

1 **Thermal consequences of increased pelt loft infer an additional utilitarian**
2 **function for grooming**

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22 Short title: *Thermal benefits of grooming*

23 **ABSTRACT**

24 A strong case has been made that the primary function of grooming is hygienic.
25 Nevertheless, its persistence in the absence of hygienic demand, and its obvious
26 tactical importance to members of primate groups, underpins the view that
27 grooming has become uncoupled from its utilitarian objectives and is now
28 principally of social benefit. We identify improved thermoregulatory function as a
29 previously unexplored benefit of grooming and so broaden our understanding of
30 the utilitarian function of this behavior. Deriving the maximum thermal benefits
31 from the pelt requires that it be kept clean and that the loft of the pelt is maintained
32 (i.e., greater pelt depth), both of which can be achieved by grooming. In a series of
33 wind-tunnel experiments, we measured the heat transfer characteristics of vervet
34 monkey (*Chlorocebus pygerythrus*) pelts in the presence and absence of
35 backcombing, which we used as a proxy for grooming. Our data indicate that
36 backcombed pelts have improved thermal performance, offering significantly
37 better insulation than flattened pelts and, hence, better protection from the cold.
38 Backcombed pelts also had significantly lower radiant heat loads compared to
39 flattened pelts, providing improved protection from radiant heat. Such thermal
40 benefits therefore furnish grooming with an additional practical value to which its
41 social use is anchored. Given the link between thermoregulatory ability and energy
42 expenditure, our findings suggest that grooming for thermal benefits may be an
43 important explanatory variable in the relationship between levels of sociability and
44 individual fitness.

45

46 **Keywords:** Fitness; Heat transfer; Pelt characteristics; Sociability;

47 Thermoregulation, Vervet monkeys

48 **INTRODUCTION**

49 Allogrooming is the most extensively studied social behavior in nonhuman
50 primates [Henzi & Barrett, 1999], and clearly serves a hygienic function: there is a
51 positive correlation between grooming rates and parasite load, body regions of
52 higher parasite infestation, and geographic regions of high parasite risk [Hutchins
53 & Barash, 1976; Barton, 1985; Saunders, 1988; Ichirou & Takefushi, 1993; Akinyi
54 et al., 2013; Grueter et al., 2013]. As increased parasite infestation can reduce
55 fitness [Lehmann, 1993], this hygienic utilitarian function of grooming is often
56 cited as the selection pressure that led to its evolution [Hutchins & Barash, 1976;
57 Barton, 1985; Saunders, 1988; Ichirou & Takefushi, 1993; Akinyi et al., 2013;
58 Grueter et al., 2013]. But evidence that grooming takes place in the absence of
59 parasite infestation [Sparks, 1967], and at rates higher than one would expect for
60 hygienic purposes alone [Dunbar & Sharman, 1984; Dunbar & Schultz, 2010; but
61 see Grueter et al., 2013], has led to the view that grooming among primates has
62 been decoupled from hygiene, so that its principal value now lies in social
63 mediation. There is, however, another possible benefit; that grooming enhances
64 the thermoregulatory capacities of the pelt and can thereby maintain a utilitarian
65 value of grooming in the absence of significant ectoparasite load.

66 The conductive and reflective properties of mammalian pelts affect the
67 amount of heat transferred to and from the body, reducing heat loss in cool
68 conditions, and preventing heat gain in hot conditions. The reduction in heat loss
69 in the cold lowers the energetic demands of autonomic thermoregulatory
70 processes, while the reduction in radiant heat gain reduces the water requirements
71 of thermoregulation [Scholander et al., 1950]. Air is a better insulator than the
72 fibers making up fur, and the more air that is trapped, the better the insulation.

73 Deeper pelts (i.e., those with a greater loft) trap a thicker layer of air and provide
74 both better insulation compared to shallower pelts, and can reduce the heat load
75 from solar radiation [Schmidt-Nielsen, 1997].

