Infrared thermography cannot be used to approximate core body temperature in wild primates

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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 noninvasive means to detect and record animal temperatures, infrared thermography alone cannot be used to approximate core body temperature in wild primates.

Research Highlights

- Body surface temperatures do not approximate core body temperatures.
- Body surface temperatures tell us more about the local climate a primate is in.

1 INTRODUCTION

As primate populations continue to decline and face an increasing risk of extinction as a consequence of climate change (Estrada et al., 2017; Graham et al., 2016), 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 (Fuller et al., 2016; Hetem et al., 2014; 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 (Lubach et al., 1992; Maloney et al., 2007; McNab & Wright, 1987; Muller et al., 1985; Robinson & Fuller, 1999; Sulzman et al., 1977; Whittow et al., 1977; Wurster et al., 1985). 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) used intra-abdominal temperature-sensitive radio transmitters to record the core body temperature patterns of chacma baboons (*Papio ursinus)* under free-ranging, natural conditions. Their study was limited by relatively few subjects and body temperature measurements being collected only intermittently during the daytime over less than a month for each animal. Nevertheless, this study revealed the importance of high heat load as a thermal stressor to chacma baboons, and the importance of drinking water to prevent hyperthermia (Brain & Mitchell, 1999). Intra-abdominal transmitters also have been used to describe the core body temperature patterns associated with daily torpor in lemurs (*Lemuridae spp*. Dausmann, 2005; Schmid, 2000; Schmid et al., 2000). More recently, we have used intra-abdominal data loggers to describe the seasonal patterns of core body temperature in wild vervet monkeys (*Chlorocebus pygerythrus*), the thermoregulatory consequences of both cold and heat stress, interindividual differences in thermal performance, and the importance of behavioral (including social) thermoregulation in body temperature regulation (Henzi et al., 2017; Lubbe et al., 2014; McFarland et al., 2015, 2019, 2020).

The use of intra-abdominal data loggers provides a good index of the thermal status of the body core but requires animals to be captured and to undergo surgical procedures for logger implantation and extraction (see McFarland et al., 2015 for a full description of methods). As an alternative to data logging approaches there has been interest in using infrared thermography to make inferences about thermoregulatory processes in free-ranging animals, including primates (Cilulko et al., 2013; McCafferty, 2007; Narayan et al., 2019; Thompson, Scheidel, et al., 2017). At face value, this appears an attractive option for the noninvasive and remote measurement of body temperature. However, infrared thermography measures animal surface temperatures, and there is contrasting evidence whether surface temperatures (i.e., skin, fur, inner-ears, and eyes) can approximate core body temperature. While some studies report no significant association between the body surface and core body temperatures (Jay et al., 2007; Larcombe, 2007; Sikoski et al., 2007; Sykes et al., 2012), others have shown a positive correlation (Dausmann, 2005; Giloh et al., 2012; Johnson et al., 2011; Warriss et al., 2006; Zanghi, 2016). An important caveat, however, is the lack of control in these analyses for the mediating effect that local climate has on both surface and core body temperatures. That is, even though body surface and core body temperatures were shown to be positively correlated, it is possible that this relationship was an artefact of the local climate influencing these variables. While it may be reasonable to assume that skin temperature more closely reflects core body temperature in small animals, the mediating effect of local climate should still be considered when attempting to make inferences about core body temperature from surface temperatures alone. In an experimental study of bats (*Carollia perspicillata*) in controlled environmental conditions, for example, it was observed that the difference between an animal's core and skin temperature was a function of ambient temperature, with the authors concluding that any inferences made about core body temperature regulation from skin temperature measurements, including in very small animals, should account for the effect of ambient conditions (Audet & Thomas, 1996). Even when care has been taken to avoid increased surface heat loads incurred by solar radiation (McCafferty, 2007; Thompson, Scheidel, et al., 2017), surface temperatures are still more influenced by local climate than body temperature. In wild mantled howling monkeys (*Alouatta palliata*), for example, dorsal fur temperature was more strongly predicted by ambient temperatures than by dorsal subcutaneous temperatures, and facial skin surface temperatures were predicted solely by ambient temperature and not by dorsal subcutaneous temperatures (Thompson, Scheidel, et al., 2017).

Here, we use data collected from wild vervet monkeys to examine the relationship between body surface and core body temperatures, while controlling for local climatic conditions. Because an endothermic animal's core body temperature is typically buffered from their environment by a range of autonomic and behavioral processes (Angilletta et al., 2010; Hetem et al., 2016; Lovegrove et al., 1991; Mitchell et al., 2018), we predict that surface temperatures will be more closely associated with local climate than with core body temperature. A better sense of the relationship between these variables will hopefully inform us whether infrared thermography can be used to approximate core body temperature. If surface temperatures are predicted by core temperatures, while controlling for the effect of the local climate, this would suggest that surface temperatures can approximate, to some extent, core body temperature. However, if surface temperatures are predicted by the local climate, and not core body temperatures, this would suggest that the surface temperatures tell us more about the environment an animal is in, and less about the body temperature of an animal in that environment. We use four body regions to test our hypothesis: the furred dorsal, ventral and tail surface and bare-skin facial surface.

