Variation in fur properties may explain differences in heat-related mortality among Australian flying-foxes

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Fur properties of Australian flying-foxes

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Abstract:
Fur properties play a critical role in the thermoregulation of mammals and are becoming of particular interest as the frequency, intensity, and duration of extreme heat events are increasing under climate change. Australian flying-foxes are known to experience mass die-offs during extreme heat events; yet, little is known about how different fur properties affect their thermoregulatory needs. In this study, we examined the differences and patterns in fur properties among and within the four mainland Australian flying-fox species: *Pteropus poliocephalus, P. alecto, P. conspicillatus, and P. scapulatus*. Using museum specimens, we collected data on fur solar reflectance, fur length and fur depth from the four species across their distribution. We found that *P. poliocephalus* had significantly longer and deeper fur, and *P. alecto* had significantly lower fur solar reflectivity, compared to the other species. Across all species, juveniles had deeper fur than adults, and females of *P. alecto* and *P. conspicillatus* had deeper fur than males. The biophysical effects of these fur properties are complex and contingent on the degree of exposure to solar radiation, but they may help to explain the relatively higher mortality of *P. alecto* and of juveniles and females that is commonly observed during extreme heat events.

**Key words:**

*Pteropus, flying-foxes, fruit bats, fur, hair, heat budget, heat stress, extreme heat events*
Introduction

One of the fundamental requirements of endotherms is to be able to defend a tolerable body temperature range in the face of environmental variation. Mammals can adopt a wide range of thermoregulatory methods: they may use behaviour to avoid exposure to hot or cold environments (Huey, Kearney et al. 2012); unlike ectotherms, they may respond physiologically by increasing or decreasing their metabolic rates and evaporative water loss (Dawson 1982; Scholander, Hock et al. 1950b); they may alter aspects of their morphology, e.g. by changing the body shape and size, posture, and by altering their pelage properties (Scholander 1955); or they may use some combination of the above (Huey, Kearney et al. 2012). It is important to have an understanding of the relative importance of each strategy for a given species across different environments, and for different species in the same environment, to predict how species will respond to climate change (Briscoe, Krockenberger et al. 2015; McKechnie, Hockey et al. 2012).

Mammals have evolved fur for diverse functions. Fur may provide a waterproof layer (Dawson and Fanning 1981), prevent physical abrasions, aid in sensory reception (Diamond and Arabzadeh 2013) and may affect camouflage via coloration (Caro 2009). Here, we focus on the role of fur in thermoregulation (Dawson and Maloney 2004; Hammel 1955; Scholander, Hock et al. 1950a; Scholander, Hock et al. 1950b; Scholander, Walters et al. 1950). Fur properties relevant to mammalian thermoregulation include the length, diameter, depth, density, thermal conductivity and solar absorptivity. These traits interact in complex and nonlinear ways to affect heat transfer, depending on the size of the organism, its physiological response and the
environment it is experiencing (Conley and Porter 1986; Dawson and Maloney 2004; Dawson, Webster et al. 2014; Walsberg 1988a).

In general, dry heat exchange between the organism and its environment occurs through conduction, convection and radiation, and fur of a mammal can influence these three processes (Gates 1980). For example, the length and diameter of individual hairs and their density can alter the heat exchange through their combined effect on fur conductivity; the heat exchange through convection depends on the boundary layer formed at the outer edge of the fur and can be affected if the fur insulation layer is disturbed; and the heat exchange through radiation can vary depending on the depth, density, positioning, colour/emissivity and texture (microstructure) of the hairs on the fur coat (Wolf and Walsberg 2000). These fur properties vary in their effect on heat transfer depending on the relative intensities of metabolic heat production, radiant heat gain and convective gradients (Walsberg 1988a; Walsberg 1988b; Walsberg and Schmidt 1989; Wolf and Walsberg 2000).

Here, we focus on three fur properties that can be non-invasively measured using museum specimens: fur depth, fur length and fur solar reflectance. Fur depth is the vertical depth of the fur layer. Since air has low thermal conductivity, the air trapped among the fur insulates the skin surface in proportion to fur depth and thus creates a resistance to conductive heat flow out of the body. Fur depth depends on fur length and fur angle. Fur length can vary from species to species depending on body size (Schmidt-Nielsen 1997), and even among different parts of the body (Underwood and Reynolds 1980). The length of the fur in part influences overall pelt thermal conductivity by altering the ratio of hair to air in a given volume of fur. It also limits the maximum potential fur depth under piloerection (Rymer, Kinahan et al. 2007;
Underwood and Reynolds 1980), a process used by mammals where the hairs take a ~90° angle to the body and thereby create a deeper insulation layer. Piloerection can allow more solar radiation to enter in between the hairs to reach the skin surface, which can consequentially increase pelt temperature (Wacker, McAllan et al. 2016) that in turn increases the radiant heat load on the skin (Gates 1980). Finally, the fur solar reflectivity quantifies the amount of incident solar radiation that is reflected by the fur surface, and thus the overall heat load via solar radiation on the pelt (Porter and Gates 1969). The reflectivity may vary with hair orientation (i.e. the angle at which the hair emerges from the skin surface), which can be controlled by piloerection (Gates 1980).

