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1 **Title:**

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

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5 **Running header:**

6 Fur properties of Australian flying-foxes

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8 **Authors:**

9 Himali Udeshinie Ratnayake (H.U.R.)*¹, Justin Arno Welbergen (J.A.W.)², Rodney van der Ree
10 (R.v.d.R.)^{1,3}, Michael Ray Kearney (M.R.K.)¹

11 *Corresponding author

12

13 **Author affiliations:**

14 ¹School of BioSciences, the University of Melbourne, Parkville, VIC 3010, Australia

15 ²Hawkesbury Institute for the Environment, Western Sydney University, NSW 2751, Australia

16 ³Ecology and Infrastructure International Pty Ltd, PO Box 6031, Wantirna, VIC 3152, Australia

17

18 **Abstract:**

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

34

35 **Key words:**

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

37 **Introduction**

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

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

58 environment it is experiencing (Conley and Porter 1986; Dawson and Maloney 2004; Dawson,
59 Webster *et al.* 2014; Walsberg 1988a).

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

71 Here, we focus on three fur properties that can be non-invasively measured using museum
72 specimens: fur depth, fur length and fur solar reflectance. Fur depth is the vertical depth of the
73 fur layer. Since air has low thermal conductivity, the air trapped among the fur insulates the
74 skin surface in proportion to fur depth and thus creates a resistance to conductive heat flow
75 out of the body. Fur depth depends on fur length and fur angle. Fur length can vary from
76 species to species depending on body size (Schmidt-Nielsen 1997), and even among different
77 parts of the body (Underwood and Reynolds 1980). The length of the fur in part influences
78 overall pelt thermal conductivity by altering the ratio of hair to air in a given volume of fur. It
79 also limits the maximum potential fur depth under piloerection (Rymer, Kinahan *et al.* 2007;

80 Underwood and Reynolds 1980), a process used by mammals where the hairs take a $\sim 90^\circ$ angle
81 to the body and thereby create a deeper insulation layer. Piloerection can allow more solar
82 radiation to enter in between the hairs to reach the skin surface, which can consequentially
83 increase pelt temperature (Wacker, McAllan *et al.* 2016) that in turn increases the radiant heat
84 load on the skin (Gates 1980). Finally, the fur solar reflectivity quantifies the amount of incident
85 solar radiation that is reflected by the fur surface, and thus the overall heat load via solar
86 radiation on the pelt (Porter and Gates 1969). The reflectivity may vary with hair orientation
87 (i.e. the angle at which the hair emerges from the skin surface), which can be controlled by
88 piloerection (Gates 1980).

89 Fur properties can vary with season and climate (Briscoe, Krockenberger *et al.* 2015; Walsberg
90 and Schmidt 1989). In broadly distributed species a compromised set of fur properties can
91 facilitate thermoregulation in several habitats and conditions, whereas fur properties of species
92 with a restricted distribution can be fine-tuned to local stable conditions (Briscoe,
93 Krockenberger *et al.* 2015; Scholander, Walters *et al.* 1950). The selective pressures on fur traits
94 are complex and it is difficult to predict how they should vary. All else being equal, we might
95 expect an animal adapted to colder climates to have a well-insulated fur coat with dense, deep
96 fur and dark, long hairs. We might also expect high fur density in organisms exposed to strong
97 sunlight, however, because it reduces solar load on the skin. We might also expect high fur
98 density and depth in organisms exposed to high radiant heat, because it reduces penetrance of
99 solar radiation into the fur to the extent that solar reflectance of fur becomes irrelevant and fur
100 colour is freer to vary for other purposes like camouflage (Dawson, Webster *et al.* 2014). An
101 additional complicating factor is the variation in thermal environments. In seasonal

102 environments we might expect fur properties to change through the year via moulting
103 (Walsberg, Weaver *et al.* 1997). Extreme weather events that occur over days or hours pose a
104 particular challenge, however, because most fur properties cannot be adjusted on such short
105 time scales.

106 A prominent example of the challenges posed by extreme weather events in mammals is found
107 in Australia's mainland flying-foxes that can suffer mass mortality during very high ambient
108 temperatures (~ 42.0 °C) (Ratnayake, Kearney, *et al.* 2019; Welbergen, Klose *et al.* 2008). The
109 frequency, intensity and duration of extreme heat events have increased, and are expected to
110 continue to increase, due to climate change (Meehl and Tebaldi 2004; Steffen, Hughes *et al.*
111 2014), and thus an increase in the frequency and magnitude of flying-fox die-offs has been
112 suggested (Welbergen, Klose *et al.* 2008). Post-mortem observations of colonies containing
113 black flying-foxes (*Pteropus alecto*) and grey-headed flying-foxes (*P. poliocephalus*) have
114 revealed a skewed proportional mortality rate towards *P. alecto*, and towards females and
115 juveniles of both species (Welbergen, Klose *et al.* 2008). The reason for these biases in mortality
116 rates may reflect the species-, sex-, and age-specific physiology, rather than the individual body
117 condition (Welbergen, Klose *et al.* 2008). However, it is also possible that differences in fur
118 properties among and within species play a role in the sensitivity to heat stress.

119 Motivated by these inter- and intra-specific patterns of heat-related mortality, we compared
120 the thermal properties of the fur of four species of flying fox: *P. alecto*, *P. poliocephalus*, *P.*
121 *conspicillatus*, and *P. scapulatus*. We aimed to assess whether the fur properties length, depth,
122 and solar reflectance varied among body parts (i.e. dorsal and ventral collar and abdominal
123 regions), among sexes and age groups (i.e. juveniles and adults), and among species. We then

124 interpreted these patterns in the context of what we know of the species' thermal
125 environments and their sensitivity to extreme heat events.

