1    **Infrared thermography cannot be used to approximate core body**

2    **temperature in wild primates**

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4    **Running title**: *Measuring vervet monkey body temperatures*

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**ABSTRACT**

Understanding the physiological processes that underpin primate performance is key if we are to assess how a primate might respond when navigating new and changing environments. Given the connection between a mammal's ability to thermoregulate and the changing demands of its thermal environment, increasing attention is being devoted to the study of thermoregulatory processes as a means to assess primate performance. Infrared thermography can be used to record the body surface temperatures of free-ranging animals. However, some uncertainty remains as to how these measurements can be used to approximate core body temperature. Here, we use data collected from wild vervet monkeys (*Chlorocebus pygerythrus*) to examine the relationship between infrared body surface temperature, core body (intra-abdominal) temperature, and local climate, to determine to what extent surface temperatures reflect core body temperature. While we report a positive association between surface and core body temperature – a finding that has previously been used to justify the use of surface temperature measurements as a proxy for core temperature regulation – when we controlled for the effect of the local climate in our analyses, this relationship was no longer observed. That is, body surface temperatures were solely predicted by local climate, and not core body temperatures, suggesting that surface temperatures tell us more about the environment a primate is in, and less about the thermal status of its body core in that environment. Despite the advantages of a non-invasive means to detect and record animal temperatures, infrared thermography alone cannot be used to approximate core body temperature in wild primates.

**INTRODUCTION**

As primate populations continue to decline and face an increasing risk of extinction as a consequence of climate change (Graham, Matthews, & Turner, 2016; Estrada et al., 2017), understanding the physiological processes that underlie the relationship between animal performance and environmental challenges is becoming increasingly important. Local climate exerts a strong selective pressure on animal behavior, physiology, and survivorship, and therefore has a profound impact on animal distributions and phenotypes (Hetem, Fuller, Maloney, & Mitchell, 2014; Fuller, Mitchell, Maloney, & Hetem, 2016; Mitchell et al., 2018). Given the obvious connection between an animal's ability to thermoregulate and the demands of its thermal environment, increasing attention is being devoted to the study of body temperature as a means to assess primate performance in variable environments.

Early studies investigating primate body temperature regulation in response to environmental variability relied on measurements obtained from captive or laboratory-housed subjects (Sulzman, Fuller, & Moore-Ede, 1977; Whittow, Scammell, Manuel, Rand, & Leong, 1977; Wurster, Murrish, & Sulzman, 1985; Müller, Nieschalk, & Meier, 1985; McNab & Wright, 1987; Lubach, Kittrell, & Coe, 1992; Robinson & Fuller, 1999; Maloney, Mitchell, Mitchell, & Fuller, 2007). While this approach provides a high degree of experimental control, such studies do not provide the data to allow conclusions to be drawn about how a free-living primate responds to change in its natural habitat. Moreover, body temperatures in laboratory conditions typically are measured with thermosensitive probes or via telemetry with a receiver in close proximity, methods that are not readily transposable to studying primates in situ.

Advancements in remote telemetry or biologging have provided insights into the body temperature of a small number of free-ranging primate populations. Brain and Mitchell (1999)

70    used intra-abdominal temperature-sensitive radio transmitters to record the core body

71    temperature patterns of chacma baboons (*Papio ursinus)* under free-ranging, natural conditions.

72    Their study was limited by relatively few subjects and body temperature measurements being

73    collected only intermittently during the daytime over less than a month for each animal.

74    Nevertheless, this study revealed the importance of high heat load as a thermal stressor to

75    chacma baboons, and the importance of drinking water to prevent hyperthermia (Brain &

76    Mitchell, 1999). Intra-abdominal transmitters also have been used to describe the core body

77    temperature patterns associated with daily torpor in lemurs (*Lemuridae spp*. Schmid 2000;

78    Schmid, Ruf, & Heldmaier, 2000; Dausmann, 2005). More recently, we have used intra-

79    abdominal data loggers to describe the seasonal patterns of core body temperature in wild vervet

80    monkeys (*Chlorocebus pygerythrus*), the thermoregulatory consequences of both cold and heat

81    stress, inter-individual differences in thermal performance, and the importance of behavioral

82    (including social) thermoregulation in body temperature regulation (Lubbe et al., 2014;

83    McFarland et al., 2015; Henzi et al., 2017; McFarland, Henzi, & Barrett, 2019; McFarland et al.,

84    2020).