Fur properties can vary with season and climate (Briscoe, Krockenberger et al. 2015; Walsberg and Schmidt 1989). In broadly distributed species a compromised set of fur properties can facilitate thermoregulation in several habitats and conditions, whereas fur properties of species with a restricted distribution can be fine-tuned to local stable conditions (Briscoe, Krockenberger et al. 2015; Scholander, Walters et al. 1950). The selective pressures on fur traits are complex and it is difficult to predict how they should vary. All else being equal, we might expect an animal adapted to colder climates to have a well-insulated fur coat with dense, deep fur and dark, long hairs. We might also expect high fur density in organisms exposed to strong sunlight, however, because it reduces solar load on the skin. We might also expect high fur density and depth in organisms exposed to high radiant heat, because it reduces penetrance of solar radiation into the fur to the extent that solar reflectance of fur becomes irrelevant and fur colour is freer to vary for other purposes like camouflage (Dawson, Webster et al. 2014). An additional complicating factor is the variation in thermal environments. In seasonal
environments we might expect fur properties to change through the year via moultng (Walsberg, Weaver et al. 1997). Extreme weather events that occur over days or hours pose a particular challenge, however, because most fur properties cannot be adjusted on such short time scales.

A prominent example of the challenges posed by extreme weather events in mammals is found in Australia’s mainland flying-foxes that can suffer mass mortality during very high ambient temperatures (~ 42.0 °C) (Ratnayake, Kearney, et al. 2019; Welbergen, Klose et al. 2008). The frequency, intensity and duration of extreme heat events have increased, and are expected to continue to increase, due to climate change (Meehl and Tebaldi 2004; Steffen, Hughes et al. 2014), and thus an increase in the frequency and magnitude of flying-fox die-offs has been suggested (Welbergen, Klose et al. 2008). Post-mortem observations of colonies containing black flying-foxes (Pteropus alecto) and grey-headed flying-foxes (P. poliocephalus) have revealed a skewed proportional mortality rate towards P. alecto, and towards females and juveniles of both species (Welbergen, Klose et al. 2008). The reason for these biases in mortality rates may reflect the species-, sex-, and age-specific physiology, rather than the individual body condition (Welbergen, Klose et al. 2008). However, it is also possible that differences in fur properties among and within species play a role in the sensitivity to heat stress.

Motivated by these inter- and intra-specific patterns of heat-related mortality, we compared the thermal properties of the fur of four species of flying fox: P. alecto, P. poliocephalus, P. conspicillatus, and P. scapulatus. We aimed to assess whether the fur properties length, depth, and solar reflectance varied among body parts (i.e. dorsal and ventral collar and abdominal regions), among sexes and age groups (i.e. juveniles and adults), and among species. We then
interpreted these patterns in the context of what we know of the species’ thermal environments and their sensitivity to extreme heat events.

Materials and Methods

Study species

Flying-foxes (*Pteropus* spp.) are large bats that form conspicuous daytime roosts in amongst the exposed branches of canopy trees (Churchill 2009). There are four species of flying-fox in mainland Australia; the grey-headed flying-fox (*P. poliocephalus*), the black flying-fox (*P. alecto*), the spectacled flying-fox (*P. conspicillatus*), and the little red flying-fox (*P. scapulatus*) (Fig. 1).

The distribution of *P. poliocephalus* is restricted to the temperate and subtropical regions of eastern and southeastern Australia (Churchill 2009; Eby 1991) (Fig. 1). *Pteropus alecto* have a widespread distribution from Western Australia to New South Wales but is mainly limited to coastal regions (Churchill 2009) (Fig. 1). *Pteropus conspicillatus* comparatively have the most restricted distribution in the tropical far north Queensland (Churchill 2009) (Fig. 1). *Pteropus scapulatus* is the most widely distributed species within Australia, with its individuals being found in Western Australia and Northern Territory, from the north to south Queensland, through New South Wales and Victoria (Churchill 2009), exposing them to temperate and (sub)tropical climates (Fig. 1). They are a nomadic species that can be found further inland compared to the other species (Churchill 2009).
Morphometric measurements

We measured fur length and fur depth of *P. poliocephalus* (*n* = 29), *P. alecto* (*n* = 12), *P. conspicillatus* (*n* = 10) and *P. scapulatus* (*n* = 22) specimens sourced from the Melbourne Museum, Victoria, and from the Australian Museum, New South Wales. Fur solar reflectance of the four species (*n* = 24, 3, 3, and 16, for *P. poliocephalus*, *P. alecto*, *P. conspicillatus*, and *P. scapulatus*, respectively) was measured from specimens sourced from the Melbourne Museum.