126

127 **Materials and Methods**

128 *Study species*

129 Flying-foxes (*Pteropus* spp.) are large bats that form conspicuous daytime roosts in amongst the
130 exposed branches of canopy trees (Churchill 2009). There are four species of flying-fox in
131 mainland Australia; the grey-headed flying-fox (*P. poliocephalus*), the black flying-fox (*P. alecto*),
132 the spectacled flying-fox (*P. conspicillatus*), and the little red flying-fox (*P. scapulatus*) (Fig. 1).
133 The distribution of *P. poliocephalus* is restricted to the temperate and subtropical regions of
134 eastern and southeastern Australia (Churchill 2009; Eby 1991) (Fig. 1). *Pteropus alecto* have a
135 widespread distribution from Western Australia to New South Wales but is mainly limited to
136 coastal regions (Churchill 2009) (Fig. 1). *Pteropus conspicillatus* comparatively have the most
137 restricted distribution in the tropical far north Queensland (Churchill 2009) (Fig. 1). *Pteropus*
138 *scapulatus* is the most widely distributed species within Australia, with its individuals being
139 found in Western Australia and Northern Territory, from the north to south Queensland,
140 through New South Wales and Victoria (Churchill 2009), exposing them to temperate and
141 (sub)tropical climates (Fig. 1). They are a nomadic species that can be found further inland
142 compared to the other species (Churchill 2009).

143

144 *Morphometric measurements*

145 We measured fur length and fur depth of *P. poliocephalus* (n = 29), *P. alecto* (n = 12), *P.*
146 *conspicillatus* (n = 10) and *P. scapulatus* (n = 22) specimens sourced from the Melbourne
147 Museum, Victoria, and from the Australian Museum, New South Wales. Fur solar reflectance of
148 the four species (n = 24, 3, 3, and 16, for *P. poliocephalus*, *P. alecto*, *P. conspicillatus*, and *P.*
149 *scapulatus*, respectively) was measured from specimens sourced from the Melbourne Museum.
150 The forearm length and total body length were also measured (Table 1 & Table 2). The age
151 category (adult, n = 60 or juvenile, n = 13), sex, date the specimen was collected, and sourced
152 location were noted where available (for further details see Supplementary material S1).

153

154 *Fur length and fur depth*

155 We measured the fur length of the head, upper (collar) and lower (abdomen) torso and legs,
156 when present, in both the dorsal and ventral sides to the nearest 0.1 mm (Fig. 2) using
157 Workzone® digital callipers (model number – ANS-16-039). Prior to measuring the fur length,
158 we combed the hair in the opposite direction of its natural orientation. Fur length was defined
159 as the length of hair from the skin surface to the tip of the hair. We measured the fur depth of
160 the collar and abdomen regions in the dorsal and ventral sides (Fig. 2). Fur depth was measured
161 when the hair was resting naturally on the skin surface and was defined as the perpendicular
162 distance between the skin surface and the outer edge of the fur coat. We recorded this
163 perpendicular distance by placing a ruler on the skin surface and marking the tip of the pelage
164 on the ruler, and then measuring the end of the ruler to the mark using the callipers.

165 Measurements were non-invasive to preserve the bat specimens in the museums, and this
166 precluded measurement of fur density as this required removal of a sample of fur.

167

168 *Solar reflectance*

169 The fur solar reflectance was measured for the upper (collar) and lower (abdomen) torso on
170 both the dorsal and ventral sides. Fur solar reflectance was measured at three replicate
171 locations dorsally and ventrally in the collar and abdominal regions using a set-up consisting of
172 two spectrometers (NIR-Quest and USB4000, Ocean Optics, USA) that were used to measure
173 spectral reflectance from 300 – 1000 nm and 1000 – 2000 nm respectively. The spectrometers
174 had two light sources (PX-2 pulsed Xenon light for the UV-Vis range and HL-2000 tungsten
175 halogen lights for the Vis-NIR range) connected to a quadrifurcated fibre optic ending in a single
176 probe, which had an oval-shaped measuring area of 5 mm x 3 mm. The probe was held in an
177 Ocean Optics RPH-1 probe holder (Ocean Optics, Inc., USA) at a constant 45° angle and constant
178 ~1 cm distance from the skin surface. Each measurement was compared against a Spectralon
179 99% white reflectance standard (Labsphere Inc., North Sutton, NH, USA). The average of the
180 measurements made for dorsal and ventral surfaces of the collar and abdominal regions were
181 converted to solar reflectivity by calculating the weighted average across 37 bandwidths
182 between 260-2600nm (Supplementary material S2) for each body region. As we could only
183 measure reflectance at wavelengths up to 2000nm, we assumed that reflectance remained
184 constant above this value. This missing region of the spectrum in our measurements accounts
185 for 4% of solar radiation and therefore deviations from this assumption would not strongly alter

186 our results.

187

188 *Statistical Analysis*

189 We used the R package lme4 (Bates, Mächler *et al.* 2015) to perform a linear mixed effects
190 analysis of the relationship between each fur trait and species. We used backward-stepwise
191 model selection, where each factor in the full model was tested for significance and the non-
192 significant terms were removed until only the significant terms remained (Dominoni *et al.*
193 2020). When the generalized linear mixed models (GLMM) were created, to minimize the
194 variation in body part fur lengths, we only considered the fur length in the torso area, i.e. the
195 collar and abdominal regions. To determine the best fitting GLMM for fur length and depth
196 species, total body length (a proxy for body size), sex, age, body part, and their interactions
197 were evaluated as fixed effects. In the GLMM for total fur solar reflectivity species, body part,
198 sex, and their interactions were considered as fixed effects. In all models, individual identity
199 was considered as a random effect. Visual inspection of residual plots did not reveal any
200 obvious deviations from homoscedasticity or normality (Supplementary material S4). We
201 assessed for autocorrelation between total body length, age, and sex; however, there were no
202 significant autocorrelations between these predictors ($|P| > 0.05$). All post hoc comparisons
203 were performed based on the t -distribution using degrees of freedom based on Satterthwaites
204 method. All values are expressed as mean \pm standard deviation and $P < 0.05$ was considered
205 statistically significant unless mentioned otherwise. All analyses were conducted in R version
206 3.4.1 (R Core Team 2017).