2 METHODS

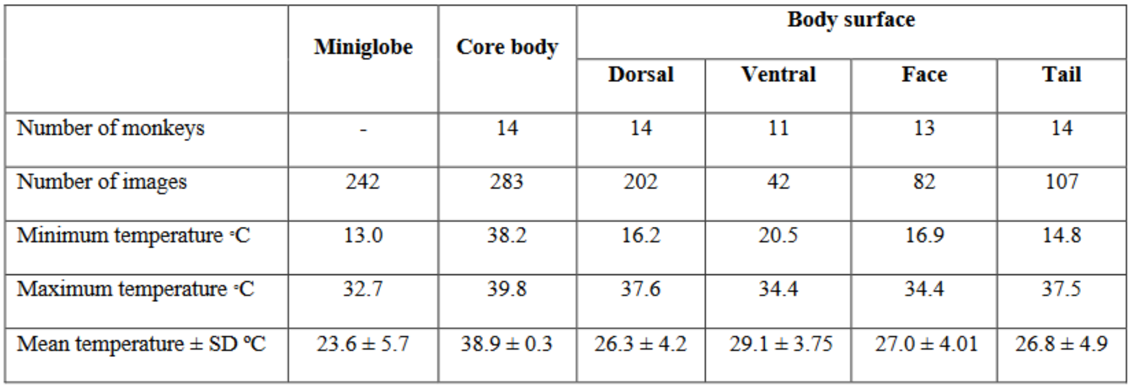
In June 2017, as part of a longitudinal project on vervet monkey thermoregulation in the Eastern Cape, South Africa (32°22’S, 24°52’E), we collected infrared thermography data from a subset of individuals living across three groups (*N* = 14: five females and nine males). These animals fed on a natural diet, were fully habituated to the presence of researchers, and were individually identifiable by means of natural markings (McFarland et al., 2014; Pasternak et al., 2013).

2.1 Infrared thermal imagery

We collected infrared thermal images (N_{total} = 294 images, $_{\text{subject}}$ = 21 ± SD 14 images) opportunistically using a handheld infrared thermograph model T360 camera (FLIR® Systems Inc.). We set emissivity to 0.98. We targeted the animal's furred dorsal, ventral, and tail surface, and bare-skin face surface, in each photo, to the point that some images could be used to measure multiple surface regions, and others not.

We used the following selection criteria to determine the usability of infrared surface temperature measurements: (i) the targeted body surface was in plain view and not obscured by foliage or another individual, (ii) the animal was within 5 m of the camera, (iii) the targeted body surface was orientated toward the camera to avoid detection errors associated with sampling curved surfaces (McCafferty, 2007), (iv) the targeted body surface was in shade or low light levels, avoiding reflective light, thereby minimizing the effect of direct solar radiation on surface measurements (McCafferty, 2007), and (v) the animal was in a relaxed state, that is, stationary and not engaged in antagonistic behavior. Table 1 outlines the distribution of the final measurements used in the current analyses.

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

At the time each image was taken, we positioned a thermocouple attached to a matte-black painted metal box within the frame of each thermal image (e.g., Figure 1). We calibrated the temperature measurements recorded by the thermal camera using the thermocouple. To ensure consistency in data collection, only one researcher extracted the FLIR temperature data, according to a strict protocol that did not rely on subjective judgement. The researcher was blind to concurrent environmental and body temperature data. For each infrared image, we used FLIR Tools® software (FLIR® Systems Inc., 2019) to extract five discrete pixel-defined temperature measurements from the targeted body surface region and the black calibration box. For the dorsal, ventral, and bare-skin face surfaces, we used the five corners of a pentagon to define the sampling locations of each discrete temperature measurement; adjusting the pentagon's size to approximately cover the area of the image that was occupied by each respective body region (Figure 2). To reduce any confounding effects of short-term temperature changes in specific facial regions that may relate to emotional states (Chotard et al., 2018), we average surface temperature over the bare-skin facial region; avoiding sampling from peri-orbital and nose tip regions. For the tail surface, we took five temperature measurements at regular intervals along the length of the tail (Figure 2). We calculated the mean black box and mean body surface temperatures for all available body regions in each image. We used the difference between the thermocouple temperature and the mean FLIR temperature of the black box to create a single-point calibration offset for all mean body surface temperatures.