The forearm length and total body length were also measured (Table 1 & Table 2). The age category (adult, *n* = 60 or juvenile, *n* = 13), sex, date the specimen was collected, and sourced location were noted where available (for further details see Supplementary material S1).

Fur length and fur depth

We measured the fur length of the head, upper (collar) and lower (abdomen) torso and legs, when present, in both the dorsal and ventral sides to the nearest 0.1 mm (Fig. 2) using Workzone® digital callipers (model number – ANS-16-039). Prior to measuring the fur length, we combed the hair in the opposite direction of its natural orientation. Fur length was defined as the length of hair from the skin surface to the tip of the hair. We measured the fur depth of the collar and abdomen regions in the dorsal and ventral sides (Fig. 2). Fur depth was measured when the hair was resting naturally on the skin surface and was defined as the perpendicular distance between the skin surface and the outer edge of the fur coat. We recorded this perpendicular distance by placing a ruler on the skin surface and marking the tip of the pelage on the ruler, and then measuring the end of the ruler to the mark using the callipers.
Measurements were non-invasive to preserve the bat specimens in the museums, and this precluded measurement of fur density as this required removal of a sample of fur.

**Solar reflectance**

The fur solar reflectance was measured for the upper (collar) and lower (abdomen) torso on both the dorsal and ventral sides. Fur solar reflectance was measured at three replicate locations dorsally and ventrally in the collar and abdominal regions using a set-up consisting of two spectrometers (NIR-Quest and USB4000, Ocean Optics, USA) that were used to measure spectral reflectance from 300 – 1000 nm and 1000 – 2000 nm respectively. The spectrometers had two light sources (PX-2 pulsed Xenon light for the UV-Vis range and HL-2000 tungsten halogen lights for the Vis-NIR range) connected to a quadrifurcated fibre optic ending in a single probe, which had an oval-shaped measuring area of 5 mm x 3 mm. The probe was held in an Ocean Optics RPH-1 probe holder (Ocean Optics, Inc., USA) at a constant 45° angle and constant ~1 cm distance from the skin surface. Each measurement was compared against a Spectralon 99% white reflectance standard (Labsphere Inc., North Sutton, NH, USA). The average of the measurements made for dorsal and ventral surfaces of the collar and abdominal regions were converted to solar reflectivity by calculating the weighted average across 37 bandwidths between 260-2600nm (Supplementary material S2) for each body region. As we could only measure reflectance at wavelengths up to 2000nm, we assumed that reflectance remained constant above this value. This missing region of the spectrum in our measurements accounts for 4% of solar radiation and therefore deviations from this assumption would not strongly alter
our results.

Statistical Analysis

We used the R package lme4 (Bates, Mächler et al. 2015) to perform a linear mixed effects analysis of the relationship between each fur trait and species. We used backward-stepwise model selection, where each factor in the full model was tested for significance and the non-significant terms were removed until only the significant terms remained (Dominoni et al. 2020). When the generalized linear mixed models (GLMM) were created, to minimize the variation in body part fur lengths, we only considered the fur length in the torso area, i.e. the collar and abdominal regions. To determine the best fitting GLMM for fur length and depth species, total body length (a proxy for body size), sex, age, body part, and their interactions were evaluated as fixed effects. In the GLMM for total fur solar reflectivity species, body part, sex, and their interactions were considered as fixed effects. In all models, individual identity was considered as a random effect. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality (Supplementary material S4). We assessed for autocorrelation between total body length, age, and sex; however, there were no significant autocorrelations between these predictors (|P| > 0.05). All post hoc comparisons were performed based on the t-distribution using degrees of freedom based on Satterthwaites method. All values are expressed as mean ± standard deviation and P < 0.05 was considered statistically significant unless mentioned otherwise. All analyses were conducted in R version 3.4.1 (R Core Team 2017).
Results

