



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



Timothy M. Eppley^{a, b, c, *}, Julia Watzek^d, Kathrin H. Dausmann^a, Jörg U. Ganzhorn^a, Giuseppe Donati^b

^a Biozentrum Grindel, Department of Animal Ecology and Conservation, University of Hamburg, Hamburg, Germany

^b Nocturnal Primate Research Group, Department of Social Sciences, Oxford Brookes University, Oxford, U.K.

^c Department of Anthropology, University of Texas, Austin, TX, U.S.A.

^d Department of Psychology, Language Research Center, Georgia State University, GA, U.S.A.

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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 utilized as an energy conservation mechanism at low ambient temperatures (T_a), thus decreasing the metabolic cost of maintaining T_b . Although unusual among primates, lemurs maintain a low metabolic rate 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 individual and conspecifics. In addition, we recorded all resting sites utilized for at least 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 probably best served by behavioural strategies, i.e. social huddling.

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Many endothermic animals have evolved different physiological and/or behavioural mechanisms to maintain optimal body temperature (T_b), i.e. thermoregulation (Boyles, Seebacher, Smit, & McKechnie, 2011; Geiser, Goodship, & Pavey, 2002; Gilbert et al., 2010; Huey & Pianka, 1977; Kauffman, Paul, Butler, & Zucker, 2003; Kearney, Shine, & Porter, 2009; Kotze, Bennett, & Scantlebury, 2008; Terrien, Perret, & Aujard, 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; Gagge & Gonzalez, 2011; McNab, 1988) 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, Perret, & Vannier, 1998; Geiser, 2004; Heldmaier, Ortmann, & Elvert, 2004; Mzilikazi & Lovegrove, 2004; Westman & Geiser, 2004). These entail prolonged periods of resting with reduced metabolic rates without time dedicated to other activities, apart from periodic arousals (Lovegrove, Kortner, & Geiser, 1999).

* Correspondence: T. M. Eppley, Biozentrum Grindel, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany.

E-mail address: eppleyti@gmail.com (T. M. Eppley).

In contrast, behavioural mechanisms are more varied, and include microhabitat selection (Downs, Wimberger, & Wilson, 2013; Hill, 2006; Huey & Pianka, 1977; Kearney et al., 2009; Terrien et al., 2011; Willis & Brigham, 2007), such as the utilization of burrows to avoid harsh environmental conditions (Long, Martin, & Barnes, 2005), basking and body positioning (Brown & Downs, 2007; Kelley, Jablonski, Chaplin, Sussman, & Kamilar, 2016; Stelzner & Hausfater, 1986; Warnecke, Schleucher, & Geiser, 2010) and social thermoregulation (Gilbert et al., 2010; Kauffman et al., 2003; Scantlebury, Bennett, Speakman, Pillay, & Schradin, 2006). 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 (Gilbert et al., 2010; Hayes, 2000). 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, Gauthier, & Larochelle, 2000), Coliiformes (McKechnie & Lovegrove, 2001), Coraciiformes (Boix-Hinzen & Lovegrove, 1998), Galliformes (Putaalaa, Hohtola, & Hissa, 1995), Passeriformes (Burns, Ben-Hamo, Bauchinger, & Pinshow, 2013; Hatchwell, Sharp, Simeoni, & McGowan, 2009; Labisky & Arnett, 2006), Pelecaniformes (Evans, 1984) and Sphenisciformes (Gilbert, Robertson, Le Maho, & Ancel, 2008), while mammalian orders include Artiodactyla (Hrupka, Leibbrandt, Crenshaw, & Benevenga, 2000), Carnivora (Riedman, 1990), Chiroptera (Willis & Brigham, 2007), Dasyuromorphia (Rhind, 2003), Didelphimorphia (Canals, Rosenmann, & Bozinovic, 1997; Canals, Rosenmann, Novoa, & Bozinovic, 1998), Lagomorpha (Gilbert et al., 2007), Primates (Donati, Ricci, Baldi, Morelli, & Borgognini-Tarli, 2011; Ogawa & Wada, 2011; Ostner, 2002; Schino & Troisi, 1990) and Rodentia (Hayes, 2000; Hayes, Speakman, & Racey, 1992; 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 (Canals, Rosenmann, & Bozinovic, 1989; Canals et al., 1998, 1997; Contreras, 1984; Geiser et al., 2002; Gilbert et al., 2010; Hayes et al., 1992; Séguy & Perret, 2005; Terrien et al., 2011).

