

Body Temperature and Thermal Environment in a Generalized Arboreal Anthropoid, Wild Mantled Howling Monkeys (*Alouatta palliata*)

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ABSTRACT Free-ranging primates are confronted with the challenge of maintaining an optimal range of body temperatures within a thermally dynamic environment that changes daily, seasonally, and annually. While many laboratory studies have been conducted on primate thermoregulation, we know comparatively little about the thermal pressures primates face in their natural, evolutionarily relevant environment. Such knowledge is critical to understanding the evolution of thermal adaptations in primates and for comparative evaluation of humans' unique thermal adaptations. We examined temperature and thermal environment in free-ranging, mantled howling monkeys (*Alouatta palliata*) in a tropical dry forest in Guanacaste, Costa Rica. We recorded subcutaneous (T_{sc}) and near-animal ambient temperatures (T_a) from 11 animals over 1586.5 sample hours during wet and dry seasons. Howlers displayed considerable variation in T_{sc} , which was largely attribut-

able to circadian effects. Despite significant seasonal changes in the ambient thermal environment, howlers showed relatively little evidence for seasonal changes in T_{sc} . Howlers experienced warm thermal conditions which led to body cooling relative to the environment, and plateaus in T_{sc} at increasingly warm T_a . They also frequently faced cool thermal conditions ($T_a < T_{sc}$) in which T_{sc} was markedly elevated compared with T_a . These data add to a growing body of evidence that non-human primates have more labile body temperatures than humans. Our data additionally support a hypothesis that, despite inhabiting a dry tropical environment, howling monkeys experience both warm and cool thermal pressures. This suggests that thermal challenges may be more prevalent for primates than previously thought, even for species living in nonextreme thermal environments. *Am J Phys Anthropol* 000:000–000, 2014. © 2014 Wiley Periodicals, Inc.

Temperature is a major factor affecting organisms because it directly impacts molecular, physiological, and behavioral processes (Pörtner et al., 2006). There is ample evidence that an animal's thermal environment and its ability to deal with temperature fluctuations have important short- and long-term consequences that are evolutionarily significant. Excess heat is known to disrupt reproductive processes and reduce cognitive ability (Dunbar, 1990; McMorris et al., 2006; Descamps et al., 2008; Megahed et al., 2008; Hansen, 2009). In free-ranging baboons, both cold and warm thermal stressors have been linked to increased interbirth interval, fewer menstrual cycles, lower conception and birth rates, higher infant and juvenile mortality, and reduced longevity (Ohsawa and Dunbar, 1984; Hill et al., 2000; Beehner et al., 2006). Thermal environment (including warm, cold, and mild habitats) has also been linked to a myriad of commonly measured behavioral variables such as rates of social contact, activity budgets, food consumption, and travel distances (Harrison, 1985; Agetsuma, 1995; Chiarello, 1995; Fernandez-Duque, 2003; Hanya, 2004; Hill, 2006; Baoping et al., 2009; Terrien et al., 2011; Nowack et al., 2013). Despite clear evidence linking temperature to behaviorally and evolutionarily important processes, we know relatively little about the

thermoregulatory responses of wild primates to their natural environment.

Laboratory studies show that animals preferentially seek ambient temperatures that allow them to maintain optimal body temperature ranges without expending additional energy to cool or warm their body (Terrien et al., 2011). Animals often achieve this "thermoneutral zone" (TNZ) through a variety of behavioral mechanisms

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such as microhabitat selection, timing of activities, use of specific postures, huddling, or sunbathing (Terrien et al., 2011). If an animal falls outside of its TNZ, it is forced to expend more energy to maintain a given body temperature. For example, mammals will warm themselves by increasing thermogenesis through elevating thyroid hormones or shivering (Silva, 2003; Silvestri et al., 2005) while conversely using skin vasodilatation, increased blood flow to the limbs, sweating, or panting to help dissipate extreme heat (Elizondo, 1977; Terrien et al., 2011). Diurnal mammals also display a strong circadian rhythm in body temperature, with peaks during the day and low temperatures exhibited at night (with nocturnal animals exhibiting the reverse pattern; Refinetti, 2010). Non-human primates display considerable variation in both the daily and absolute range of body temperatures (Table 1). Although most of these thermoregulatory patterns have been examined experimentally under laboratory conditions, such studies fail to replicate the numerous factors that influence temperature regulation in the wild such as spatial and temporal variation in temperature; weather related variables including humidity, wind speed, and precipitation; food supply, quality, and distribution; predation; and social interactions. Additionally, many laboratory studies manipulate light cycles or temperature conditions in ways that may create artificial thermoregulatory patterns (Table 1). Given these challenges, thermoregulatory data from lab studies may not provide an ecologically, and therefore evolutionarily, relevant representation of how wild primates respond to thermal challenges throughout their environment (e.g., Geiser et al., 2007; Warnecke et al., 2007).

