Huddling is more important than rest site selection for thermoregulation in southern bamboo lemurs

Timothy M. Eppley1,2,3,*, Julia Watzek4, Kathrin H. Dausmann1, Jörg U. Ganzhorn1, Giuseppe Donati2

1 Biozentrum Grindel, University of Hamburg, Hamburg, Germany
2 Nocturnal Primate Research Group, Department of Social Sciences, Oxford Brookes University, Oxford, United Kingdom
3 Department of Anthropology, University of Texas, Austin, TX, United States of America
4 Department of Psychology, Language Research Center, Georgia State University, GA, United States of America

***Correspondence: Timothy M. Eppley**
Biozentrum Grindel
University of Hamburg
Martin-Luther-King Platz 3
20146 Hamburg
Germany
Telephone: +1 (512) 800-0269
Email: eppleyti@gmail.com

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Abstract

Resting site selection can have important effects on the behaviour and fitness of organisms. The maintenance of optimal body temperatures (T_b) when faced with environmental variables has often been attributed to either specific microhabitat rest site characteristics or to behavioural strategies. Among many small group living endotherms, social thermoregulation (i.e., huddling) is utilised as a behavioural energy conservation mechanism at low ambient temperatures (T_a), thus decreasing the metabolic cost of maintaining T_b. Though unusual among primates, lemurs are hypometabolic and exhibit a diversity of thermoregulatory strategies; however, objective T_b measurements have thus far been limited to small-bodied lemurs (e.g., Cheirogaleids). As such, we sought to determine whether a medium-sized lemur model, the southern bamboo lemur (*Hapalemur meridionalis*), would maintain thermoregulation through microhabitat rest site selection, huddling behaviour, or potentially both strategies. Within a degraded littoral forest fragment in southeast Madagascar, we conducted full-day focal observations on three groups of *H. meridionalis* between January and December 2013. Adult individuals were collared with data-loggers that collected instantaneous skin temperature T_{sk} (°C). We calculated the mean T_{sk} of the focal individual during each resting bout, and the proportional rate of huddling between the focal and conspecifics. In addition, we recorded all resting sites utilised ≥15 min and collected standard tree characteristics. We fitted Linear Mixed-Effects Models to determine the thermoregulatory combined effect of specific resting site characteristics, huddling behaviour, and environmental variables on T_{sk}. Our results showed that lemurs selected tree sites with larger diameter at breast height; however, huddling was most predictive of increasing T_{sk} whereas resting site characteristics were not included in the best-fit model. It is possible that microhabitat rest site selection is not significant in a degraded forest as the potential environmental buffering is limited, thus thermoregulatory mechanisms are likely best served by behavioural strategies, i.e., social huddling.

Key-words: huddling; skin temperature; *Hapalemur meridionalis*; energy conservation; thermal ecology; southern bamboo lemur; Madagascar; strepsirrhines

Introduction

Many endothermic animals have evolved different physiological and/or behavioural mechanisms to maintain optimal body temperature (T_b), i.e., thermoregulation (Huey and Pianka 1977; Geiser et al. 2002; Kauffman et al. 2003; Kotze et al. 2008; Kearney et al. 2009; Gilbert et al. 2010; Boyles et al. 2011; Terrien et al. 2011). These autonomic mechanisms include vasodilation and sweating to reduce T_b in high ambient/environmental temperatures (T_a), increased blood pressure via vasoconstriction to reduce heat loss and increase T_b at low T_a (Daniels 1984; McNab 1988; Gagge and Gonzalez 2011) and insulation provided by seasonal changes of plumage or fur (Gilbert et al. 2010). More extreme physiological strategies, e.g., daily torpor and hibernation, involve a dramatic reduction of metabolic processes/metabolic rate to face cold and resource lean periods (Aujard et al. 1998; Westman and Geiser 2002; Geiser 2004; Heldmaier et al. 2004; Mzilikazi and Lovegrove 2004). These entail prolonged periods of resting with reduced metabolic rates without time dedicated to other activities, apart from periodic arousals (Lovegrove et al. 1999).

