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ORIGINAL PAPER

The functional requirements of mammalian hair: a compromise between crypsis and thermoregulation?

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Abstract Mammalian fur often shows agouti banding with a proximal dark band near the skin and a lighter distal band. We examined the function of both bands in relation to camouflage, thermal properties of pelts, and thermal energetics of dunnarts (*Sminthopsis crassicaudata*), which are known to use torpor and basking. Although the distal band of dunnart fur darkened with increasing latitude, which is important for camouflage, it did not affect the thermal properties and the length of the dark band and total hair length were not correlated. In contrast, the length of the proximal dark band of preserved pelts exposed to sunlight was positively correlated ($r^2 = 0.59$) with the temperature underneath the pelt (T_{pelt}). All dunnarts offered radiant heat basked by exposing the dark band of the hair during both rest and torpor. Basking dunnarts with longer dark bands had lower resting metabolism ($r^2 = 0.69$), warmed faster from torpor ($r^2 = 0.77$), required less energy to do so ($r^2 = 0.32$), and reached a higher subcutaneous temperature (T_{sub}) at the end of rewarming ($r^2 = 0.75$). We provide the first experimental evidence on the possible dual function of the color banding of mammalian fur. The distal colored band appears to be important for camouflage, whereas the length of the dark proximal hair band facilitates heat gain for energy conservation and allows animals to rewarm quickly and economically from torpor.

Keywords Fur · Thermal energetics · Basking · Torpor · Marsupial · *Sminthopsis*

Introduction

The hair color of many mammals is not uniform but is often divided into two or more bands (agouti banding) with a proximal band closest to the animal's skin and a differently colored distal band farthest from the skin (Searle 1968). While the distal band is largely responsible for an animal's appearance, coloration, and camouflage, it is also important in thermoregulation as it affects the insulative effectiveness of the entire coat. Although absorption of radiant heat is usually associated with reptiles, it can also substantially affect the energy expenditure of mammals during the day when they are normothermic with a high body temperature (T_b) and also during rewarming from torpor (Geiser et al. 2002, 2016; Schradin et al. 2007; Warnecke et al. 2008; Signer et al. 2011; Thompson et al. 2015). Torpor is a state of reduced metabolic rate (MR) and (T_b) that allows many small endotherms to save energy normally expended during normothermic thermoregulation (Lyman et al. 1982).

While the state of torpor reduces the energy expenditure of mammals enormously, the required endothermic rewarming at the end of a torpor bout is energetically costly and is widely viewed as its main disadvantage (Lyman et al. 1982). However, recent evidence shows that several mammalian species bask in the sun during the rewarming phase from torpor, similar to ectotherms (Geiser et al. 2002; Warnecke et al. 2008; Thompson et al. 2015). Basking in these mammals reduces the cost of rewarming from torpor and the energy expenditure during rest by up to 85 % (Geiser and Drury 2003; Geiser et al. 2004; Schradin et al. 2007;

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Warnecke and Geiser 2010; Signer et al. 2011). Interestingly, mammals that have been observed basking during rewarming from torpor are considered to be primarily nocturnal and basking in the sun is obviously possible only when solar radiation is available (Stannard et al. 2015). To be able to bask, these animals have to leave their refuge and become partially diurnal and basking most often occurs in the morning. A clear drawback of this behavior is the potentially increased exposure to diurnal predators (Geiser et al. 2002; Pavey and Geiser 2008). It is then imperative that animals balance the overall costs and benefits associated with basking (Rojas et al. 2012).

One desert mammal known to bask in the wild is the fat-tailed dunnart (*Sminthopsis crassicaudata*, hereafter "dunnarts"), a small insectivorous marsupial. In autumn and winter, wild dunnarts usually have only brief activity periods in the late afternoon/early evening, enter torpor early in the night, and remain torpid until they exit their shelters to bask in the morning (Warnecke et al. 2008). The coloration and markings of dunnart hair must therefore allow them to blend in with the background to avoid predation (Hope and Godfrey 1988; Caro 2005) but also gain heat from the sun (Withers 1992; Caro 2005; Margalida et al. 2008). Dunnart hair is primarily underfur with few sparse guard hairs throughout and has the following two main color bands that vary in length among individuals: a pronounced dark, almost black proximal band near the skin and a paler sand-colored distal band and a minor dark-colored tip that is of very similar length in all dunnarts (Brunner et al. 2002).