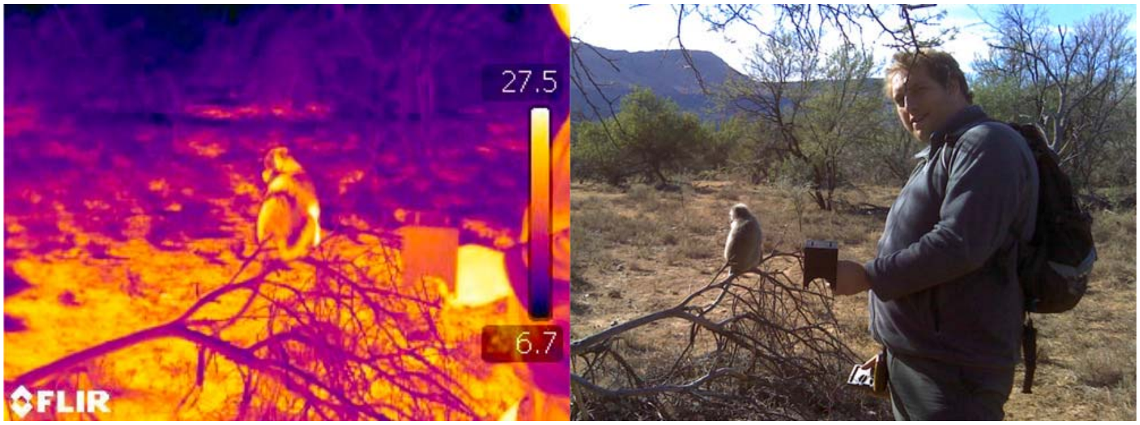


Figure 1. An infrared image and time-matched photograph of data collection (zoomed out for illustrative purposes) of a vervet monkey implanted with a temperature-sensitive data logger

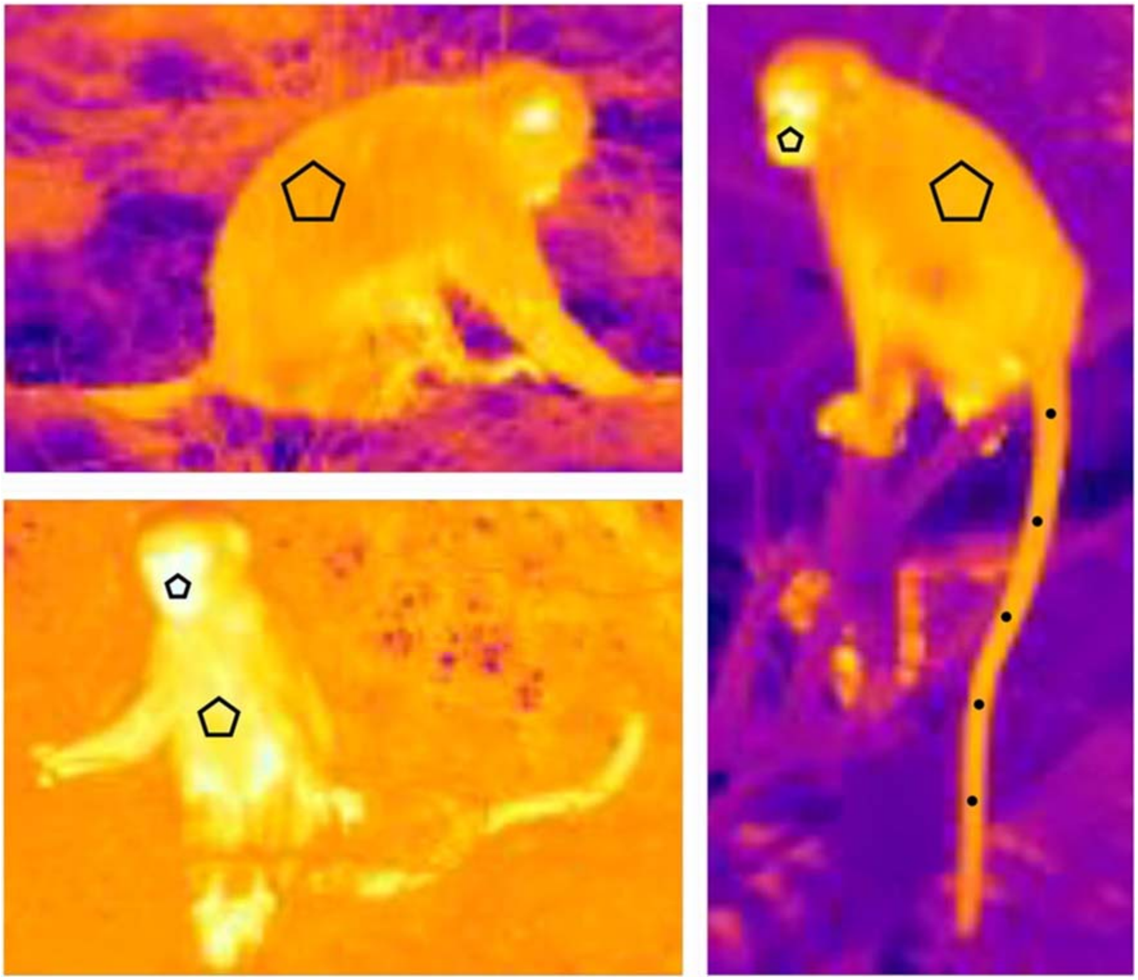


Figure 2. *Figure*Three example infrared images demonstrating the location of discrete temperature sampling from the dorsal, ventral, tail, and bare-skin face image surfaces

2.2 Local climate

We used black globe temperature to measure the local climate experienced by our study animals. Black globe temperature integrates the influence of air temperature, solar radiation and wind speed, and is thus considered a better measure of the thermal heat load experienced by an animal than air temperature alone (Hetem et al., 2007; McFarland et al., 2014). We recorded black globe temperatures every minute using a calibrated, temperature-sensitive Thermochron 4 K iButton (model DS1921G; Maxim Integrated™) housed inside a matte-black painted copper ball with a diameter of 30 mm (hereafter, miniglobe). iButtons recorded miniglobe temperature at one-minute intervals at a resolution of 0.06°C and were individually calibrated to an accuracy of 0.1°C. We recorded miniglobe temperatures at the time each image was taken, within 5 m of the target animal. Miniglobe temperatures ranged from 13.0 to 32.7°C across the study period with a mean daily temperature of 23.6 ± SD 5.7°C.