There have been few attempts to understand the thermoregulatory strategies employed by free-ranging primates in their natural environment. The only available body temperatures of wild primates have been measured on terrestrial hamadryas baboons living in an open and highly arid environment, nocturnal galagos, and fat-tailed dwarf and mouse lemurs which undergo torpor (although temperatures during non-torpor periods are also available) (Table 1). Hamadryas baboons living in their extreme environment offer only limited insight into generalized anthropoid thermoregulation as they likely possess their own derived heat-stress adaptations. Nocturnal, small-bodied, and torpid strepsirrhines also offer little comparative insight into the essential thermal responses of most primate species to their environment.

Developing an understanding of the thermoregulatory patterns of more generalized anthropoids is critical for informing field primatological studies that examine variables impacted by thermoregulation, as well as providing baseline data for interpreting the evolution of human thermoregulation. Humans possess unmistakable adaptations to dissipate heat relative to non-human primates. In addition to lacking body fur, human skin has an increased concentration of eccrine sweat glands that can produce up to five times more sweat than chimpanzees and up to 100 times more than some mammals (Whitford, 1976; Zihlman and Cohn, 1988; Folk and Semken, 1991; Kenny and Journeay, 2010). This sweating greatly enhances evaporative cooling (Hanna and Brown, 1983; Folk and Semken, 1991; Jablonski, 2004; Kenny and Journeay, 2010) and can provide an additional avenue of heat loss during strenuous activities such as running (Carrier et al., 1984). Similarly, vasodilatation in

humans enables heat loss by generating a 16-fold increase in blood flow to the skin, compared with only a three-fold increase in baboons (Wyss and Rowell, 1976; Kenny and Journeay, 2010). In comparison to the wide temperature variation seen in non-human primates, human core body temperatures vary only minimally for healthy individuals under a variety of thermal stressors (Table 1). While the unique thermoregulation of humans is well understood from a clinical perspective, we currently have little knowledge of the baseline anthropoid condition from which these adaptations evolved.

To characterize temperature and thermal environment of a generalized arboreal anthropoid, we monitored subcutaneous and near-animal ambient temperatures of free-ranging mantled howling monkeys (*Alouatta palliata*) living in a seasonally dry tropical forest at La Pacifica, Costa Rica. Using data from these animals, we will address five aims:

1. Assess the impact of sex and interindividual variation on body temperatures.
2. Document circadian variation in subcutaneous and ambient temperatures.
3. Evaluate seasonal temperature variation.
4. Analyze the temporal association between subcutaneous and ambient temperatures during circadian shifts.
5. Assess the response of subcutaneous temperature to the range of ambient environmental conditions experienced by howlers.

METHODS

Data collection

We collected data on mantled howling monkeys at Hacienda La Pacifica, a private 1,980 hectare ranch located in the Province of Guanacaste, Costa Rica (10°28'N, 85°07'W). La Pacifica is in the lowland tropical dry forest life zone and comprised of seasonally dry deciduous forest (Holdridge, 1967). During the dry season, daily temperature ranges from 22.5 to 34.1°C with a mean temperature of 28.1°C and 42% average relative humidity. Wet season temperatures range from 21.8 to 33.8°C (\bar{x} = 26.1°C) with 94% average relative humidity. Mean annual precipitation is 1368 mm (range: 831–2701), with heavy rains occurring during the wet season from May to October and relatively little precipitation during the dry season months of November–April (Daubenmire, 1972; Glander, unpublished data). Mantled howlers are mid-sized diurnal anthropoids (at La Pacifica, adult males: \bar{x} = 5.79 kg; adult females: \bar{x} = 4.73 kg; Glander, 2006) that feed primarily on fruit (12.5–49.9% of diet) and leaves (48.2–69.3%; Di Fiore et al., 2011). Despite living in large, mixed sex social groups (group size averages 10.2–21.8 individuals at various field sites in Guanacaste, Costa Rica; Di Fiore et al., 2011), rates of social interaction and physical contact (including huddling) are extremely low (Zucker and Clarke, 1998; Wang and Milton, 2003; Di Fiore et al., 2011). While howlers spend a relatively large amount of time resting (56.0–79.7% of total activity budget; Di Fiore et al., 2011), their basal metabolism is comparable to other primates of similar body size (Milton et al., 1979; Ross, 1992). They also lack the digestive specializations of other folivorous primates (Milton, 1998) and have no known adaptive thermal specializations. Mantled

TABLE 1. Absolute maximum and daily maximum body temperature ranges displayed by primates