Primates represent a behaviourally and physiologically diverse order of small- and large-bodied endotherms that are distributed throughout various climatic and geographical zones (Lehman & 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 (Anderson, 1998; Cowlshaw, 1994). In addition to predator avoidance, resting sites are often sought to buffer against environmental variables such as rain and temperature fluctuation (De Vere, Warren, Nicholas, Mackenzie, & Higham, 2011; Han & Hu, 2012; Samson & Hunt, 2012), whereby the location and microhabitat variations may optimize physiological processes (Schino & 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, Quan, & Xiao, 2006). In fact, many primates are challenged with seasonally harsh environmental conditions, and exhibit optimal body temperature maintenance via postural changes, e.g. hunched, huddling and sun-basking positions (Danzy, Grobler, Freimer, & Turner, 2012; Dasilva, 1993; Donati et al., 2011; Hanya, Kiyono, & Hayaishi, 2007; Kelley et al., 2016; Morland, 1993; Ogawa & Wada, 2011; Stelzner & Hausfater, 1986; Terrien et al., 2011). Yellow baboons, *Papio cynocephalus*, utilize a hunched position to reduce heat loss during cold weather (Stelzner & Hausfater, 1986), while Japanese macaques, *Macaca fuscata*, have been observed to

habitually utilize hot springs during cold weather (Zhang, Watanabe, & Eishi, 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 characterized by seasonality and climatic stochasticity, both presumed to have had a major influence on the evolution of lemur life history traits (Dewar & Richard, 2007; Wright, 1999). So far, all lemurs studied have a comparatively low metabolic rate (Genoud, 2002; Schmid & Ganzhorn, 1996; Simmen et al., 2010), which suggests they rely on behavioural thermoregulatory strategies as an adaptation to scarce and unpredictable resources (Donati et al., 2011; McNab, 1986; Morland, 1993; Wright, 1999). In fact, during the cold and resource-deficient austral winter months, many species of Cheirogaleid lemurs (e.g. *Microcebus murinus*, *Microcebus griseorufus*, *Cheirogaleus medius*) reduce their metabolism and enter a temporary state of torpor or prolonged hibernation to conserve energy (Dausmann, 2005, 2014; Dausmann, Glos, & Heldmaier, 2009). Additionally, microhabitat variations such as constructing nests, utilizing tree holes or burrowing may reduce the physiological cost of thermoregulation (Blanco, Dausmann, Ranaivoarisoa, & Yoder, 2013; Dausmann, Glos, Ganzhorn, & Heldmaier, 2004; Kappeler, 1998; Lutermann, Verburt, & Rendigs, 2010; Radespiel, Ehresmann, & Zimmermann, 2003; Schmid, 1998). 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 (Donati et al., 2011; Kelley et al., 2016; Morland, 1993). For example, collared lemurs, *Eulemur collaris*, and red-fronted lemurs, *Eulemur rufifrons*, regularly hunch and form huddling groups more often during colder seasons (Donati et al., 2011; Ostner, 2002). While ring-tailed lemurs, *Lemur catta*, occasionally huddle within an open-canopy habitat, sun basking was shown to be utilized 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 antipredator 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 the selection of a rest site may have important fitness consequences (Anderson, 1998; Cowlshaw, 1994), 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 than rest sites only used once. In our second model, we sought to determine which factors maintained thermoregulation via skin temperatures (T_{sk}). Climatic seasons (e.g. wet and dry) within Madagascar often differ substantially (Dewar & Richard, 2007), with many animals displaying different behavioural and physiological responses (Wright, 1999). As such, we predicted seasonal differences in microhabitat selection, as greater environmental buffering would provide additional thermoregulation during the relatively 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 lower. 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 recherche 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 above sea level) along the south-east coast of Madagascar. This area consists of 230 ha of fragmented littoral forest and interspersed, seasonally inundated swamp (Eppley, Donati et al., 2015). Littoral forests are characterized as having a relatively low canopy that grows on sandy substrates and occur within 3 km of the coast (Dumetz, 1999; Consiglio, Schatz, Mcpherson, Lowry, Rabenantoandro, et al., 2006), yet due to the degree of degradation in Mandena, the vertical structure of this littoral forest is relatively low compared to less-degraded sites (Campera et al., 2014; Eppley, Donati et al., 2015).