2.3 Body temperature data

In June 2016, we surgically implanted 14 adult vervet monkeys (five females, nine males; distributed across three groups) with miniature temperature-sensitive data loggers (model: DST Centi-T) intra-abdominally. Data loggers recorded core body temperature at five-minute intervals at a resolution of 0.03°C and were individually calibrated to an accuracy of 0.1°C.

We recorded the body mass (kg) of all animals ($_{\text{female}}$ = 3.4 ± SD 0.4 g, $_{\text{male}}$ = 5.1 ± SD 0.3 g). We removed the data loggers at the end of June 2017. For full details of the capture and surgery procedure see McFarland et al. (2015). Data loggers measured the core intra-abdominal body temperature (to the nearest 5 min) of the same animals that were sampled using the infrared camera. Importantly, we implanted our subjects with data loggers in fulfillment of a long-term study of vervet monkey thermal physiology. That is, our subjects were not solely exposed to this procedure for the purpose of the current project.

Observational data collection protocols were approved by the University of Lethbridge under Animal Welfare Protocols 0702 and 1505. Capture and surgical procedures were approved by the University of the Witwatersrand Animal Ethics Research Committee (Protocol # 2015-04-14B-2017), and were treated in accordance with international ethical standards. No long-term sequelae were observed as a consequence of surgical intervention. Overall, this study adhered to the legal requirements of South Africa, and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

2.4 Statistical analysis

We used a series of Bland–Altman plots to visually compare the measurement of vervet monkeys' core body temperature using intra-abdominal data loggers, with surface temperature measured using infrared thermography (Altman & Bland, 1983).

We performed our analyses in R v.3.6.0 (R-Core-Team, 2019) using the "lme4" package to model outcomes (Bates et al., 2019), the "rsq" package to generate adjusted R^2 values for the fixed effects (Zhang, 2018), and the "lmertest" package to generate p values (Kuznetsova et al., 2019). Before running each model, we checked for intercollinearity by calculating variance inflation factors (VIFs) for the predictor variables using the "car" package (Fox et al., 2020). The VIF scores in all of our models were <2 and were therefore not considered collinear. We scaled and centered our predictor variables so we could directly compare the resulting coefficients. We specified a Gaussian error structure with a log link function in all of our models to normalize the residuals.

We originally ran a series of linear mixed models, entering subject ID as a random effect. However, these random effects did not explain any meaningful variance and their inclusion produced overfitted models with the singular fit. We, therefore, ran a series of linear models, removing this random effect. The results of the linear mixed models and linear models were qualitatively the same. We present the results of the linear models below.

We first ran a series of four linear models entering our four surface temperatures (i.e., dorsal, ventral, tail, and face) in turn as the dependent variable, and time-matched miniglobe as the sole predictor variable. We ran a second series of four linear models entering our four surface temperatures in turn as the dependent variable, and time-matched core body temperature as the sole predictor variable. We ran a third series of four linear models entering our four surface temperatures in turn as the dependent variable and entered time-matched miniglobe temperature and core body temperature as predictor variables, to determine whether this model improved upon either of the single predictor variable models described in the first two series of linear models.

For the first two series of linear models (i.e., the single predictor variable models), we follow Colquhoun (2014) in describing outcomes as indicating weak (p = .05), moderate (p = .01), or strong (p = .001) evidence for effects. Following the third series of linear models, we used a reduction in the Akaike Information Criterion (AIC: Akaike, 1974) of a model, using a ΔAICc (to control for small sample sizes) threshold of >2.0 (Burnham & Anderson, 2004), to indicate whether the composite model was better than its single predictor variable equivalent. We used adjusted R^2 values to describe how much variance in a model's dependent variable was explained by its predictor variables.