Species	Max range (°C)	Max daily range (°C)	Measurement location	Environment	References
<i>Cheirogaleus crossleyi</i>	(25.0)	(25.0)	S	Wild	Blanco and Rahalinarivo, 2010
<i>Cheirogaleus medius</i>	>10.0 (24.9)	(24.9)	IP, S	Wild	Dausmann et al., 2004, 2005
<i>Eulemur fulvus</i>	1.0		IP	Captive	Erkert and Cramer, 2006 ^{a,b}
<i>Galago moholi</i>	6.6 (>10.0)	5.3 (>10.0)	IP	Wild	Mzilikazi et al., 2006; Nowack et al., 2010 ^c
<i>Microcebus berthae</i> ^d	6.7 (>30.0)	2.7 (>30.0)	IP	Wild	Schmid et al., 2000 ^c ; Ortmann et al., 1997 ^c
<i>Microcebus griseorufus</i>	(27.0)	(23)	S	Wild	Kobbe and Dausmann, 2009; Kobbe et al., 2011
<i>Microcebus murinus</i>	<4.0 (>25.0)	<4.0	S	Wild	Schmid and Speakman, 2000, 2009; Schmid, 2001; Vuarin et al., 2013; Ortmann et al., 1997 ^c
<i>Microcebus murinus</i>	2.2 (>20.0)	2.2 (>20.0)	IP	Captive	Aujard and Vasseur, 2001; Perret and Aujard, 2001 ^b ; Genin and Perret, 2003 ^{b,e} ; Séguy and Perret, 2005
<i>Microcebus ravelobensis</i>	>2.1 (>10.0)	>2.1 (>10.0)	IP	Wild	Lovegrove et al., in press
<i>Nycticebus coucang</i>	5.6	4	R	Captive	Müller, 1979 ^a
<i>Otolemur crassicaudatus</i>	0.6		R	Captive	Hiley, 1976 ^a
<i>Tarsius syrichta</i>	>4.0	>2.0	S	Wild	Lovegrove et al., in press
<i>Tarsius syrichta</i>	2.0		R	Captive	McNab and Wright, 1987 ^a
<i>Aotus trivirgatus</i>	3.8	1.3–2.1	R	Captive	Le Maho et al., 1981 ^a ; Hoban et al., 1985 ^b
<i>Aotus lemurinus</i>	2.0	1.5	IP	Captive	Erkert and Gröber, 1986 ^b
<i>Cebus albifrons</i>	3.0	3.0	IP	Captive	Winget et al., 1968
<i>Saimiri sciureus</i>	2.5–2.7	2.0–2.7	H, IP, R	Captive	Stitt and Hardy, 1971 ^a ; Fuller, 1984 ^a ; Fuller et al., 1985; Robinson and Fuller, 1999 ^a
<i>Erythrocebus patas</i>	2.1	2.0	A	Captive	Simpson and Galbraith, 1906
<i>Macaca fuscata</i>	3.4	3.4	IP, R	Captive	Nakayama et al., 1971 ^a ; Takasu et al., 2002 ^b
<i>Macaca mulatta</i>	1.6–2.6	1.0–1.6	A, IP, R, RP	Captive	Simpson and Galbraith, 1906; Johnson and Elizondo, 1979 ^a ; Tapp and Natelson, 1989; Honnebiere et al., 1992
<i>Macaca fascicularis</i>	3.5		A	Captive	Simpson and Galbraith, 1906
<i>Papio cynocephalus</i>	1.8		R	Captive	Hiley, 1976 ^a
<i>Papio hamadryas</i>	2.5	2.5	A	Captive	Simpson and Galbraith, 1906
<i>P. hamadryas ursinus</i>	>3.0	1.7	IP	Captive	Mitchell et al., 2009 ^{a,f} ; Nyakudya et al., 2012
<i>P. hamadryas ursinus</i>	5.3	5.3	IP	Wild	Brain and Mitchell, 1999
<i>Pan troglodytes</i>	4.0		R	Captive	Hiley, 1976 ^a
<i>Homo sapiens</i>	0.5–1.6	1.6	AC, E, O, R	See citations	Mackowiak et al., 1992; Refinetti and Menaker, 1992 ^g ; Webb, 1992 ^a ; Refinetti, 2010 ^g

Temperatures in parentheses denote torpid/hibernating animals.

Measurement location: A: axillary; AC: auditory canal; E: esophageal; H: hypothalamic; IP: intraperitoneal; O: oral; R: rectal; RP: retroperitoneal; S: skin (for small mammals, skin temperature approximates core body temperature: Dausmann, 2005).

^a Study manipulated ambient temperature.

^b Manipulated light cycle.

^c Animals were wild caught and housed in outdoor cages.

^d Published as *M. myoxinus*: Rasoloarison et al., 2000.

^e Manipulated access to food.

^f Manipulated access to water.

^g Review article with varying methods.

howlers at La Pacifica inhabit both riparian forests and more seasonal dry, nonriver forest patches (Glander, 1975; Glander and Nisbett, 1996).

We recorded subcutaneous (T_{sc}) and near-animal ambient temperature (T_a) from 11 animals from two groups during intermittent field seasons from March 2010 to August 2012, yielding a total of 1586.5 sample hours ($N = 9519$ temperature sample points; Table 2). Sampling was conducted during both wet (1396.0 hr; $N = 8376$) and dry (190.5 hr; $N = 1143$) seasons and var-

ied in length for subjects (Table 2). Animals were darted following Glander et al. (1991). We recorded T_{sc} by implanting a small ($17 \times 6 \times 6$ mm 3.3 g) sterile and intact temperature data logger (iButton DS1922T: Maxim Integrated Products) directly under the skin between the shoulder blades under general anesthesia (Lovegrove, 2009). Temperature loggers were accurate to $\pm 0.06^\circ\text{C}$. A second iButton temperature logger was loosely attached (i.e., not touching the skin) to an anklet or neck collar to record T_a . This placement has the

