

Do black-furred animals compensate for high solar absorption with smaller hairs? A test with a polymorphic squirrel species

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Abstract In polymorphic mammalian species that display multiple color forms, those with dark, or melanic pelage would be prone to overheating, especially if they live in warm climates, because their fur absorbs solar energy at a higher rate. However, experimental studies indicate that certain physical properties of fur of dark individuals appear to prevent, or minimize heat stress, although it is not clear what properties do so. Here, we tested the possibility that black-furred individuals simply have shorter or thinner hair fibers, which would create a lighter (in terms of weight) coat or one that allows greater air flow for evaporative cooling. We examined museum specimens of eastern fox squirrels *Sciurus niger*, a species native to the United States and one that displays brown, grey or all-black pelage color, and used image analysis procedures to quantify hairs from the dorsal surface and tail. From examination of 43 specimens (19 brown, 9 black and 15 grey), and 1,720 hairs, we found no significant difference in hair lengths across color morphs, but significant differences in hair fiber widths. Black squirrels had thinner body hairs than other forms (7% thinner), but thicker tail hairs (9% thicker) than the others. Given that the dorsal surface would be directly exposed to solar radiation, we interpret this to be an adaptation to prevent heat stress during the day. The thicker tail hairs may be an adaptation for nighttime thermoregulation, since squirrels sleep with their tails wrapped around their bodies. These results add to a growing literature body of the functional significance of mammalian pelage [*Current Zoology* 57 (6): 731–736, 2011].

Keywords Polymorphism, Melanism, Fox squirrels, *Sciurus niger*, Heat stress, Hair morphology

Solar radiation greatly affects the lives of terrestrial animals by providing heat for metabolic purposes. For ectotherms, it is the principal form of energy for metabolism (Pough 1980), and even for endothermic animals, solar heat gain makes up a sizeable amount of the total energy budget (e.g. Walsberg and Wolf, 1995; Walsberg et al., 1997, Cooper et al., 2003). For mammals, the physical characteristics of their fur can greatly impact the amount of solar energy absorbed (e.g. Walsberg, 1988). Characteristics such as hair length, width and density can all influence the overall depth of the fur, which ultimately regulates how much heat is reflected versus trapped in individuals (Jacobsen, 1980; Walsberg, 1988). In addition, coat color can also impact the level of solar heat gain, since darker fur tends to absorb greater amounts of solar energy than lighter fur (Armitage, 2009). For polymorphic species where integument color varies among individuals, this can lead to significant physiological and/or behavioral differences between color forms. For example, in springbok (*Antidorcas marsupialis*, an African ungulate), white individuals maintained lower body temperatures in winter while black individuals were at a disadvantage in

the hot summer (Hetem et al., 2009). Further, black individuals were less active during the day and foraged less than other morphs, either because of avoidance of sun or because its metabolic needs were less than those of other morphs. While such behavioral thermoregulation is one form of adaptation by dark individuals to increased solar absorption, few researchers have considered that melanic individuals may have physical compensatory mechanisms in their fur that prevent or at least minimize overheating.

While there could be many physical characteristics of pelage that dark animals could have that differ from other forms, one obvious and easily-measured trait is the fine-scale morphology of the hair fibers themselves (Davis, 2010). For example, given that melanic animals would be prone to overheating in hot climates, it may be that their guard hairs (the large hairs on the outer layer of the fur) are shorter, which would create a thinner overall coat. Or, the guard hair fibers may be thinner (along the shaft), leading to a lighter (in terms of weight) coat overall, or one that allows more air penetration. In the current study, we tested these two ideas using museum specimens of a polymorphic squirrel species, the

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eastern fox squirrel *Sciurus niger*. This species is native to the eastern half of the United States (Steele and Koprowski, 2001) and there are at least three color forms throughout its range; individuals can have brown-colored, grey-colored or black fur (Fig. 1). It is not clear what mechanism regulates the frequency of color morphs in this species, although predation has been examined (Kiltie, 1992) as well as frequency of fires in the environment (Kiltie, 1989). Regardless of the reason, the three color forms makes this species ideal for examining the fine-scale characteristics of hairs across color morphs, especially since in the southern portion of its range (such as the state of Georgia), summer temperatures can be extremely hot, and black morphs would be prone to heat stress unless they had some way of reducing solar heat gain.