207

208 Results

209 There was considerable variation among morphometric measurements both among and within
210 species (Table 1 – 3). Fur length varied significantly among species, body part and their
211 interaction (GLMM; species: $F_{3,9} = 17.40$, $P < 0.001$; body part: $F_{3,9} = 73.91$, $P < 0.001$;
212 interaction: $F_{9,3} = 2.35$, $P = 0.01$; Supplementary material Fig. S1). Fur depth also varied
213 significantly among the species, sex, age, and body part (GLMM; species: $F_{3,1} = 55.57$; $P < 0.001$;
214 sex: $F_{1,3} = 17.23$, $P = 0.0001$; age: $F_{1,3} = 5.41$; $P = 0.023$; body part: $F_{3,1} = 35.60$; $P < 0.001$)
215 (Supplementary material Fig. S2). There was no significant effect by body size on either fur
216 length or fur depth ($F_{1,3} = 3.39$, $P = 0.07$ and $F_{1,3} = 2.77$, $P = 0.100$, respectively). Fur solar
217 reflectivity varied significantly among species, body parts, and their interaction (GLMM;
218 species: $F_{3,9} = 6.27$, $P = 0.001$; body parts: $F_{3,9} = 39.06$, $P < 0.001$; interaction: $F_{9,3} = 3.52$, $P <$
219 0.001) (Supplementary material Fig. S3).

220

221 Variation in fur length of Australian flying-foxes

222 *Pteropus poliocephalus* had the highest mean fur length (Table 1), while *P. scapulatus* had the
223 lowest mean fur length, and *P. alecto* and *P. conspicillatus* had similar, intermediate, mean fur
224 lengths (Supplementary material S5; Fig. S5, S8 & S9). Fur lengths of each body part were
225 significantly different from each other ($P < 0.001$), except between the ventral and dorsal
226 abdominal regions ($P = 0.80$; Supplementary material S5; Fig. 3). Across all four species, the
227 dorsal collar had the longest fur, and the ventral collar had the second longest fur, while the
228 dorsal and ventral abdomen furs were the third longest and of similar length (Fig. 4). In all body

229 regions, *P. poliocephalus* had longer hair compared to the other three species, and *P.*
230 *scapulatus* consistently had shorter fur length in all body parts compared to the other species
231 (Fig. 4). The greatest variation in fur lengths among species was found in the dorsal collar region
232 (Fig. 4). The interaction term in the GLMM reflected the fact that differences in fur length
233 between body parts were most pronounced in *P. poliocephalus* and least pronounced in *P.*
234 *scapulatus* with the other two species in between.

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

238

239 Variation in fur depth of Australian flying-foxes

240 *Pteropus poliocephalus* had significantly deeper fur compared to the other three species ($P <$
241 0.001) (Supplementary material S5; Fig. S6, S8 & S9). The fur depths among the other three
242 species were not significantly different (*P. alecto* - *P. scapulatus* $P = 0.010$; *P. alecto* - *P.*
243 *conspicillatus* $P = 0.250$; *P. scapulatus* - *P. conspicillatus* $P = 0.440$) (Supplementary material S5).

244 Fur depths were significantly different between all body parts considered (Supplementary
245 material S5). In all species a general pattern was for fur to be deeper in the collar region
246 compared to the abdominal region (Table 1).

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

248 There was a significant interaction between species and sex in the GLMM for fur depth
249 (Supplementary material Fig. S2). Specifically, there is a difference in the fur depths between

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

256

257 Variation in fur solar reflectance of Australian flying-foxes

258 The solar reflectivity of *P. alecto* fur was significantly lower compared to that of the other three
259 species ($P < 0.010$) (Supplementary material S5; Fig. S7 & S9). The dorsal collar fur had a
260 significantly higher solar reflectivity compared to the other body parts (Supplementary material
261 S5, Fig. 5). There was a significant interaction between species and body part in the GLMM for
262 fur solar reflectivity (Supplementary material Fig. S3), whereby the black headed flying fox had
263 lower reflectance overall, but this was especially strong for the ventral collar region.

264 There was no effect of sex on the solar reflectivity of fur, and sex was thus not considered in the
265 final GLMM (Supplementary material Fig. S3). There were only three juvenile *P. poliocephalus*
266 specimens and one juvenile *P. scapulatus* specimen to measure fur solar reflectance; thus, we
267 did not consider differences in fur solar reflectivity between age groups.

268

269 **Discussion**

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

287

288 *Distribution, climate and fur properties*

289 Compared to the other species, *P. poliocephalus* had the longest and deepest fur, which implies
290 greater thermal insulation. This is consistent with the species' more temperate distribution

291 (Churchill 2009; Hall and Richards 2000) and thus greater exposure to cold. The similarly short
292 fur lengths of *P. alecto* and *P. conspicillatus* is reflected in their similar geographic distributions;
293 *P. conspicillatus* is restricted to the tropics and *P. alecto* shares this distribution and also
294 expands to the subtropical regions (Churchill 2009). Similar observations have been made in
295 koalas where fur depth substantially decreases clinally towards the tropics (Briscoe,
296 Krockenberger *et al.* 2015).