76 Deriving the maximum thermal benefits from the pelt requires it to be kept
77 clean, and that the loft of the fur is maintained. Grooming involves the removal of
78 dirt and ectoparasites [Hutchins & Barash, 1976], and the untangling of fibers,
79 making it an obvious way to achieve loft. Additionally, the backcombing that
80 characterizes grooming can augment the effectiveness of piloerection, in species
81 with this capability, both by removing dirt and by mechanically distributing sebum
82 along the hair shaft, which increases both loft and shine (and therefore spectral
83 reflectance: [Robbins, 2012]).

84 Here, we test the hypothesis that increased loft promotes thermoregulatory
85 efficiency. Specifically, we predict that the increased loft associated with the
86 backcombing of the pelt will increase total insulation (i.e., protection from the
87 cold) and reduce the heat load from radiation (i.e., protection from the heat), when
88 compared to flattened pelts.

89

90 **METHODS**

91 This research complied with protocols approved by the University of the
92 Witwatersrand Animal Ethics Screening Committee and adhered to the legal
93 requirements of South Africa and Australia, and the American Society of
94 Primatologists (ASP) principles for the ethical treatment of nonhuman primates.

95 We collected pelts from seven adult vervet monkeys that died of natural
96 causes in the Eastern Cape, South Africa. All pelts were collected within a few
97 hours of death, and were tanned by a taxidermist. Circular samples were cut from

98 the mid-dorsal region of each pelt, with a diameter of 120 mm. The reflectance of
99 the pelt samples was measured by the spectrophotometric facilities at the National
100 Metrology Institute of South Africa, Pretoria. The pelts were then shipped to the
101 wind-tunnel laboratory at the University of Western Australia (CITES permit
102 number: PWS2013-AU-000035) where their heat transfer characteristics were
103 measured following established techniques [Maloney & Dawson, 1995; Dawson &
104 Maloney, 2004; Hetem et al., 2009]. Specifically, we calculated each pelt's total
105 insulation (combined pelt and air boundary layer insulation), the proportion of
106 radiation that was reflected by the pelt, radiation penetrance, the distance from the
107 skin that radiation penetrated, and the radiant heat load at the skin surface (Fig. 1)
108 -- Fig.1 here --

109 **Spectral reflectance**

110 A double beam spectrophotometer (Hitachi, model U-3400), with a
111 bandwidth of 2 nm and geometry of normal/diffuse (0/d), was used to measure the
112 reflectance of the samples in 5 nm bands from 250 to 2500 nm, in both the
113 backcombed and flattened conditions. The measurements were repeated at three
114 sites, evenly spaced across each pelt sample. The measurements were made
115 against a calibrated, matt white Spectralon reflectance standard.

116 Total reflectance to the radiation source used in the wind tunnel
117 experiments (see below) was calculated by integrating the reflectance measured in
118 each 50nm waveband with the relative spectral power of the radiation source in
119 each waveband as measured by the spectrophotometric facilities of the Australian
120 Broadcasting Corporation at Gore Hill, New South Wales, Australia. The total
121 reflectance was used to calculate the amount of incident radiation that was either
122 absorbed or reflected by the pelt in the wind tunnel.

123 Thermal insulation

124 In a temperature-controlled room (air temperature 21–22 °C), the pelt
125 samples were mounted, hair upwards, on the upper surface of a temperature-
126 controlled metal plate (100 mm diameter), maintained at 37 °C via a temperature-
127 controlled water bath (Isotemp 5150, Fisher Scientific Inc., Pittsburgh, U.S.A.). A
128 20x30 mm heat flux transducer (model HA13-18-10P, Thermonetics Corporation,
129 U.S.A.) was embedded in the upper surface of the plate. The heat flux transducer
130 was calibrated using a certified thermal blanket of known thermal conductance
131 (National Institute of Standards and Technology, U.S.A.). Voltage output from the
132 heat flux transducer was recorded using an analog/digital (A/D) converter
133 (Datataker 500, Data Electronics, Australia). The samples were set inside a
134 rectangular glass wind tunnel that allowed laminar-flow wind to pass over the pelt
135 surface in a cranial-caudal direction. Wind speed was measured 20 mm above the
136 pelt surface using a thermoanemometer (Schiltknecht 39400, Technical &
137 Scientific Equipment Co., Melbourne, Australia) and maintained at 1 m.s⁻¹ by
138 adjusting the power supplied to a fan driving air through the tunnel.

