Biophysical properties of the pelt of a diurnal marsupial, the numbat (*Myrmecobius fasciatus*), and its role in thermoregulation

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Summary

Numbats are unusual marsupials in being exclusively diurnal and termitivorous. They have a sparse (1921 hairs cm^{-2}) and shallow (1.19 mm) pelt compared with other marsupials. Coat reflectivity is low (19%) for numbats compared with nocturnal marsupials, but absorptivity is similar to that of diurnal North American ground squirrels (72%), indicating that the coat of the numbat may be adapted for acquisition of solar heat. Numbat coat thermal resistance decreases significantly with wind speed from 45.9 s m^{-1} (at 0.5 m s^{-1}) to 29.8 s m^{-1} (at 3 m s^{-1}). Erecting the fur significantly increases pelt depth (6.5 mm) and coat resistance (79.2–64.2 s m^{-1}) at wind speeds between 0.5 m s^{-1} and 3 m s^{-1}. Numbat coat resistance is much lower than that of other marsupials, and wind speed has a greater influence on coat resistance for numbats than for other mammals, reflecting the low pelt density and thickness.

Solar heat gain by numbats through the pelt to the level of the skin (60–63%) is similar to the highest value measured for any mammal. However the numbat's high solar heat gain is not associated with the same degree of reduction in coat resistance as seen for other mammals, suggesting that its pelt has structural and spectral characteristics that enhance both solar heat acquisition and endogenous heat conservation. Maximum solar heat gain is estimated to be 0.5–3.6 times resting metabolic heat production for the numbat at ambient temperatures of 15–32.5°C, so radiative heat gain is probably an important aspect of thermoregulation for wild numbats.

Key words: pelt, thermoregulation, numbat, *Myrmecobius fasciatus*, thermal resistance, solar heat gain, marsupial.

Introduction

The numbat *Myrmecobius fasciatus* is a medium-sized (550 g) marsupial found only in areas of open woodland in the south-west of Western Australia, although prior to European settlement it inhabited open woodland, grassland and desert across much of southern Australia (Friend, 1993). Unlike other marsupials, numbats are exclusively diurnal and they feed only on termites collected from shallow sub-surface soil galleries. Their daily activity pattern has been related to the mainly diurnal activity of termites in these subsurface galleries (Friend, 1982).

Solar heat gain (SHG) is a potentially important factor in the energy budget of a diurnal animal (Walsberg, 1988a). If numbats can exploit solar heat to aid in thermoregulation, then they can reduce their metabolism at ambient temperatures (T_a) below the thermoneutral zone. This may be particularly significant for a mammal feeding exclusively on poor quality food, such as termites, which have a low energy density and variable availability (McNab, 1984, 2000; Redford and Dorea, 1984; Anderson et al., 1997). There are anecdotal reports of numbats sun basking, especially on cold winter mornings (Calaby, 1960; Friend, 1993), suggesting that SHG may indeed

have an important thermoregulatory role for the numbat. SHG by mammals is determined by a complex array of factors, including selection of microhabitat and orientation to incident radiation (Walsberg, 1988a). For mammals that have an insulating covering of fur, the pelt plays an important role in thermoregulation, influencing both passive heat loss and radiative heat gain (Walsberg, 1988b). Consequently, the biophysical characteristics of the pelt, including insulation, structure, colour, hair spectral properties and skin colour, are all important determinates of heat balance for a mammal (Walsberg, 1988b).

This study investigates the biophysical properties of the numbat's pelt in relation to insulation and SHG and assesses the thermoregulatory importance and potential for energy conservation of exploiting solar heat for this unusual, diurnal, termitivorous marsupial.

Materials and methods

Bodies of three numbats (*Myrmecobius fasciatus* Waterhouse 1836; two females and one male; all in good

physical condition) were obtained from Perth Zoo during summer and early autumn. Only this limited number of individuals was available for this study due to the endangered status of the numbat. The pelts were removed, rinsed with water and pinned out to dry, with the fur in a normally depressed state. When dry, two 6 cm^2 sections were removed from the mid-dorsal section of each pelt, one from the mid-scapular region (reddish-brown fur) and the other from the lumbar region (black-and-white striped; Fig. 1). Measurements of the depressed pelts were carried out first, then the skin sections were moistened and the fur brushed into a maximally erect state and dried before the measurements were repeated.