In contrast, behavioural mechanisms are more varied, and include microhabitat selection (Huey and Pianka 1977; Hill 2006; Willis and Brigham 2007; Kearney et al. 2009; Terrien et al. 2011; Downs et al. 2013), including the utilisation of burrows to avoid harsh environmental conditions (Long et al. 2005), basking and body positioning (Stelzner and Hausfater 1986; Brown and Downs 2007; Warnecke et al. 2010; Kelley et al. 2016), and social thermoregulation (Kauffman et al. 2003; Gilbert et al. 2010; Scantlebury et al. 2010). This last strategy, social thermoregulation (i.e., a behavioural energy conservation mechanism) is the active and close aggregation of animals in order to keep warm and is achieved by adopting hunched and/or curled positions with conspecifics (Hayes 2000; Gilbert et al., 2010). Colloquially, this is referred to as huddling, and has been recorded in numerous avian and mammalian orders (Gilbert et al. 2010). These include birds from the orders Anseriformes (Fortin et al. 2000), Coliiformes (McKechnie and Lovegrove 2001), Coraciiformes (Boix-Hinzen and Lovegrove 1998), Galliformes (Putaala et al. 1995), Passeriformes (Hatchwell et al. 2009; Labisky and Arnett 2006; Burns et al. 2013), Pelecaniformes (Evans 1984), and Sphenisciformes (Gilbert et al. 2008), while mammalian orders include Artiodactyla (Hrupka et al. 2000), Carnivora (Riedman 1990), Chiroptera (Willis and Brigham 2007), Dasyuromorphia (Rhind 2003), Didelphimorphia (Canals et al. 1997, 1998), Lagomorpha (Gilbert et al. 2007), Primates (Schino and Troisi 1990; Ostner 2002; Donati et al. 2011; Ogawa and Wada 2011), and Rodentia (Hayes et al. 1992; Hayes 2000; Kotze et al. 2008). The strategy may improve an individual's (or group's) ability to survive via maintaining optimal T_b and conserving heat (i.e., metabolic energy) by reducing the total body surface area exposed to the environment (Contrera 1984; Hayes et al. 1992; Canals et al. 1989, 1997, 1998; Geiser et al. 2002; Séguy and Perret 2005; Gilbert et al. 2010;

Primates represent a behaviourally and physiologically diverse order of small- and large-bodied endotherms that are distributed throughout various climatic and geographic zones (Lehman and Fleagle 2006). As it is estimated that primates spend approximately half of their lives at sleeping sites, site selection is a vital aspect of an individual's fitness and group's overall performance and behavioural ecology (Cowlishaw 1994; Anderson 1998). In addition to predator avoidance, resting sites are often sought to buffer against environmental variables such as rain and temperature fluctuation (De Vere et al. 2011; Han and Hu 2012; Samson and Hunt 2012), whereby the location and microhabitat variations may optimize physiological processes (Schino and Troisi 1990). For example, in a seasonally harsh environment, black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) select sleeping trees with large diameters at breast height (DBH) and broad crown diameters presumably to provide effective shelter from precipitation and cold exposure (Cui et al. 2006). In fact, many primates are challenged with seasonally harsh environmental conditions, and have exhibited optimal body temperature maintenance via postural changes, e.g., hunched, huddling, and sun-basking positions (Stelzner and Hausfater 1986; Dasilva 1993; Moreland 1993; Hanya et al. 2007; Donati et al. 2011; Ogawa and Wada 2011; Terrien et al. 2011; Danzy et al. 2012; Kelley et al. 2016). Yellow baboons (*Papio cynocephalus*) utilise a hunched position to reduce heat loss during cold weather (Stelzner and Hausfater 1986), while Japanese macaques (*Macaca fuscata*) have been observed to habitually utilise hot springs during cold weather (Zhang et al. 2007). When exposed to low temperatures in environments without the advantage of hot springs, *M. fuscata* huddle and sun-bask during the winter as an effective means of raising T_b (Hanya et al. 2007).

The strepsirrhine primates of Madagascar live in an island environment characterised by seasonality and climatic stochasticity, both presumed to have had a major influence on the evolution of lemur life history traits (Wright 1999; Dewar and Richard 2007). So far, all lemurs studied are hypometabolic (Genoud 2002; Simmen et al. 2010), which suggests they rely on behavioural thermoregulatory strategies as an adaptation to scarce and unpredictable resources (Kurland and Pearson 1986; McNab 1986; Morland 1993; Donati et al. 2011). In fact, during the cold and resource deficient austral winter months, many species of Cheirogaleid lemurs (e.g., *Microcebus murinus*, *M. griseorufus*, *Cheirogaleus medius*) reduce their metabolism and enter a temporary state of torpor or prolonged hibernation in order to conserve energy (Dausmann 2005, 2014; Dausmann et al. 2009). Additionally, microhabitat variations such as constructing nests, utilising tree holes or burrowing may reduce the physiological cost of thermoregulation (Kappeler 1998; Schmid 1998; Radespiel et al. 2003; Dausmann et al. 2004; Lutermann et al. 2010; Blanco et al. 2013). Torpor is most often found in mammals with a body mass below 200 g, with reduced energetic savings as body mass increases (Geiser 2004; Heldmaier et al. 2004), potentially providing an explanation why hibernation and torpor are not exhibited by larger, non-Cheirogaleid lemurs (Dausmann et al. 2009).

Postural behaviour, such as huddling and sun-basking, have also been shown to assist in reducing these physiological thermoregulatory costs in certain groups (Morland 1993; Donati et al. 2011; Kelley et al. 2016). For example, collared lemurs (*Eulemur collaris*) and red-fronted lemurs (*E. rufifrons*) regularly hunch and form huddling groups more often during colder seasons (Ostner 2002; Donati et al. 2011). While ring-tailed lemurs (*Lemur catta*) occasionally huddle within an open-canopy habitat, sun-basking was shown to be utilised most often under cold weather conditions (Kelley et al. 2016). However, as anthropogenic pressure in Madagascar grows and forests become further degraded and fragmented (Schwitzer et al. 2014), lemurs are likely to be left with fewer suitable microhabitat resting options to meet thermoregulatory and anti-predator needs.