139 Air temperature (T_a), plate temperature (T_p), skin surface temperature (T_s)
140 and fur surface temperatures (T_f) were measured using copper/constantan (Type-
141 T) thermocouples (0.7 mm diameter). Thermocouple outputs were referenced
142 against an isothermal block (Datataker, Data Electronics, Australia) and recorded
143 on the A/D converter mentioned above. The thermocouples were individually
144 calibrated against a certified (National Association of Testing Authorities,
145 Australia) mercury-in-glass thermometer to an accuracy of 0.1 °C. Two
146 thermocouples mounted near the inlet of the wind tunnel measured T_a . Two
147 thermocouples mounted directly onto the hot plate surface beside the embedded

148 heat flux transducer measured T_p . Two thermocouples that were fed to the
149 hair/skin interface through oblique holes from beneath the skin measured T_s . Two
150 thermocouples mounted on the outer fur surface on flexible wires, avoiding
151 compression, were used to measure T_f .

152 Once room temperature, water bath temperature, wind tunnel temperatures,
153 and wind speed had stabilized (~2 h), thermocouple temperatures and heat flow
154 were recorded for 30 min. Mean values across this period were then used to
155 calculate pelt insulation ($\text{m}^2 \cdot \text{C} \cdot \text{W}^{-1}$) following the equation: $I_p = (T_s - T_a) / Q$, where
156 Q is the heat flow ($\text{W} \cdot \text{m}^{-2}$) through the pelt as measured by the transducer. The
157 contribution of the air boundary layer to total insulation was obtained from
158 calculations of fur insulation $I_f = (T_s - T_f) / Q$ and air boundary layer insulation
159 $I_{abl} = (T_f - T_a) / Q$. All measurements were made on each pelt in both the backcombed
160 and flattened conditions.

161 **Radiant heat load**

162 The average depth to which radiation penetrates can be calculated from
163 measures of incident radiation, heat load beneath the skin, coat reflectance, and
164 coat insulation [Hutchinson & Brown, 1969; Walsberg et al., 1978; Maloney &
165 Dawson, 1995]. The measurements described above were repeated while the pelt
166 surface was exposed to a simulated solar radiant heat load (ARRI daylight 575 W,
167 equipped with a 575 W metal halide lamp, DM1575, ILC Technology) delivered
168 through a 100 mm diameter hole in a cover of aluminium foil on the glass pane
169 that formed the top of the wind tunnel. The aluminium foil prevented any short or
170 long wave radiation (from the lamp itself, or the hot lamp body, respectively)
171 heating the wind tunnel. The lamp emits a similar relative spectral distribution of
172 radiation in the visible spectrum to that of the solar spectrum [Maloney &

173 Dawson, 1995; Dawson & Maloney, 2004].

174 The incident radiation on the pelts was measured at the level of the pelt
175 surface with a radiometer (Model 8-48, Eppley Laboratory, Rhode Island, U.S.A.)
176 and averaged 563 W.m^{-2} at the top of the flattened pelts and 671 W.m^{-2} at the top
177 of the backcombed pelts.

178 The heat load from radiation at the skin level was then calculated by
179 subtracting the heat flow through the pelt exposed to radiation from the heat flow
180 without radiation. That heat load was then expressed as a proportion of the radiant
181 heat load by dividing the heat load from radiation by the incident radiation; a value
182 that expresses the proportion of incident radiation that acts as a heat load at the
183 skin. Due to difficulties in exactly matching T_p and T_a between the trials with and
184 without radiation, the heat flow without radiation was adjusted to the exact T_p and
185 T_a conditions that existed during the radiation trial. These adjustments were
186 calculated by dividing the temperature gradient between T_p and T_a that existed
187 when the pelt was exposed to radiation, by the insulation provided by the entire
188 sample (from plate to air) that was measured in the no-radiation condition. The
189 adjustment was generally no more than a few percent of the heat flow.