297

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

300 The discrepancies and biases shown in flying-fox mortality rates during extreme heat events are
301 consistent with the expected heat transfer consequences of the variation we observed in the
302 fur properties of the different species, ages, and sexes. In mixed-species colonies, different
303 species often vary in their roost height under benign weather conditions, e.g. *P. alecto* tend to
304 roost higher in the canopy compared to *P. poliocephalus* (Welbergen 2005). However, during an
305 extreme heat event, there are no known roosting differences between species as all are then
306 generally found near or on the ground in the coolest spots in the roost. Nevertheless, due to
307 limited shade availability, spaces between branches and leaves, and scattered light, most flying-
308 foxes are not completely covered from sunlight and their fur solar reflectivity would still be
309 relevant in reducing their heat load. Thus, the greater mortality rates of *P. alecto* compared to
310 *P. poliocephalus* observed in mixed-species colonies in the field may in part relate to the lower
311 fur solar reflectivity of *P. alecto* (Welbergen, Klose *et al.* 2008). The shorter fur of *P. alecto* may

312 also allow heat to penetrate deeper into the fur and thus render it more vulnerable to heat
313 stress than *P. poliocephalus*. A more complete answer to this question will require biophysical
314 analyses and quantification of radiant conditions within the roost during heat stress events that
315 jointly consider the combined influences fur has on radiant heat gain through solar radiation
316 penetrance and heat loss by conduction and radiation through the fur (e.g. Conley and Porter
317 1986; Dawson and Maloney 2004; Mathewson and Porter 2013). These analyses will also need
318 to consider the role of fur properties in influencing the evaporative cooling mechanisms that
319 these species use, such as licking their wings, fur and skin (Welbergen, Klose et al. 2008).

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

325 Although the higher relative mortality rates of adult females and juveniles during flying-fox
326 extreme heat events may be explained by their differences in physiology (Welbergen, Klose *et*
327 *al.* 2008), the differences in their fur properties can also contribute to this disparity. Our results
328 show that juveniles had deeper fur than adults, and *P. alecto* and *P. conspicillatus* females have
329 significantly deeper fur than males. New-born bats are naked and poikilothermic and, in a few
330 days, they develop fur and become normothermic (Noll 1979; Weigold 1973). While the deeper
331 fur in juveniles would assist to prevent hypothermia, during an extreme heat event the deep fur
332 which provides a good insulation layer may become detrimental to them, depending on the
333 depth of radiant heat penetration, which was not measured in the current study. Moreover,

334 since juveniles have a smaller mass to surface area ratio compared to adults, they have a lower
335 thermal inertia, and thus could rapidly overheat, necessitating more pronounced evaporative
336 cooling and access to water/milk. However, we did not see a significant effect by age on fur
337 length (potentially due to the small sample size).

338 Furthermore, it should be noted that even though in the majority of instances darker fur results
339 in higher solar heat loads compared to light fur, there are sometimes complex interactions
340 between pelage colour, microstructure, optical properties, behaviour and convective heat loss,
341 especially under certain environmental conditions (e.g. windy) that can result in higher heat
342 gain for light coloured pelages (Wolf and Walsberg 2000). As flying-foxes can be exposed to
343 high wind speeds if there is less understory vegetation in their roosting trees, species with
344 lighter fur may gain a greater solar heat load than those with darker pelage (Wolf and
345 Walsberg, 2000). Moreover, since solar penetrance is greater in shorter fur, the impact of
346 colour is greater on shallower pelts (Dawson and Maloney 2004; Dawson, Webster *et al.* 2014).
347 Small mammals, such as flying-foxes, have comparatively short fur, and thus the differences in
348 pelt colouration of different species may have a considerable effect on the absorbed heat load
349 (Dawson, Webster *et al.* 2014).

350

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

352 Although significant variations in fur properties in different body parts has been observed in
353 some bats (Madej, Mikulová *et al.* 2013), their relative effect on thermoregulation, especially
354 under extreme heat conditions, has not been thoroughly explored. When heat stressed, flying-

355 foxes fan their wings (Bartholomew, Leitner *et al.* 1964; Welbergen, Klose *et al.* 2008) and we
356 have observed that this inwardly-directed fanning created a movement of air along the ventral
357 surface of the body, which allowed heat to be lost through forced convection (Ratnayake 2018).
358 Since these wing fanning effects are not directed to the dorsal side of the body, the higher fur
359 solar reflectivity on the dorsal side as observed in our results across all species may help to
360 minimize the heat gain from solar radiation.

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

375

376 *Concluding remarks and future work*

377 In addition to the fur properties considered in this study, fur density (Dawson and Maloney
378 2004; Hutchinson and Brown 1969; Rymer, Kinahan *et al.* 2007) is an important trait relevant
379 for thermoregulation, especially through its effect on solar penetrance to the skin. Thermal
380 conductance (insulation) and conductivity are also common variables used to measure the
381 thermal properties of mammalian pelage (Dawson and Maloney 2004; Hammel 1955). The
382 conductivity of a pelage is defined as the heat flowing per unit area per unit time divided by the
383 temperature gradient (Hammel 1955) and can provide valuable insights about the
384 thermoregulatory purposes of a pelage. All these different fur traits play an important role in
385 flying-fox thermoregulation. However, to understand the effect of each property and their
386 relative importance on heat exchange we must consider the joint physical relationships among
387 the fur structure, fur-air interface, solar radiation, infrared radiation, convection, conduction
388 and the other factors involved in this heat and mass transfer. For instance, the effects of
389 piloerection and multiple sources of heat on one surface (e.g. skin) create complexities that
390 must be carefully analysed to gain a full understanding of the effect on the animal's heat
391 budget. The information from this study can be used to further explore the adaptive
392 significance of the variation in fur, which can be achieved using the principles of biophysical
393 ecology (Kearney and Porter 2017; Porter and Mitchell 2006; Porter, Munger *et al.* 1994) and
394 this is an obvious future direction that would enable us to make better predictions of how
395 flying-foxes would cope in future climate change scenarios.