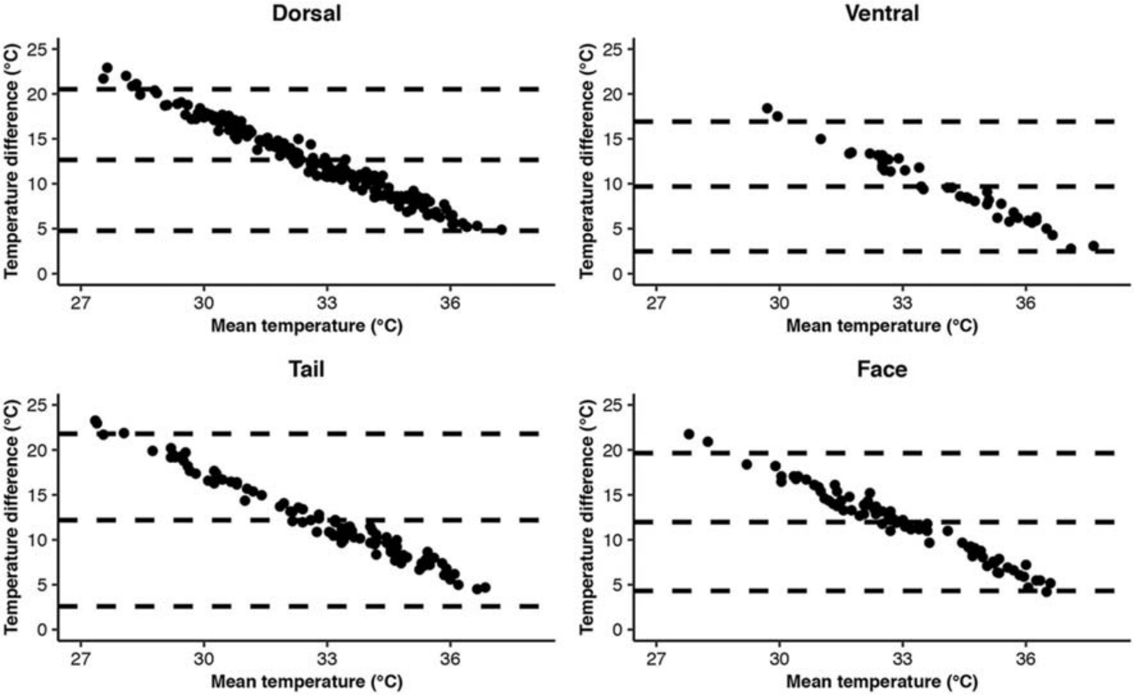


Figure 3. A Bland–Altman plot showing the relationship between vervet monkeys' core body temperature (°C) and each of the four body surface temperatures (°C) (i.e., dorsal, ventral, tail, and face). The *x*-axis represents the combined mean of core body and specified surface temperatures (°C). The *y*-axis represents the difference in temperature between core body and specified surface temperatures. Dashed lines represent the mean ± 1.96 *SD*

3 RESULTS

In a series of four Bland–Altman plots (Figure 3), we observed large differences between the measurements of core body and surface temperatures ($\bar{x}_{\text{dorsal}} = 12.6 \pm \text{SD } 4.4°\text{C}$, $\bar{x}_{\text{ventral}} = 9.4 \pm \text{SD } 3.9°\text{C}$, $\bar{x}_{\text{tail}} = 12.3 \pm \text{SD } 5.5°\text{C}$, $\bar{x}_{\text{face}} = 12.0 \pm \text{SD } 4.3°\text{C}$). Temperature differences in excess of 15°C were common and occasionally exceeded 20°C at low temperatures. When the mean of core body and surface body temperatures were higher as a result of increased surface temperature in warm conditions (Table 2), the differences between these variables were smaller. However, core body and surface temperatures were never equivalent.

Table 2. Results of the linear model analyses testing the relationship between miniglobe temperature and infrared surface temperatures from the following body regions: dorsal, ventral, tail, and face. We ran the analyses at the level of the image/subject

	β ± 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		

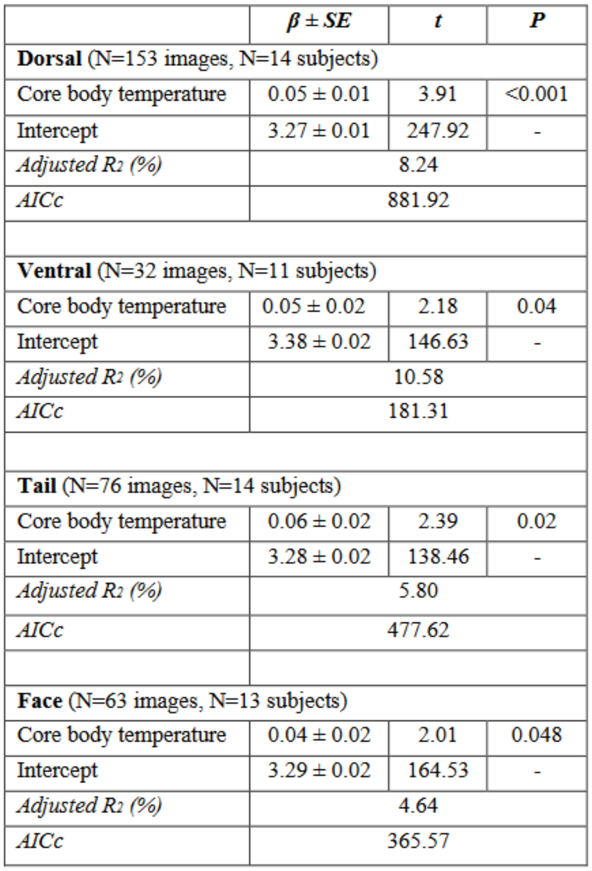
3.1 Miniglobe temperature

In a series of four linear models (Table 2) with miniglobe temperature as the sole predictor variable, globe temperature had a strong positive effect on dorsal, ventral, face, and tail infrared surface temperatures (all $p < .001$). Miniglobe temperature explained 81% (dorsal), 76% (ventral), 87% (tail), and 77% (face) of the variance in infrared body surface temperatures (Table 2).