Within a degraded habitat, we studied a medium-sized strepsirrhine, the southern bamboo lemur (*Hapalemur meridionalis*), as a model to determine which factor(s) most influenced thermoregulation for resting individuals. As rest site selection may have important fitness consequences (Cowlishaw 1994; Anderson 1998), we first sought to determine what factors most influenced an individual to return to a rest site. We predicted that lemurs would select rest areas of greater environmental protection (e.g., shade, wind protection), whereby individuals would more often return to larger trees with greater crown volumes compared to rest sites only used once. In our second model, we sought to determine which factors maintained thermoregulation via skin temperatures (T_{sk}). We predicted seasonal differences in microhabitat selection, as greater environmental buffering would provide addition thermoregulation during the cool, austral winter. As prolonged social contact during resting bouts (i.e., huddling) is a frequent energy preservation strategy among many mammals and birds (Gilbert et al. 2010), we hypothesized that T_{sk} would increase as a result of increased huddling behaviour. In addition, we predicted that huddling would occur more frequently when T_a is colder. We also predicted that huddling bouts would occur most often at smaller, single-use resting sites that provided limited environmental buffers.

Methods

Ethical note

All data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. This research was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherché N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

Study Site and Species

Our study was conducted in the protected littoral area of Mandena (24°95’S 46°99’E, 0–20 m asl) along the southeast coast of Madagascar. This area consists of 230 ha of fragmented littoral forest and interspersed, seasonally-inundated swamp (Eppley et al. 2015a). Littoral forests are characterised as having a relatively low canopy that grows on sandy substrates and occur within 3 km of the coast (Dumetz 1999; Consiglio et al. 2006), yet due to the degree of degradation in Mandena, the vertical structure of this littoral forest is relatively low (Eppley et al. 2015a).

Southern bamboo lemurs (*H. meridionalis*) are medium-sized lemurs (albeit small-bodied primates) with an average body mass of 1.1 kg that exhibit a cathemeral activity pattern (Eppley et al. 2015b, 2015c, 2017). This species is also known to feed heavily on a low-quality folivorous diet, the bulk of which is composed of various terrestrial grasses and sedges (Eppley et al. 2011, 2016a).

Climatic data

To assess daily climatic factors, temperature (°C) was recorded in 30-mins intervals using four Lascar EL-USB-1 data loggers (Lascar Electronics, Inc.; Erie, PA, USA), operated by custom software (EasyLog USB Version 5.45, Lascar Electronics, Inc.). These were positioned throughout the Mandena study site, i.e., two placed in the littoral forest and two in the swamp, at 1.5 m above the ground and protected from direct sun. In 2013, the mean temperature in Mandena was 22.5°C, with an absolute range between 9.5 – 35.0°C (Eppley et al. 2016b; Fig. 1). Furthermore, precipitation (mm) was measured daily at 6:00 h using a rain gauge placed within the study site. Total precipitation in Mandena during the study period was 2,815.1mm (Fig. 1).

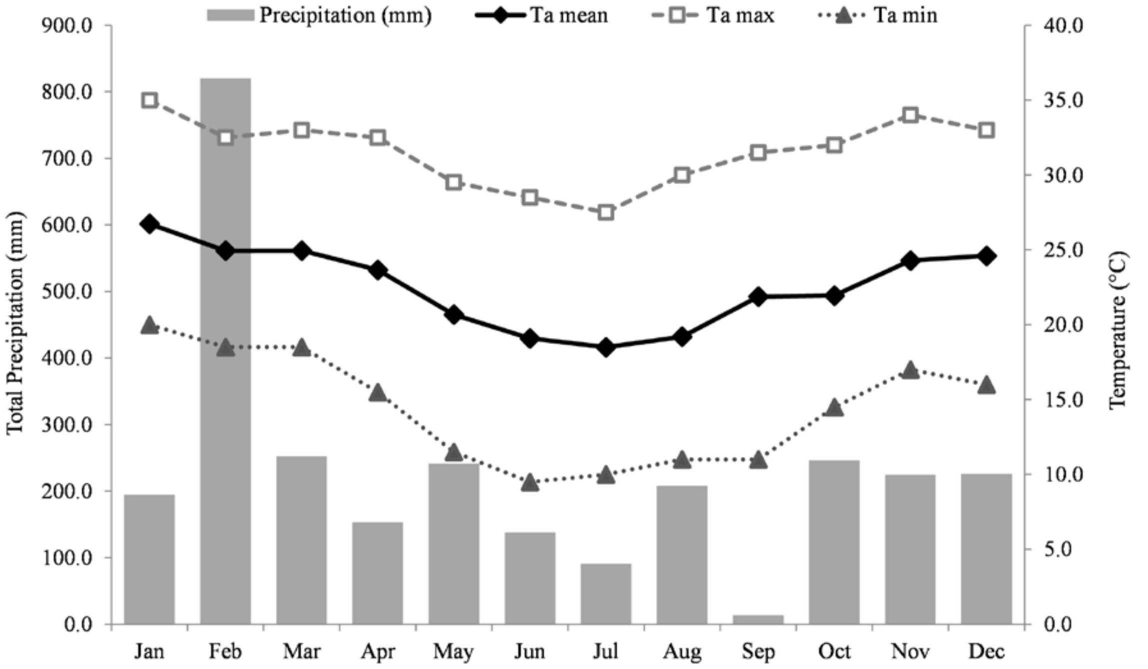

Fig. 1. Monthly total precipitation and mean temperature (including monthly maxima and minima recorded) in Mandena from January to December 2013.