Structural characteristics

Hair density was determined by shaving a 1 cm^2 section of pelt with an electric shaver and counting the numbers of guard and underfur hair stumps in 10×1 mm^2 areas using a compound microscope with an ocular grid micrometer. The mean hair

1 cm

Fig. 1. (A) Anterior reddish-brown and (B) posterior black-and-white-striped sections of a numbat pelt.

density (cm^{-2}) was calculated. Pelt depth was measured with a vernier caliper from the skin surface to the surface of the hairs for depressed pelts and from the skin surface to the tips of the guard hairs for erect pelts. Hair length and diameter were measured using a compound microscope with an ocular micrometer for the longest and widest point of 10 hairs of each type for each sample.

Spectral characteristics

Pelt samples were placed flat under a solar simulator (SS1000X; Kratos Analytical, Ramsey, NJ, USA) that generated simulated solar radiation at 900 W m^{-2}. Coat reflectivity (ρ_c) was measured using a pyroelectric radiometer (model 7080; Oriel, Stratford, CO, USA) held at 45° to the pelt (after Walsberg, 1988b). A single optical quartz fiber, connected to the radiometer and an Oriel model 17070 photomultiplier system, was threaded through a tiny hole in the skin to measure coat transmissivity (τ_c). The pelt was mounted on an Oriel precision vertical translator, and τ_c was measured at intervals of 5% of the pelt depth from skin surface to fur surface. Unless otherwise stated, τ_c refers to transmissivity through the coat at the level of the skin. Values for reflectivity and transmissivity are closely repeatable, within 0.5–1%. Coat absorptivity (α_c) was calculated as $1-\rho_c-\tau_c$. The coat interception function (I) was calculated using equation 15 of Cena and Monteith (1975), after Walsberg (1988a).

Thermal resistance and solar heat gain

The 6 cm^2 sections of pelt were mounted on the upper surface of a temperature-controlled stage with a 1 cm^2 heat-flux transducer embedded on its upper surface (after Walsberg, 1988a,b). Laminar wind flow was produced using a wind tunnel with an 18 cm^2 cross section (after Walsberg, 1988b; Walsberg and Schmidt, 1989), and wind speed was measured with a thermoanemometer (HHF 52; Omega, Stamford, CO, USA) held 2 cm above the pelt surface. Air flowed in an anterior-to-posterior direction across the pelt sample, at velocities of 0.25, 0.5, 1, 2 and 3 m s^{-1}. Room temperature was 23 ± 0.5°C for the duration of the experiments. Signal output from the heat flux transducer was measured with a datalogger (CR21x; Campbell Scientific, Loughborough, UK).

Conductance (W m^{-2} °C^{-1}) was determined from heat flux across the pelt, as a function of skin to environment temperature gradient (Walsberg, 1988b), and was then converted to total thermal resistance (s m^{-1}) as a function of the volumetric specific heat of air at 20°C (1200 J m^{-3} K^{-1}): total thermal resistance (r_t) = 1200/(heat flux/temperature gradient). Coat resistance (r_c) was calculated from r_t by subtracting environmental resistance (r_e), calculated as $1/r_e=1/r_r+1/r_a$, where r_r (radiative heat transfer resistance) was calculated after Campbell (1977) and the aerodynamic (boundary layer) resistance (r_a) was approximated after Webster and Weathers (1988).