There was considerable variation among morphometric measurements both among and within species (Table 1 – 3). Fur length varied significantly among species, body part and their interaction (GLMM; species: $F_{3,9} = 17.40, P < 0.001$; body part: $F_{3,9} = 73.91, P < 0.001$; interaction: $F_{9,3} = 2.35, P = 0.01$; Supplementary material Fig. S1). Fur depth also varied significantly among the species, sex, age, and body part (GLMM; species: $F_{3,1} = 55.57; P < 0.001$; sex: $F_{1,3} = 17.23, P = 0.0001$; age: $F_{1,3} = 5.41; P = 0.023$; body part: $F_{3,1} = 35.60; P < 0.001$) (Supplementary material Fig. S2). There was no significant effect by body size on either fur length or fur depth ($F_{1,3} = 3.39, P = 0.07$ and $F_{1,3} = 2.77, P = 0.100$, respectively). Fur solar reflectivity varied significantly among species, body parts, and their interaction (GLMM; species: $F_{3,9} = 6.27, P = 0.001$; body parts: $F_{3,9} = 39.06, P < 0.001$; interaction: $F_{9,3} = 3.52, P < 0.001$) (Supplementary material Fig. S3).

Variation in fur length of Australian flying-foxes

*Pteropus poliocephalus* had the highest mean fur length (Table 1), while *P. scapulatus* had the lowest mean fur length, and *P. alecto* and *P. conspicillatus* had similar, intermediate, mean fur lengths (Supplementary material S5; Fig. S5, S8 & S9). Fur lengths of each body part were significantly different from each other ($P < 0.001$), except between the ventral and dorsal abdominal regions ($P = 0.80$; Supplementary material S5; Fig. 3). Across all four species, the dorsal collar had the longest fur, and the ventral collar had the second longest fur, while the dorsal and ventral abdomen furs were the third longest and of similar length (Fig. 4). In all body
regions, *P. poliocephalus* had longer hair compared to the other three species, and *P. scapulatus* consistently had shorter fur length in all body parts compared to the other species (Fig. 4). The greatest variation in fur lengths among species was found in the dorsal collar region (Fig. 4). The interaction term in the GLMM reflected the fact that differences in fur length between body parts were most pronounced in *P. poliocephalus* and least pronounced in *P. scapulatus* with the other two species in between.

There was no effect of sex on the fur length and sex was thus not considered in the final GLMM (Supplementary material Fig. S1). There was no significant effect of age class on the fur length, i.e. there was no significant difference between adult and juvenile fur length (*P* = 0.34).

Variation in fur depth of Australian flying-foxes

*Pteropus poliocephalus* had significantly deeper fur compared to the other three species (*P* < 0.001) (Supplementary material S5; Fig. S6, S8 & S9). The fur depths among the other three species were not significantly different (*P. alecto* - *P. scapulatus* *P* = 0.010; *P. alecto* - *P. conspicillatus* *P* = 0.250; *P. scapulatus* - *P. conspicillatus* *P* = 0.440) (Supplementary material S5). Fur depths were significantly different between all body parts considered (Supplementary material S5). In all species a general pattern was for fur to be deeper in the collar region compared to the abdominal region (Table 1).

Females had a significantly deeper fur than males (*P* < 0.001; Supplementary material S5).

There was a significant interaction between species and sex in the GLMM for fur depth (Supplementary material Fig. S2). Specifically, there is a difference in the fur depths between
males and females in *P. alecto* and *P. conspicillatus*, but not in *P. poliocephalus* and *P. scapulatus*. Overall, juveniles had significantly deeper fur than adults (*P* = 0.02; Supplementary material S5). There was also a significant interaction between body part and age in the GLMM for fur depth (Supplementary material Fig. S2). The collar region of the adults had deeper fur compared to the abdomen; however, such a pattern could not be clearly observed in juveniles. A more distinguished pattern may be observed if there was a larger sample size for juveniles.

Variation in fur solar reflectance of Australian flying-foxes

The solar reflectivity of *P. alecto* fur was significantly lower compared to that of the other three species (*P* < 0.01) (Supplementary material S5; Fig. S7 & S9). The dorsal collar fur had a significantly higher solar reflectivity compared to the other body parts (Supplementary material S5, Fig. S5). There was a significant interaction between species and body part in the GLMM for fur solar reflectivity (Supplementary material Fig. S3), whereby the black headed flying fox had lower reflectance overall, but this was especially strong for the ventral collar region. There was no effect of sex on the solar reflectivity of fur, and sex was thus not considered in the final GLMM (Supplementary material Fig. S3). There were only three juvenile *P. poliocephalus* specimens and one juvenile *P. scapulatus* specimen to measure fur solar reflectance; thus, we did not consider differences in fur solar reflectivity between age groups.