TABLE 2. Mantled howler subjects and data collection conditions

Group	Subject	Weight (kg) ^a	Sex	Recording Date	Jacket	Season	Sample (h)	
1	Abita	5.20	F	July 2010	Y ^b	Wet	24.5	
				July 2010	N	Wet	252.3	
		5.20		March 2010	Y	Dry	46.8	
	Alana	4.25	F	March 2010	Y	Dry	47.5	
		4.40		July 2010	Y	Wet	24.0	
		4.40		July 2010	Y	Wet	48.7	
	Dyani	6.40	M	March 2010	Y	Dry	47.7	
		6.00		July 2010	Y	Wet	47.7	
	St Patrick	6.35	M	July 2011	Y	Wet	63.3	
		6.00		March 2010	Y	Dry	48.5	
		6.30		July 2010	Y ^b	Wet	47.8	
				July 2010	N	Wet	306.7	
				August 2012	Y	Wet	34.0	
	2	Agate	4.75	F	August 2012	Y	Wet	34.0
		Audio Monkey	4.25	F	August 2012	Y	Wet	35.3
Audrey		3.80	F	August 2012	N	Wet	83.0	
Wingette		3.75	F	August 2012	Y	Wet	32.8	
Orf		6.50	M	July 2011	N	Wet	194.0	
Wings		6.00	M	July 2011	N	Wet	204.8	

^a Taken after capture.

^b Individual initially wore jacket for 1–2 days and then was re-captured, jacket removed and re-released with only temperature recording devices.

advantage of recording ambient temperatures at the animal's location, rather than at a remote weather station, providing more accurate measurement of the animal's actual thermal environment (Hetem et al., 2007). We synchronized loggers to record temperatures at 10 min intervals. At the end of sampling periods, animals were recaptured to explant temperature sensors using the same procedures involved in capture and implant. The minimum time between subsequent captures was 46 hr; recaptures were needed to remove extra devices carried by animals for a concurrent project (below). In all cases, we waited >14 hr postcapture to collect temperature data to avoid thermal effects of tiletamine-based anesthesia on primates (Lopez et al., 2002). During some sampling periods (500.1 hr; 31.5% of total sampling time; Table 2), animals were fitted with a jacket designed for primates (Lomir Biomedical) to carry devices for a concurrent project (Williams et al., 2008; Vinyard et al., 2012). The total weight carried by jacketed subjects was ~300 g, which is less than the weight of infants carried by females. Jackets did not hinder movement. The jacket did not have a significant impact on daily T_{sc} minimum (ANCOVA: $F = 0.44$, $P = 0.513$), maximum ($F = 0.58$, $P = 0.463$), or mean ($F = 0.01$, $P = 0.933$) when controlling for T_a , season, and individual. For the two individuals with jacketed and nonjacketed sample periods, both showed significant, but minimal effects of the jacket on T_{sc} (two sample t -test: Abita: $t = 2.72$, $P = 0.007$, mean difference = 0.24°C ; St. Patrick: $t = -7.15$, $P < 0.001$, mean difference: -0.53°C), with the presence or absence of the jacket explaining 0.5% of variation in T_{sc} for Abita and 2.4% for St. Patrick during the same season. The jacket did not have a significant effect on daily T_{sc} and T_a cross-correlation coefficients (CCF; two sample t -test; $t = -1.01$, $P = 0.318$) nor on CCF lag time (two sample t -test; $t = -0.52$, $P = 0.602$), indicating the jacket did not change the nature of the T_a/T_{sc} relationship. Given these results, we have taken a conservative approach and opted to control for the relatively small effect of jackets in appropriate statistical analyses. All procedures were approved by the NEOMED, Duke University, and Ohio University IACUCs.

Data analysis

Data were analyzed in two formats: (1) the data set containing all samples taken at 10 min intervals ($N = 9519$), and (2) a data set summarizing temperature variables by day (e.g., daily mean temperature, daily minimum, daily maximum), for days with >14 sampling hr ($N = 67$). To test the effects of sex and season on T_{sc} , we conducted ANCOVAs on the impact of sex, jacket, season, and T_a (covariate) on daily mean, minimum, and maximum T_{sc} (Aims 1, 3). For a more general assessment of the variables impacting T_{sc} , we conducted ANCOVAs for mean, minimum, and maximum daily T_{sc} , testing the effect of the interindividual differences, jacket, and season while controlling for T_a as a covariate (Aims 1, 3). [Sex and interindividual differences could not be combined in a single ANCOVA due to multicollinearity.] For both tests, the T_a covariate selected was analogous to the T_{sc} variable analyzed (e.g., minimum T_a was used as covariate for the ANCOVA on minimum T_{sc}). Interindividual differences were a significant variable in the ANCOVA, so we conducted an ANOVA comparing all animals via a Tukey HSD post hoc test to better quantify pairwise individual differences in T_{sc} (Aim 1).