85         The use of intra-abdominal data loggers provides a good index of the thermal status of

86    the body core, but requires animals to be captured and to undergo surgical procedures for logger

87    implantation and extraction (see McFarland et al., 2015 for a full description of methods). As an

88    alternative to data logging approaches there has been interest in using infrared thermography to

89    make inferences about thermoregulatory processes in free-ranging animals, including primates

90    (McCafferty, 2007; Cilulko, Janiszewski, Bogdaszewski, & Szczygielska, 2013; Thompson et

91    al., 2017; Narayan, Perakis, & Meikle, 2019). At face value, this appears an attractive option for

92    non-invasive and remote measurement of body temperature. However, infrared thermography

4

93    measures animal surface temperatures, and there is contrasting evidence whether surface

94    temperatures (i.e., skin, fur, inner-ears, eyes) can approximate core body temperature. While

95    some studies report no significant association between body surface and core body temperatures

96    (Jay et al., 2007; Larcombe, 2007; Sikoski et al., 2007; Sykes et al., 2012), others have shown a

97    positive correlation (Dausmann, 2005; Warriss, Pope, Brown, Wilkins, & Knowles, 2006;

98    Johnson, Rao, Hussey, Morley, & Traub-Dargatz, 2011; Giloh, Shinder, & Yahav, 2012; Zanghi,

99    2016). An important caveat, however, is the lack of control in these analyses for the mediating

100    effect that local climate has on both surface and core body temperatures. That is, even though

101    body surface and core body temperatures were shown to be positively correlated, it is possible

102    that this relationship was an artefact of the local climate influencing these variables. While it

103    may be reasonable to assume that skin temperature more closely reflects core body temperature

104    in small animals, the mediating effect of local climate should still be considered when attempting

105    to make inferences about core body temperature from surface temperatures alone. In an

106    experimental study of bats (*Carollia perspicillata*) in controlled environmental conditions, for

107    example, it was observed that the difference between an animal's core and skin temperature was

108    a function of ambient temperature, with the authors concluding that any inferences made about

109    core body temperature regulation from skin temperature measurements, including in very small

110    animals, should account for the effect of ambient conditions (Audet & Thomas, 1996). Even

111    when care has been taken to avoid increased surface heat loads incurred by solar radiation

112    (McCafferty, 2007; Thompson et al., 2017), surface temperatures are still more influenced by

113    local climate than body temperature. In wild mantled howling monkeys (*Alouatta palliata*), for

114    example, dorsal fur temperature was more strongly predicted by ambient temperatures than by

115    dorsal subcutaneous temperatures, and facial skin surface temperatures were predicted solely by

116    ambient temperature and not by dorsal subcutaneous temperatures (Thompson et al., 2017).

117          Here, we use data collected from wild vervet monkeys to examine the relationship

118    between body surface and core body temperatures, while controlling for local climatic

119    conditions. Because an endothermic animal's core body temperature is typically buffered from

120    their environment by a range of autonomic and behavioural processes (Lovegrove, Heldmaier, &

121    Ruf, 1991; Angilletta, Cooper, Schuler, & Boyles, 2010; Hetem, Maloney, Fuller, & Mitchell,

122    2016; Mitchell et al., 2018), we predict that surface temperatures will be more closely associated

123    with local climate than with core body temperature. A better sense of the relationship between

124    these variables will hopefully inform us whether infrared thermography can be used to

125    approximate core body temperature. If surface temperatures are predicted by core temperatures,

126    while controlling for the effect of the local climate, this would suggest that surface temperatures

127    can approximate, to some extent, core body temperature. However, if surface temperatures are

128    predicted by the local climate, and not core body temperatures, this would suggest that the

129    surface temperatures tell us more about the environment an animal is in, and less about the body

130    temperature of an animal in that environment. We use four body regions to test our hypothesis:

131    the furred dorsal, ventral and tail surface and bare-skin facial surface.

132

133    **METHOD**

134    In June 2017, as part of a longitudinal project on vervet monkey thermoregulation in the Eastern

135    Cape, South Africa (32º22'S, 24º52'E), we collected infrared thermography data from a subset

136    of individuals living across three groups (N=14: 5 females, 9 males). These animals fed on a

137    natural diet, were fully habituated to the presence of researchers, and were individually

138    identifiable by means of natural markings (Pasternak et al., 2013; McFarland, Barrett, Boner,

139    Freeman, & Henzi, 2014).

140

141    ***Infrared thermal imagery***

142    We collected infrared thermal images ($N_{total}$ = 294 images, $\bar{x}_{subject}$ = 21 ± SD 14 images)

143    opportunistically using a handheld infrared thermograph model T360 camera (FLIR® Systems

144    Inc.). We set emissivity to 0.98. We targeted the animal's furred dorsal, ventral, and tail surface,

145    and bare-skin face surface, in each photo, to the point that some images could be used to measure

146    multiple surface regions, and others not.