Discussion
Our findings indicate substantial variation in the fur traits that affect thermal responses among mainland Australian flying-fox species, with *P. poliocephalus* having the longest and deepest fur and *P. alecto* having the lowest fur reflectivity compared to the other species. Within all species, juveniles had deeper fur than adults, and adult females of *P. alecto* and *P. conspicillatus* had deeper fur than adult males. Together, these results suggest that *P. poliocephalus* and *P. alecto*, adult females, and juveniles have fur thermal properties that would reduce heat flow out of the body (or increase heat flow into the body) and thus may compromise their survival during extreme heat events, a notion consistent with observed mortality biases (Welbergen, Klose *et al.* 2008). However, further modelling and experimental work will be required to fully understand the consequences of this variation. Additionally, lactation in adult females will have higher energetic costs (Racey and Speakman 1987) that may contribute to the higher mortality rates observed among lactating females during extreme heat events (Welbergen, Klose *et al.* 2008). Although the layer of fur can protect an animal from short term exposures through insulation during an extreme heat event, they are exposed to environmental conditions that are effectively above core body temperature for periods long enough to reach steady state given their body mass (i.e. > 1 hour, see Kearney *et al.* (2021) for further details on transient heat budget calculations).

**Distribution, climate and fur properties**

Compared to the other species, *P. poliocephalus* had the longest and deepest fur, which implies greater thermal insulation. This is consistent with the species’ more temperate distribution.
(Churchill 2009; Hall and Richards 2000) and thus greater exposure to cold. The similarly short
fur lengths of *P. alecto* and *P. conspicillatus* is reflected in their similar geographic distributions;
*P. conspicillatus* is restricted to the tropics and *P. alecto* shares this distribution and also
expands to the subtropical regions (Churchill 2009). Similar observations have been made in
koalas where fur depth substantially decreases clinally towards the tropics (Briscoe,
Krockenberger *et al.* 2015).

Variation in fur properties of different species and demographics and their effect during extreme
heat events

The discrepancies and biases shown in flying-fox mortality rates during extreme heat events are
consistent with the expected heat transfer consequences of the variation we observed in the
fur properties of the different species, ages, and sexes. In mixed-species colonies, different
species often vary in their roost height under benign weather conditions, e.g. *P. alecto* tend to
roost higher in the canopy compared to *P. poliocephalus* (Welbergen 2005). However, during an
extreme heat event, there are no known roosting differences between species as all are then
generally found near or on the ground in the coolest spots in the roost. Nevertheless, due to
limited shade availability, spaces between branches and leaves, and scattered light, most flying-
foxes are not completely covered from sunlight and their fur solar reflectivity would still be
relevant in reducing their heat load. Thus, the greater mortality rates of *P. alecto* compared to
*P. poliocephalus* observed in mixed-species colonies in the field may in part relate to the lower
fur solar reflectivity of *P. alecto* (Welbergen, Klose *et al.* 2008). The shorter fur of *P. alecto* may
also allow heat to penetrate deeper into the fur and thus render it more vulnerable to heat stress than *P. poliocephalus*. A more complete answer to this question will require biophysical analyses and quantification of radiant conditions within the roost during heat stress events that jointly consider the combined influences fur has on radiant heat gain through solar radiation penetrance and heat loss by conduction and radiation through the fur (e.g. Conley and Porter 1986; Dawson and Maloney 2004; Mathewson and Porter 2013). These analyses will also need to consider the role of fur properties in influencing the evaporative cooling mechanisms that these species use, such as licking their wings, fur and skin (Welbergen, Klose et al. 2008).

Currently, *P. alecto* is not considered a threatened species (Roberts, Eby et al. 2017) or a priority in conservation efforts; however, our findings and the empirical evidence for their heightened sensitivity to heat increase the importance of monitoring of *P. alecto* population sizes and potential decline rates, particularly in more temperate regions where extreme heat events are more common (Buckley and Huey 2016; see also Welbergen et al 2008).

Although the higher relative mortality rates of adult females and juveniles during flying-fox extreme heat events may be explained by their differences in physiology (Welbergen, Klose et al. 2008), the differences in their fur properties can also contribute to this disparity. Our results show that juveniles had deeper fur than adults, and *P. alecto* and *P. conspicillatus* females have significantly deeper fur than males. New-born bats are naked and poikilothermic and, in a few days, they develop fur and become normothermic (Noll 1979; Weigold 1973). While the deeper fur in juveniles would assist to prevent hypothermia, during an extreme heat event the deep fur which provides a good insulation layer may become detrimental to them, depending on the depth of radiant heat penetration, which was not measured in the current study. Moreover,
since juveniles have a smaller mass to surface area ratio compared to adults, they have a lower thermal inertia, and thus could rapidly overheat, necessitating more pronounced evaporative cooling and access to water/milk. However, we did not see a significant effect by age on fur length (potentially due to the small sample size).