Solar heat gain (SHG) was determined as for thermal resistance, but measurements were carried out under the Kratos SS1000X solar simulator at 900 W m^{-2}. SHG was calculated

Table 1. *Structural characteristics of numbat fur*

	Anterior pelt		Posterior pelt	
	Guard hair	Underfur	Guard hair	Underfur
Coat depth depressed (mm)	1.2±0.26	0.6±0.12	1.1±0.11	0.54±0.07
Coat depth erect (mm)	7.3±0.65	3.5±0.41	5.8±0.66	2.4±0.38
Hair length (mm)	12.7±0.29	6.0±0.21	14.1±1.4	5.7±0.17
Hair diameter (mm)	0.11±0.01	0.03±0.00	0.13±0.02	0.02±0.02
Hair density (cm^{-2})	112±6	1863±168	74±7	1794±136

Values are means ± S.E.M. (*N*=3).

as the net heat flux with radiation minus the net heat flux without solar radiation (Walsberg, 1990).

The proportion of metabolic heat production met by SHG for numbats was predicted by (SHG × PSA)/MR, where MR is metabolic rate (W; Cooper and Withers, 2002) and PSA is projected surface area (m^2). PSA for numbats was calculated as $1.69M^{0.667}$ after Walsberg and Wolf (1995), where mass (*M*) was 550 g (Cooper and Withers, 2002). This equation was validated for numbats by tracing the shadow area of a deceased numbat (frozen into a natural position with a depressed pelt and illuminated from directly overhead), held normal to a horizontal surface, onto paper of known mass per unit area and then weighing the paper. The measured PSA was 96% of that predicted using Walsberg and Wolf's equation (Walsberg and Wolf, 1995).

Statistics

Repeated-measure analysis of variance (ANOVA) with the Greenhouse–Geisser test for sphericity was used to determine any effect of fur section (anterior or posterior), state (erect or depressed) or wind speed on the structural, spectral and thermal properties of the numbat pelts using SPSS version 10. Values are presented as means ± 1 S.E.M.

Results
Structural characteristics

There were no significant differences between anterior and posterior sections of numbat pelts with regard to structural characteristics such as pelt depth, fur length, hair diameter or hair density (Table 1). Erect coats were significantly deeper than depressed coats with regard to both the total pelt depth ($F_{1,2}$=361, *P*=0.003) and the depth of the underfur ($F_{1,2}$=77, *P*=0.013). The larger guard hairs were always much more sparse (97±11 cm^{-2}; *N*=6) than the finer underfur hairs (1828±98 cm^{-2}; *N*=6). White stripes comprised 35±2.5% of the posterior sections of the pelts (*N*=3), with the remainder being black.

Thermal resistance

Mean r_t across all wind speeds and sections of pelt

was 90.3 s m^{-1} for depressed pelts and 124.9 s m^{-1} for erect pelts (Fig. 2). Erecting the fur significantly increased r_t ($F_{1,2}$=187, *P*=0.005) to 138% of the r_t for depressed pelts. The r_t decreased significantly ($F_{1.2,2.3}$=1042, *P*<0.001) as wind speed increased from 0.25 m s^{-1} to 3 m s^{-1}. There was no difference in r_t between the anterior and posterior sections of pelt.

Calculated r_e decreased with increasing wind speed; r_e=48.1 × wind speed$^{-0.44}$ (r^2=0.997). Mean r_c across all wind speeds and sections of pelt was significantly higher for erect pelts (71 s m^{-1}) than for depressed pelts (37 s m^{-1}; $F_{1,2}$=187, *P*=0.005). There was no difference in r_c between anterior and posterior sections of the pelt. r_c decreased significantly ($F_{1.2,2.3}$=50, *P*=0.011) as wind speed increased above 0.5 m s^{-1}.
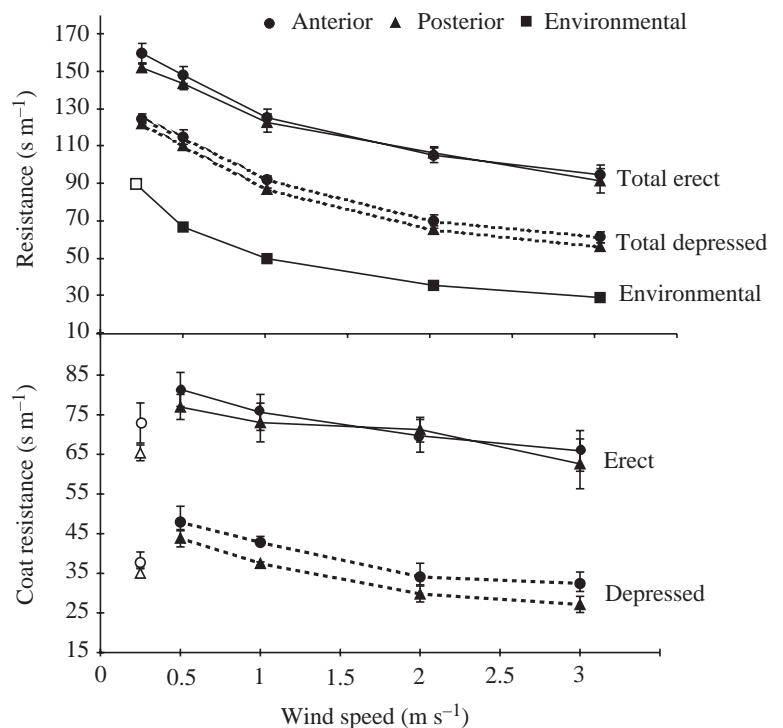