147         We used the following selection criteria to determine the usability of infrared surface

148    temperature measurements: (i) the targeted body surface was in plain view and not obscured by

149    foliage or another individual, (ii) the animal was within 5 m of the camera, (iii) the targeted body

150    surface was orientated toward the camera to avoid detection errors associated with sampling

151    curved surfaces (McCafferty, 2007), (iv) the targeted body surface was in shade or low light

152    levels, avoiding reflective light, thereby minimizing the effect of direct solar radiation on surface

153    measurements (McCafferty, 2007), and (v) the animal was in a relaxed state, i.e., stationary and

154    not engaged in antagonistic behavior. Table 1 outlines the distribution of the final measurements

155    used in the current analyses.

156         At the time each image was taken, we positioned a thermocouple attached to a matte-

157    black painted metal box within the frame of each thermal image (e.g., Figure 1). We calibrated

158    the temperature measurements recorded by the thermal camera using the thermocouple. To

159    ensure consistency in data collection, only one researcher extracted the FLIR temperature data,

160    according to a strict protocol that did not rely on subjective judgement. The researcher was blind

161    to concurrent environmental and body temperature data. For each infrared image, we used FLIR

162    Tools® software (FLIR® Systems Inc., 2019) to extract five discrete pixel-defined temperature

163    measurements from the targeted body surface region and the black calibration box. For the

164    dorsal, ventral, and bare-skin face surfaces, we used the five corners of a pentagon to define the

165    sampling locations of each discrete temperature measurement; adjusting the pentagon's size to

166    approximately cover the area of the image that was occupied by each respective body region

167    (Figure 2). To reduce any confounding effects of short-term temperature changes in specific

168    facial regions that may relate to emotional states (Chotard et al. 2018), we average surface

169    temperature over the entire bare-skin facial region; avoiding sampling from peri-orbital and nose

170    tip regions. For the tail surface, we took five temperature measurements at regular intervals along

171    the length of the tail (Figure 2). We calculated the mean black box and mean body surface

172    temperatures for all available body regions in each image. We used the difference between the

173    thermocouple temperature and the mean FLIR temperature of the black box to create a single-

174    point calibration offset for all mean body surface temperatures.

175

176    ***Local climate***

177    We used black globe temperature to measure the local climate experienced by our study animals.

178    Black globe temperature integrates the influence of air temperature, solar radiation and wind

179    speed, and is thus considered a better measure of the thermal heat load experienced by an animal

180    than air temperature alone (Hetem, Maloney, Fuller, Meyer, & Mitchell, 2007; McFarland et al.,

181    2014). We recorded black globe temperatures every minute using a calibrated, temperature-

182    sensitive Thermochron 4K iButton (model DS1921G; Maxim Integrated[TM]) housed inside a

183    matte-black painted copper ball with a diameter of 30mm (hereafter, miniglobe). iButtons

184    recorded miniglobe temperature at one-minute intervals at a resolution of 0.06°C and were

185    individually calibrated to an accuracy of 0.1°C. We recorded miniglobe temperatures at the time

186    each image was taken, within 5m of the target animal. Miniglobe temperatures ranged from 13.0-

187    32.7ºC across the study period with a mean daily temperature of 23.6 ± SD 5.7ºC.

188

189    ***Body temperature data***

190    In June 2016, we surgically implanted 14 adult vervet monkeys (5 females, 9 males; distributed

191    across three groups) with miniature temperature-sensitive data loggers (model: DST Centi-T,

192    Star-Oddi, Iceland) intra-abdominally. Data loggers recorded core body temperature at five-

193    minute intervals at a resolution of 0.03°C and were individually calibrated to an accuracy of

194    0.1°C. We recorded the body mass (kg) of all animals ($\bar{x}_{female} = 3.4 \pm$ SD 0.4g, $\bar{x}_{male} = 5.1 \pm$ SD

195    0.3g). We removed the data loggers at the end of June 2017. For full details of the capture and

196    surgery procedure see McFarland et al. (2015). Data loggers measured the core intra-abdominal

197    body temperature (to the nearest five minutes) of the same animals that were sampled using the

198    infrared camera. Importantly, we implanted our subjects with data loggers in fulfilment of a

199    long-term study of vervet monkey thermal physiology. That is, our subjects were not solely

200    exposed to this procedure for the purpose of the current project.

201         Observational data collection protocols were approved by the University of Lethbridge

202    under Animal Welfare Protocols 0702 and 1505. Capture and surgical procedures were approved

203    by the University of the Witwatersrand Animal Ethics Research Committee (Protocol # 2015-04-

204    14B-2017), and were treated in accordance with international ethical standards. No long-term

205    sequelae were observed as a consequence of surgical intervention. Overall, this study adhered to

9

206    the legal requirements of South Africa, and the American Society of Primatologists (ASP)

207    Principles for the Ethical Treatment of Non-Human Primates.

208

209    *Statistical analysis*

210    We used a series of Bland-Altman plots to visually compare the measurement of vervet

211    monkeys' core body temperature using intra-abdominal data loggers, with surface temperature

212    measured using infrared thermography (Altman & Bland, 1983).