To assess circadian variation, ranges and CVs were calculated for daily T_{sc} and T_a values (Aim 2). To further assess seasonal effects, we compared daily mean, minimum, and maximum T_{sc} of individuals that were sampled in both seasons via a permutation test for matched pairs conducted with 1000 random permutations created from the original data set (Aim 3). Although the original (nonpermuted) sample size was very low (4 individuals: Abita, Alana, St. Patrick, and Dyani), this test does provide an additional means of assessing seasonal effects (compared with the ANCOVA) on individuals. To assess whether animals experience seasonal shifts in their thermal environment, we compared daily mean, maximum, and minimum T_a between wet and dry seasons via two sample t -tests (Aim 3). A nested ANOVA (no covariates) was also performed on T_{sc} to directly compare the variation attributable to circadian vs. seasonal effects (Aims 2, 3).

TABLE 3. Daily and absolute minimum, maximum, and mean subcutaneous and near-animal ambient temperatures by season and sex

Season	Sex	T_{sc} (°C)						T_a (°C)						Sample Hours
		Absolute		\bar{x} Daily			Absolute		\bar{x} Daily					
		Min	Max	Min	Max	\bar{x}	Min	Max	Min	Max	\bar{x}			
Dry	Male	35.23	40.87	35.95	40.07	37.52	25.29	44.89	21.29	39.47	32.62	96.2		
	Female	35.29	39.70	35.93	39.54	37.36	26.50	41.01	29.21	37.35	32.38	94.3		
Wet	Male	30.97	42.34	35.44	40.18	37.57	22.59	42.58	25.06	36.30	29.83	863.2		
	Female	32.42	42.64	34.60	39.70	36.78	22.34	40.25	24.30	36.46	29.15	532.8		

TABLE 4. ANCOVA for the effect of season, individual, and ambient temperature on daily maximum, minimum, and mean subcutaneous temperatures

Variable	T_{sc} Maximum			T_{sc} Minimum			T_{sc} Mean		
	F	P	Partial η^2	F	P	Partial η^2	F	P	Partial η^2
Season	0.46	0.502	0.09	3.72	0.059	0.07	1.32	0.256	0.02
T_a	12.06	0.001	0.19	10.25	0.002	0.16	11.57	0.001	0.18
Individual	2.33	0.023	0.31	3.70	<0.001	0.43	5.74	<0.001	0.52

Significant values ($P < 0.05$) in **bold**.

We conducted cross-correlations between T_a and T_{sc} on a per day interval for days with >14 hr of data (Aim 4). CCFs were evaluated at lags up to ± 2.3 hr (preliminary tests with greater lags did not yield higher CCF values). To determine whether the relationship between T_a and T_{sc} varied with specific thermal conditions, we conducted a regression for maximum daily CCF values including daily means, maximums, and minimums for T_a and T_{sc} and CCF lag times (Aim 4). The Bayesian Information Criterion (BIC) was used to determine the best model. Regression residuals from reported models displayed normality (Kolmogorov-Smirnov test: $K-S = 0.10$, $P = 0.20$), indicating the test passed parametric criteria. We also calculated maximum CCF and lag values separately for daylight (6:30–18:30) and nighttime (all other hours) samples. We compared the respective daily daytime and nighttime maximum CCFs via paired t -tests (Aim 4).

To determine the range of T_{sc} displayed at various T_a (Aim 5), we calculated the mean and coefficients of variation (CV) for observed T_{sc} over 0.5°C increments of T_a . Mean and CV T_{sc} values were correlated with the lower limit of the ambient interval range via Pearson's product-moment (Aim 5). Large variation in T_{sc} within T_a intervals suggests animals are within their TNZ, as body temperatures can vary in this range without energetic expense and active thermoregulation (Romanovsky et al., 2002). Low variation suggests animals are actively controlling body temperature. All tests were evaluated at a two-tailed $\alpha = 0.05$ except where noted above.

RESULTS

Sex and interindividual effects

Absolute and daily values for T_a and T_{sc} varied with sex and season (Table 3). There was a significant impact of sex (when controlling for T_a , jacket, and season) on daily mean (ANCOVA: sex: $F = 7.37$, $P = 0.009$) and maximum T_{sc} values (ANCOVA: $F = 4.38$, $P = 0.041$) with males displaying warmer temperatures than females (Table 3). There was not a significant sex effect on mini-

mum T_{sc} (ANCOVA: $F = 2.08$, $P = 0.154$). There were significant interindividual differences in T_{sc} (Table 4) and post hoc tests (with no covariates) revealed that 72.7% ($N = 40$) of all possible pairwise interindividual comparisons showed significant differences. For individual animals over the entire study period, T_{sc} varied from 3.8 – 11.4°C with a mean range of $7.5 \pm 2.2^\circ\text{C}$.