3.2 Core body temperature

In a series of four linear models with core body temperature as the sole predictor variable, core body temperature had a strong positive effect on dorsal surface temperatures ($p < .001$) and a weak positive effect on ventral ($p = .04$), tail ($p = .02$), and face ($p = .048$) infrared surface temperatures. Core body temperature explained 8% (dorsal), 11% (ventral), 6% (tail), and 5% (face) of the variance in infrared body surface temperatures (Table 3).

Table 3. Results of the linear model analyses testing the relationship between core body temperature and infrared surface temperatures from the following body regions: dorsal, ventral, tail, and face. We ran the analyses at the level of the image/subject

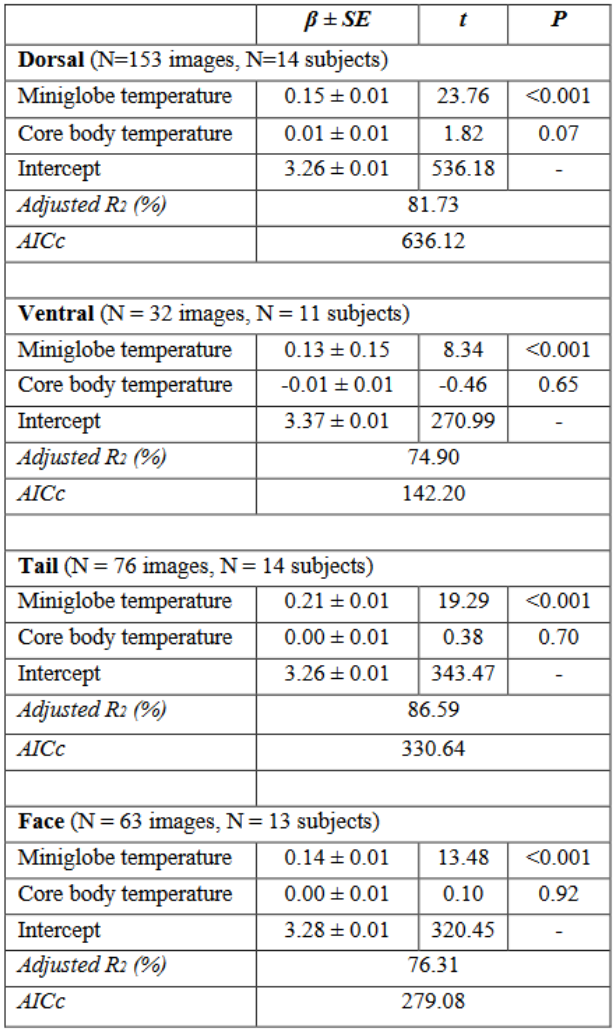


	β* ± *SE	***t***	***P***
Dorsal (N=153 images, N=14 subjects)			
Core body temperature	0.05 ± 0.01	3.91	<0.001
Intercept	3.27 ± 0.01	247.92	-
Adjusted R_2 (%)	8.24		
AICc	881.92		
Ventral (N=32 images, N=11 subjects)			
Core body temperature	0.05 ± 0.02	2.18	0.04
Intercept	3.38 ± 0.02	146.63	-
Adjusted R_2 (%)	10.58		
AICc	181.31		
Tail (N=76 images, N=14 subjects)			
Core body temperature	0.06 ± 0.02	2.39	0.02
Intercept	3.28 ± 0.02	138.46	-
Adjusted R_2 (%)	5.80		
AICc	477.62		
Face (N=63 images, N=13 subjects)			
Core body temperature	0.04 ± 0.02	2.01	0.048
Intercept	3.29 ± 0.02	164.53	-
Adjusted R_2 (%)	4.64		
AICc	365.57		

3.3 Miniglobe temperature and core body temperature

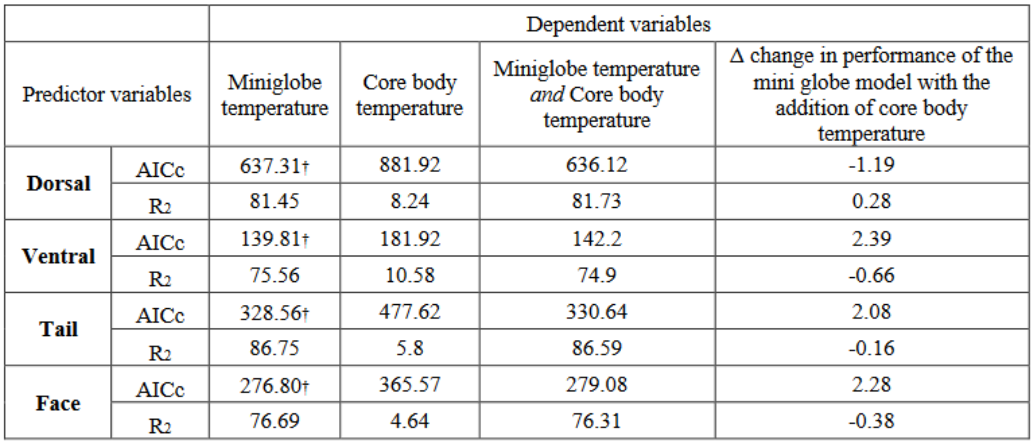
Given that globe temperature was a stronger predictor of infrared surface temperatures than core body temperature (Tables 2 and 3), we ran a series of four linear models including both globe temperature and core body temperature as predictor variables, to examine whether the addition of core body temperature improved the performance of the model with globe temperature as the sole predictor (Table 4). The dorsal, ventral, tail, and face infrared surface temperature models were not improved by the addition of core body temperature. AICc values did not decrease by >2.0, and less than 1% additional variance was explained, following the addition of core body temperature as a predictor in all cases (Table 5). The best-fitting models, for all infrared body surface temperatures, therefore, were those that included globe temperature as a sole predictor variable.