Fig. 2. Mean (± S.E.M.) total thermal resistance (r_t), environmental resistance (r_e) and coat thermal resistance (r_c) of three numbat pelts at wind speeds of 0.25, 0.5, 1, 2 and 3 m s^{-1}. Open symbols are used for calculated r_c and r_e at wind speeds of 0.25 m s^{-1}, where r_e has probably been overestimated.

Table 2. *Spectral characteristics of numbat pelts; where values are proportions of incident solar radiation*

	Depressed			Erect			
	Anterior	Posterior black	Posterior white	Anterior	Posterior black	Posterior white	Significance
Coat absorptivity (α_c)	0.724±0.049	0.842±0.039	0.584±0.034	0.839±0.062	0.902±0.028	0.755±0.0760	
Coat reflectivity (ρ_c)	0.180±0.022	0.070±0.006	0.320±0.023	0.051±0.009	0.023±0.003	0.123±0.023	*,†
Coat transmissivity (τ_c)	0.096±0.028	0.088±0.037	0.096±0.031	0.109±0.053	0.074±0.030	0.122±0.097	
Interception function (I)	80±33.7	52±7.4	52±7.4	9±1.27	12±3.3	12±3.3	†
Skin reflectivity	0.158±0.060	0.144±0.067	0.144±0.067	0.158±0.060	0.144±0.067	0.144±0.067	

Values are means ± S.E.M. (N=3). * indicates a significant ($P<0.05$) difference between sections (anterior, posterior black and posterior white) of the pelt; † indicates a significant difference ($P<0.05$) between depressed and erect pelts.

Spectral characteristics

Depressed coats had a higher ρ_c ($F_{1,2}=49$, $P=0.02$) than erect coats, while there was no significant difference in α_c or τ_c between erect and depressed coats (Table 2). Anterior and posterior pelt sections differed significantly in ρ_c ($F_{2,4}=97$, $P=0.003$) but not in α_c or τ_c. For erect coats, τ_c increased gradually from the skin surface to approximately 40–50% of the coat depth, before increasing sharply to approach 100% at depths of >50% from the skin. I was significantly greater for depressed pelts (mean for all animals and all sections=66±17; N=6, $P<0.05$) than for erect pelts (10±2).

Solar heat gain

Mean SHG at the level of the skin, across all pelts, anterior and posterior sections and wind speeds was 60% of total irradiance for depressed pelts and 63% for erect pelts. Neither the state of the fur (erect or depressed) nor the section of the pelt (anterior or posterior) had a statistically significant effect on SHG (Fig. 3). SHG significantly decreased ($F_{1,2.1}=71$,

$P=0.012$) as wind speed increased from 0.25 m s⁻¹ to 3 m s⁻¹. Solar absorption efficiency (SAE), calculated as SHG (% irradiation)/(1 – reflectivity/100), was very high, ranging from 85% at a wind speed of 0.25 m s⁻¹ to 55% at 3 m s⁻¹, with a highly significant reduction with increasing wind speed ($F_{1,2.1}=71$, $P=0.012$).