213        We performed our analyses in R v.3.6.0 (R-Core-Team, 2019) using the 'lme4' package

214    to model outcomes (Bates et al., 2019), the 'rsq' package to generate adjusted $R^2$ values for the

215    fixed effects (Zhang, 2018), and the 'lmertest' package to generate p-values (Kuznetsova,

216    Brockhoff, Christensen, & Jensen, 2019). Prior to running each model, we checked for

217    intercollinearity by calculating variance inflation factors (VIF) for the predictor variables using

218    the 'car' package (Fox et al., 2020). The VIF scores in all of our models were < 2 and were

219    therefore not considered collinear. We scaled and centered our predictor variables so we could

220    directly compare the resulting coefficients. We specified a gaussian error structure with a log

221    link function in all of our models to normalize the residuals.

222        We originally ran a series of linear mixed models, entering subject ID as a random effect.

223    However, these random effects did not explain any meaningful variance and their inclusion

224    produced overfitted models with singular fit. We therefore ran a series of linear models,

225    removing this random effect. The results of the linear mixed models and linear models were

226    qualitatively the same. We present the results of the linear models below.

227        We first ran a series of four linear models entering our four surface temperatures (i.e.,

228    dorsal, ventral, tail, and face) in turn as the dependent variable, and time-matched miniglobe as

229    the sole predictor variable. We ran a second series of four linear models entering our four surface

230    temperatures in turn as the dependent variable, and time-matched core body temperature as the

231    sole predictor variable. We ran a third series of four linear models entering our four surface

232    temperatures in turn as the dependent variable and entered time-matched miniglobe temperature

233    and core body temperature as predictor variables, to determine whether this model improved

234    upon either of the single predictor variable models described in the first two series of linear

235    models.

236        For the first two series of linear models (i.e., the single predictor variable models), we

237    follow Colquhoun (2014) in describing outcomes as indicating weak ($P \sim 0.05$), moderate ($P \sim$

238    $0.01$) or strong ($P \sim 0.001$) evidence for effects. Following the third series of linear models, we

239    used a reduction in the Akaike Information Criterion (AIC: Akaike, 1974) of a model, using a

240    ΔAICc (to control for small sample sizes) threshold of $> 2.0$ (Burnham & Anderson, 2002), to

241    indicate whether the composite model was better than its single predictor variable equivalent. We

242    used adjusted $R^2$ values to describe how much variance in a model's dependent variable was

243    explained by its predictor variables.

244

245    **RESULTS**

246    In a series of four Bland-Altman plots (Figure 3), we observed large differences between the

247    measurements of core body and surface temperatures ($\bar{x}_{dorsal} = 12.6 \pm$ SD 4.4ºC, $\bar{x}_{ventral} = 9.4 \pm$

248    SD 3.9ºC, $\bar{x}_{tail} = 12.3 \pm$ SD 5.5ºC, $\bar{x}_{face} = 12.0 \pm$ SD 4.3ºC). Temperature differences in excess of

249    15ºC were common and occasionally exceeded 20ºC at low temperatures. When the mean of

250    core body and surface body temperatures were higher as a result of increased surface temperature

251    in warm conditions (Table 2), the differences between these variables were smaller. However,

252    core body and surface temperatures were never equivalent.

253

*Miniglobe temperature*

255 In a series of four linear models (Table 2) with miniglobe temperature as the sole predictor

256 variable, globe temperature had a strong positive effect on dorsal, ventral, face, and tail infrared

257 surface temperatures (all P<0.001). Miniglobe temperature explained 81% (dorsal), 76%

258 (ventral), 87% (tail), and 77% (face) of the variance in infrared body surface temperatures (Table

259 2).

260

*Core body temperature*

262 In a series of four linear models with core body temperature as the sole predictor variable, core

263 body temperature had a strong positive effect on dorsal surface temperatures (P<0.001) and a

264 weak positive effect on ventral (P=0.04), tail (P=0.02) and face (P=0.048) infrared surface

265 temperatures. Core body temperature explained 8% (dorsal), 11% (ventral), 6% (tail), and 5%

266 (face) of the variance in infrared body surface temperatures (Table 3).

267

*Miniglobe temperature and core body temperature*

269 Given that globe temperature was a stronger predictor of infrared surface temperatures than core

270 body temperature (Tables 2 and 3), we ran a series of four linear models including both globe

271 temperature and core body temperature as predictor variables, to examine whether the addition of

272 core body temperature improved the performance of the model with globe temperature as the

273 sole predictor (Table 4). The dorsal, ventral, tail, and face infrared surface temperature models

274 were not improved by the addition of core body temperature. AICc values did not decrease by >

275 2.0, and less than 1% additional variance was explained, following the addition of core body

276 temperature as a predictor in all cases (Table 5). The best fitting models, for all infrared body

277  surface temperatures, therefore, were those that included globe temperature as a sole predictor

278  variable.