Southern bamboo lemurs are medium-sized lemurs (albeit small-bodied primates) with an average body mass of 1.1 kg that exhibit a cathemeral activity pattern (Eppley, Ganzhorn, & Donati, 2015; Eppley, Hall, Donati, & Ganzhorn, 2015; Eppley, Watzek, Ganzhorn, & Donati, 2017). This species is also known to have a low-quality folivorous diet, the bulk of which is composed of various terrestrial grasses and sedges (Eppley, Donati, & Ganzhorn, 2016a; Eppley, Verjans, & Donati, 2011).

Climatic Data

To assess daily climatic factors, temperature (°C) was recorded in 30 min intervals using four Lascar EL-USB-1 data-loggers (Lascar Electronics, Inc.; Erie, PA, U.S.A.), 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 and 35.0 °C (Eppley, Donati, & Ganzhorn, 2016b; Fig. 1). Precipitation (mm) was measured daily at 0600 hours using a rain gauge placed within the study site. Total precipitation in Mandena during the study period was 2815 mm (Fig. 1).

Temperature Measurements

As part of a larger behavioural ecology study, we captured 10 adult individuals and fitted them with external radio-transmitting tags equipped with data-logging sensors for T_{sk} (ARC400, Advanced Telemetry Systems, Isanti, MN, U.S.A.). 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, Ganzhorn, and Donati (2016c). Our data-logging collars collected T_{sk} in degrees Celsius (°C) 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 \pm SD T_{sk} of *H. meridionalis* was 32.8 \pm 2.9 °C; however, when data-logging tags of individuals registered 0.0% activity, the mean T_{sk} of *H. meridionalis* was 35.8 \pm 1.2 °C. This fluctuation was due to movement when travelling and foraging, and thus the temperatures recorded while resting with minimal movement are considered accurate (Dausmann, 2005).

Behavioural Data

From January to December 2013, we conducted behavioural focal follows (from sunrise to sunset) every 5 min. Data were collected from three social groups, and totalled 1762 h. During the study period, Group 1 consisted of three to five individuals (three adult females, one adult male), Group 2 consisted of three to four individuals (one adult female, one adult male) and Group 4 consisted of eight to nine individuals (two adult females, two adult males) (Eppley et al., 2016c). Individuals were identified using radio-tracking tags with coloured pendants, with all adult individuals ($N = 10$) from our three focal groups sampled for at least 1 day each month. As general activity has a large influence on T_{sk} (Dausmann, 2005), our T_{sk} analyses are limited to resting bouts of 15 min or more.

All instances of continuous resting bouts of 15 min or more were recorded. Specifically, we recorded the full duration of the resting bout, the height of the focal individual, whether the focal individual 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 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' DBH (cm), height (m) and crown volume (m^3 ; Eppley, Donati et al., 2015) and the site's microhabitat location (i.e. littoral forest or swamp). We also recorded whether the rest site also acted as a feeding site or was utilized 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 defined 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 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 lemur's sex (female/male), huddle rate (i.e. proportion of huddling during rest bout), duration of the resting bout (min), group size,

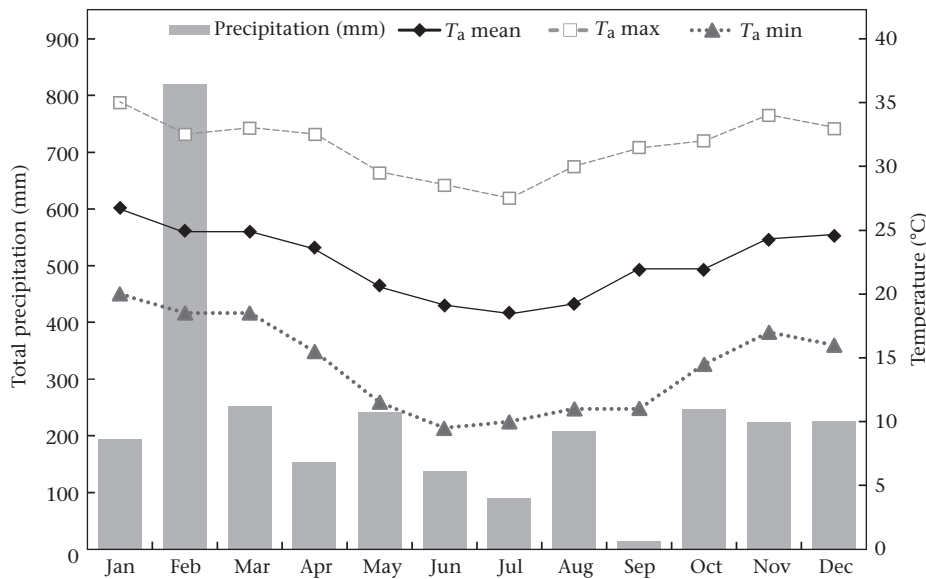


Figure 1. Monthly total precipitation and mean temperature (including monthly maxima and minima recorded) in Mandena from January to December 2013.