396

397 **Conflicts of Interest:**

398 The authors declare no conflicts of interest.

399

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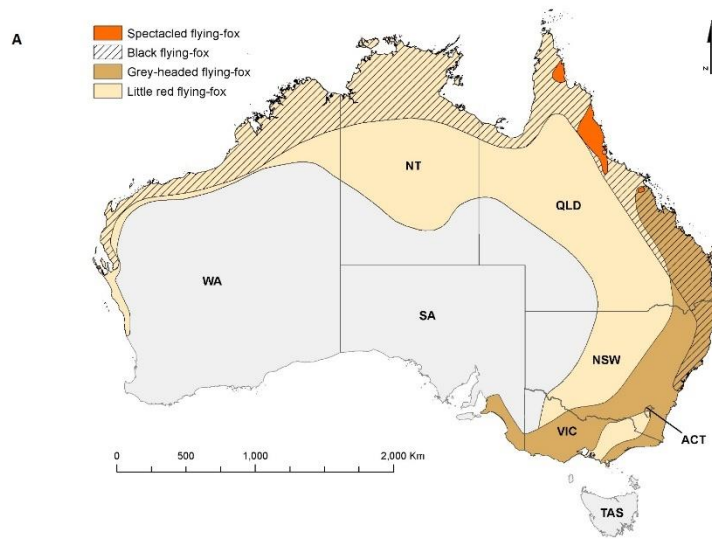
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1 **Figures**

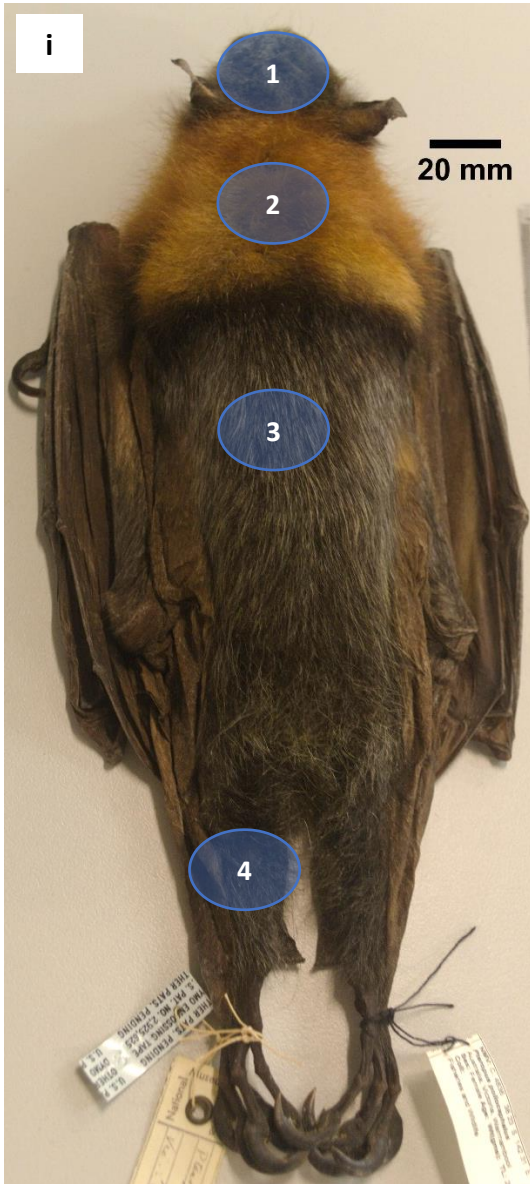


2

3 Fig. 1. **(A)** Reproduced distribution map of the four species of mainland Australian flying-foxes (Currey
4 *et al.* 2018), and **(B)** photographs of these species demonstrating their fur colouration (all photos
5 taken by Justin Welbergen).

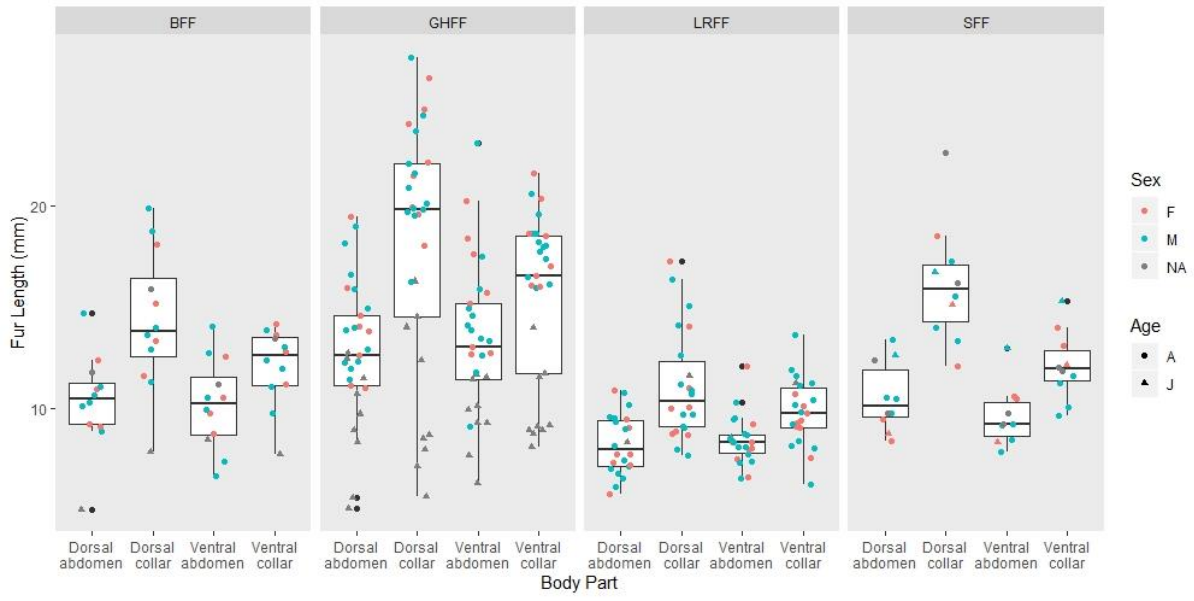
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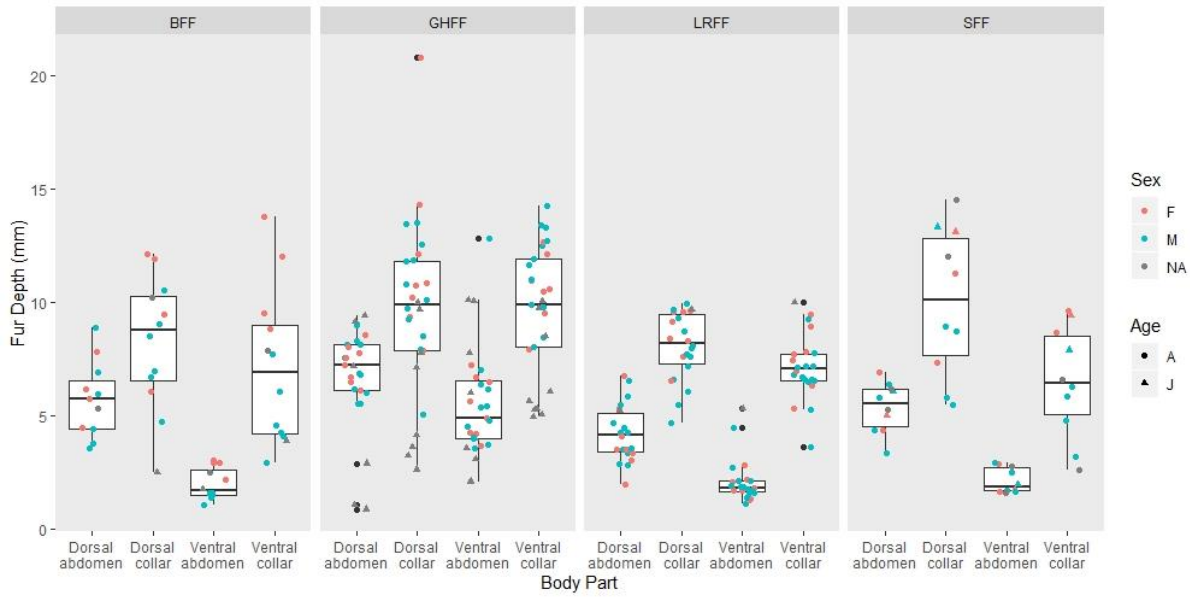