Temperature measurements

As part of a larger behavioural ecology study, we captured ten adult individuals and fitted them with external radio-transmitting tags equipped with data-logging sensors for T_{sk} (ARC400, Advanced Telemetry Systems, Isanti, MN, USA). Individuals were recaptured immediately following the completion of the study, and tags/collars were removed. For information on this and the capture, anaesthesia, and collaring processes, see Eppley et al. (2016c). Our data-logging collars collected T_{sk} in degrees Celsius every 15 min. Between January and December 2013, we recorded 269,436 T_{sk} data points, which were matched to the corresponding T_a. The mean (± SD) T_{sk} of *H. meridionalis* was 32.8 ± 2.9°C; however, when data-logging tags of individuals registered 0.0% activity, the mean T_{sk} of *H. meridionalis* was 35.8 ± 1.2°C. This fluctuation was due to movement when traveling and foraging, and thus the temperatures recorded while resting with minimal movement are considered accurate.

Behavioural data

From January to December 2013, we conducted behavioural focal follows (from sunrise to sunset) every 5 mins. Data were collected from three social groups, and totalled 1,762 h. During the study period, Group 1 consisted of 3-5 individuals (3 adult females, 1 adult male), Group 2 consisted of 3-4 individuals (1 adult female, 1 adult male), and Group 4 consisted of 8-9 individuals (2 adult females, 2 adult males) (Eppley et al. 2016c). Identification of individuals was made using radio-tracking tags with coloured pendants, with all adult individuals ($N = 10$) from our three focal groups sampled for at least one day each month. As general activity largely influences T_{sk} (Dausmann 2005), our T_{sk} analyses are limited to resting bouts ≥15 min.

All instances of continuous resting bouts ≥ 15 min were recorded. Specifically, we recorded the full duration of the resting bout, the height of the focal individual, whether the focal was huddling (i.e., within contact) with social group members, and the proportion of huddling (referred to as 'huddling rate') that occurred during each resting bout. Huddling rate was calculated as the total time an individual was in physical contact with the resting focal subject, divided by the total resting bout time. All plants (trees, lianas, etc.) selected as rest sites were marked with flagging tape, given a unique code, and were identified for their scientific family, genus, and species names by on-site Malagasy botanists. This allowed us to determine whether sites were returned to multiple times, i.e., a preference site. We also recorded the plants' diameter at breast height (DBH; cm), height (m), crown volume (m^3; Eppley et al. 2015a), and the site's microhabitat location (i.e., littoral forest or swamp). Furthermore, we recorded whether the rest site also acted as a feeding site or was utilised solely for resting.

Data analyses

To determine which factors influenced the repeated use of resting sites, we fitted Generalized Linear Mixed-effects Models (GLMMs) with preference site as a binomial dependent variable. We define preference sites as those sites that were visited more than once by a focal group. Group was included as a random effect to account for different baseline rates of returning to a rest site. As fixed effects, both as independent terms and in interactions, we included DBH (cm), height (m), crown volume (m^3), habitat (littoral forest or swamp), and whether a site was also a feeding site (0/1). We standardized DBH, height, and crown volume, as they were on very different scales of magnitude.

To determine which factors influenced lemurs' T_{sk} (a proxy for body temperature), we fitted ~~a~~ Linear Mixed-effects Models (LMMs). As random effects, we included individual identity (nested within groups) to account for different baseline T_{sk}. As fixed effects, both as independent terms and in interactions, we included the focal lemurs' sex (female/male), huddle rate (i.e., proportion of huddling during rest bout), duration of the resting bout (mins), group size, whether the resting site was a preference site (0/1), the crown volume (m^3), and cover (the position of the focal, in meters, beneath the tree canopy). In addition, we included climatic variables as fixed effects, specifically temperature (°C), as the mean T_a from the nearest data-logger during the sleeping bout duration, daily total precipitation (mm), and the general season (dry or wet). We standardized huddle rate, duration, and ambient temperature, as they were on very different scales of magnitude.

For both the preference site GLMM and the T_{sk} LMM, we used an information-theoretic approach with model averaging to generate a set of candidate models and assess the relative strength of evidence for our hypotheses (Burnham and Anderson 2002). We inspected the Variance Inflation Factors (VIF) of a full model, including all fixed effects, to assess multicollinearity. To obtain unbiased parameter estimates, we did not include collinear terms (VIF > 3) in the same model. Highly related predictors could, however, occur in separate models of the model set. We ranked the models using Akaike's Information Criterion corrected for finite sample sizes (AICc) and defined a subset of top models as those models within two AICc units from the best model ($\Delta_i < 2$). We then computed the model-averaged parameter estimates and the relative importance for each term included in this model set. Importance is the sum of the Akaike weights w_i of all models which include the term in question. As model weights represent the probability of a model to be the best model in the model set and thus reflect model uncertainty, importance can be understood as the likelihood of a term to be included in the best model. We used the lme4 (Bates et al. 2015) and MuMIn (Bartoń 2016) packages in R statistical software version 3.3.2 (R Core Team 2016) for these analyses.