279

280  **DISCUSSION**

281  Our findings reveal that infrared thermography cannot be used to approximate core body

282  temperature. Vervet monkey surface temperatures measured on the furred dorsal, ventral and tail

283  region, as well as the bare-skin facial region, were more strongly predicted by miniglobe (i.e.,

284  environmental) temperatures than core body temperatures. At low miniglobe temperatures,

285  surface temperatures dropped substantially and furred surfaces could be more than 20ºC below

286  core body temperature. Since an animal's body surface is the interface where heat is gained by,

287  and dissipated from, the body, it is unsurprising that animal surface temperature is strongly

288  influenced by environmental temperature. While the core body temperatures of free-ranging

289  primates can also vary in response to environmental variability (e.g., Brain & Mitchell, 1999;

290  Schmid, 2000; Schmid et al., 2000; Dausmann, 2005; Lubbe et al., 2014; McFarland et al., 2015,

291  Henzi et al., 2017; McFarland et al., 2020), core body temperature is much more tightly

292  regulated through a range of behavioral and physiological processes.

293      Primates, like all mammals, employ a range of physiological mechanisms to cope with

294  environmental challenges and maintain homeostasis. Autonomic processes involve the activation

295  of pathways in the preoptic area of the hypothalamus that regulate the balance of heat production

296  and loss (Morrison & Nakamura, 2019), including altering blood flow to the skin through

297  peripheral vasoconstriction and vasodilation. Individuals can also engage in behaviors that alter

298  body temperature, such as changing activity patterns, posture, or selecting appropriate

299  microclimates (McFarland et al., 2015, 2019, 2020; Henzi et al., 2017). Morphological features,

300    such as the color, depth, density, and condition of the pelage, can further modulate heat transfer

301    to and from the body (Scholander, 1950; Schmidt-Nielsen, 1997; McFarland et al., 2016). For

302    example, a thick pelage would act to insulate the animal, reducing the rate of heat loss in cold

303    environments and the rate of heat gain in hot environments, thereby resulting in outer fur surface

304    temperatures that differ substantially from skin temperatures.

305        Given the complexities surrounding core body temperature regulation, it would be

306    surprising if surface temperatures did approximate core body temperatures. Yet, a number of

307    studies have shown an association between surface temperature and core body temperature

308    (Dausmann, 2005; Warris et al., 2006; Johnson et al., 2011; Giloh et al., 2011; Zanghi, 2016),

309    including the current manuscript. However, the variance in surface temperature that could be

310    explained by core body temperature in our study was an order of magnitude lower than that

311    explained by miniglobe temperature. In addition, after controlling for the effect of miniglobe

312    temperature, the relationship with surface and core temperatures became trivial. We recommend

313    that future studies do not use surface temperature measurements to approximate core body

314    temperature, without a full understanding of the interactions between core, surface, and

315    environmental variables.

316        In an apparent attempt to avoid the invasiveness of intra-abdominal data logging, several

317    research teams have used skin or subcutaneous temperature measurements to make inferences

318    about core body temperature in primates. These methods have provided information on the

319    hibernation patterns of the Lesser bushbaby (*Galago moholi*: Mzilikazi, Masters, & Lovegrove,

320    2006; Nowack, Mzilikazi, & Dausmann, 2010; Nowack, Wippich, Mzilikazi, & Dausmann,

321    2013) and several lemur species (*Lemuridae spp.,* Schmid, 2001; Dausmann, Glos, Ganzhorn, &

322    Heldmaier, 2004; Dausmann, 2005; Blanco, Dausmann, Faherty, & Yoder, 2013; Kobbe,

323 Nowack, & Dausmann, 2014), as well as the seasonal variability in the body temperature rhythm

324 of the larger, diurnal mantled howling monkey (Thompson et al., 2014). While subcutaneous

325 body temperatures, typically recorded using devices implanted between the scapula, may more

326 closely reflect core body temperature than surface temperature, they also are likely to be

327 influenced by a core to periphery gradient, particularly in large mammals. The temperature of

328 peripheral tissue is more strongly influenced by local climate, and peripheral blood flow, than is

329 core body temperature (Mitchell et al., 2018). The subcutaneous body temperatures of mantled

330 howling monkeys, for example, were strongly influenced by environmental temperature

331 (Thompson et al., 2014). Furthermore, although a positive association between core body and

332 subcutaneous body temperatures has been documented (Brown & Bernard, 1991; Navarro-Serra

333 & Sanz-Cabañes, 2018), this does not mean that the measures are equivalent or interchangeable.