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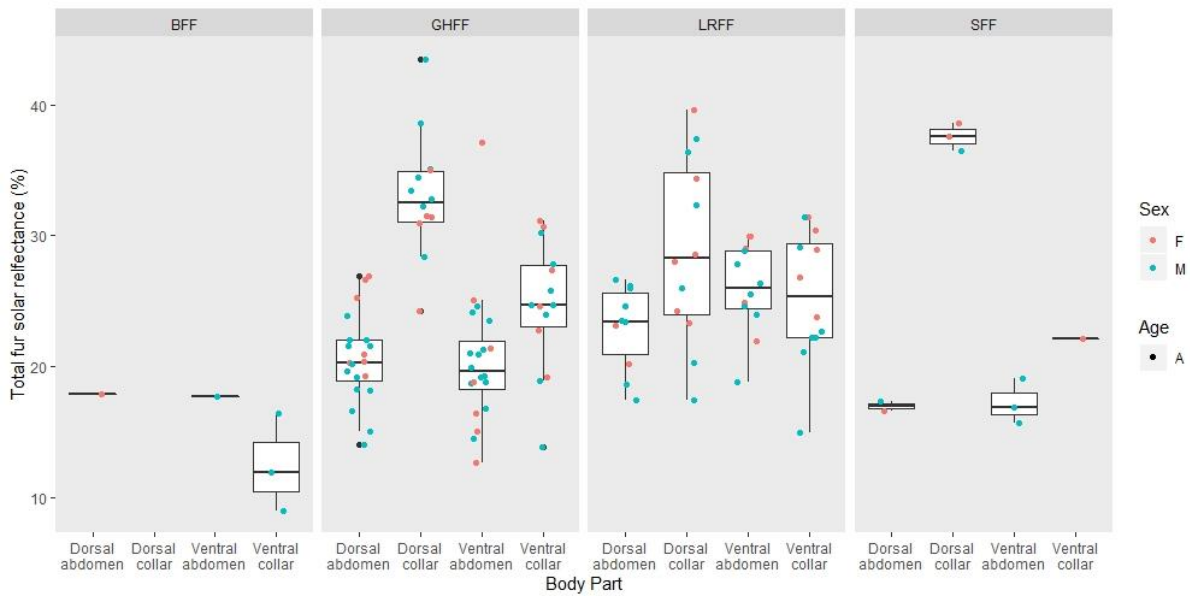
10 Fig. 2. Body regions used in measuring morphometric variables of museum specimens. i, ventral side
 11 of grey-headed flying-fox body, ii, dorsal side of grey-headed flying-fox body. The regions were
 12 categorized in the following manner: 1, dorsal head; 2, dorsal collar; 3, dorsal abdomen; 4, dorsal leg;
 13 5, ventral head; 6, ventral collar; 7, ventral abdomen; 8, ventral leg.