Although the hair properties of mammals in relation to thermal biology have been previously investigated (Cooper et al. 2003; Dawson et al. 2014), the possible dual function of camouflage and thermal biology of the color banding have not been examined. The aims of our study were (i) to determine if there was a correlation between the length of the dark band and temperature under preserved pelts, (ii) to examine if the color of dunnart fur was correlated with distribution, and (iii) to provide the first data on whether and how the length of colored hair bands affect the thermal properties of pelts and thermal energetics of normothermic and torpid dunnarts during basking/passive rewarming. We emphasized work on whole animals to provide a strong ecological perspective and used pelts only to further strengthen the results. Specifically, we tested the hypothesis that (i) the dark band of the hair assists in heat absorption through the skin, (ii) animals in more southern locations have darker fur than those in the north, and (iii) individual hair banding is correlated with energy expenditure during basking/passive rewarming when at rest and when rewarming from torpor. We predicted that animals with a long dark band should have a thermal advantage over those with short band because, in general, dark surfaces absorb more radiant heat.

Material and methods

The dark band and pelt temperature in deceased animals

Nine pelts in good condition and with dense hair from deceased captive (5+ generations) adult dunnarts were used. Pelts were collected on the day of death, 12 weeks before measurements began. Tissue was removed, the skins salt cured (Martin et al. 2011), and stored in the dark. Two weeks before measurements, skins were relaxed and washed in cold water, drained, and pinned to prevent shrinkage during drying. We assessed hair color while the skin was still attached to the animal and after curing the skins (Downing 1945), and it did not change. We assessed fur color (Munsell soil color chart 10YR, Munsell soil color systems 2009, Munsell Color, Grand Rapids, USA), using a fur sample from the same mid-dorsal region (Munsell 2009).

To test the uptake of radiant heat by pelts under natural sunlight, we pinned cured skins to a piece of Styrofoam board 4 cm thick, with >6-cm space between each pelt, and the Styrofoam board was placed perpendicular to the sun to ensure even sunlight exposure across all pelts. We measured the thermal properties of dried pelts with the hair brushed up, exposing the dark band of the hair, but not the skin, as observed during basking. These measurements were repeated when the hair was brushed down against the skin. To read the temperature underneath the pelt (T_{pelt}), we placed a calibrated thermocouple (precision reference thermometer to the nearest 0.1 °C; Wacker et al. 2012) mid-dorsally underneath the skin, and the temperature was read to the nearest 0.1 °C after 5 min with a digital thermometer (HH-71 T, Omega, Stamford, CT, USA). The T_a was measured with a shielded thermocouple (HH-71 T, Omega, Stamford, CT, USA) in the shade. These measurements were completed within three sunny days during winter in July 2012 between 10:00 and 11:00 Australian Eastern Standard Time (AEST) in a sheltered location without wind at near-constant ambient temperature (T_a). To ensure consistent sun exposure, we measured the light intensity (Gossen light metre, Panlux Electronics, 2 lux resolution, Nürnberg, Germany) throughout the experiment; light intensity was between 114,000 and 116,000 lux throughout measurements.

Four individual hairs were removed from the mid-dorsal area of each pelt, and these were straightened over 24 h using 100 % ethanol. This did not affect the hair color. Initially, more individual hairs were measured, but as they did not vary, four were used each time. Photographs of each hair were taken using a digital camera (IC80 HD Digital Camera for Stereo Microscopes, Leica, Heerbrugg, Switzerland) and microscope (M80 Stereo Microscope with 8:1 Zoom, Leica, Heerbrugg, Switzerland). Total hair length, excluding the hair root, and the length of the dark and light bands and hair tip were measured under a stereomicroscope.

Fur color and latitude

Fur color was assessed in living wild dunnarts. Dunnarts were caught using pitfall traps at the following two field locations: Fowlers Gap Field Research Station in western New South Wales (31° 21′ S, 141° 39′ E) in December 2010 and Neds Corner Station in Victoria (34° 08′ S, 141° 19′ E) in January 2011. Five animals were caught at the New South Wales site and 14 animals were caught at the Victorian site.

Dunnart specimens were also examined at the Queensland Museum in Brisbane, Queensland ($n = 14$), and the Australian Museum in Sydney, New South Wales ($n = 26$), including specimens from all Australian mainland states. Because wet specimens were not used, numbers were limited to only whole dried specimens and pelts that were clearly identified as *S. crassicaudata*. Museum pelts were tested for color fading by comparison with new pelts. Fur color was assessed using Munsell soil color chart 10YR. The "YR" refers to hue (relationship to red and yellow). The two numbers that follow the hue (e.g., 10YR5/4) refer to value (lightness) and strength (departure from a neutral of the same lightness), respectively (Munsell 2009).