190 The average level of the coat to which radiation penetrated before being
191 absorbed was calculated by assuming that radiation that was not reflected from the
192 pelt penetrated to an average level, z , within the coat. Because the resultant heat
193 flows to either the skin or to the environment in proportion to the insulation in
194 each direction, z was calculated as a proportion of pelt insulation, and converted to
195 distance by multiplying by coat depth [Maloney & Dawson, 1995; Hetem et al.,
196 2009].

197 **Pelt conditions**

198 All heat transfer measurements were made on each pelt in both the
199 backcombed and flattened conditions. For the backcombed condition, the fur was
200 combed backwards (50 strokes). For the flattened condition, the fur was combed
201 flat (50 strokes). Our backcombed condition represents a pelt in its typical form,
202 and was our proxy for the intrinsic loft associated with a groomed pelt. The
203 flattened condition represents the reduced loft associated with an ungroomed pelt.
204 Insofar as our pelts were free of dirt and ectoparasites, and were not matted, our
205 measure of the ungroomed condition was highly conservative; a complete absence
206 of grooming would not only reduce pelt loft, but would also allow it to become
207 matted, and infiltrated with dirt and ectoparasites.

208 In both conditions, the depth of each pelt was calculated by averaging three
209 caliper measurements made at points evenly spaced across each sample (Table 1).
210 Descriptive statistics are presented as means and standard deviations. The heat
211 transfer characteristics of backcombed and flattened pelts were analysed using
212 two-tailed paired sample t-tests. Significance was set a $P < 0.05$.

213 -- Table.1 here --

214

215 **RESULTS**

216 Backcombed pelts were significantly deeper than flattened pelts (paired t-
217 test: $t=14.7$, $df=6$, $P<0.001$) and had significantly more total insulation than
218 flattened pelts ($t=8.20$, $df=6$, $P<0.001$); a consequence of significantly better
219 insulation from the fur ($t=-12.80$, $df=6$, $P<0.001$), with no significant difference in
220 the insulation provided by the air boundary layer ($t=1.92$, $df=6$, $P=0.10$; Table 1).

221 There was no significant difference in the proportion of incident radiation
222 that was reflected by the backcombed and flattened pelts ($t=1.8$, $df=6$, $P=0.12$),

223 and therefore the pelt in both conditions absorbed the same proportion of incident
224 radiant heat. Although radiation penetrated significantly deeper in to the
225 backcombed pelts than the flattened pelts ($t=3.1$, $df=6$, $P=0.02$), the backcombed
226 pelts were nearly six times as deep as the flattened pelts, resulting in radiation
227 being absorbed further from the skin in the backcombed condition ($t=9.9$, $df=6$,
228 $P<0.001$). Therefore, significantly less of the incident radiation absorbed by the
229 coat acted as a heat load at the skin level in the backcombed pelts compared to the
230 flattened pelts ($t=6.56$, $df=6$, $P<0.001$); that is, more of the absorbed heat flowed
231 back to the environment before it reached the skin in the backcombed pelts.

232

233 **DISCUSSION**

234 We provide positive evidence to suggest that the thermal performance of
235 vervet monkey pelts provides an additional utilitarian function of grooming. Our
236 data indicate that backcombing pelts – a condition similar to that achieved through
237 grooming – increases the total insulation and reduces the radiant heat absorbed at
238 the skin, offering thermal benefits under both cold and hot conditions. Regardless
239 of its proximate benefits, functionally we suggest that in the complete absence of
240 grooming (for which our flattened condition provides a conservative estimate), an
241 animal will lose the inherent thermal benefits afforded by its pelt (for which our
242 backcombed condition provides an estimate). We emphasize the inherent
243 conservatism of our test conditions because grooming is likely to improve the
244 condition of a vervet monkey's pelt beyond the maintenance of loft alone, by also
245 removing dirt and ectoparasites. Such thermal benefits may also vary in response
246 to different environmental conditions, such as variable heat load, wind speed and
247 direction. In addition, we should note that our study considered only vervet

248 monkey pelts, which have a uniform coat color. Species-specific differences in
249 pelt color, depth, hair length and density, may also have an impact on the thermal
250 properties of primate pelts.