Our study involved gathering samples of hairs from the dorsal surface and tail of museum specimens, and using image analysis procedures (Davis, 2010; Davis et al., 2010) to quantify hair length and shaft width on individuals from each color type. We envisioned two possible scenarios: 1) that black-furred individuals would have shorter hairs than other color forms, which would create thinner coats overall (i.e. coats with less depth), or 2) that hair shafts on black individuals would tend to be thinner, to allow for greater air flow through the fur layer and/or make the coat lighter in weight.

1 Materials and Methods

1.1 Specimens

This study was conducted on a collection of 50+ fox squirrel specimens housed at the Georgia Museum of Natural History at the University of Georgia campus (Athens, GA, USA). The specimens all originated from within the state of Georgia and were collected between 1948 and 1995. A small number of specimens had only partial tails, and we did not consider these individuals, since we were partially interested in hairs from the tail tip (see below). Further, certain individuals could not be reliably assigned to a color form (see below) and these were not considered. With these criteria, our final sample size was 43 specimens. For each specimen we recorded the total length of the animal (nose to tail), which was reported on its museum specimen tag (i.e. the length before preparation) as well as the gender, if reported. We also assigned each to a color form: brown, black or grey (Fig. 1). Finally, we extracted a small tuft of hair from each specimen at two locations, on the dorsal surface over the rump and from the distal tip of the tail. Hair samples were placed in labeled plastic

bags until measurement.



Fig. 1 Three eastern fox squirrel *Sciurus niger* specimens that display the brown, black or grey pelage forms typical of this species

Although the black individual in this image is larger than the others, there was no statistical difference in body size among color forms (see text).

1.2 Measuring hair

Hairs were measured using an image analysis procedure outlined previously (Davis, 2010). Briefly, 20 random hairs were selected from each tuft sample and mounted with clear laminating material on a transparent plastic sheet. Note that only the long, thick guard hairs were examined here (i.e. not the small fuzzy body hairs that lay beneath the guard hairs). Sheets were then scanned with a standard flatbed scanner at 1,200 dpi. The resulting images were imported into an image analysis program (FoveaPro, Reindeer Graphics, Inc.) where we obtained measures of each hair's length (in mm, regardless of the curvature of the shaft) and width (in μm), which was measured at the midpoint of the shaft (Davis et al., 2010).

1.3 Data analysis

We first tested for possible differences in overall specimen size (total length) among color forms using one-way ANOVA. This test revealed no statistical difference ($F_{2, 38} = 2.36$, $P = 0.108$). We also tested for a

possible effect of specimen age on hair characteristics (Davis and Castleberry, 2010) by correlating the mean hair values for each specimen against the year the specimen was collected. There was no relationship between specimen age and dorsal hair length ($r = -0.106$, $P = 0.496$), or age and dorsal hair width ($r = -0.155$, $P = 0.320$). Similar results were found with tail hair measurements. Then, to address the central question in this study (are there differences in hair characteristics [length, width] among color forms), we used mixed model ANOVA designs with the hair as the unit of replication in each case. In the first model, hair *length* was the response variable, specimen number was a random effect, while sex, color and sample location (body or tail) were fixed effects. All two-way interaction effects were also included. We performed a similar analysis using hair *width* as the response variable. All tests were conducted using the Statistica 6.1 software package (Statistica, 2003) and tests were considered significant when $P < 0.05$.

2 Results

2.1 General

We examined 19 brown, 9 black and 15 grey specimens for this study. From these 43 specimens a total of 1,720 hairs were examined, 860 from the body and 860 from the tail. Of the squirrels of known sex ($n=40$), their basic hair characteristics are presented in Table 1, which shows that body hairs of this species were approximately 18 mm long on average and 100 μm in width, while tail hairs were nearly 80 mm in length and 86 μm in width. While statistical comparison of male and female hair parameters is considered below, this table shows that in general, male fox squirrels tended to have thicker body hairs than did females, but tail hair widths were similar between sexes.

2.2 Hair length

In the statistical model describing variation in hair

shaft lengths there was an expected effect of sample location ($F_{1, 1559} = 102.3$, $P < 0.0001$), reflecting the longer hairs in the tail than the body in this species, there was an effect of specimen number ($F_{36, 1559} = 102.3$, $P < 0.0001$), which indicates substantial individual variation (also expected), but there were no other significant main effects or interactions. Thus, hair lengths did not differ between sexes ($F_{1, 36} = 0.63$, $P = 0.432$) or among color forms ($F_{2, 36} = 0.32$, $P = 0.728$).