Furthermore, it should be noted that even though in the majority of instances darker fur results in higher solar heat loads compared to light fur, there are sometimes complex interactions between pelage colour, microstructure, optical properties, behaviour and convective heat loss, especially under certain environmental conditions (e.g. windy) that can result in higher heat gain for light coloured pelages (Wolf and Walsberg 2000). As flying-foxes can be exposed to high wind speeds if there is less understory vegetation in their roosting trees, species with lighter fur may gain a greater solar heat load than those with darker pelage (Wolf and Walsberg, 2000). Moreover, since solar penetrance is greater in shorter fur, the impact of colour is greater on shallower pelts (Dawson and Maloney 2004; Dawson, Webster et al. 2014).

Small mammals, such as flying-foxes, have comparatively short fur, and thus the differences in pelt colouration of different species may have a considerable effect on the absorbed heat load (Dawson, Webster et al. 2014).

Variation of fur properties in different body parts and their effect during extreme heat events

Although significant variations in fur properties in different body parts has been observed in some bats (Madej, Mikulová et al. 2013), their relative effect on thermoregulation, especially under extreme heat conditions, has not been thoroughly explored. When heat stressed, flying-
foxes fan their wings (Bartholomew, Leitner et al. 1964; Welbergen, Klose et al. 2008) and we have observed that this inwardly-directed fanning created a movement of air along the ventral surface of the body, which allowed heat to be lost through forced convection (Ratnayake 2018). Since these wing fanning effects are not directed to the dorsal side of the body, the higher fur solar reflectivity on the dorsal side as observed in our results across all species may help to minimize the heat gain from solar radiation.

In general, the collar region had longer and deeper fur in all four species (Table 1 & Table 2). The reason for the longer, and in some species different coloured, fur (e.g. P. poliocephalus, P. conspicillatus, and P. scapulatus) in this body region is not yet understood. It may reflect the individual’s condition or have sexual signalling implications as it may help retain odiferous marking secretions in males (e.g. Wagner 2008) like the lion’s mane (West and Packer 2002), although there was no apparent sexual dimorphism in the flying-fox collar. Interestingly, instead of having the same long and deep fur coat all over the body, they show shorter fur in the abdominal regions, which may enable them to lose heat more efficiently. Previous work on other mammals show that variation in fur properties across the body can have consequences for behavioural thermoregulation. For instance, depending on their thermal needs, the black-and-gold howling monkeys (Alouatta caraya) changes its posture to optimize solar radiation absorption or reflection, making use of the heterogeneous fur density in different body parts (Bicca-Marques and Calegaro-Marques 1998) – a phenomenon referred to as ‘thermal windows’ (e.g. Klir and Heath).
Concluding remarks and future work

In addition to the fur properties considered in this study, fur density (Dawson and Maloney 2004; Hutchinson and Brown 1969; Rymer, Kinahan et al. 2007) is an important trait relevant for thermoregulation, especially through its effect on solar penetrance to the skin. Thermal conductance (insulation) and conductivity are also common variables used to measure the thermal properties of mammalian pelage (Dawson and Maloney 2004; Hammel 1955). The conductivity of a pelage is defined as the heat flowing per unit area per unit time divided by the temperature gradient (Hammel 1955) and can provide valuable insights about the thermoregulatory purposes of a pelage. All these different fur traits play an important role in flying-fox thermoregulation. However, to understand the effect of each property and their relative importance on heat exchange we must consider the joint physical relationships among the fur structure, fur-air interface, solar radiation, infrared radiation, convection, conduction and the other factors involved in this heat and mass transfer. For instance, the effects of piloerection and multiple sources of heat on one surface (e.g. skin) create complexities that must be carefully analysed to gain a full understanding of the effect on the animal’s heat budget. The information from this study can be used to further explore the adaptive significance of the variation in fur, which can be achieved using the principles of biophysical ecology (Kearney and Porter 2017; Porter and Mitchell 2006; Porter, Munger et al. 1994) and this is an obvious future direction that would enable us to make better predictions of how flying-foxes would cope in future climate change scenarios.
Conflicts of Interest:

The authors declare no conflicts of interest.