251 Although our findings are not intended to negate the idea that social factors
252 play a critical part in shaping grooming patterns, the idea that “in the absence of
253 such [i.e., social] explanation, it is difficult to explain why such intense (and
254 otherwise functionless) grooming should apparently play so important a role in
255 primate sociality” ([Dunbar & Schultz, 2010]: p782) may need some revision:
256 such ‘functionless’ grooming maintains pelt loft, expanding the utilitarian function
257 of grooming beyond hygiene alone.

258 The insulation provided by an animal’s pelt is proportional to its depth
259 [Scholander et al., 1950; Schmidt-Nielsen, 1997], and many mammals (and birds)
260 can acutely adjust the depth of their pelt by piloerection. While piloerection can
261 achieve some of the benefits we here ascribe to grooming, the effectiveness of
262 piloerection depends fundamentally on the condition of the hair, for which
263 grooming is essential. Without grooming, the pelt would become matted, as well
264 as infiltrated with dirt and parasites, and the efficiency of piloerection would be
265 greatly reduced. Thus, we argue that the two are not independent, and should be
266 considered as inseparable parts of the same thermoregulatory strategy: piloerection
267 and grooming can be combined to compensate for changes in the environment by
268 improving insulation, while reducing the energy expenditure associated with other
269 autonomic thermoregulatory processes.

270 Similar reasoning explains the ability of animals to remain active while
271 exposed to a radiant heat load that, during summer, can be up to twenty times the
272 metabolic heat production of a resting animal [Maloney & Dawson, 1995;

273 Walsberg & Wolf, 1995]. Although it was originally surmised that solar heat load
274 was a simple function of pelt color, it is now recognized that the factors
275 determining solar heat load are complex, and include other coat characteristics that
276 determine how far radiation penetrates into a coat before absorption. Radiation that
277 penetrates further results in radiant heat being produced closer to the skin,
278 increasing the heat load on an animal [Hutchinson & Brown, 1969; Walsberg et
279 al., 1978; Maloney & Dawson, 1995]. We show that simulated grooming reduces
280 the radiant heat load significantly by increasing pelt depth and causing radiation to
281 be absorbed further from the skin. While radiation did penetrate further into the
282 groomed coat, possibly because the looser structure of the hairs permitted such
283 penetration, the increase in pelt depth far exceeded the increased penetration.
284 These results support the argument that radiant heat load is largely independent of
285 radiation absorption, and therefore of animal coloration [Dawson et al., 2014].

286 Given that animals can only groom a circumscribed fraction of their own
287 bodies [Barton, 1985], this thermoregulatory benefit provides allogrooming with
288 an additional, utilitarian, value as an exchangeable commodity within a social
289 group [Barrett et al., 1999; Henzi & Barrett, 1999] which, given constant
290 degradation of pelt condition, is likely to remain relatively consistent over time.
291 Grooming is also likely to be especially important for strepsirrhines and tarsiers,
292 which lack the musculature necessary for pilomotor control [Chaplin et al., 2014].
293 These thermoregulatory-related advantages have implications for analyses of
294 grooming, not only at the proximate level of value matching, but also functionally,
295 since the thermal benefits of grooming might contribute to the documented
296 positive relationship between measures of social engagement and individual
297 fitness [Silk et al., 2009; McFarland & Majolo, 2013; Archie et al., 2014;

298 McFarland et al., 2015]. Social thermoregulation among primates (e.g., grooming
299 and huddling) can help buffer thermal fluctuations within an environment, reduce
300 the energetic costs associated with autonomic thermoregulation, and should
301 promote the establishment of larger social networks [Dunbar, 2009; Satinoff,
302 2011; IJzerman et al., 2015; McFarland et al., 2015].

303

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388 **FIGURES AND TABLE LEGENDS**

389 **Figure 1.** A model of the pelt heat-transfer characteristics recorded during the

390 wind-tunnel experiments

391

392 **Table 1.** Physical and thermal properties of flattened and backcombed vervet

393 monkey pelts (mean \pm SD)