334 Similar to surface temperatures, subcutaneous temperatures may deviate substantially from core

335 body temperature, particularly in cold environments when endotherms peripherally vasoconstrict

336 to conserve core body heat (Torrao, Hetem, Meyer, & Fick, 2011).

337 　　　　Other less invasive measures of an animal's body temperature include measuring the

338 temperature of an animal's feces to approximate its core body temperature. For example, fecal

339 temperature has been used as a proxy for core body temperature in chimpanzees (Jensen,

340 Mundry, Nunn, Boesch, & Leendertz, 2009; Negrey, Sandel, & Langergraber, 2020) based on

341 limited evidence that fecal temperatures approximate rectal temperature in humans. However,

342 given the infrequency of defecation point-sampling, and the fact that core body temperatures can

343 fluctuate over 24h, and over even shorter time intervals for a multitude of reasons (e.g., drinking,

344 behavioral thermoregulation, microclimate selection, intensity of activity: McFarland et. al.,

345 2015, 2019, 2020), this method offers very little information on the regulation of core body

346  temperature. Continuous and remote measurement of core body temperature through implanted

347  intra-abdominal data loggers is a relatively simple and feasible technique that provides far

348  greater insight into an individual's thermal balance with its environment.

349        That is not to say that infrared thermography cannot provide important insights on

350  thermoregulatory or other physiological processes. Surface temperatures not only inform us

351  about the heat load experienced at an animal's surface, but may also provide information on

352  peripheral blood flow, and the effect of pelage properties on heat transfer (McCafferty, 2007;

353  Cilulko et al., 2013; Mathewson et al., 2018). Infrared thermography can also provide valuable

354  insights on animal behavior and physiology, or can be used to test the accuracy of biophysical

355  heat transfer models (e.g., Mathewson et al., 2018). Moreover, facial infrared thermography has

356  been used to quantify the emotional states of non-human primates (Nakayama, Goto, Kuraoka, &

357  Nakamura, 2005; Kuraoka & Nakamura, 2011; Ioannou, Chotard, & Davila-Ross, 2015;

358  Chotard, Ioannou, & Davila-Ross, 2018), including in wild chimpanzees (*Pan troglodytes*:

359  Dezecache, Zuberbühler, Davila-Ross & Dahl, 2017), and other animals (McCafferty, 2007).

360  The experimental protocols used in these studies typically rely on small short-term changes in

361  the skin-surface temperature of particular facial regions to make inferences about emotional

362  responses that invoke autonomic changes in blood flow at the surface of the skin (Kreibig, 2010).

363  For example, reductions in nasal skin temperature associated with negative emotional states were

364  relatively small in magnitude, <0.8°C, even in 'raging' monkeys (Kuraoka & Nakamura 2011),

365  and these short terms changes in facial temperature are not influenced by the thermal

366  environment to which the monkeys were exposed (Nakayama et al. 2005). The magnitudes of

367  these emotion-driven temperature changes are unlikely to have had a significant influence on the

368  much larger differences that we report between core and surface body temperatures. Nonetheless,

369    our experimental protocol attempted to reduce the confounding effects of emotional state by

370    focusing our thermal images on relaxed monkeys and using relatively discrete temperature

371    measurements collected across the day. Any small skin temperature differences as a result of

372    emotional state would likely be further diluted by our protocol that averaged the temperatures

373    across all bare-skin facial regions, as different facial regions may differ in the direction of

374    temperature change (Chotard et al. 2018).

375         When alternative methods are used to measure an animal's surface or peripheral tissue

376    temperature, one should acknowledge that these data do not necessarily reflect the thermal status

377    of an animal's core in a given environment. For subcutaneous data logging methods, in

378    particular, the limited scientific value afforded by these methods should be weighed carefully

379    against the ethical considerations surrounding the required animal capture and intervention.

380    When it is not possible to measure body temperature within the animal's core, we suggest that

381    alternative, non-invasive physiological measures are used to provide information on a primate's

382    energy balance, hormone levels, or metabolic activity in response to environmental variability

383    (e.g., Cristóbal-Azkarate, Maréchal, Semple, Majolo, & MacLarnon, 2016; Behringer &

384    Deschner, 2017; Thompson, 2017; Thompson et al., 2017b). Biophysical models (e.g., Niche

385    Mapper$^{TM}$: Porter & Mitchell, 2006) that use principles of heat and mass transfer, coupled with

386    information on an animal's morphology, behavior, and microclimate, have also been used to

387    predict an animal's energetic requirements as a function of environmental conditions (e.g.,

388    Moyer-Horner, Mathewson, Jones, Kearney, & Porter, 2015; Natori & Porter, 2007; Zhang,

389    Mathewson, Zhang, Porter, & Ran, 2018; Long et al., 2014; Mathewson & Porter, 2013; Briscoe,

390    Kearney, Taylor, & Brendan, 2016; Mathewson et al., 2018), including in vervet monkeys

391    (Mathewson, 2018). Ultimately, an integrative approach to understanding heat transfer and

392  physiological plasticity can complement accurate measures of core body temperature, to provide

393  greater insight into how primates respond to environmental stress.