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Fig. 1. (A) Reproduced distribution map of the four species of mainland Australian flying-foxes (Currey *et al.* 2018), and (B) photographs of these species demonstrating their fur colouration (all photos taken by Justin Welbergen).
Fig. 2. Body regions used in measuring morphometric variables of museum specimens. i, ventral side of grey-headed flying-fox body, ii, dorsal side of grey-headed flying-fox body. The regions were categorized in the following manner: 1, dorsal head; 2, dorsal collar; 3, dorsal abdomen; 4, dorsal leg; 5, ventral head; 6, ventral collar; 7, ventral abdomen; 8, ventral leg.
Fig. 3. Detailed box plots including (i) fur length, (ii) fur depth, and (iii) fur solar reflectance values of each measured individual. The different colours represent sex, the points represent all the measurements, and the shape represents the age classes. In the ‘Sex’ legend the pink colour represents females (F), blue colour represents males (M), and grey colour represents individuals whose sex could not be determined (NA). In the ‘Age’ legend the circle represents adults (A) and the triangle represents juveniles (J); solar reflectance of juveniles was not measured. BFF, *P. alecto*; GHFF, *P. poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*
Fig. 4. Fur lengths of different body parts in the four flying-fox species – BFF, *P. alecto*; GHFF, *P. poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*. The values in the boxplots represent the median and interquartile range of the distributions of the data.
Fig. 5. Total fur solar reflectivity of different body parts in the four flying-fox species – BFF, *P. alecto*; GHFF, *P. poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*. The values in the boxplots represent the median and interquartile range of the distributions of the data.
Table 1. Summary of morphometric measurements of all adult flying-foxes

<table>
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<tr>
<th>Species</th>
<th>Forearm Length (mm)</th>
<th>Total Body Length (mm)</th>
<th>Fur Length (mean ± standard deviation)</th>
<th>Fur Depth (mean ± standard deviation)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dorsal Head</td>
<td>Dorsal Collar</td>
<td>Dorsal Abdomen</td>
<td>Dorsal Leg</td>
</tr>
<tr>
<td>P. poliocephalus</td>
<td>155.9</td>
<td>257.4</td>
<td>115.7 ±</td>
<td>216.1 ±</td>
</tr>
<tr>
<td>(n = 20)</td>
<td></td>
<td></td>
<td>26.7</td>
<td>28.0</td>
</tr>
<tr>
<td>P. alecto</td>
<td>155.2</td>
<td>233.7</td>
<td>90.3 ±</td>
<td>149.8 ±</td>
</tr>
<tr>
<td>(n = 11)</td>
<td></td>
<td></td>
<td>26.6</td>
<td>28.8</td>
</tr>
<tr>
<td>P. conspicillatus</td>
<td>157.9</td>
<td>239.8</td>
<td>79.9 ±</td>
<td>162.1 ±</td>
</tr>
<tr>
<td>(n = 8)</td>
<td></td>
<td></td>
<td>±18.1</td>
<td>33.5</td>
</tr>
<tr>
<td>P. scapulatus</td>
<td>130.8</td>
<td>198.8</td>
<td>52.9 ±</td>
<td>111.1 ±</td>
</tr>
<tr>
<td>(n = 21)</td>
<td></td>
<td></td>
<td>17.4</td>
<td>27.8</td>
</tr>
</tbody>
</table>
**Table 2. Summary of morphometric measurements of all juvenile flying-foxes**

<table>
<thead>
<tr>
<th>Species</th>
<th>Forearm Length (mm)</th>
<th>Total Body Length (mm)</th>
<th>Fur Length (mean ± standard deviation)</th>
<th>Fur Depth (mean ± standard deviation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. poliocephalus</td>
<td>81.4</td>
<td>127.3</td>
<td>62 ± 106.0 ± 94.6 ± 64.5 ± 75.1 ± 100.4 ± 97.1 ± 86.2 ± 60.5 ± 51.1 ± 67.4 ± 54.4 ±</td>
<td></td>
</tr>
<tr>
<td>(n = 9)</td>
<td></td>
<td></td>
<td>16.0 37.7 27.7 14.6 15.4 19.4 18.3 21.5 29.8 39.4 20.9 32.1</td>
<td></td>
</tr>
<tr>
<td>P. alecto (n = 1)</td>
<td>70.0</td>
<td>100.0</td>
<td>61.9 78.8 50.4 41.1 70.3 77.4 84.6 76.7 25.1 - 38.8 17.8</td>
<td></td>
</tr>
<tr>
<td>P. conspicillatus</td>
<td>146.0</td>
<td>20.0</td>
<td>58.8 ± 2 159.5 ± 107.2 ± 79.4</td>
<td>75.8 ± 137.3 ± 106.8 ± 74.8 ± 132.3 ± 55.5 ± 86.8 ± 18.7 ±</td>
</tr>
<tr>
<td>(n = 2)</td>
<td></td>
<td></td>
<td>.6 11.3 27.3 4.7 22.4 33.1 12.6 1.5 7.7 10.8 1.5</td>
<td></td>
</tr>
<tr>
<td>P. scapulatus (n</td>
<td>114.0</td>
<td>118.0</td>
<td>56.9 116.1 83.6 - 44.4 112.5 85.6 - 96.9 52.3 100.3 53.5</td>
<td></td>
</tr>
<tr>
<td>= 1)</td>
<td></td>
<td></td>
<td></td>
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</tr>
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</table>
Table 3. Summary of fur solar reflectivities for different body regions