14

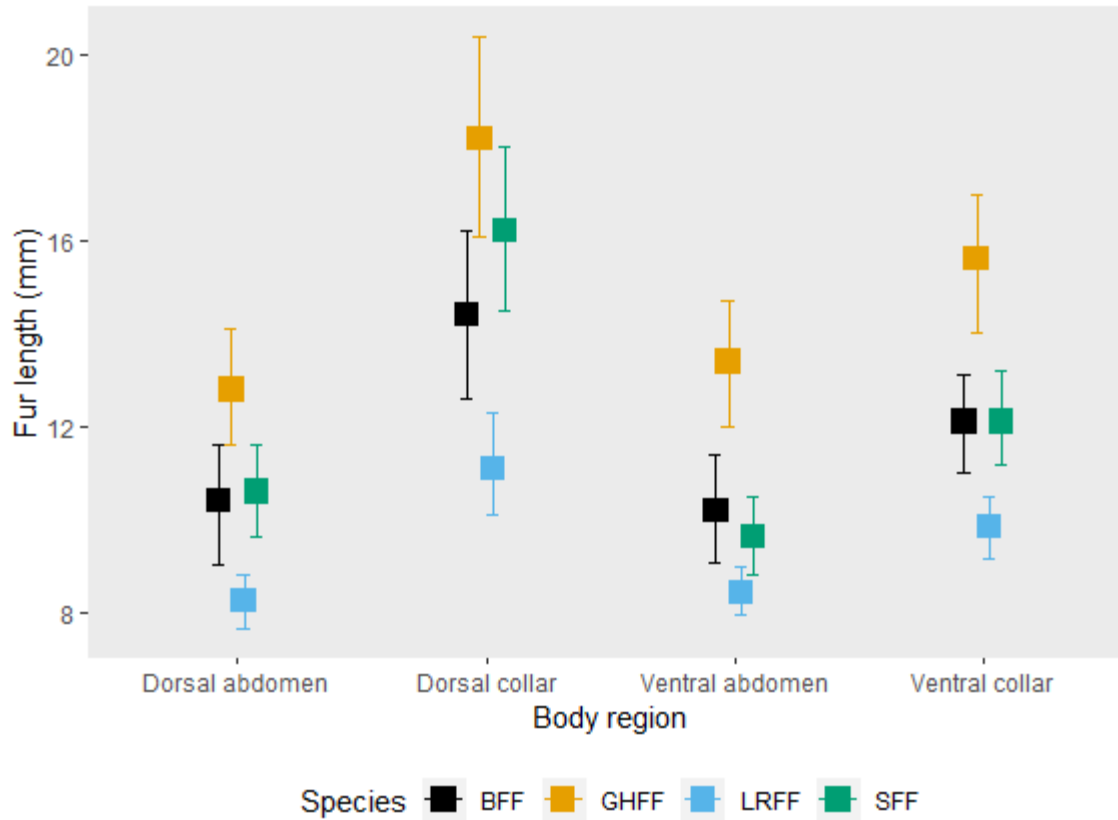


15



16

17 Fig. 3. Detailed box plots including (i) fur length, (ii) fur depth, and (iii) fur solar reflectance values of
 18 each measured individual. The different colours represent sex, the points represent all the
 19 measurements, and the shape represents the age classes. In the 'Sex' legend the pink colour
 20 represents females (F), blue colour represents males (M), and grey colour represents individuals
 21 whose sex could not be determined (NA). In the 'Age' legend the circle represents adults (A) and the
 22 triangle represents juveniles (J); solar reflectance of juveniles was not measured. BFF, *P. alecto*; GHFF,
 23 *P. poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*



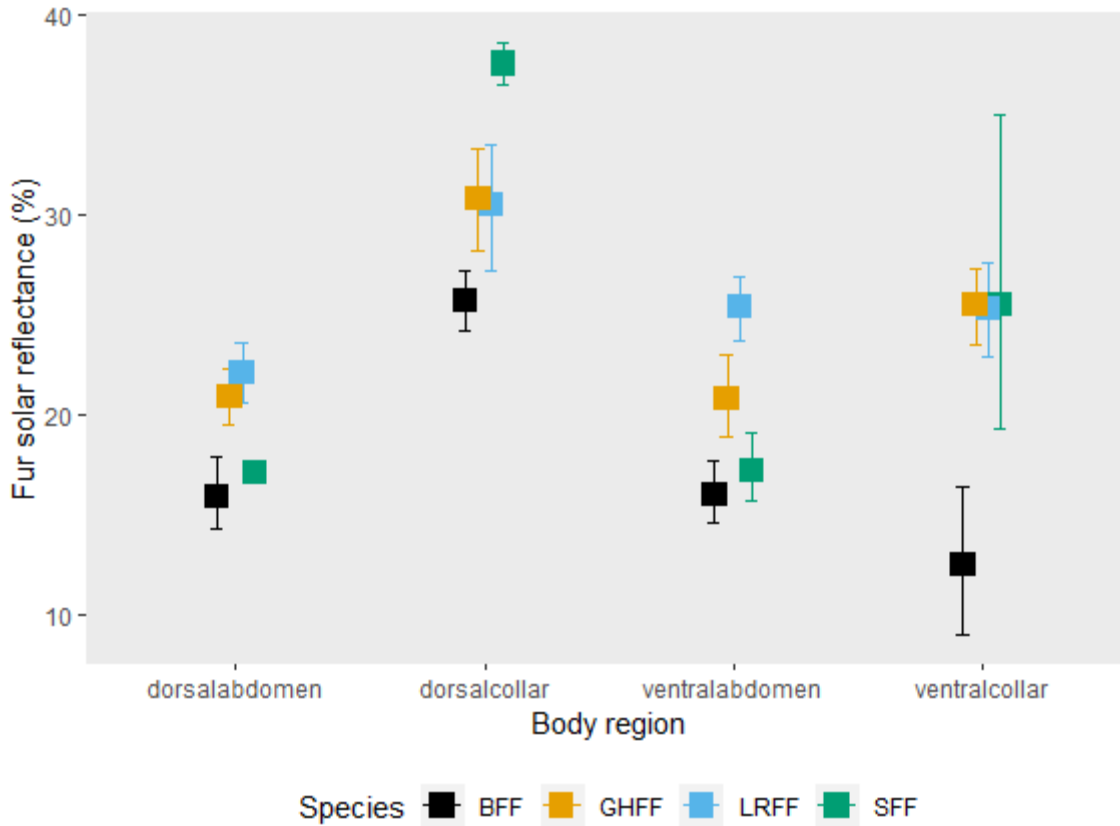
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25

26 Fig. 4. Fur lengths of different body parts in the four flying-fox species – BFF, *P. alecto*; GHFF, *P.*

27 *poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*. The values in the boxplots represent

28 the median and interquartile range of the distributions of the data.