2.3 Hair width

As in the statistical model of hair lengths, there was significant individual variation in hair widths, although the effect depended on the sample location (specimen \times location interaction effect; $F_{36, 1520} = 5.72$, $P < 0.0001$). There was also a sample location effect ($F_{1, 36} = 54.81$, $P < 0.0001$), with hairs from the body being thicker than those from the tail (Fig. 2). Moreover, while there was no other significant main effects, there was a significant color \times sample location interaction ($F_{2, 36} = 5.27$, $P = 0.009$), meaning that there was significant variation in hair widths among color forms but the direction of the effect differed between body and tail. The patterns are displayed in Fig. 2. From this figure it is clear that black-furred squirrels had thinner hair fibers on their body (Fig. 2A), but thicker hairs on their tails (Fig. 2B) than brown or grey-colored individuals. As a follow-up to this, a one-way ANOVA of body hair widths across color forms again found significant variation ($F_{2, 857} = 8.78$, $P = 0.0002$) and Tukey's post-hoc tests showed that black individuals differed significantly from brown ($P = 0.002$) and grey ($P < 0.001$) but brown did not differ from grey ($P = 0.511$). Similarly, a one-way ANOVA of tail hair widths showed significant variation among color forms ($F_{2, 857} = 18.02$, $P < 0.0001$) and Tukey's post-hoc test indicated that black-furred individuals differed from brown ($P < 0.0001$) and grey ($P < 0.0001$), but brown did not differ from grey ($P = 0.427$).

Table 1 Summary of basic hair characteristics of fox squirrels examined in this study, grouped by sample location and gender

Location	Sex	<i>n</i> (hairs)	Hair Length (mm)	Hair Width (μm)
Body	Males	400	18.4 \pm 3.5	106.4 \pm 23.8
	Females	400	18.1 \pm 3.6	100.2 \pm 25.7
	All	800	18.3 \pm 3.5	103.3 \pm 25.0
Tail	Males	400	82.0 \pm 16.3	86.7 \pm 17.2
	Females	400	77.8 \pm 18.3	86.5 \pm 17.9
	All	800	79.9 \pm 17.4	86.6 \pm 17.5

Only animals of known sex are included in the table ($n=40$). Numbers in parentheses indicate standard deviations of the mean.

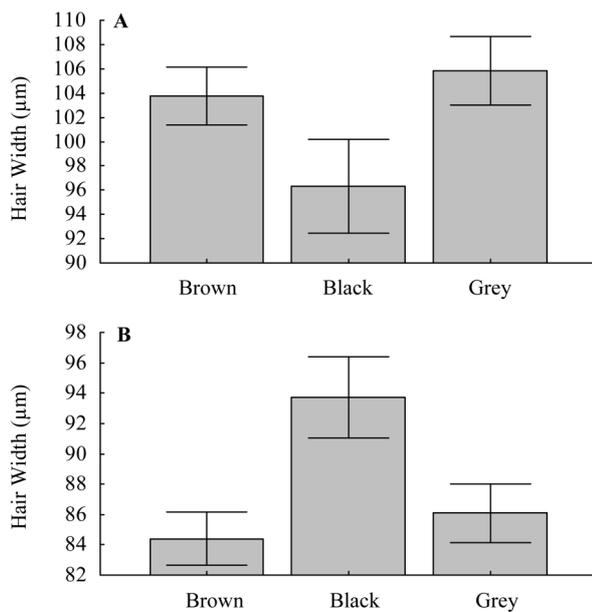


Fig. 2 Average hair shaft diameter of body (A) and tail (B) hairs from fox squirrels in this study

Twenty dorsal and 20 tail hairs were measured each from 43 specimens (19 brown, 9 black and 15 grey). Error bars represent 95% confidence intervals.

3 Discussion

While only one of our predictions was met in this study (black individuals did not have shorter hairs than others), our results concerning hair widths indicate that, at least within this polymorphic species, black-furred individuals appear to have certain hair characteristics (hair widths in the body and tail) that deviate from those of brown or grey individuals. We argue that these deviations are likely a compensatory mechanism for the increased solar heat absorption that typifies melanistic animals (Watt, 1968; Ellers and Boggs, 2004; Armitage, 2009). In fact, we can think of no other adaptive reason why melanistic forms would have these traits, especially given that the black squirrels tended to have thinner hairs on the very region where their solar absorption would be the greatest during the day (their dorsal surface). Here, their hairs were an average of 96.3 µm in width, compared to 103.7 µm and 105.8 µm for brown and grey squirrels, respectively (Fig. 2A), which is a difference of approximately 7% per hair. Given that there are hundreds of thousands of hairs on the dorsal surface of any given squirrel (Voipio and Hissa 1970), this seemingly small difference would no doubt translate into considerable differences in overall coat mass between color types.