whether the resting site was a preference site (0/1), the crown volume (m^3) and cover (the position of the focal, in metres, beneath the tree canopy). In addition, we included climatic variables as fixed effects, specifically temperature ($^{\circ}C$), as the mean T_a from the nearest data-logger during the sleeping bout duration, daily total precipitation (mm) and the 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 & Anderson, 2002). We inspected the variance inflation factors (VIF) of a full model, including all fixed effects, to assess multicollinearity. VIF were computed from the variance-covariance matrix of the fixed effects conditional on the random effects, using the method of Davis, Hyde, Bangdiwala, and Nelson (1986), which is based on the correlation matrix. 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 that include the term in question. As model weights represent the probability of a model being the best model in the model set and thus reflect model uncertainty, importance can be understood as the likelihood of a term being included in the best model. We used the lme4 (Bates, Maechler, Bolker, & Walker, 2015) and MuMIn (Bartoń, 2016) packages in R statistical software version 3.3.2 (R Core Team, 2016) for these analyses, with P values derived for the averaged model with the MuMIn package.

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).

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. Our correlation matrix showed that DBH was positively correlated with height (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 (Table 2) included only DBH and only height, respectively, which explain the data significantly better than random effects, and were supported two times and 1.7 times more strongly than the model that included only crown volume (Table 2). 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% more likely to be a component of the best model (relative importance of

Table 1
Comparison of preferred and single-use resting sites

Resting sites	N	Feeding	DBH (cm)	Height (m)	Crown volume (m^3)
Preferred site	52	4	16.0	7.0	16.5
Median			8.0–25.3	5.0–9.3	6.3–62.8
Single-use site	378	41	11.0	6.0	6.3
Median			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; DBH = diameter at breast height. In addition to tree species, unidentified fallen dead trees and the ground (including burrows) were occasionally used by all groups.

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

Measure	PS	H	FS	DBH	HT	CV
Preferred site (PS)	–					
Habitat (H, forest=0, swamp=1)	–0.04	–				
Feeding site (FS)	–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 < 0.05; **P < 0.01; ***P < 0.001.

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

Model <i>i</i>	b_0	DBH	HT	CV	FS	Δ_i	w_i	χ^2	χ^2 df
1	–1.95	0.30				0.00	0.30	4.69*	1
2	–1.95		0.30			0.39	0.25	4.29*	1
3	–1.91	0.33			–0.48	1.22	0.17	3.27	1
4	–1.93			0.27		1.42	0.15	5.51	2
5	–1.91		0.33		–0.47	1.66	0.13	5.07	2
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 (FS). 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). Comparisons with the null model are provided via likelihood ratio tests. Bottom rows show model-averaged parameter estimates (β), unconditional standard errors which incorporate model uncertainty (SE), odds ratios and relative importance.
*P < 0.05; ***P < 0.001.

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 did 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 1 SD (11.03 cm and 2.96 m, respectively).

Thermoregulation: Huddling versus Resting Site

Considering all 505 resting bouts, 45.1% involved huddling behaviour. A total of 349 of these resting bouts were observed with radiocollared focal individuals; thus, our data set 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

Table 4
Correlation coefficients between model variables to predict thermoregulation

Measure	T_{sk}	Season	GS	Sex	PS	T_a	HR	D	P	Cover	CV
Season	0.17**	–									
Group size (GS)	0.17**	0.04	–								
Sex	–0.13*	–0.03	–0.61***	–							
Preference site (PS)	0.07	–0.15**	–0.03	0.03	–						
Temperature (T_a)	0.32***	0.50***	0.05	0.04	–0.11*	–					
Huddle rate (HR)	0.43***	–0.02	0.09	–0.18***	0.17**	–0.15**	–				
Duration (D)	0.48***	0.11*	–0.06	–0.02	0.18**	0.14*	0.28***	–			
Precipitation (P)	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 (CV)	–0.06	–0.11	–0.05	–0.03	0.09	–0.25***	0.10	–0.01	0.07	0.63***	–

N = 322. T_{sk} = skin temperature; season (dry = 0, wet = 1); sex (female = 0, male = 1); duration = length of resting bout.
*P < 0.05; **P < 0.01; ***P < 0.001.