Discussion

Structural characteristics

The summer pelt of the numbat is sparse and shallow compared with that of most other mammals (Scholander et al., 1950; Dawson and Brown, 1970; Dawson and Degabriele, 1973; Hulbert and Dawson, 1974; Degabriele and Dawson, 1979; Hofmeyr and Louw, 1987; Walsberg, 1988a; Walsberg and Schmidt, 1989), with exceptions being the eland (*Taurotragus oryx*; 1.05 mm; Hofmeyr and Louw, 1987) and the round-tailed ground squirrel (*Spermophilus tereticaudus*; 0.85 mm; Walsberg, 1988a). Both these species inhabit regions characterised by high environmental temperatures and extreme solar radiation, where a shallow, sparse pelt may facilitate heat loss. However, such an advantage of heat loss must outweigh potentially increased evaporative water loss and SHG (Schmidt-Nielsen, 1983).

Resistance

Numbats have poor coat insulation compared with other marsupials. Their r_c of 40 s m⁻¹ at a wind speed of 1 m s⁻¹ is much lower than that of the euro (*Macropus robustus*; 145 s m⁻¹; Dawson and Brown, 1970), red kangaroo (*Macropus rufus*; 161 s m⁻¹; Dawson and Brown, 1970) and koala (*Phascolarctos cinereus*; 605 s m⁻¹; Degabriele and Dawson, 1979), as expected for a thin pelt (Hofmeyr and Louw, 1987). This low r_c is consistent with the high thermal conductance (C) of the numbat (131% of that predicted for a marsupial of equivalent mass; Cooper and Withers, 2002). Pelt depths, densities and resistances appear to be correlated with the general habits of marsupials and their degree of exposure to the elements. The koala, which does not shelter from inclement weather conditions, living in the exposed treetops, has a deep, dense pelt, high r_c and low C (Degabriele and Dawson, 1979). At the other extreme, the numbat, with a
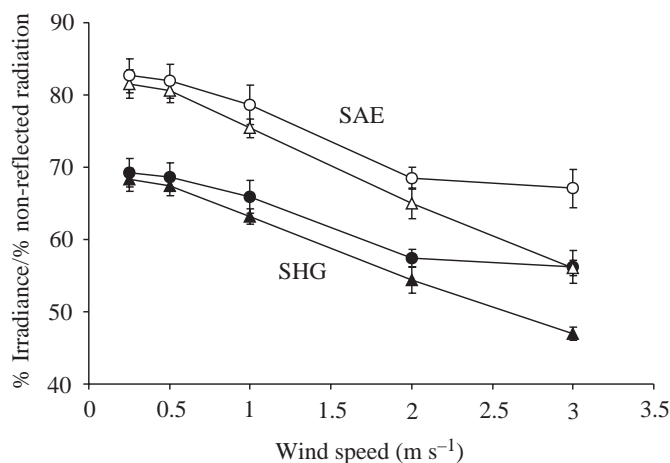

Fig. 3. Solar heat gain (SHG) at the level of the skin (% irradiance; solid symbols) and solar absorption efficiency (SAE; % of non-reflected radiation that acts as SHG at the level of the skin; open symbols) for numbats (N=3; means ± S.E.M. of anterior and posterior sections of pelt) for both erect (circles) and depressed (triangles) pelts at varying wind speeds. There was a significant effect of wind speed ($P<0.05$) on both SHG and SAE.

sparse, thin pelt, low r_c and high C, avoids undesirable weather by sheltering in hollow logs or burrows during cold, wet and windy conditions (Friend, 1982, 1993).

Numbats are similar, with respect to pelt structure and r_c values, to a number of diurnal North American ground squirrels, which have thin, sparse fur and r_c values of between 13 s m^{-1} (Walsberg, 1988a) and 63 s m^{-1} (Walsberg, 1988b). These ground squirrels, which inhabit extremely hot environments with high incident solar radiation, have thin coats and low r values to avoid overheating. Like the numbat, they are active during the day and are also semi-fossorial, avoiding inclement weather by sheltering below ground (Walker, 1975).