Circadian and seasonal effects

Individual T_{sc} varied up to 11.4°C within a day (minimum daily range = 2.1°C), with a mean daily range of $4.7 \pm 1.9^\circ\text{C}$ (Fig. 1; Supporting Information). Within-day T_{sc} CVs ranged from 1.3–6.7% with a mean CV of $3.1 \pm 1.3\%$. For comparison, the total range of all observed T_{sc} was 11.7°C with a CV of 4.0%. T_a was more variable than T_{sc} , with maximum daily ranges up to 18.7°C (minimum: 5.9°C) and a mean daily range of $11.4 \pm 2.5^\circ\text{C}$. Within-day T_a CVs ranged from 3.1–16.1% with a mean CV of $9.9 \pm 3.1\%$; total variation for all recorded T_a was 12.7%. During the nighttime, T_a ranged from 22.3 – 36.9°C ($\bar{x} = 28.1 \pm 3.2^\circ\text{C}$) compared with daytime temperatures between 22.4 – 44.9°C ($\bar{x} = 31.8 \pm 3.5^\circ\text{C}$). T_{sc} varied from 31.9 to 39.7°C ($\bar{x} = 36.5 \pm 1.3^\circ\text{C}$) at night and 31.0 – 42.6°C ($\bar{x} = 38.1 \pm 1.2^\circ\text{C}$) during the day. A nested ANOVA found that circadian effects explained 33.7% of variation in T_{sc} , compared with only 0.2% explained by seasonal effects.

T_a measures showed that howlers experience seasonal changes in their thermal environment (Table 3). Daily T_a means and minimums were significantly cooler in the wet season (means: mean difference = 3.53°C , two sample t -test: $t = 4.49$, $P < 0.001$; minimums: mean difference = 4.08°C , two sample t -test: $t = 6.53$, $P < 0.001$), while maximums did not significantly differ (mean difference = 2.05°C , two sample t -test: $t = 1.52$, $P = 0.171$). Despite these changes in thermal environment, season did not affect daily T_{sc} measures when controlling for jacket, sex, and T_a (Table 4). Removing T_a as a covariate did not change these relationships. For the four individuals sampled in both seasons, animals had lower, but non-significant, absolute minimum T_{sc} during the wet

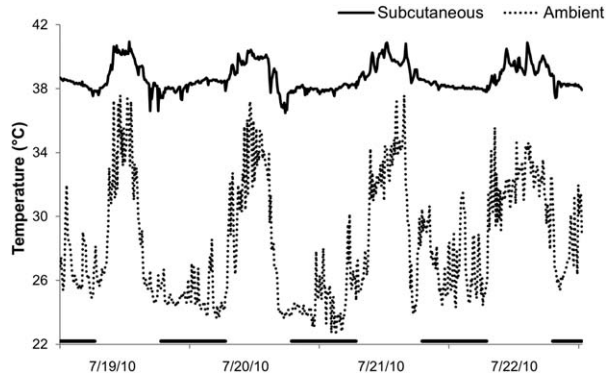


Fig. 1. Representative temperature sequence from a male howler (Wings) during the wet season, showing circadian variation in T_a and T_{sc} . Horizontal bars indicate nighttime hours (06:30–18:30).

season (mean difference: 1.66°C , permutation test: $P = 0.058$), while maximums and means did not appreciably differ between seasons (maximums: mean difference = -0.48°C , permutation test: $P = 0.349$; means: mean difference = 0.18°C , permutation test: $P = 0.483$).

The relationship between T_{sc} and T_a

Daily maximum CCFs between T_{sc} and T_a were positive for 66 out of 67 days ($\bar{x} = 0.70 \pm 0.18$) and all but one day yielded significant values. However, the maximum CCFs spanned a wide range of lag times. The modal lag time (in 10 min increments) was 0, which represented 43.3% ($N = 29$) of days. Positive lag times, in which T_a led changes in T_{sc} characterized 32.8% ($N = 22$) of days, while 23.9% ($N = 16$) of days displayed negative lag times, in which T_{sc} led changes in T_a . The model best predicting daily CCF values (using BIC) included the variables daily mean T_a (standardized $\beta = -0.48$, $P < 0.001$) and daily maximum T_a (standardized $\beta = 0.54$, $P < 0.001$). The second best model included these variables in addition to maximum T_{sc} , but this variable was not significant (standardized $\beta = 0.13$, $P = 0.380$). For temperature samples over all sample days, CCFs between T_{sc} and T_a were much stronger during daytime hours (\bar{x} CCF = 0.524) than nighttime hours (\bar{x} CCF = 0.184; paired t -test: $t = -4.81$, $P < 0.001$), reflecting that T_{sc} rises and falls concurrently with daytime T_a shifts (Fig. 1), but T_{sc} remains level as T_a declines to cooler nighttime lows. These differences also indicate that T_a measurements were not being impacted by residual body heat from the animal.

Overall, the average T_{sc} displayed was strongly correlated with observed T_a (Pearson's: $r = 0.96$, $P < 0.001$; Fig. 2). However, T_{sc} values plateaued at $T_a > 41^\circ\text{C}$ (Fig. 2, box). Likewise, 95% of dry season samples with $T_{sc} < T_a$ occurred at $T_a > 38.1^\circ\text{C}$. The CVs for T_{sc} at observed T_a were relatively constant at lower T_a , but decreased at warmer T_a (Pearson's: $r = -0.48$, $P = 0.001$; Fig. 2), suggesting that T_{sc} is being actively controlled at these warm T_a .