Results

Resting sites

We recorded 505 resting bouts of ≥15 min at 430 different rest sites in Mandena. Typically, *H. meridionalis* groups maintain synchronous activity, thus groups tended to rest for similar durations within the same tree site. There were 52 sites (12.1% of the total resting sites observed) that were returned to at least once (between two and five times), henceforth referred to as 'preferred' sites, constituting a total of 127 resting bouts (25.1% of all bouts). Additionally, 7.7% of preferred sites were also known feeding resources, while 10.8% of single-use rest sites were also feeding resources (Table 1).

Table 1. Comparison of preferred and single-use rest sites

Resting Sites	N	Feeding	DBH (cm)	Height (m)	Crown volume (m^3)
Preferred site	52	4			
Median			16.0	7.0	16.5
Quartiles			8.0 – 25.3	5.0 – 9.3	6.3 – 62.8
Single-use site	378	41			
Median			11.0	6.0	6.3
Quartiles			6.0 – 18.0	5.0 – 8.0	1.1 – 24.7

N = total number of sites; Feeding = number of sites used for resting and feeding.
*Note that in addition to tree species, unidentified fallen dead trees and the ground (including burrows) were occasionally used by all groups

Preferred Resting Sites

From the 430 rest sites, DBH values were missing from 24 sites while two additional sites were found to be outliers for crown volume, thus these were removed from the GLMM. According to our correlation matrix, DBH was positively correlated with height, $r(404) = 0.74$, $P < 0.001$, and crown volume, $r(404) = 0.73$, $P < 0.001$ (Table 2), indicating that trees with larger DBH tended to be taller and tended to have larger crown volumes. Each of these three metrics was a component of at least one model within two AICc of the best-fit model to explain the repeated use of a rest site (Table 3). The two most likely models included only DBH ($\Delta_1 = 0.00$, $w_1 = 0.30$) and only height ($\Delta_2 = 0.39$, $w_2 = 0.25$), respectively, and were supported 2 times and 1.7 times more strongly than the model including only cover (evidence ratios $w_1/w_4 = 0.30/0.15 = 2$, $w_1/w_4 = 0.25/0.15$). Indeed, the estimate for crown volume was imprecise, suggesting that it was not driving resting site selection. Further, whether a resting site also served as a feeding site was 30% likely to be a component of the best model (relative importance of Feed), in addition to either DBH or height. However, the direction of the effect could not be estimated with sufficient confidence, and the more parsimonious models that do not include feeding site were better supported by the data.

Overall, bamboo lemurs were seven times more likely *not* to return to a resting site than to return (odds ratio $^{1}/_{0.14}$). However, lemurs preferentially returned to resting sites with wider or taller trees, being 37% more likely to return to a site with a DBH or height increased by one standard deviation (11.03 cm and 2.96 m, respectively).

Table 2. Correlation coefficients between model variables to predict resting site selection

Measure	Pref	Hab	Feed	DBH	HT	CV
Preferred Site (Pref)	–					
Habitat (Hab, forest = 0, swamp = 1)	-0.04	–				
Feeding Site (Feed)	-0.02	-0.04	–			
Diameter at Breast Height (DBH)	0.11^{*}	-0.08	0.21^{***}	–		
Height (HT)	0.10^{*}	-0.21^{***}	0.19^{***}	0.74^{***}	–	
Crown Volume (CV)	0.07	-0.14^{**}	0.10^{*}	0.73^{***}	0.66^{***}	–

$N = 404$. $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$

Table 3. GLMMs for returning to a resting site ($\Delta_i < 2$)

Model *i*	b_0	DBH	HT	CV	Feed	Δ_i	w_i
1	-1.95	0.30				0.00	0.30
2	-1.95		0.30			0.39	0.25
3	-1.91	0.33			-0.48	1.22	0.17
4	-1.93			0.27		1.42	0.15
5	-1.91		0.33		-0.47	1.66	0.13
β	-1.93^{***}	0.31^{*}	0.31^{*}	0.27	-0.48		
SE	0.17	0.18	0.18	0.11	0.38		
Odds Ratio	0.14	1.37	1.37	1.32	0.62		
Importance		0.47	0.38	0.15	0.30		

$N = 404$. Model terms include the intercept (b_0), diameter at breast height (DBH), height (HT), crown volume (CV), and feeding site (Feed). Columns on the right show the difference in AICc values between Model *i* and the model with the lowest AICc, Model 1 (Δ_i) and the Akaike weight of Model *i* (w_i). Bottom rows show model-averaged parameter estimates (β), unconditional standard errors which incorporate model uncertainty (*SE*), odds ratios, and relative importance. $^{*}P < .05$, $^{***}P < .001$.