Table 4. Results of the linear model analyses testing the effects of miniglobe temperature and core body temperature on infrared surface temperatures from the following body regions: dorsal, ventral, tail, and face. We ran the analyses at the level of the image/subject



	β* ± *SE	***t***	***P***
Dorsal (N=153 images, N=14 subjects)			
Miniglobe temperature	0.15 ± 0.01	23.76	<0.001
Core body temperature	0.01 ± 0.01	1.82	0.07
Intercept	3.26 ± 0.01	536.18	-
Adjusted R_2 (%)	81.73		
AICc	636.12		
Ventral (N = 32 images, N = 11 subjects)			
Miniglobe temperature	0.13 ± 0.15	8.34	<0.001
Core body temperature	-0.01 ± 0.01	-0.46	0.65
Intercept	3.37 ± 0.01	270.99	-
Adjusted R_2 (%)	74.90		
AICc	142.20		
Tail (N = 76 images, N = 14 subjects)			
Miniglobe temperature	0.21 ± 0.01	19.29	<0.001
Core body temperature	0.00 ± 0.01	0.38	0.70
Intercept	3.26 ± 0.01	343.47	-
Adjusted R_2 (%)	86.59		
AICc	330.64		
Face (N = 63 images, N = 13 subjects)			
Miniglobe temperature	0.14 ± 0.01	13.48	<0.001
Core body temperature	0.00 ± 0.01	0.10	0.92
Intercept	3.28 ± 0.01	320.45	-
Adjusted R_2 (%)	76.31		
AICc	279.08		

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



		Dependent variables			
Predictor 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

4 DISCUSSION

Our findings reveal that infrared thermography cannot be used to approximate core body temperature. Vervet monkey surface temperatures measured on the furred dorsal, ventral, and tail region, as well as the bare-skin facial region, were more strongly predicted by miniglobe (i.e., environmental) temperatures than core body temperatures. At low miniglobe temperatures, surface temperatures dropped substantially and furred surfaces could be more than 20°C below core body temperature. Since an animal's body surface is the interface where heat is gained by, and dissipated from, the body, it is unsurprising that animal surface temperature is strongly influenced by environmental temperature. While the core body temperatures of free-ranging primates can also vary in response to environmental variability (e.g., Brain & Mitchell, 1999; Dausmann, 2005; Henzi et al., 2017; Lubbe et al., 2014; McFarland et al., 2015, 2020; Schmid, 2000; Schmid et al., 2000), core body temperature is much more tightly regulated through a range of behavioral and physiological processes.

Primates, like all mammals, employ a range of physiological mechanisms to cope with environmental challenges and maintain homeostasis. Autonomic processes involve the activation of pathways in the preoptic area of the hypothalamus that regulate the balance of heat production and loss (Morrison & Nakamura, 2019), including altering blood flow to the skin through peripheral vasoconstriction and vasodilation. Individuals can also engage in behaviors that alter body temperature, such as changing activity patterns, posture, or selecting appropriate microclimates (Henzi et al., 2017; McFarland et al., 2019, 2020). Morphological features, such as the color, depth, density, and condition of the pelage, can further modulate heat transfer to and from the body (McFarland et al., 2016; Schmidt-Nielsen, 1997; Scholander et al., 1950). For example, a thick pelage would act to insulate the animal, reducing the rate of heat loss in cold environments and the rate of heat gain in hot environments, thereby resulting in outer fur surface temperatures that differ substantially from skin temperatures.

Given the complexities surrounding core body temperature regulation, it would be surprising if surface temperatures did approximate core body temperatures. Yet, a number of studies have shown an association between surface temperature and core body temperature (Dausmann, 2005; Giloh et al., 2012; Johnson et al., 2011; Warriss et al., 2006; Zanghi, 2016), including the current manuscript. However, the variance in surface temperature that could be explained by core body temperature in our study was an order of magnitude lower than that explained by miniglobe temperature. In addition, after controlling for the effect of miniglobe temperature, the relationship with surface and core temperatures became trivial. We recommend that future studies do not use surface temperature measurements to approximate core body temperature, without a full understanding of the interactions between core, surface, and environmental variables.