29

30 Fig. 5. Total fur solar reflectivity of different body parts in the four flying-fox species – BFF, *P.*
 31 *alecto*; GHFF, *P. poliocephalus*; LRFF, *P. scapulatus*; SFF, *P. conspicillatus*. The values in the
 32 boxplots represent the median and interquartile range of the distributions of the data.

33 **Tables**

34 Table 1. Summary of morphometric measurements of all adult flying-foxes

Species	Forearm Length (mm)	Total Body Length (mm)	Fur Length (mean ± standard deviation)								Fur Depth (mean ± standard deviation)			
			Dorsal		Dorsal Abdomen		Ventral		Ventral Abdomen		Dorsal	Dorsal Abdomen	Ventral	Ventral Abdomen
			Head	Collar	Head	Collar	Head	Collar	Head	Collar	Collar	Abdomen	Collar	Abdomen
<i>P. poliocephalus</i> (n = 20)	155.9	257.4	115.7 ± 26.7	216.1 ± 28.0	143.1 ± 25.4	104.2 ± 25.9	79.9 ± 14.5	180.3 ± 16.3	150.1 ± 31.7	115.7 ± 26.5	110.6 ± 31.9	72.9 ± 11.0	110.6 ± 18.3	55.6 ± 20.9
<i>P. alecto</i> (n = 11)	155.2	233.7	90.3 ± 26.6	149.8 ± 28.8	108.6 ± 16.8	76.5 ± 16.1	69.5 ± 16.7	125.1 ± 13.7	104.0 ± 22.5	86.3 ± 18.3	87.7 ± 24.0	57.4 ± 16.7	74.4 ± 34.6	20.3 ± 7.1
<i>P. conspicillatus</i> (n = 8)	157.9	239.8	79.9 ± 18.1	162.1 ± 33.5	105.5 ± 16.2	90.2 ± 21.7	56.1 ± 14.0	117.2 ± 14.3	93.5 ± 9.4	86.8 ± 17.6	92.6 ± 31.6	53.4 ± 12.2	59.7 ± 24.4	22.2 ± 6.1
<i>P. scapulatus</i> (n = 21)	130.8	198.8	52.9 ± 17.4	111.1 ± 27.8	82.4 ± 15.1	54.5 ± 17.4	51.8 ± 12.4	97.8 ± 16.6	84.4 ± 12.4	73.1 ± 20.1	80.0 ± 14.9	41.7 ± 12.4	70.2 ± 13.3	19.7 ± 7.1

36 Table 2. Summary of morphometric measurements of all juvenile flying-foxes

Species	Forearm Length (mm)	Total Body Length (mm)	Fur Length (mean ± standard deviation)						Fur Depth (mean ± standard deviation)					
			Dorsal		Dorsal Abdomen	Ventral		Ventral		Dorsal	Dorsal Abdomen	Ventral		Ventral
			Head	Collar	en	Head	Collar	en	Collar	en	Collar	en	Collar	en
<i>P. poliocephalus</i> (n = 9)	81.4	127.3	62 ± 16.0	106.0 ± 37.7	94.6 ± 27.7	64.5 ± 14.6	75.1 ± 15.4	100.4 ± 19.4	97.1 ± 18.3	86.2 ± 21.5	60.5 ± 29.8	51.1 ± 39.4	67.4 ± 20.9	54.4 ± 32.1
<i>P. alecto</i> (n = 1)	70.0	100.0	61.9	78.8	50.4	41.1	70.3	77.4	84.6	76.7	25.1	-	38.8	17.8
<i>P. conspicillatus</i> (n = 2)	146.0	20.0	58.8 ± 2.6	159.5 ± 11.3	107.2 ± 27.3	79.4	75.8 ± 4.7	137.3 ± 22.4	106.8 ± 33.1	74.8 ± 12.6	132.3 ± 1.5	55.5 ± 7.7	86.8 ± 10.8	18.7 ± 1.5
<i>P. scapulatus</i> (n = 1)	114.0	118.0	56.9	116.1	83.6	-	44.4	112.5	85.6	-	96.9	52.3	100.3	53.5

37

38 Table 3. Summary of fur solar reflectivities for different body regions

Species	Body region	Ultraviolet region solar reflectivity (%)	Visible region 1 solar reflectivity (%)	Visible region 2 solar reflectivity (%)	Infrared region 1 solar reflectivity (%)	Infrared region 2 solar reflectivity (%)	Total solar reflectivity (%)
<i>P.</i>	Dorsal collar	5.1	6.9	19.7	44.5	40.7	30.8
<i>poliocephalus</i> (n=24)	Dorsal abdomen	4.6	5.5	7.1	29.0	43.3	20.9
	Ventral collar	3.8	4.6	12.3	38.7	35.9	25.5
	Ventral abdomen	3.9	4.8	7.6	29.8	39.7	20.8
<i>P. alecto</i> (n=3)	Dorsal collar	3.9	4.2	10.8	39.0	40.7	25.7
	Dorsal abdomen	2.3	2.8	3.9	22.3	36.8	15.9
	Ventral collar	2.6	2.7	3.2	16.9	29.9	12.5
	Ventral abdomen	2.7	2.8	3.6	22.3	38.0	16.0
<i>P.</i>	Dorsal collar	4.3	9.2	29.8	52.9	41.7	37.5
<i>conspicillatus</i> (n=3)	Dorsal abdomen	0.8	1.8	2.9	26.5	35.3	17.1
	Ventral collar	3.2	4.4	11.4	38.3	39.8	25.5
	Ventral abdomen	1.8	2.6	3.3	25.5	37.8	17.2
	Dorsal collar	3.8	5.3	15.3	45.3	46.3	30.5

<i>P.</i> <i>scapulatus</i>	Dorsal						
	abdomen	2.0	2.9	6.4	33.6	42.0	22.1
(n=16)	Ventral collar	3.4	4.6	14.5	37.7	33.9	25.3
	Ventral abdomen	3.4	3.8	9.6	38.2	43.7	25.4