Thermoregulation: huddling vs resting site

Considering all 505 resting bouts, 45.1% involved huddling behaviour. A total of 349 of these resting bouts were observed with radio-collared focal individuals, thus our dataset was limited to those bouts in which T_{sk} was measured. Similar to the GLMM, incomplete cases and outliers were excluded from the LMM, leaving 322 resting bouts. Correlation coefficients between our model variables revealed that T_{sk} was higher during the wet season, for females, at non-feeding rest sites, when T_a was higher, when huddle rates were higher, and when resting bouts lasted longer (Table 4). Additionally, huddle rates were higher and resting bouts lasted longer at preference sites, whereas the opposite was seen at dual resting-feeding sites. Furthermore, the larger the crown volume of the resting site, the deeper below the canopy the focal individual tended to rest. Our full T_{sk} dataset show that *H. meridionalis* did not exhibit torpor at any point during the 12-month study, with individuals often wakeful when resting, occasionally opening their eyes at small disturbances.

Table 4. Correlation coefficients between model variables to predict thermoregulation

Measure	T_{sk}	Ssn	Size	Sex	Pref	T_a	Hud	Dur	Precip	Cover	CV
Season	0.17^{**}	–									
Group Size	0.17^{**}	0.04	–								
Sex	-0.13^{*}	-0.03	-0.61^{***}	–							
Preference Site	0.07	-0.15^{**}	-0.03	0.03	–						
T_a	0.32^{***}	0.50^{***}	0.05	0.04	-0.11^{*}	–					
Huddle rate	0.43^{***}	-0.02	0.09	-0.18^{***}	0.17^{**}	-0.15^{**}	–				
Duration	0.48^{***}	0.11^{*}	-0.06	-0.02	0.18^{**}	0.14^{*}	0.28^{***}	–			
Precipitation	0.03	0.27^{***}	-0.01	0.09	-0.06	0.17^{**}	0.03	-0.03	–		
Cover under canopy	-0.07	-0.05	-0.10	0.04	0.08	-0.12^{*}	0.05	0.02	0.05	–	
Crown volume	-0.06	-0.11	-0.05	-0.03	0.09	-0.25^{***}	0.10	-0.01	0.07	0.63^{***}	–

$N = 322$. $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$.
Season (dry = 0, wet = 1); Sex (female = 0, male = 1); Duration = length of resting bout

Table 5. Model-averaged LMM parameters for predicting an increase in *H. meridionalis* T_{sk}

Term	β	*SE*	95% *CI*	Model	Importance
Intercept	33.20^{***}	0.41	(32.39, 34.01)	1, 2	
Group Size	0.13^{*}	0.08	(0.01, 0.25)	1	0.7
Huddle Rate (Hud)	0.64^{***}	0.08	(0.48, 0.81)	1, 2	1
Duration (Dur)	0.74^{***}	0.09	(0.56, 0.92)	1, 2	1
Temperature (T_a)	0.58^{***}	0.08	(0.42, 0.75)	1, 2	1
Hud × Dur	-0.26^{**}	0.08	(-0.42, -0.10)	1, 2	1
Hud × T_a	-0.51^{**}	0.08	(-0.67, -0.36)	1, 2	1
Dur × T_a	-0.16	0.10	(-0.35, 0.03)	1, 2	1
Hud × Dur × T_a	0.24^{**}	0.09	(0.08, 0.41)	1, 2	1

$N = 322$. Akaike weights: $w_1 = 0.70$, $w_2 = 0.30$. Difference in AICc values between Model *i* and the model with the lowest AICc, Model 1: $\Delta_1 = 0$, $\Delta_2 = 1.68$. Parameters shown are model-averaged parameter estimates (β), unconditional standard errors which incorporate model uncertainty (*SE*), 95% confidence intervals, models that included the term, and relative importance. $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$

The top two models to explain lemurs' T_{sk} both included huddle rate, T_a, and duration, their two-way interactions, and their three-way interaction (Table 5). Model 1 additionally includes group size as a model component and was supported 2.3 times more strongly than Model 2, which does not include group size (evidence ratio $w_1/w_2 = 0.70/0.30$). Specifically, every additional group member was associated with an increase in T_{sk} by 0.13°C. Further, an increase in huddling rate by one standard deviation (0.42) was associated with an increase in T_{sk} by 0.48 - 0.81°C. This relationship was stronger when T_a was low (Fig. 2); e.g., for a decrease by one standard deviation in T_a (4.95°C), the slope of huddle rate increased by 0.51°C (huddle rate × T_a interaction). Specifically, in the absence of huddling, lemurs' T_{sk} was lower when T_a was low than when it was high, but that difference vanished at high huddle rates. Finally, the huddle rate × T_a × duration three-way interaction indicates that the two-way interaction between huddle rate and T_a changed across different durations. That is, the moderating effect of T_a on the effect of huddle rate on T_{sk} was stronger for short resting bouts than for long ones. Thus, huddling elevated T_{sk} most when T_a was low and resting bouts were short.