Warm thermal conditions ($T_a > T_{sc}$) occurred less frequently than cool conditions ($T_a < T_{sc}$), with only 10.4% of dry season samples and 0.06% of wet season samples displaying $T_a > T_{sc}$ (Fig. 3). Additionally, under cool thermal conditions animals displayed a greater magnitude of difference between T_a and T_{sc} than under warm condi-

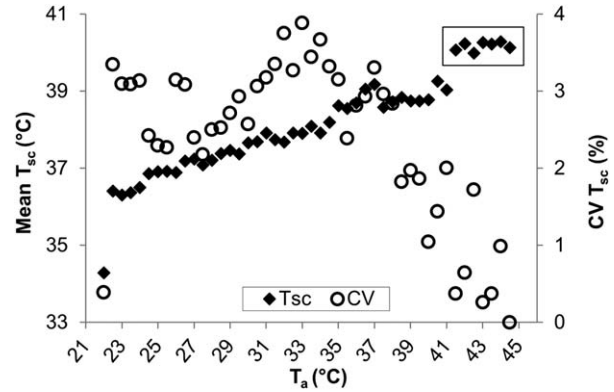


Fig. 2. Observed mean subcutaneous temperatures (T_{sc}) and their coefficients of variation (CV) at near-animal ambient temperatures (T_a). Box = plateau in T_{sc} ($\bar{x} = 40.2^\circ\text{C}$) at warm T_a . Increased CV values indicate more variable heat loss from the skin at energetically neutral T_a values.

tions, with a maximum difference of 15.4°C in cool conditions vs. 4.8°C in warm conditions (Fig. 3).

DISCUSSION

We have provided the first characterization of temperatures and thermal environment in a free-ranging, thermally generalized arboreal anthropoid. Howling monkeys experience a dynamic thermal environment and appear to have flexible body temperatures that respond to ambient conditions. Despite living in a dry tropical forest, howlers at La Pacifica also appear to be influenced by both warm and cool thermal pressures. While many primate studies invoke thermoregulatory explanations, we rarely have measures of body temperatures or even a basic understanding of the species' thermoregulatory patterns to support these hypothesized relationships. Our data show that thermal pressures (both cool and warm) may be more widespread in primates than previously thought, including species living in thermal environments traditionally viewed as "mild." Understanding the biology behind how free-ranging primates mediate ambient thermal conditions and body temperature will allow us to more accurately model how behavioral and physiological variables are impacted by thermoregulatory processes. This is critical for primatological studies that measure variables heavily influenced by thermoregulation such as ranging behavior, dietary preferences, or food consumption.

Howlers displayed an impressive amount of total, daily, and within-individual variability in T_{sc} , as well as significant variation between individuals and the sexes (Tables 3 and 4). The sex differences in body temperatures found here are common for many mammals (e.g., Gordon, 1990; Cryan and Wolf, 2003; Lu and Dai, 2009). Despite the limited data available on wild primates (Table 1), this adds to growing evidence that body temperatures are more labile in non-human primates than in humans. In addition to the minimal overall deviation in human core body temperature (Table 1), the average difference in core temperature between the onset of shivering and sweating ranges only 0.1 – 0.2°C in humans, with mean T_{sc} varying only 5.2°C between these behaviors (Webb, 1992). As an illustrative comparison, howler T_{sc} in this study varied over twice this range (11.7°C : Table 3) with no observed sweating or shivering

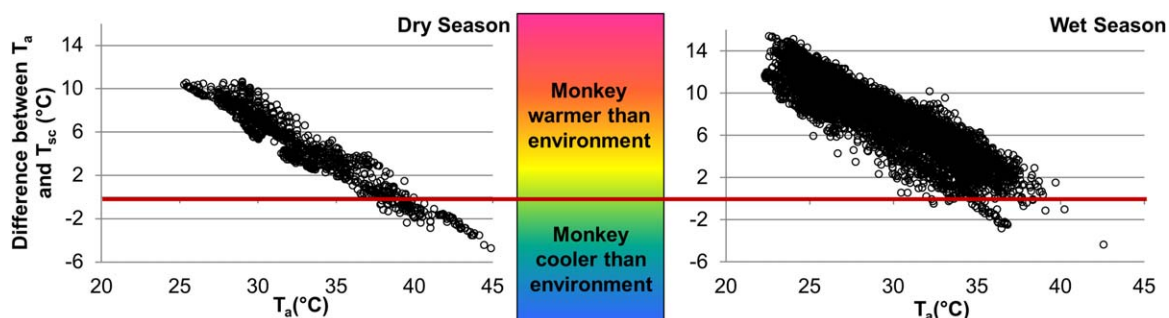


Fig. 3. Magnitude of differences between subcutaneous (T_{sc}) and near-animal ambient temperatures (T_a), by season. Temperatures above red line indicate $T_{sc} > T_a$, temperatures below, $T_{sc} < T_a$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

(although animals were only visually observed during the day). Likewise, human TNZ estimates have a range of $\sim 2^\circ\text{C}$ (Erikson et al., 1956; Andersen and Hellström, 1960; Brengelmann and Savage, 1997) while the estimated TNZs for captive primates are much broader: 5.9°C ($24.7\text{--}30.6^\circ\text{C}$) for rhesus macaques (*Macaca mulatta*; Johnson and Elizondo, 1979), 10.0°C ($25.0\text{--}35.0^\circ\text{C}$) for squirrel monkeys (*Saimiri sciureus*; Stitt and Hardy, 1971), and 8.0°C ($25.0\text{--}33.0^\circ\text{C}$) for slow lorises (*Nycticebus coucang*; Müller, 1979). Wild fat-tailed dwarf lemurs (*Cheirogaleus medius*) have a $\sim 3^\circ\text{C}$ ($25.0\text{--}28.0^\circ\text{C}$) estimated TNZ during nontorpid periods (Dausmann et al., 2009). While captivity may not provide the most ecologically relevant measure of TNZ, the consistent difference in temperature variability seen between humans and non-human primates supports the notion that non-human primates have more labile body temperatures.