In an apparent attempt to avoid the invasiveness of intra-abdominal data logging, several research teams have used skin or subcutaneous temperature measurements to make inferences about core body temperature in primates. These methods have provided information on the hibernation patterns of the Lesser bushbaby (*Galago moholi*: Mzilikazi et al., 2006; Nowack et al., 2010, 2013) and several lemur species (*Lemuridae spp.*, Blanco et al., 2018; Dausmann, 2005; Dausmann et al., 2004; Kobbe et al., 2014; Schmid, 2001), as well as the seasonal variability in the body temperature rhythm of the larger, diurnal mantled howling monkey (Thompson et al., 2014). While subcutaneous body temperatures, typically recorded using devices implanted between the scapula, may more closely reflect core body temperature than the surface temperature, they also are likely to be influenced by a core to periphery gradient, particularly in large mammals. The temperature of peripheral tissue is more strongly influenced by local climate, and peripheral blood flow, than is core body temperature (Mitchell et al., 2018). The subcutaneous body temperatures of mantled howling monkeys, for example, were strongly influenced by environmental temperature (Thompson et al., 2014). Furthermore, although a positive association between core body and subcutaneous body temperatures has been documented (Brown & Bernard, 1991; Navarro-Serra & Sanz-Cabañes, 2019), this does not mean that the measures are equivalent or interchangeable. Similar to surface temperatures, subcutaneous temperatures may deviate substantially from core body temperature, particularly in cold environments when endotherms peripherally vasoconstrict to conserve core body heat (Torrao et al., 2011).

Other less invasive measures of an animal's body temperature include measuring the temperature of an animal's feces to approximate its core body temperature. For example, fecal temperature has been used as a proxy for core body temperature in chimpanzees (Jensen et al., 2009; Negrey et al., 2020) based on limited evidence that fecal temperatures approximate rectal temperature in humans. However, given the infrequency of defecation point-sampling, and the fact that core body temperatures can fluctuate over 24 h, and over even shorter time intervals for a multitude of reasons (e.g., drinking, behavioral thermoregulation, microclimate selection, the intensity of activity: McFarland et al., 2015, 2019, 2020), this method offers very little information on the regulation of core body temperature. Continuous and remote measurement of core body temperature through implanted intra-abdominal data loggers is a relatively simple and feasible technique that provides far greater insight into an individual's thermal balance with its environment.

That is not to say that infrared thermography cannot provide important insights on thermoregulatory or other physiological processes. Surface temperatures not only inform us about the heat load experienced at an animal's surface, but may also provide information on peripheral blood flow, and the effect of pelage properties on heat transfer (Cilulko et al., 2013; Mathewson, Hanson-Dorr, et al., 2018; McCafferty, 2007). Infrared thermography can also provide valuable insights on animal behavior and physiology, or can be used to test the accuracy of biophysical heat transfer models (e.g., Mathewson, Hanson-Dorr, et al., 2018). Moreover, facial infrared thermography has been used to quantify the emotional states of nonhuman primates (Chotard et al., 2018; Ioannou et al., 2015; Kuraoka & Nakamura, 2011; Nakayama et al., 2005), including in wild chimpanzees (*Pan troglodytes*: Dezecache et al., 2017), and other animals (McCafferty, 2007). The experimental protocols used in these studies typically rely on small short-term changes in the skin-surface temperature of particular facial regions to make inferences about emotional responses that invoke autonomic changes in blood flow at the surface of the skin (Kreibig, 2010). For example, reductions in nasal skin temperature associated with negative emotional states were relatively small in magnitude, <0.8°C, even in “raging” monkeys (Kuraoka & Nakamura, 2011), and these short terms changes in facial temperature are not influenced by the thermal environment to which the monkeys were exposed (Nakayama et al., 2005). The magnitudes of these emotion-driven temperature changes are unlikely to have had a significant influence on the much larger differences that we report between core and surface body temperatures. Nonetheless, our experimental protocol attempted to reduce the confounding effects of the emotional state by focusing our thermal images on relaxed monkeys and using relatively discrete temperature measurements collected across the day. Any small skin temperature differences as a result of emotional state would likely be further diluted by our protocol that averaged the temperatures across all bare-skin facial regions, as different facial regions may differ in the direction of temperature change (Chotard et al., 2018).

When alternative methods are used to measure an animal's surface or peripheral tissue temperature, one should acknowledge that these data do not necessarily reflect the thermal status of an animal's core in a given environment. For subcutaneous data logging methods, in particular, the limited scientific value afforded by these methods should be weighed carefully against the ethical considerations surrounding the required animal capture and intervention. When it is not possible to measure body temperature within the animal's core, we suggest that alternative, noninvasive physiological measures are used to provide information on a primate's energy balance, hormone levels, or metabolic activity in response to environmental variability (e.g., Behringer & Deschner, 2017; Cristóbal-Azkarate et al., 2016; Thompson, Powell, et al., 2017; Thompson, Scheidel, et al., 2017). Biophysical models (e.g., Niche Mapper™: Porter & Mitchell, 2006) that use principles of heat and mass transfer, coupled with information on an animal's morphology, behavior, and microclimate, have also been used to predict an animal's energetic requirements as a function of environmental conditions (e.g., Briscoe et al., 2016; Long et al., 2014; Mathewson & Porter, 2013; Mathewson, Hanson-Dorr, et al., 2018; Moyer-Horner et al., 2015; Natori & Porter, 2007; Zhang et al., 2018), including in vervet monkeys (Mathewson et al., in press). Ultimately, an integrative approach to understanding heat transfer and physiological plasticity can complement accurate measures of core body temperature, to provide greater insight into how primates respond to environmental stress.

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