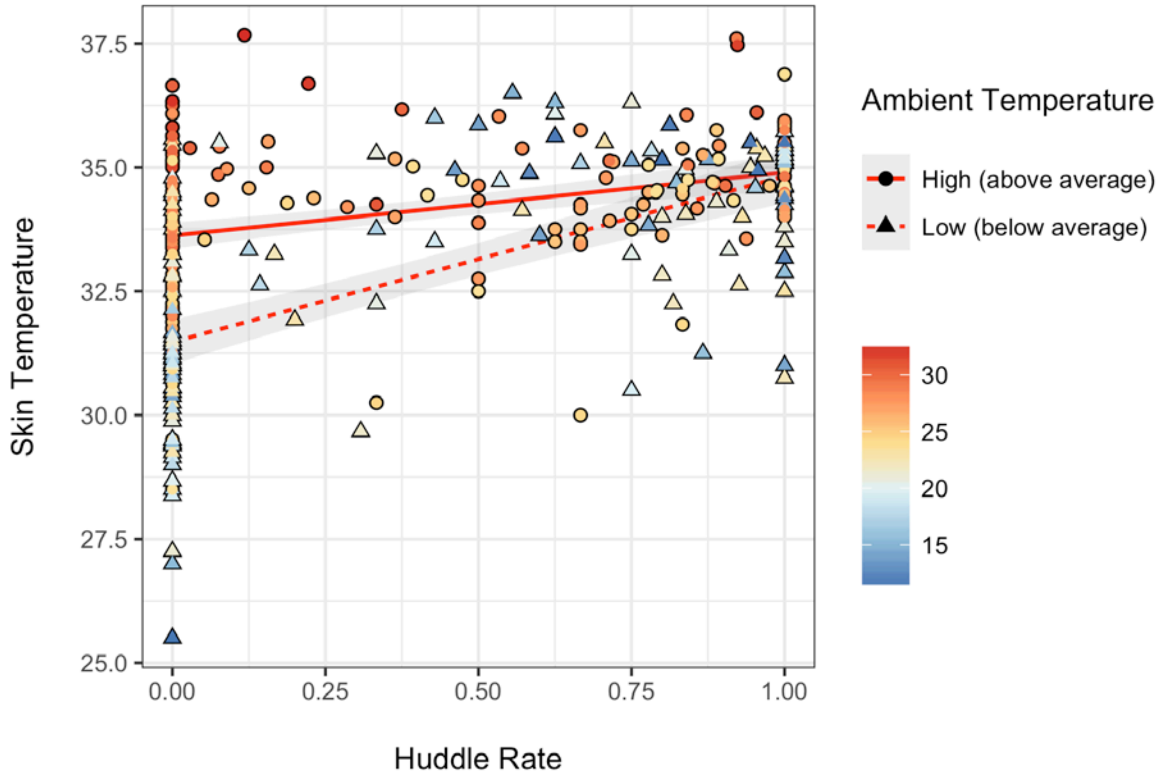

Figure 2. Lemur T_{sk} as a function of huddle rate, by ambient temperature. Resting bouts during ambient temperatures below the average of 23.4°C are indicated by triangles; those above average by circles. Plotted lines indicate the linear regression models for low (dashed) and high (solid) ambient temperatures; shaded areas indicate 95% confidence intervals.

Discussion

Southern bamboo lemurs displayed a preference for resting in larger trees and potentially increased buffering from environmental variables, e.g., rainfall, exposure to wind and cold air, and/or direct sun exposure. This environmental buffering, however, was not found to be as influential as huddling behaviour for increasing T_{sk}, especially at lower T_a.

Microhabitat rest site selection

Rest sites in larger trees may confer greater thermoregulatory benefits, such as protection from the direct sun and/or exposure to cold weather. In fact, chimpanzees (*Pan troglodytes*) have been observed to become more terrestrial during warm T_a (Takemoto 2004; Kosheleff and Anderson 2009), while chacma baboons (*Papio ursinus*) rest in the shade during midday, taking advantage of thermal microclimates (Hill 2006). Furthermore, both of these species occasionally utilise caves, which provide consistent T_a as well as shelter from extreme weather (Barrett et al. 2004; Pruetz 2007). Moreover, research on Cape ground squirrels (*Xerus inauris*) has shown that using a burrow consistently reduced T_b by 1-2°C (Fick et al. 2009). Similarly, southern bamboo lemurs were occasionally observed to rest on the ground and in terrestrial burrows, an unusual behaviour potentially attributed to increased T_a (Eppley et al. 2016b); however, their overall general selection of larger trees for resting were not shown to confer any thermal benefit. Considering the ecological characteristics of the Mandena littoral forest, large trees are not particularly large compared to less-degraded nearby littoral forests (Campera et al. 2014; Eppley et al. 2015a), so the environmental buffering effect at our site may be potentially limited. Furthermore, microhabitat resting sites selected for thermal characteristics may lack optimal anti-predator protection, or in the case of resources, may lack quick access to food and water (Angilletta et al. 2010).