394

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403

404  **Data sharing**

405  The data and analysis code that support the findings of this study are openly available on figshare

406  at https://doi.org/10.6084/m9.figshare. ####### [to be published at time of manuscript

407  publication].

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667

668    **TABLES**

669

670    **Table 1**. Sample of miniglobe, core body, and infrared body surface temperature measurements

671    across four sites recorded from wild vervet monkeys

| | Miniglobe | Core body | Body surface | | | |
|---|---|---|---|---|---|---|
| | | | Dorsal | Ventral | Face | Tail |
| Number of monkeys | - | 14 | 14 | 11 | 13 | 14 |
| Number of images | 242 | 283 | 202 | 42 | 82 | 107 |
| Minimum temperature °C | 13.0 | 38.2 | 16.2 | 20.5 | 16.9 | 14.8 |
| Maximum temperature °C | 32.7 | 39.8 | 37.6 | 34.4 | 34.4 | 37.5 |
| Mean temperature ± SD °C | 23.6 ± 5.7 | 38.9 ± 0.3 | 26.3 ± 4.2 | 29.1 ± 3.75 | 27.0 ± 4.01 | 26.8 ± 4.9 |

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678    **Table 2**. Results of the linear model analyses testing the relationship between miniglobe

679    temperature and infrared surface temperatures from the following body regions: dorsal, ventral,

680    tail, and face. We ran the analyses at the level of the image/subject.

| | $\beta \pm SE$ | $t$ | $P$ |
|---|---|---|---|
| **Dorsal** (N=153 images, N=14 subjects) | | | |
| Miniglobe temperature | 0.16 ± 0.01 | 25.02 | <0.001 |
| Intercept | 3.26 ± 0.01 | 532.10 | - |
| *Adjusted $R^2$ (%)* | 81.45 | | |
| *AICc* | 637.31 | | |
| | | | |
| **Ventral** (N=32 images, N=11 subjects) | | | |
| Miniglobe temperature | 0.12 ± 0.01 | 9.30 | <0.001 |
| Intercept | 3.37 ± 0.01 | 274.70 | - |
| *Adjusted $R^2$ (%)* | 75.56 | | |
| *AICc* | 139.81 | | |
| | | | |
| **Tail** (N=76 images, N=14 subjects) | | | |
| Miniglobe temperature | 0.21 ± 0.01 | 20.27 | <0.001 |
| Intercept | 3.26 ± 0.01 | 345.44 | - |
| *Adjusted $R^2$ (%)* | 86.75 | | |
| *AICc* | 328.56 | | |
| | | | |
| **Face** (N=63 images, N=13 subjects) | | | |
| Miniglobe temperature | 0.14 ± 0.01 | 14.26 | <0.001 |
| Intercept | 3.28 ± 0.01 | 322.88 | - |
| *Adjusted $R^2$ (%)* | 76.69 | | |
| *AICc* | 276.80 | | |

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687  **Table 3**. Results of the linear model analyses testing the relationship between core body

688  temperature and infrared surface temperatures from the following body regions: dorsal, ventral,

689  tail, and face. We ran the analyses at the level of the image/subject.

| | $\beta \pm SE$ | $t$ | $P$ |
|---|---|---|---|
| **Dorsal** (N=153 images, N=14 subjects) | | | |
| Core body temperature | $0.05 \pm 0.01$ | 3.91 | <0.001 |
| Intercept | $3.27 \pm 0.01$ | 247.92 | - |
| *Adjusted R$^2$ (%)* | 8.24 | | |
| *AICc* | 881.92 | | |
| | | | |
| **Ventral** (N=32 images, N=11 subjects) | | | |
| Core body temperature | $0.05 \pm 0.02$ | 2.18 | 0.04 |
| Intercept | $3.38 \pm 0.02$ | 146.63 | - |
| *Adjusted R$^2$ (%)* | 10.58 | | |
| *AICc* | 181.31 | | |
| | | | |
| **Tail** (N=76 images, N=14 subjects) | | | |
| Core body temperature | $0.06 \pm 0.02$ | 2.39 | 0.02 |
| Intercept | $3.28 \pm 0.02$ | 138.46 | - |
| *Adjusted R$^2$ (%)* | 5.80 | | |
| *AICc* | 477.62 | | |
| | | | |
| **Face** (N=63 images, N=13 subjects) | | | |
| Core body temperature | $0.04 \pm 0.02$ | 2.01 | 0.048 |
| Intercept | $3.29 \pm 0.02$ | 164.53 | - |
| *Adjusted R$^2$ (%)* | 4.64 | | |
| *AICc* | 365.57 | | |