Both r_t and r_c decreased for the numbat as wind speed increased from 0.5 m s^{-1} to 3 m s^{-1} (Fig. 2), presumably due to forced convection disrupting insulation within the pelt (Walsberg, 1988a) and, in the case of r_t, the additional effect of a reduction in the still air boundary layer above the pelt. The unexpectedly low r_c for both erect and depressed pelts measured at 0.25 m s^{-1} (Fig. 2) may be due to overestimation of r_e and difficulty in controlling the airflow velocity at very low wind speeds. A similar reduction in r_c was reported by Dawson and Brown (1970) for red kangaroo and euro pelts at wind speeds of <1 m s^{-1}.

Wind speed had a much greater effect on r_c for numbats than has been measured for other marsupials (koala, red kangaroo and euro; Dawson and Brown, 1970; Degabriele and Dawson, 1979) and for ground squirrels (Walsberg, 1988a, 1990; Walsberg and Schmidt, 1989). Erecting the pelt increased the numbat's r_c by an average of 92% across all wind speeds (Fig. 2). The reduction in r_c with wind speed (between 0.5 m s^{-1} and 3 m s^{-1}) was greater for depressed pelts (34%) than for erect pelts (19%). By erecting their fur when exposed to low T_as (Cooper and Withers, 2002), numbats are potentially able to double the thermal resistance of their pelts and also reduce the effect of wind, therefore reducing the loss of metabolic heat.

Spectral properties

Coat reflectivity of the numbat, measured for the mid dorsal region (19%, on average, for red and black-and-white sections of depressed pelts), was less than that measured for other marsupials (20.1–57%; Dawson and Brown, 1970; Dawson and Degabriele, 1973). Coat absorptivity (71.7% on average) is within the wide range of 18–85% measured for placental mammals (Walsberg, 1988a,b, 1990, 1991; Hofmeyr and Louw, 1987; Walsberg and Schmidt; 1989) and is consistent with that of several ground squirrel species (67–81%; Walsberg 1988a,b, 1990; Walsberg and Schmidt, 1989). Like the structural and thermal characteristics, the low ρ_c and high α_c of numbat pelts are more similar to those of diurnal ground squirrels than to nocturnal marsupials, suggesting that the numbat's pelt may be adapted to the acquisition of solar heat, which is not available to nocturnal marsupials.

Numbat ρ_c was significantly reduced by erecting the pelt, probably as a result of a decrease in I, resulting in an overall increase of penetration of radiation through the pelt. This must be accompanied by an increase in τ_c and/or α_c, so the lack of a statistically significant change in either of these factors with pelt erection is likely to be an artefact of the small (N=3) sample size.

White stripes reflect more solar radiation (32%) than do black (7%) stripes, but the overall reflectance, weighted for the relative proportions of white and black (16%), is very similar to that of anterior, reddish fur (18%; Table 2). So, the fraction of sunlight reflected by the striped portion of the pelt is similar to that of non-striped regions, and the striking banded pattern of the numbat might not have any role in thermal radiative relations. Rather, it may have evolved for crypsis, breaking up the outline of the numbat when it is foraging in dappled light. The low reflectivity of the numbat's pelt may also enhance crypsis, as the albedo for woodlands of about 16–18% (Campbell, 1977) is the same as the reflectivity of numbat pelts, thereby minimising the contrast between the numbat and its background.

Solar heat gain

The SHG of numbats is potentially remarkably high. Indeed, SHG for erect coats (62%) is the highest value measured for mammals, equivalent to the very high values measured for the round-tailed ground squirrel of 59% for erect and 61% for depressed pelts (Walsberg, 1988a). However, despite differences in ρ_c and r_c, erection of the pelt did not significantly increase SHG for numbat pelts (Fig. 3), in contrast to the increased SHG by fur erection in some ground squirrels (Walsberg, 1988a). This may be due to the lower ρ_c (and increased penetration of radiation into the pelt) of an erect coat being opposed by increased free convection with coat erection, resulting in a reduced heat load at the skin surface, with the end result being no net change in SHG. Increasing wind speed significantly reduces SHG, as forced convection increases (Fig. 3).

