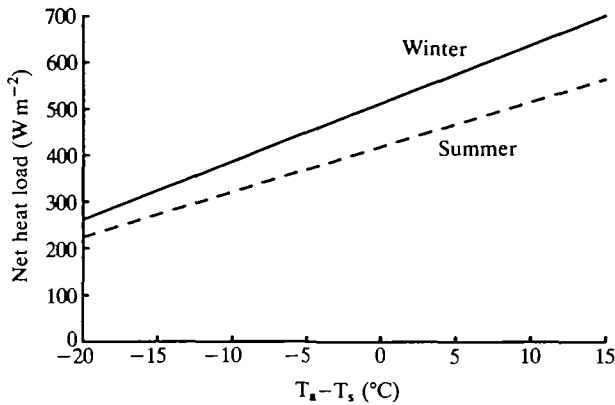


Fig. 5. Estimated thermal behaviour of summer and winter coats of rock squirrel. Values represent the net heat load on the skin, combining the effects of changes in coat resistance and solar heat gain when solar irradiance = $1000 W m^{-2}$. T_a , air temperature; T_s , skin temperature.

calculating the net heat load on the animal's skin as a function of air temperature and solar irradiance:

$$Q = Q_s + k(T_a - T_s)/(r_c + r_e). \quad (12)$$

Note that this equation predicts changes only for those portions of the animal directly facing the sun; the total effect on the animal will be less than these estimates, and will depend upon factors such as animal orientation. Thermal behaviour of rock squirrel coats was estimated using measured data collected at a wind speed of $0.5 m s^{-1}$. Values were calculated over a probable annual range of air-to-skin temperature gradients likely to be experienced during the midday activity period (i.e. $T_a - T_s = -20^\circ C$ to $+15^\circ C$) and assuming that solar irradiance is $1000 W m^{-2}$, an intensity typically observed in the Sonoran Desert.

Under these conditions, winter coats are predicted to transmit net heat loads averaging $38-126 W m^{-2}$ greater than summer coats. This 16-22% increase in heat load is 1.0-3.4 times the estimated area-specific basal metabolic heat production of *S. variegatus* (Walsberg, 1988b), equating to the change in heat load across those portions of the skin directed towards the sun that would be produced by a change in air temperature of 4-14°C (Fig. 5). Such substantial declines in the heat load clearly are advantageous for mammals inhabiting a subtropical desert.

Determinants of seasonal changes in solar heat gain

The increased solar heat gain observed in winter coats compared with summer coats results from alterations in a suite of coat and hair properties (Tables 1 & 2). The relative importance of these various seasonal changes can be estimated using simulations incorporating the validated model subsumed in equations 5-9, data presented in Tables 1 and 2, and assuming that wind speed is $1.0 m s^{-1}$. Radiative heat gain was estimated for a coat resembling the summer pelage except

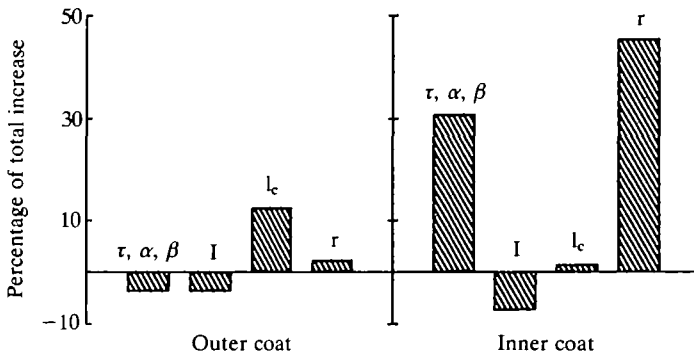


Fig. 6. Predicted sensitivity of solar heat gain to seasonal changes in individual coat variables. Data reflect the increase in solar heat gain predicted for a summer coat if the mean value characteristic of winter fur is substituted for the identified variable. Substituted variables are the radiation interception function (I), coat depth (l_c), coat thermal resistance per unit depth (r), and the set of hair optical properties (τ, α, β). Results are expressed as a percentage of the total predicted change between winter and summer coats when all variables act in concert.

characterized for one variable by the mean value typical of winter fur. Substituted variables were coat depth, the interception function (I), coat thermal resistance per unit depth, and hair optical properties. Factors characteristic of inner and outer coats were used separately. An associated set of hair optical properties (α, β, τ) was treated as a single variable. Simulation results suggest that the two most important factors producing increased heat gain during winter months are changes in the inner coat in thermal resistance per unit fur depth, and in the optical properties of individual hairs (Fig. 6). The net effect of alterations in hair optical properties in the inner coat during the winter (i.e. increased forward scattering, decreased backward scattering and absorptivity) is to enhance penetration of radiation and consequently elevate solar heat gain. Decreased thermal resistance in the inner coat tends to increase radiative heat gain by reducing the fraction of the total thermal resistance ($r_c + r_e$) between a point of ray absorption and the skin.

Though illustrative, these simulations provide only a crude approximation of the relative importance of various factors, because interaction effects among the variables were ignored. This lack of interaction effects is reflected by the failure of the sum of the changes predicted to result from altering individual variables to equal the net effect predicted when all factors act in concert. A more sophisticated analysis would require knowledge of the functional relationships between all variables subsumed in the model. Unfortunately, the relationship between hair density and coat thermal resistance is inadequately understood. The complexity of this relationship is illustrated by the association in winter pelages of decreased fur insulation with increased hair density. Although it may initially appear improbable, a negative effect of hair density on coat insulation is explicable in the context of likely effects of fur structure on major avenues of nonevaporative heat flow (radiation, convection, conduction through the air contained in the coat, and

conduction along hairs). The relative importance of these transport modes undoubtedly varies with coat structure (see, for example, Davis & Birkebak, 1974; Cena & Monteith, 1975*a,b*; Gebremedhin *et al.* 1983). In general, radiation and convection are most likely to be important in sparse coats. Because the thermal conductivity of hair is much greater than that of air (Davis & Birkebak, 1974), conduction should be maximized in dense coats. If thermal conduction along hairs is sufficiently important, increases in hair density will decrease coat insulation. Unfortunately, estimating the net effect of changes in hair density requires unavailable data describing the thermal conductivity of individual hairs. It is clearly possible, however, that the increased hair density observed in winter coats of rock squirrels may be a mechanism for reducing coat insulation and consequently increasing solar heat gain.

In conclusion, the seasonal alteration in solar heat gain acquired by the pelage of rock squirrels is in a direction expected to be adaptive and is substantial, being equivalent to the change in heat load that would be produced by major changes in air temperature or the animal's surface coloration. Such results suggest the existence of a previously unknown mode of long-term thermoregulation by varying coat optics and structure to alter solar heat gain independently of the animal's coloration. Use of such mechanisms may therefore uncouple the selective pressures related to thermal and social signalling effects of animal coloration.

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