The dark band and basking

Captive-bred adult fat-tailed dunnarts (six females, eight males; body mass 16.1 ± 1.9 g) were housed in cages (550 × 380 × 220 mm) provided with wood shaving substrate and with nesting boxes filled with shredded paper. Water and food were always available if not otherwise specified. Animals were kept under the natural photoperiod (30.50° S, 151.65° E) and at T_a 20.0 ± 2.0 °C. All measurements were conducted during January 2012 (austral summer).

Implantable temperature transponders ($n = 14$; IPTT-300, 0.13 g, 14 × 2 mm, Bio Medic Data Systems, Seaford, DE, USA) were calibrated prior to use to the nearest 0.1 °C between 10.0 and 40.0 °C (Wacker et al. 2012). Transponders were implanted subcutaneously in the dorsal region (Wacker et al. 2012).

Metabolic rate was measured using open flow respirometry following the procedures detailed in Warnecke and Geiser (2010). Respirometry chambers were clear Perspex tubes fitted with a cardboard tube refuge, allowing animals to select or avoid radiant heat by moving under or away from the basking lamp. The decrease in resting MR from non-basking to basking was considered proportional to the heat uptake by the animals. T_a was measured with a calibrated thermocouple, shielded from radiation, in the respirometry chamber.

The transponder signal (T_{sub}) was read with a DAS-7006/7R/S Handheld Reader (Bio Medic Data Systems, Seaford, DE, USA) modified and connected to a computer and read automatically via a Visual Basic V6 program. Oxygen concentration was measured in sequence; respirometry chamber was measured once per minute for 12 min, followed by a reference (outside air) measurement once per minute for 3 min. Transponder readings were taken every minute and were timed to coincide with oxygen consumption readings.

Approximately 1 week after transponder implantation, the dunnarts were placed between 15:30 and 16:30 (AEST; under a natural photoperiod) into respirometry chambers overnight, without food and water to induce torpor. Animals were weighed (to the nearest 0.1 g, MAXI, pro-fit 63–9534; InterTan, Newcastle, Australia) immediately before and immediately after respirometry measurements, and a linear mass loss over the measurement period was assumed. We maintained the temperature inside the respirometry chamber at T_a 15.0 ± 0.7 °C even with the basking lamp on. If the animal was torpid (which always occurred in the refuge) the following morning, and once its T_{sub} was between 19.5 and 20.0 °C, a basking lamp (SunGlo basking spot lamp, 50-W tight beam color rendering index of 98, 6700 K color temperature, ExoTerra, Montreal, Canada; placed at a 45° angle to horizontal and 20-cm distance from the respirometer ceiling) was switched on to aid rewarming. The lux generated by the heat lamp was ~5 % of that of solar radiation during bright sunlight (~110,000 lux) but has been shown previously to effectively induce basking behavior and reduce energy expenditure required from thermoregulation in dunnarts (Geiser and Drury 2003; Warnecke and Geiser 2010). A camera (Swann SecuraView, Security Monitoring Kit, Melbourne, Australia) in the temperature cabinet was used to observe whether the animal was either resting, active, basking, or sheltered in the cardboard tube. Four individual hairs taken from the mid-dorsal area of each individual were straightened using 100 % ethanol as outlined in part a pelts. Measurements were repeated after 1 week, but this time, animals did not have access to a basking lamp and instead needed to rewarm actively.

Data analysis

Data are presented as mean ± standard deviation. Least squares linear regression analyses were used to test for the effect of dark band length on T_{pelt} with the hair brushed up or brushed down and hair length. A paired t test was used to determine differences in T_{pelt} between the measurements obtained when the hair was brushed up and brushed down.

To test for significance in distribution patterns seen in fur color at different latitudes, a chi-squared analysis was used.

Dunnarts were considered torpid when their T_{sub} was <30.0 °C (Barclay et al. 2001; Geiser and Mzilikazi 2011), and torpor bout duration (TBD) was defined as the time T_{sub} remained below 30.0 °C. The maximum basking T_{sub} refers to the maximum reached within 2 h of the basking lamp being switched on; after 2 h, most animals had begun to reduce their

T_{sub}. The maximum non-basking T_{sub} was determined as the maximum T_{sub} recorded after the animals had rewarmed from torpor. The oxygen consumption during resting periods of normothermic individuals was calculated using the average of three 5-min intervals of the lowest, stable, non-torpid values. For non-basking measurements, these intervals were before entry into torpor, and for basking individuals, these intervals were after rewarming from torpor. We calculated the rate of rewarming from torpor using the average rewarming rate (time it took for T_{sub} to rise to 30.0 °C) over the time the animal warmed from its lowest torpid T_{sub} backup to a T_{sub} of 30.0 °C. The cost of rewarming from torpor was calculated by integrating the oxygen consumption from the time the basking lamp was switched on until when the animals were no longer torpid (T_{sub} of 30 °C) and converting this to a mass-specific average. Least squares linear regression analysis was used to test for the effect of the dark band length on resting metabolic rate (RMR), rewarming rate, highest T_{sub} after torpor, and cost of rewarming from torpor with and without a basking lamp. Repeated measure ANOVAs were used to test for differences between RMR, rewarming rate, and highest T_{sub} after torpor with and without a basking lamp.