The significant negative relationship between r_c and SHG for the depressed pelts of ground squirrels at a wind speed of 1 m s^{-1} (SHG=$-0.36r_c$+64.3; r^2=0.97, P=0.0028) indicates a trade off between the conservation of metabolic heat (by high r_c) and the acquisition of solar heat (by low r_c) for these mammals. Surprisingly, the numbat falls well outside the predicted relationship, with a much higher SHG than ground squirrels based on r_c (Fig. 4). Therefore, the numbat's pelt is remarkably effective in trapping heat from insolation, without as much of a decrease in r_c. How this is achieved is unclear, but it does suggest that the numbat's pelt has some special combination of structural and spectral properties not measured here. Further investigation would require analysis of changes in the biophysical properties of the pelt with depth, but this is challenging for such a shallow (1.2 mm) pelt.

For a numbat, SHG to the skin surface is high compared with metabolic heat production. SHG at the skin surface is predicted to range from 135% to 580% of the resting energetic requirements (RMR; Cooper and Withers, 2002) of a numbat, at T_as between 15°C and 32.5°C, with incident radiation of
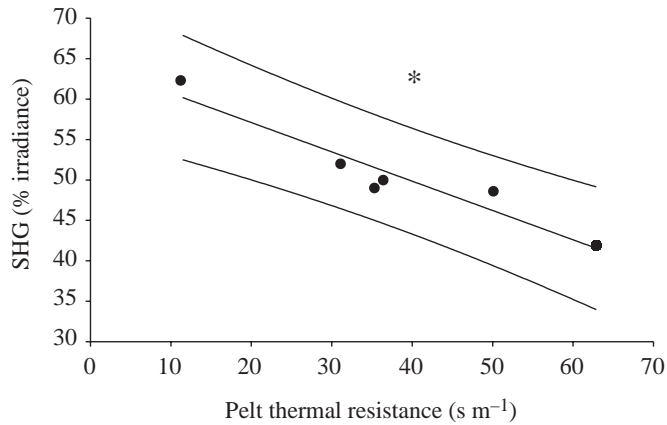
2776 C. E. Cooper, G. E. Walsberg and P. C. Withers

Fig. 4. The relationship between solar heat gain (SHG) and coat thermal resistance (r_c, of depressed fur; measured at a wind speed of 1 m s^{-1}) of six ground squirrel species (circles; round-tailed, rock, two antelope and two golden-mantled ground squirrels; data from Walsberg, 1988a,b, 1990; Walsberg and Schmidt, 1989) and for the numbat (asterisk; N=3). The regression line for ground squirrels is y=$-0.36x$+64.3 (r^2=0.97), with 95% confidence limits for predicting a further point.

900 W m^{-2} and at wind speeds between 0.25 m s^{-1} and 3 m s^{-1}. However, predictions of whole animal SHG made from isolated coat samples may be 32–48% higher than values measured for live animals (Walsberg and Wolf, 1995). Measurement of whole-animal SHG is not possible for live numbats, due to their endangered status, but we can estimate it. Calculations of SHG to the animal's core (Q_A) were made after Walsberg and Wolf (1995), using two values for tissue thermal resistance (r_{tissue}; 100 W m^{-2} and 75 W m^{-2}; Monteith and Unsworth, 1989; Walsberg and Wolf, 1995), which provide a range of estimations of Q_A. Predicted SHG to the numbat's core range from 50% to 357% of RMR, dependent on T_a and wind speed (Table 3). The proportions of RMR met by SHG at higher wind speeds may be overestimated if there is an increase in RMR at high wind speed, so these values represent maximal proportions of SHG/RMR at higher wind speeds.