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696　　**Table 4**. Results of the linear model analyses testing the effects of miniglobe temperature and

697　　core body temperature on infrared surface temperatures from the following body regions: dorsal,

698　　ventral, tail, and face. We ran the analyses at the level of the image/subject.

| | $\beta \pm SE$ | $t$ | $P$ |
|---|---|---|---|
| **Dorsal** (N=153 images, N=14 subjects) | | | |
| Miniglobe temperature | $0.15 \pm 0.01$ | 23.76 | <0.001 |
| Core body temperature | $0.01 \pm 0.01$ | 1.82 | 0.07 |
| Intercept | $3.26 \pm 0.01$ | 536.18 | - |
| *Adjusted $R^2$ (%)* | 81.73 | | |
| *AICc* | 636.12 | | |
| | | | |
| **Ventral** (N = 32 images, N = 11 subjects) | | | |
| Miniglobe temperature | $0.13 \pm 0.15$ | 8.34 | <0.001 |
| Core body temperature | $-0.01 \pm 0.01$ | -0.46 | 0.65 |
| Intercept | $3.37 \pm 0.01$ | 270.99 | - |
| *Adjusted $R^2$ (%)* | 74.90 | | |
| *AICc* | 142.20 | | |
| | | | |
| **Tail** (N = 76 images, N = 14 subjects) | | | |
| Miniglobe temperature | $0.21 \pm 0.01$ | 19.29 | <0.001 |
| Core body temperature | $0.00 \pm 0.01$ | 0.38 | 0.70 |
| Intercept | $3.26 \pm 0.01$ | 343.47 | - |
| *Adjusted $R^2$ (%)* | 86.59 | | |
| *AICc* | 330.64 | | |
| | | | |
| **Face** (N = 63 images, N = 13 subjects) | | | |
| Miniglobe temperature | $0.14 \pm 0.01$ | 13.48 | <0.001 |
| Core body temperature | $0.00 \pm 0.01$ | 0.10 | 0.92 |
| Intercept | $3.28 \pm 0.01$ | 320.45 | - |
| *Adjusted $R^2$ (%)* | 76.31 | | |
| *AICc* | 279.08 | | |

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**Table 5.** A summary of the performance (AICc and Adjusted $R^2$ %) of the infrared surface temperature linear models (i.e., dorsal, ventral, face, and tail) as explained by miniglobe temperature and core body temperature as sole predictors, and a composite model including both predictor variables. [†] denotes best fitting model. A ΔAICc threshold of < -2.0 was used indicate whether a composite model was better than its single predictor variable equivalent.

| Surface temperature | | Dependent variables | | | |
|---|---|---|---|---|---|
| | | Miniglobe temperature | Core body temperature | Miniglobe temperature *and* Core body temperature | Δ change in performance of the mini globe model with the addition of core body temperature |
| **Dorsal** | AICc | 637.31[†] | 881.92 | 636.12 | -1.19 |
| | $R^2$ | 81.45 | 8.24 | 81.73 | 0.28 |
| **Ventral** | AICc | 139.81[†] | 181.92 | 142.2 | 2.39 |
| | $R^2$ | 75.56 | 10.58 | 74.9 | -0.66 |
| **Tail** | AICc | 328.56[†] | 477.62 | 330.64 | 2.08 |
| | $R^2$ | 86.75 | 5.8 | 86.59 | -0.16 |
| **Face** | AICc | 276.80[†] | 365.57 | 279.08 | 2.28 |
| | $R^2$ | 76.69 | 4.64 | 76.31 | -0.38 |

720    **FIGURES LEGENDS**

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722    **Figure 1.** An infrared image and time-matched photograph of data collection (zoomed out for

723    illustrative purposes) of a vervet monkey implanted with a temperature-sensitive data logger

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725    **Figure 2.** Three example infrared images demonstrating the location of discrete temperature

726    sampling from the dorsal, ventral, tail and bare-skin face image surfaces.

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728    **Figure 3.** A Bland-Altman plot showing the relationship between vervet monkeys' core body

729    temperature ($^\circ$C) and each of the four body surface temperatures ($^\circ$C) (i.e., dorsal, ventral, tail

730    and face). The x-axis represents the combined mean of core body and specified surface

731    temperatures ($^\circ$C). The y-axis represents the difference in temperature between core body and

732    specified surface temperatures. Dashed lines represent the mean $\pm$ 1.96SD.