Results

The dark band and pelt temperature in deceased animals

When the hair was brushed up and away from the skin, the length of the proximal dark band (6.7 ± 1.9 mm) of the mid-dorsal hair affected the thermal properties of the pelt exposed to solar radiation. Pelts with a longer dark band reached a higher T_{pelt} than those with a shorter dark band ($y = 2.57x - 9.59$, $r^2 = 0.59$, $p = 0.009$; Fig. 1a) at a T_a of 17.5 ± 1.0 °C in the shade. When the hair was brushed down against the skin (Fig. 1b), the length of the dark band and T_{pelt} were not correlated ($p = 0.125$). In a paired comparison, the mean T_{pelt} differed between the hair brushed down (41.6 ± 2.9 °C) and hair brushed up (69.1 ± 5.8 °C) measurements (paired t test, $t = 11.15$, $df = 8$, $p < 0.001$). The total length of the hair (9.7 ± 1.6 mm) and T_{pelt} when the hair was brushed down were not correlated ($p = 0.285$) nor was the total hair length correlated with T_{pelt} (0.4 ± 0.1 mm) when the hair was brushed up ($p = 0.149$). The length of the dark band was also not related to the total length of the hair ($p = 0.243$).

Individual dunnart hair consisted of the following four sections: the hair root (Fig. 1c; A); a dark, almost black band (B); a light-colored band (C); and a dark distal tip (D). The dark band was proximal to the skin and was the same color in all dunnarts examined but differed in length among individuals. No seasonal variation in hair length or hair color in captive fat-tailed dunnarts was observed. The light-colored band (C) differed in color and length among individuals, whereas the short, dark distal hair tip (D) was a similar length in all dunnarts examined and of similar dark brown/black color in all individuals.

Fur color and latitude

Dunnarts with a darker distal colored band originated from more southern latitudes (Fig. 2). The darkest distal colored band (fur value 3) was only present at latitude 32°S, while the lightest distal colored band (fur value 6) was present at both southern and northern latitudes (chi-squared = 7.06, $df = 2$, $p = 0.029$).

The dark band and basking

When the basking lamp was available, all animals, normothermic and torpid, moved their whole body from the cardboard refuge, turned their back to the basking lamp, and exposed their entire dorsal surface to the heat source with hair spread apart, making it possible for radiant heat to penetrate to the proximal dark band and skin. All animals had rewarmed within 2 h of the basking lamp being switched on and continued to bask even once they had rewarmed completely from torpor.

Torpor depth (mean T_b 18.5 ± 4.1 °C) and duration (mean 243.7 ± 139.5 min) varied greatly among individuals (one short bout and one longer bout; examples in Fig. 3). Both individuals in these examples (data for all animals in Figs. 4 and 5) remained normothermic for most of the night and entered torpor in the early morning. One individual with a 7.1-mm dark band (Fig. 3a) showed a rapid rate of passive rewarming from torpor (0.25 °C min^{-1}, T_a 14.6 ± 0.4 °C) with the aid of radiant heat from 08:35. The mean RMR of this individual was 3.89 ± 0.62 ml g^{-1} h^{-1} without radiant heat; with radiant heat, RMR was reduced by 67 % to 1.30 ± 0.23 ml g^{-1} h^{-1}. Although patterns of activity and torpor entry of the two animals were similar, the dunnart with the shorter dark hair band rewarmed more slowly from torpor at T_a 15.4 ± 0.3 °C (Fig. 3b). When the T_{sub} was 19.6 °C and the heat lamp was switched on at 08:02, the passive rewarming rate of this dunnart was only 0.14 °C min^{-1} until the end of arousal. The average RMR without radiant heat was 3.78 ± 0.14 ml g^{-1} h^{-1} in comparison to 2.1 ± 0.20 ml g^{-1} h^{-1} with radiant heat, a reduction of 44 %.