Along the same line, if the thinner hairs on the dorsal

surface of black squirrels are a compensatory mechanism for their increased solar absorption, then perhaps their thicker tail hairs are a nighttime compensation for the reduction in thermoregulation garnered by their body fur. Since the average tail hair width of black squirrels was 93.7 µm, compared to 84.4 µm and 86.1 µm for brown and grey forms (Fig. 2B), this means that black squirrels have tail hairs that are approximately 9% thicker than brown and grey squirrels. At night, when body heat must be generated internally (and conserved by the fur), the thicker tail hairs of black squirrels could compensate for their thinner body hairs given that squirrels tend to sleep with their tails wrapped around them (Steele and Koprowski, 2001).

When interpreting our results concerning hair color of fox squirrels, it might help to consider certain research in the related fields of investigative dermatology and even forensic science (Ozeki et al., 1995, Vaughn et al., 2009), where microscopic examination of mammalian (including human) hair is routinely done. This body of work shows that the most important factors in determining hair color in mammals are the quantity and type of melanin pigments embedded in the hair shaft (Ozeki et al., 1995). Melanin pigments can be generally classed as either eumelanins (which produce black and dark brown color) or pheomelanins (which produce yellow to reddish colors). Prior laboratory experiments with other small mammals has shown how black hairs have twice as much total melanin pigment than brown or grey hairs, as well as a greater amount of eumelanin pigment (Ozeki et al., 1995). How this difference in melanin content relates to variation in hair diameter is not known, although work with human hairs has shown a negative relationship between hair lightness and diameter, so that individuals with darker hair (and presumably with more melanin) have thicker hair shafts and vice versa (Vaughn et al., 2009). Interestingly though, this pattern is not consistent with the results from the current project, at least for the hairs on the squirrel bodies, where black-furred individuals had the thinnest hair shafts relative to the brown and grey individuals.

There is little other work in non-human mammals comparing hair color and thickness that we can draw upon to aid understanding of our data. One exception is a study of red squirrels *Sciurus vulgaris* conducted 40 years ago that found thicker hairs (and more dense hairs) on dark-colored individuals compared to red-colored ones (Voipio and Hissa, 1970), which is at first glance in contrast to our results. We point out, however, that those animals were from a population in central Finland

(>60°N latitude), where summer temperatures may not be sufficiently high as to cause heat stress. Therefore, having dark fur at this location may not be costly. Conversely, the fox squirrels studied here all originated from the state of Georgia, USA, where summer temperatures can often reach 40°C (Davis, *pers. obs.*). In such conditions, dark animals would be at a disadvantage during the day (Hetem et al., 2009), and any physical trait that would alleviate or minimize heat stress would be advantageous.

It also should be noted that prior experimental work on two closely-related squirrel species with contrasting colors demonstrated little difference in overall solar heat gain in dark versus pale-colored individuals (Walsberg, 1990; Walsberg and Wolf, 1995), which was attributed to differences between species in the physical properties of the hair which in turn leads to differences in the depth of penetration (through the fur) by solar radiation (Walsberg, 1990). While in that study the hair properties that led to the differences in solar penetration were thought to be optical qualities of the hair fibers (i.e. the amount of solar energy reflected versus absorbed), we point out that this argument is not dissimilar from that given here; certain hair characteristics of darker animals seem to compensate for the increase in solar absorption typical of dark integuments, leading to a similar overall energy gain across color forms.

Finally, our results add to the growing body of work detailing the many physical (e.g. Voipio and Hissa, 1970; Sacchi et al., 2007), physiological (e.g. Cotter et al., 2008; Davis and Milanovich, 2010; Galeotti et al., 2010) and behavioral (e.g. Armitage, 2009; Hetem et al., 2009) differences among color morphs of polymorphic species in the animal kingdom. Indeed, this field of research contains many avenues for scientific exploration, since by studying animals of the same species that vary in some characteristic, we can learn about the very nature of evolutionary adaptation and the forces that drive it.

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