The ratio of SHG to basal metabolic rate (BMR) is high for the numbat (i.e. Q_A=1.5–3.6×BMR) compared with other species. Ground squirrels (e.g. *Spermophilus saturatus* and *S. lateralis*) have a much lower ratio (0.8–1.0×BMR for *S. saturatus*; 1.3–1.7×BMR for *S. lateralis*; Walsberg and Wolf, 1995). Thus, for numbats, potential SHG can be a substantial fraction of their heat budget compared with resting/basal metabolism, due to a combination of high radiative heat gain and low basal metabolism (numbat BMR is only 48% of that predicted for a typical placental mammal of equivalent mass; Cooper and Withers, 2002).

Pelt specialisations

The biophysical properties of numbat pelts presumably reflect adaptation to their diurnal lifestyle. Compared with other marsupials, their pelt is sparse and shallow and has poor insulative and low reflective properties, probably to maximise SHG. As termites are a poor quality food source (MacNab, 1984, 2000; Redford and Dorea, 1984; Anderson et al., 1997), it is beneficial for the exclusively termitivorous numbat to conserve energy by utilising SHG in preference to metabolic heat production for thermoregulation. The structural and spectral properties of numbat pelts in comparison to other marsupials suggest that SHG may indeed be a major source of heat, and the numbat's pelt is adapted to favour SHG at the expense of resistance to metabolic heat loss. Foraging timing of numbats is closely timed with diurnal termite activity in shallow sub-surface soil galleries (Friend, 1986, 1993), so numbats are active under environmental conditions that favour SHG. During summer, numbats (like the termites they feed on) are most active in early morning and evenings and seek shelter during the heat of the day. In winter, the pattern is reversed, and numbats remain in their hollows or burrows in the mornings and evenings, emerging only during the warmest part of the day (Friend, 1986). Thus, numbats may avoid potential overheating in the hot summer and utilize solar radiation for thermoregulation during the cooler winter.

Considering the differences in ecophysiology between diurnal numbats and other nocturnal marsupials, it is not

Table 3. *The percentage of heat produced that is met by solar heat gain for numbats*

T_a (°C)	MR (W)	SHG as a % of MR at different wind speeds (m s^{-1})*				
		0.25	0.5	1	2	3
15	3.55	108–122	102–116	86–99	63–74	50–59
20	3.02	127–143	120–136	100–115	73–86	59–70
25	1.96	196–220	186–210	155–178	113–133	90–107
30	1.20	320–361	304–344	253–292	185–218	148–176
32.5	1.21	317–357	301–341	251–289	183–216	146–174

MR, metabolic rate; T_a, ambient temperature; SHG, solar heat gain.

Data were obtained at ambient temperatures of 15–32.5°C, at wind speeds of 0.25–3 m s^{-1}, with incident radiation of 900 W m^{-2} (resting metabolic data from Cooper and Withers, 2002), calculated for a whole numbat after Walsberg (1995).

*Lower values are for a tissue resistance of 100 W m^{-2}, and higher values are for a tissue resistance of 75 W m^{-2}. Values represent maximal proportions of MR at the higher wind speeds, as resting metabolic rate (RMR) might increase as wind speed increases.

surprising that the structural, spectral and thermal properties of numbat pelts are more like those of small diurnal placental mammals. Ground squirrels make the best comparison. They have similar coat absorptivity and r_c values to those of the numbat, and their high fractional SHG is like that of the numbat. The similarity in coat structure and function for numbats and desert-dwelling ground squirrels is a clear case of convergent evolution, responding to selection pressures to use solar radiation in balancing the energy budget. However, the numbat has achieved a high level of heat gain without the same extent of reduction in r_c of ground squirrel pelts, indicating different structural and spectral properties that adapt the numbat for both heat acquisition and conservation.

List of symbols

α_a	coat absorptivity
I	coat interception function
M	mass
Q_A	solar hear gain to the animal's core
ρ_c	coat reflectivity
r_a	aerodynamic (boundary layer) resistance
r_c	coat thermal resistance
r_e	environmental resistance
r_r	radiative heat transfer resistance
r_t	total thermal resistance
r_{tissue}	tissue thermal resistance
τ_c	coat transmissivity
T_a	ambient temperature

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