The length of the dark band of the hair in $n = 14$ dunnarts was negatively correlated with the average energetic cost of rewarming from torpor ($y = -0.44x + 4.45$, $r^2 = 0.32$, $p = 0.036$; Fig. 4a) with animals with longer dark bands having lower oxygen demands while rewarming from torpor. Two adult males with dark band lengths of 7.10 and 7.88 mm had very low average MRs while rewarming (0.28 and 0.41 ml g^{-1} h^{-1}, respectively), initially rewarming completely passively, with very little active input. Basking RMR

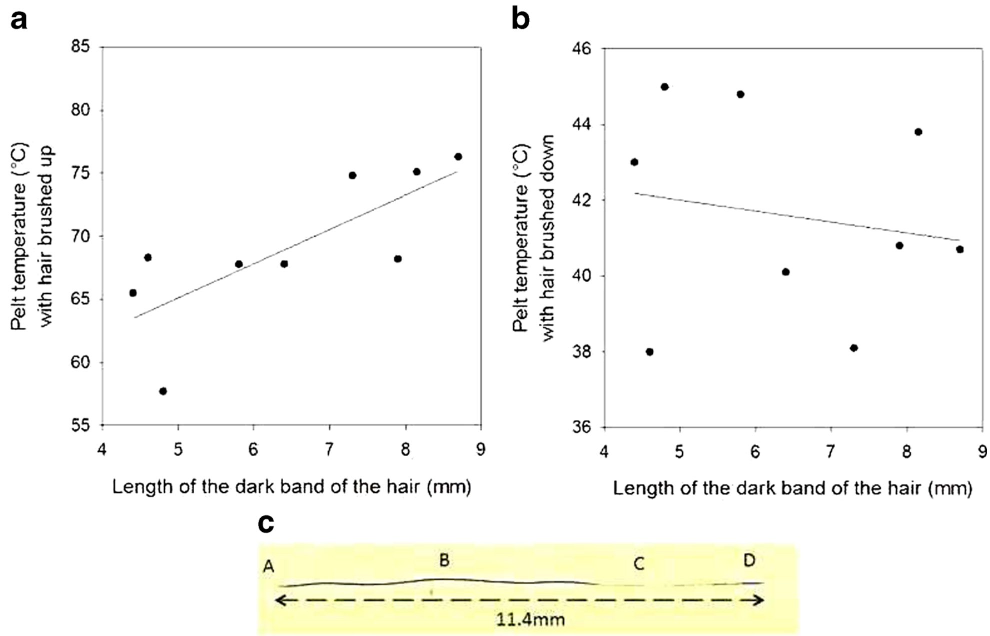

Fig. 1 The pelt temperature (T_{pelt}) as a function of the dark band of the mid-dorsal hair of dunnart pelts ($y = 2.57x - 9.59$, $r^2 = 0.59$, $p = 0.009$) with the hair brushed up (**a**). No correlation was observed when the hair was brushed down (**b**). T_a in the shade = 17.5 ± 1.0 °C. An example (**c**) of a single hair from the mid-dorsal region of an adult fat-tailed dunnart showing the position of the hair root (A), the proximal dark band (B), distal light band (C), and the dark hair tip (D)

(measured once the animals had rewarmed, 1.70 ± 0.25 ml g^{-1} h^{-1}; Fig. 4b) was 60 % lower than the non-basking RMR (4.26 ± 0.41 ml g^{-1} h^{-1}). The length of the dark band of the hair was correlated with basking RMR ($y = -0.46x + 4.64$, $r^2 = 0.69$, $p < 0.001$) but not with non-basking RMR ($r^2 = 0.02$, $p = 0.680$).

The rate of passive rewarming (0.32 ± 0.11 °C/min) in $n = 14$ dunnarts measured at T_a of 14.8 ± 0.7 °C was strongly