<table>
<thead>
<tr>
<th>Species</th>
<th>Body region</th>
<th>Ultraviolet region</th>
<th>Visible region 1</th>
<th>Visible region 2</th>
<th>Infrared region 1</th>
<th>Infrared region 2</th>
<th>Total solar reflectivity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. poliocephalus</em> (n=24)</td>
<td>Dorsal collar</td>
<td>5.1</td>
<td>6.9</td>
<td>19.7</td>
<td>44.5</td>
<td>40.7</td>
<td>30.8</td>
</tr>
<tr>
<td></td>
<td>Dorsal abdomen</td>
<td>4.6</td>
<td>5.5</td>
<td>7.1</td>
<td>29.0</td>
<td>43.3</td>
<td>20.9</td>
</tr>
<tr>
<td></td>
<td>Ventral collar</td>
<td>3.8</td>
<td>4.6</td>
<td>12.3</td>
<td>38.7</td>
<td>35.9</td>
<td>25.5</td>
</tr>
<tr>
<td></td>
<td>Ventral abdomen</td>
<td>3.9</td>
<td>4.8</td>
<td>7.6</td>
<td>29.8</td>
<td>39.7</td>
<td>20.8</td>
</tr>
<tr>
<td><em>P. alecto</em> (n=3)</td>
<td>Dorsal collar</td>
<td>3.9</td>
<td>4.2</td>
<td>10.8</td>
<td>39.0</td>
<td>40.7</td>
<td>25.7</td>
</tr>
<tr>
<td></td>
<td>Dorsal abdomen</td>
<td>2.3</td>
<td>2.8</td>
<td>3.9</td>
<td>22.3</td>
<td>36.8</td>
<td>15.9</td>
</tr>
<tr>
<td></td>
<td>Ventral collar</td>
<td>2.6</td>
<td>2.7</td>
<td>3.2</td>
<td>16.9</td>
<td>29.9</td>
<td>12.5</td>
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<tr>
<td></td>
<td>Ventral abdomen</td>
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<td>2.8</td>
<td>3.6</td>
<td>22.3</td>
<td>38.0</td>
<td>16.0</td>
</tr>
<tr>
<td><em>P. conspicillatus</em> (n=3)</td>
<td>Dorsal collar</td>
<td>4.3</td>
<td>9.2</td>
<td>29.8</td>
<td>52.9</td>
<td>41.7</td>
<td>37.5</td>
</tr>
<tr>
<td></td>
<td>Dorsal abdomen</td>
<td>0.8</td>
<td>1.8</td>
<td>2.9</td>
<td>26.5</td>
<td>35.3</td>
<td>17.1</td>
</tr>
<tr>
<td></td>
<td>Ventral collar</td>
<td>3.2</td>
<td>4.4</td>
<td>11.4</td>
<td>38.3</td>
<td>39.8</td>
<td>25.5</td>
</tr>
<tr>
<td></td>
<td>Ventral abdomen</td>
<td>1.8</td>
<td>2.6</td>
<td>3.3</td>
<td>25.5</td>
<td>37.8</td>
<td>17.2</td>
</tr>
<tr>
<td></td>
<td>Dorsal collar</td>
<td>3.8</td>
<td>5.3</td>
<td>15.3</td>
<td>45.3</td>
<td>46.3</td>
<td>30.5</td>
</tr>
<tr>
<td></td>
<td>Dorsal abdomen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------</td>
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<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td></td>
</tr>
<tr>
<td><em>P. scapulatus</em> (n=16)</td>
<td>2.0</td>
<td>2.9</td>
<td>6.4</td>
<td>33.6</td>
<td>42.0</td>
<td>22.1</td>
<td></td>
</tr>
<tr>
<td>Ventral collar</td>
<td>3.4</td>
<td>4.6</td>
<td>14.5</td>
<td>37.7</td>
<td>33.9</td>
<td>25.3</td>
<td></td>
</tr>
<tr>
<td>Ventral abdomen</td>
<td>3.4</td>
<td>3.8</td>
<td>9.6</td>
<td>38.2</td>
<td>43.7</td>
<td>25.4</td>
<td></td>
</tr>
</tbody>
</table>