Many studies of primate resting site selection have focused on anti-predator characteristics (Anderson and McGrew 1984; Anderson 1998; Albert et al. 2011; Barnett et al. 2012; Feilen and Marshall 2014), whereby protection from potential predators is presumably provided via large tree crowns. For example, golden-handed tamarins (*Saguinus midas midas*) utilised resting trees that were larger (in both DBH and height) compared to other trees (Day and Elwood 1999), presumably providing protection from potential aerial and terrestrial predators. This is similar to *H. meridionalis* in Mandena, whereby large trees provide larger canopy crowns and multiple escape routes in the case of potential predators. In fact, irregular sleeping site usage pattern (e.g., many rest sites were used only once) may support the predator avoidance strategy by reducing odour that might be cues for predators (Reichard 1998; José-Domínguez et al. 2015).

Huddling behaviour

Our results suggest that huddling confers an immediate effect as a thermoregulatory mechanism, and assists in maintaining an optimal T_b during longer duration resting bouts. Huddling has been shown to confer higher and more constant T_b than solitary resting, thus, it is an effective strategy to maintain homeothermy and reduce energy expenditure (Gilbert et al. 2010; Nuñez-Villegas et al. 2014; McFarland et al. 2015). This social behaviour, along with decreased inter-individual distances, has been shown to increase in colder weather conditions (i.e., lower T_a), and as such, is a typical behavioural response to thermal stress (Riedman 1990; Yahav and Buffenstein 1991; Gilbert et al. 2008; Donati et al. 2011; Sugita and Ueda 2013). Unlike most endothermic birds and mammals, many lemurid species display an unusual trait by exhibiting even or male-biased adult sex ratios, which may lead to potential benefits (Kappeler 2000, 2009). One proposed benefit for having surplus adult males in a group is for increased energy conservation via social thermoregulation (Morland 1993); however, this is not always the case (Ostner 2002). Furthermore, increased social links have been shown to lead to energy conservation advantages in gregarious vervet monkeys (*Chlorocebus pygerythrus*; McFarland et al. 2015). Nevertheless, bamboo lemur groups in Mandena are typically limited to small family units with one adult male and one to two adult females, and in fact, only one of our three studied groups had a surplus adult male (Eppley et al. 2016c). Thus, it is unlikely that this peculiar lemurid trait confers a thermoregulatory benefit among *H. meridionalis*. Southern bamboo lemur group size, however, did significantly predict an increase in T_{sk}. It is possible that with larger groups sizes, individuals may experience greater opportunity for social thermoregulation among group mates.

Huddling is not exhibited by all lemurids, however; in fact, both ring-tailed lemurs (*Lemur catta*) and ruffed lemurs (*Varecia* spp.) use sun-basking as a warming strategy (Jolly 1966; Morland 1993; Vasey 2002; Kelley et al. 2016). Specifically, they decrease the energetic demands during cold periods by positioning themselves to maximize surface area exposure to sunlight (Terrien et al. 2011). Similar to *L. catta* (Jolly 1966; Kelley et al. 2016), this is a strategy commonly used by many mammalian taxa living in arid or semi-arid habitats (Stelzner and Hausfater 1986; Brown and Downs 2007; Warnecke et al. 2010; Terrien et al. 2011; Danzy et al. 2012). On the contrary, *Varecia* spp. are restricted to the humid forests of eastern Madagascar, but sun-bask regardless (Morland 1993; Vasey 2002). This is perplexing given that sun-basking behaviour is absent in brown lemurs (*Eulemur* spp.) despite widespread geographic distribution (Sussman 1974; Pereira et al. 1999; Donati et al. 2011). *H. meridionalis* was never observed to sun-bask at any period during our study. It has been postulated that this behaviour within humid forests would only be possible on the emergent portion of the canopy, thus predation pressure from diurnal raptors would be high (Donati et al. 2011).

Compared to microhabitat rest site selection, huddling appears to be most important in terms of thermoregulation. Neither of the microhabitat variables (i.e., cover, crown volume) were correlated with the rate of huddling during a resting bout (Table 4), and furthermore, bamboo lemurs displayed no preference in where they chose to huddle in spite of the potential increased buffering effects against environmental variables that larger trees may confer. Our findings are similar to what has been shown among big brown bats (*Eptesicus fuscus*), with social thermoregulation being more effective in decreasing energy expenditure compared to microhabitat rest site selection (Willis and Brigham 2007).

Conclusion

Both microhabitat resting site selection and behavioural positioning (e.g., huddling, sun-basking, etc.) have been shown to play a large role in the thermoregulation of a multitude of endothermic birds and mammals. While rest site selection and the microhabitat may confer thermoregulatory benefits to individuals, our data only supported huddling among the southern bamboo lemurs to help increase T_b on cold days. This is potentially due to the increasing degradation and fragmented state of Mandena, whereby relatively few large trees exist and lemurs must adjust behaviourally to cope within increasingly anthropogenic landscapes. Furthermore, this leads us to question whether huddling in a small group is a cooperative benefit conferred to all group members, or if inclusion is determined via reciprocal exchange of services.

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