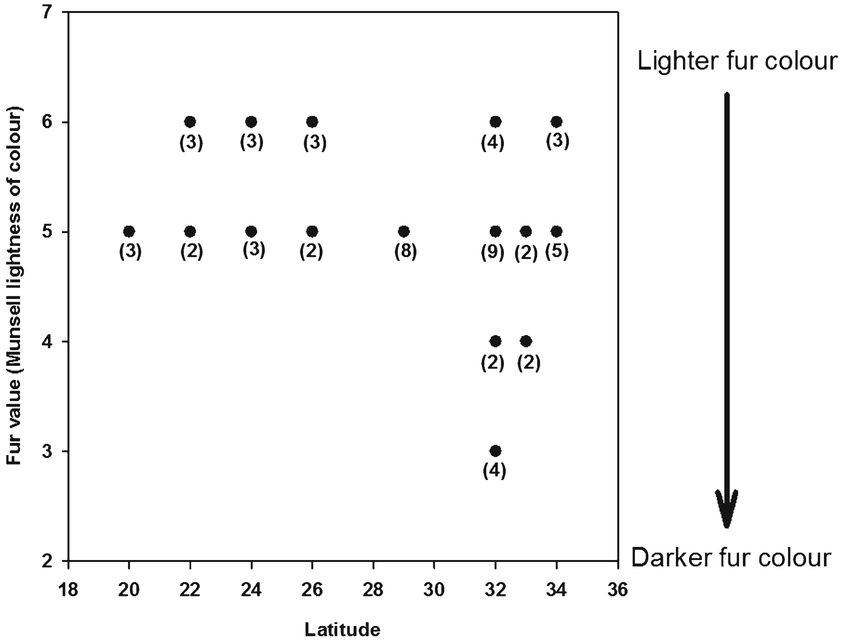

Fig. 2 Fur value (lightness) in wild caught dunnarts and museum specimens from eight latitudes. Each point represents between two and nine individuals. Fur color is darker at more southern latitudes (chi-squared = 7.06, $df = 2$, $p = 0.029$). Fur value (lightness) 3 ($n = 4$, the darkest color) was present at only latitude 32°; fur value 4 was observed at latitudes 32° ($n = 2$) and 33° ($n = 2$); fur value 5 was present at all eight latitudes, 20° ($n = 3$), 22° ($n = 2$), 24° ($n = 3$), 26° ($n = 2$), 29° ($n = 8$), 32° ($n = 9$), 33° ($n = 2$), and 34° ($n = 5$); and fur value 6 was present at five latitudes, 22° ($n = 3$), 24° ($n = 3$), 26° ($n = 3$), 32° ($n = 4$), and 34° ($n = 3$)

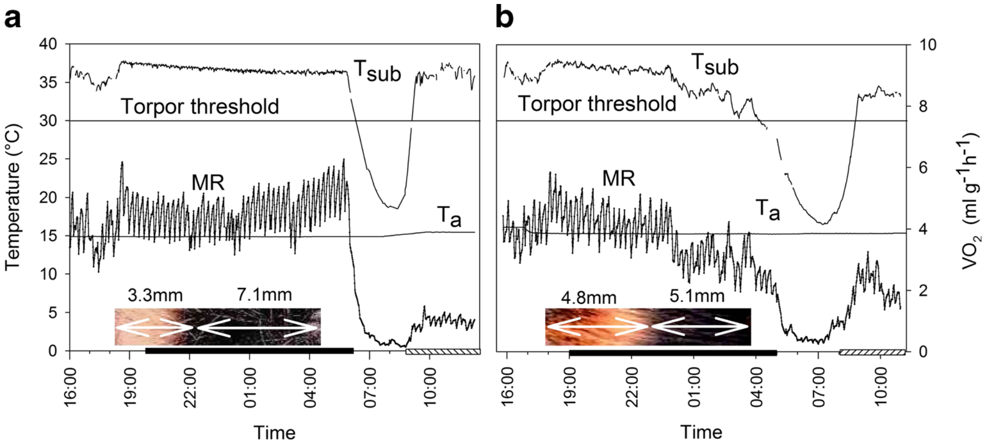

Fig. 3 T_{sub} and V O$_2$ cycle at T_a 14.9 ± 0.4 °C for an animal **a** with a long dark hair band and T_{sub} and V O$_2$ for an animal **b** with a short dark hair band. The *black bar* indicates the scotophase, and the *cross-hatch bar* is the time the basking lamp was on. Note the large difference in V O$_2$ between the individuals during rewarming (~10:00) with access to radiant heat

and positively correlated with the length of the dark band ($y = 0.11x - 0.41$, $r^2 = 0.77$, $p < 0.001$; Fig. 5a). In contrast, in the absence of radiant heat, there was no correlation between the length of the dark band of the hair and rate of active rewarming ($r^2 = 0.03$, $p = 0.750$).

Animals ($n = 14$) with a longer dark hair band also reached a higher T_{sub} at the end of arousal from torpor using radiant heat ($y = 1.29x + 28.36$, $r^2 = 0.75$, $p = 0.00$; Fig. 5b), but interestingly, a similar, albeit weaker correlation was observed when dunnarts rewarmed activity without radiant heat ($y = 0.69x + 30.05$, $r^2 = 0.31$, $p = 0.041$).