In this study, daily T_{sc} variation within individuals was nearly as high as the variation in the total data set, suggesting that the thermal factors most frequently impacting howlers are short-term, circadian variations, rather than longer-term seasonal changes or multiday weather patterns (e.g., storms, hot spells, etc.). The prevalence of howlers experiencing cool conditions ($T_a < T_{sc}$) and the reduced nighttime correlation between T_{sc} and T_a in this study also support the idea that daily variation, particularly cooler nighttime temperatures, may be the most frequent thermal pressure for howlers. This observation has far reaching implications for the study of primate nocturnal activity, including night ranging and sleeping site selection. It also means that the period of the coolest thermal stress is often not being monitored by observers. Precipitation may also be a significant contributing factor in short-term thermal pressures, since the evaporation of water from animals will produce a cooling effect. Yet, it should be noted that the relative constancy of T_{sc} over seasons, despite experiencing significantly cooler temperatures in the wet season, does imply that animals are using either behavioral or physiological mechanisms to maintain stable body temperatures in the face of a changing thermal environment. This varying thermoregulatory load could help explain various seasonal changes observed in primates including shifts in feeding and ranging behavior (e.g., Brockman and van Schaik, 2005).

Warm conditions and the potential for heat stress occurred less frequently than cool conditions, but appeared to evoke a stronger physiological response. Howlers' T_{sc} were tightly positively correlated with T_a ,

yet showed a distinct plateau at $T_a > 41^\circ\text{C}$, in which T_{sc} remained at $\sim 40.2^\circ\text{C}$, despite increasingly warmer ambient conditions (Fig. 2). For comparison, human core body temperatures above 40°C are considered a criterion for heat stroke and can be associated with delirium, convulsions, and coma (Bouchama and Knochel, 2002). The reduced variation in howler T_{sc} at higher T_a (Fig. 2) suggests that animals are actively controlling their body temperature, while high variation in T_{sc} is indicative of flexible heat loss from the body at energetically neutral temperatures (Romanovsky et al., 2002). The mechanism for this cooling is unknown. Sweating appears to be important for some primate species (Stitt and Hardy, 1971; Johnson and Elizondo, 1979; Elizondo, 1988), although it does not occur to the extent seen in humans (Hanna and Brown, 1983). Howlers possess eccrine sweat glands on their palms and soles, glabrous portion of the tail, and throughout the hairy skin of the body (Montagna, 1972; Perkins, 1975), yet we have never observed visible sweating by howlers. Likewise, heat loss through panting is negligible in most primates (Elizondo, 1977, 1988) and we have never observed panting in howlers. Other common mammalian mechanisms to dissipate body heat include posture and microhabitat use, skin vasodilatation, decreased locomotor activity, and decreased energy intake (to reduce the heat generated by digestion) (Terrien et al., 2011). We predict that howlers are using many of these mechanisms, particularly extended (heat-dissipating) postures and selection of cool microhabitats to aid in thermoregulation. It is also likely that these commonly measured variables are being impacted by thermoregulation in a wide range of primate species, particularly those living in more extreme thermal environments. Our data imply that howlers experience warm thermal pressures, but that these events are acute and relatively infrequent while cool thermal pressures pose less intense physiological challenges, but are faced more often. The observation that primates in a dry tropical forest potentially experience both cool and warm thermal challenges suggests that thermoregulatory pressures may currently be underestimated for many tropical and midlatitude primates (Dausmann, 2014).

The maintenance of an optimal range of body temperature in the face of a changing thermal environment likely involves adjustments in many physiological and behavioral variables of interest to primate researchers. For instance, many mammals seasonally increase levels of the thyroid hormones triiodothyronine (T_3) and

thyroxine (T₄) (Magdub et al., 1982; Tomasi, 1991). These hormones increase heat production by boosting basal metabolic rate and in turn lead to heightened food consumption and modifications in nutrient ingestion (Pijl et al., 2001; Silva, 2003; Silvestri et al., 2005). Thermoregulatory efforts may also impact short-term behavior including microhabitat choice, travel, activity budgets, and social contact. Given the prevalence of these variables in primatological studies and the dearth of body temperatures data from wild primates, we may be currently overlooking a key factor influencing physiology and behavior. An increased understanding of primate thermoregulation is needed to evaluate how thermal pressures impact the biology of free-ranging primates. This evaluation should consider simultaneously collected body and environmental temperatures, as well as additional thermal factors such as wind speed, humidity, precipitation, and solar radiation.

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