Discussion

Our study provides the first evidence of the functional significance of the color banding of mammalian hair. Whereas the color of the distal light band is correlated with latitude and likely soil color (Searle 1968; Smith et al. 1972; Kaufman 1974), the length of the uniform dark band proximal to the skin strongly affects thermal energetics. We show that dunnarts with a longer dark hair band had a lower RMR, rewarmed more quickly and energetically cheaply from torpor, reached a higher T_{sub} at the end of rewarming, and used less energy maintaining this high T_{sub}. Each one millimeter of hair dark band increased the T_{sub} by as much as 6.6 °C/h and reduced basking RMR by more than 10 %. In addition, dried dunnart pelts with a longer proximal dark band also absorbed more solar radiation and attained a higher temperature under the skin. Resting MR values in basking dunnarts at T_a 15.0 °C were as low as 1.40 ml g^{-1} h^{-1} in animals with a dark band >7 mm. This is only slightly above the BMR of fat-tailed dunnarts at T_a 30.0 °C (1.33 ml g^{-1} h^{-1}; Dawson and Hulbert 1970; Geiser and Baudinette 1987). Although the

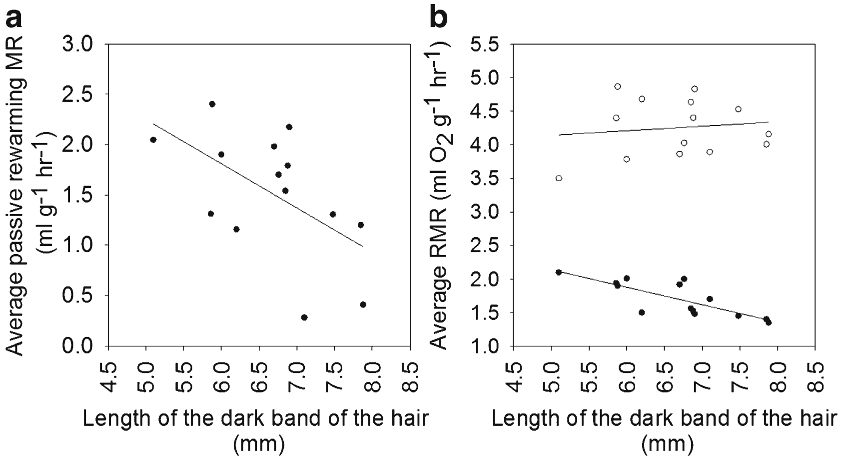

Fig. 4 The length of the dark band of the hair (**a**) in $n = 14$ dunnarts was correlated with the energetic cost of passive rewarming ($p = 0.036$). The RMR (**b**) when basking under the heat lamp (*filled symbols*) was correlated with the length of the dark band of the hair ($y = -0.46x + 4.64$, $r^2 = 0.69$, $p < 0.001$) unlike in non-basking animals with a higher RMR (*open symbols*; $p = 0.680$). $T_a = 14.8 \pm 0.7$ °C

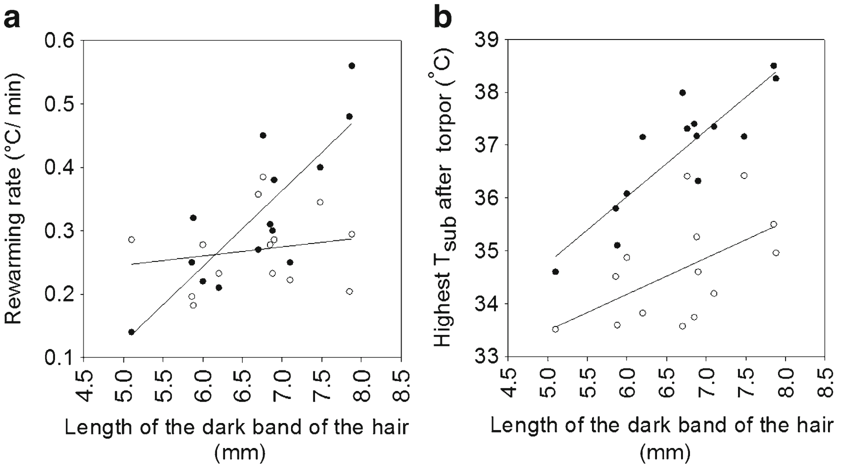

Fig. 5 The rate of passive rewarming from torpor under a heat lamp and the length of the dark band of the hair (**a**) were correlated (*filled symbols*; $y = 0.11x - 0.41$, $r^2 = 0.77$, $p < 0.001$) but not without a basking lamp (*open circles*; $p = 0.750$). The highest basking T_{sub} and the length of the dark band of the hair (**b**) were correlated (*filled symbols*; $y = 1.29x + 28.36$, $r^2 = 0.75$, $p = 0.001$). The highest T_{sub} reached during active rewarming from torpor and the length of the dark band was weakly correlated (*open circles*; $y = 0.69x + 30.05$, $r^2 = 0.31$, $p = 0.041$). $T_a = 14.8 \pm 0.7$ °C

density of the dunnart hair was not measured in this investigation, coats were assessed visually and coat thickness appeared similar. While the effect of hair density on the thermal biology of the dunnarts does need to be kept in mind (Walsberg 1992; Cooper et al. 2003), the fact that there was no correlation between the total hair length and T_{pelt}, nor between the length of the dark band and T_{pelt} when the hair was brushed down, indicates that the length of the dark band is playing an important part in the rate of rewarming.

The dark band of the hair only influenced rewarming rate and energy saved during passive rewarming but not active rewarming. Therefore, the dark hair band was involved in absorption of more radiant heat and appears to have little influence on overall hair length and therefore likely did not affect insulation. The thermal advantages of darker hair or skin have been well established (Scholander 1955; Svihla 1956; Burtt 1981), with dark hair typically absorbing more energy in the visible and near-infrared wavelengths than lighter hair (McNab 2002). The length of the dark hair band in fat-tailed dunnarts did not influence and was not influenced by the total hair length, so this dark band did not affect the overall insulative efficiency of the coat. While some larger animals have different hair lengths in summer and winter (Chappell 1980; Calder 1984), it is more feasible for smaller animals to change other properties of the hair (Underwood and Reynolds 1980; Geiser and Baudinette 1987; Steudel et al. 1994). Very few dunnarts (12–18-g body mass) have a coat that is deeper than 11.5 mm as it is difficult for small mammals to increase their hair length beyond a certain level before the coat becomes too cumbersome or energetically costly to carry (Underwood and Reynolds 1980).

Most species used for studies on fur color and thermoregulation are diurnal (Endler 1978; Kearney and Predavec 2000; Merilaita et al. 2001), and the relationship between basking, nocturnal activity, and crypsis remains uncertain (Schmidt-Nielsen 1964; Endler 1978). The length of the dark band did not influence overall hair color when the animal was not basking. However, during basking, the mid-dorsal hairs parted; exposing the dark band to the heat source changed the animal's appearance. Balancing thermal biology and the ability to camouflage can be difficult because having darker hair means an animal is theoretically better suited to habitats with darker soil or foliage (Kaufman 1974; Krupa and Geluso 2000; Ioannou and Krause 2009). Our data generally followed Gloger's rule; areas with higher rainfall have darker-colored soil, and the animals that inhabit these areas are more heavily pigmented. Arid areas, as in latitudes further north in our study, tend to have lighter soil, and the dunnarts that inhabit them are more lightly pigmented (Hope and Godfrey 1988), which is also the case for other mammals (Burtt 1981).

Consequently, fur color appears important for camouflage in fat-tailed dunnarts. As they have been observed leaving their nests with a T_b as low as 14.6 °C in the morning (Warnecke et al. 2008), fast rewarming rates are important to increase the T_b to normothermic values and avoid predation (Rojas et al. 2012). We propose that the proximal dark band allows the hair to have a dual function while basking. Animals basking in the morning sun are exposing themselves to greater predation risks because they are not only vulnerable to nocturnal predators at night when they are active but also to diurnal predators while rewarming in the morning. While torpor does provide significant energetic benefits, rewarming from torpor can be energetically costly and can take some time without the aid of an external heat source (Geiser and Drury 2003). By altering the basking posture, exposing the dark hair band to direct sunlight, and thus increasing the rate of rewarming, animals are significantly decreasing the amount of time they are exposed to diurnal predators without increasing energy expenditure. In this way, the hair can perform two functions, a dark band to aid in faster rewarming from torpor and a lighter band that allows the animal to blend into its arid environment and aid predator avoidance. This agouti banding in mammalian hair is relatively widespread, especially among Australian arid zone rodents (Brunner et al. 2002), and this dual functionality of hair may be relatively common. While it seems that there would be no advantage to having a shorter dark band, because there is a limit to the length of fur small animals can carry, there is a limit to how long the dark band can be without compromising the camouflage ability of the light band.

We have provided evidence of a dual function of the banding in fat-tailed dunnarts, crypsis, and thermoregulation, and, considering that many mammalian species have this agouti hair band pattern, this dual functionality may be widespread. The hair patterning in mammals has been rarely studied with respect to thermoregulation, ecological niche, and predator avoidance, and our study provides the first evidence of its functional significance.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Statement of human rights and informed consent This article does not contain any studies with human participants performed by any of the authors.

Statement on the welfare of animals All applicable international, national, and/or institutional guidelines for the care and use of animals were followed under the University of New England Animal ethics authority number AEC11/033.

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