Table 5
Model-averaged LMM parameters for predicting an increase in skin temperature (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 (HR)	0.64***	0.08	(0.48, 0.81)	1, 2	1
Duration (D)	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
HR*D	–0.26**	0.08	(–0.42, –0.10)	1, 2	1
HR* T_a	–0.51**	0.08	(–0.67, –0.36)	1, 2	1
D* T_a	–0.16	0.10	(–0.35, 0.03)	1, 2	1
HR*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: $\Delta_1 = 0.00$, $\Delta_2 = 1.68$. Parameters shown are model-averaged parameter estimates (β), unconditional standard errors that incorporate model uncertainty (SE), 95% confidence intervals (CI), models that included the term and relative importance. Both models fit the data better than a null model including only the random effects (Model 1: $\chi^2_8 = 245.89$, $P < 0.001$; Model 2: $\chi^2_7 = 242.05$, $P < 0.001$).
*P < 0.05; **P < 0.01; ***P < 0.001.

variables revealed that T_{sk} was higher during the wet season, for females, at nonfeeding 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} data set shows 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.

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 included group size as a model component and was supported 2.3 times more strongly than Model 2, which did not include group size (evidence ratio $w_1/w_2 = 0.70/0.30$). Specifically, every additional group

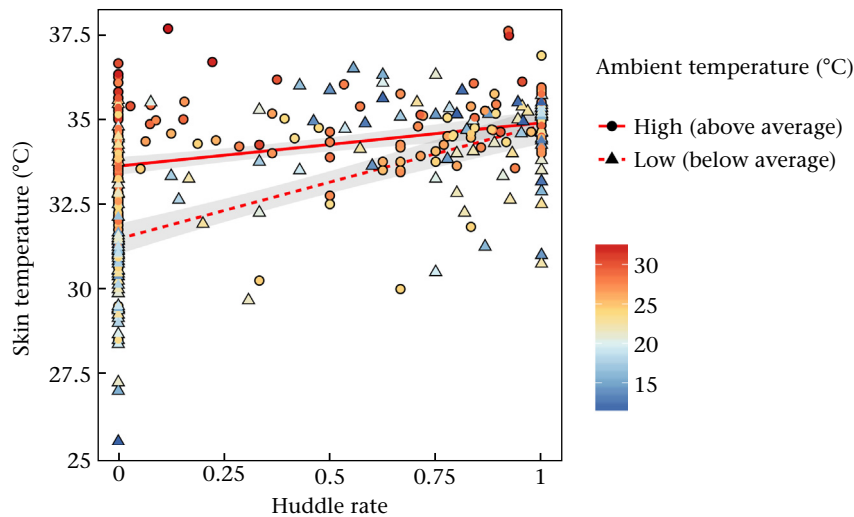


Figure 2. Lemur T_{sk} as a function of huddle rate, by ambient temperature. Resting bouts during ambient temperatures below the average of 23.4 °C are indicated by triangles; those above average by circles. Plotted lines indicate the linear regression models for low (dashed) and high (solid) ambient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

member was associated with an increase in T_{sk} by 0.13 °C. Further, an increase in huddling rate by 1 SD (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 1 SD 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.

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 at high T_a (Kosheleff & Anderson, 2009; Takemoto, 2004), while chacma baboons, *Papio ursinus*, rest in the shade during midday, taking advantage of thermal microclimates (Hill, 2006). Furthermore, both of these species occasionally utilize caves, which provide consistent T_a as well as shelter from extreme weather (Barrett, Gaynor, Rendall, Mitchell, & Henzi, 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, Kucio, Fuller, Matthee, & Mitchell, 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 was 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, Donati et al., 2015), 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, Cooper, Schuler, & Boyles, 2010).

Many studies of primate resting site selection have focused on antipredator characteristics (Albert, Savini, & Huynen, 2011; Anderson, 1998; Anderson & McGrew, 1984; Barnett, Shaw, Spironello, MacLarnon, & Ross, 2012; Feilen & Marshall, 2014), whereby protection from potential predators is presumably provided via large tree crowns. For example, golden-handed tamarins, *Saguinus midas midas*, utilized resting trees that were larger (in both DBH and height) than other trees (Day & 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 from potential predators. In fact, an 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 (José-Domínguez, Asensio, García, Huynen, & Savini, 2015; Reichard, 1998).

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 resting bouts. Huddling has been shown to confer higher and more constant T_b than solitary resting and is thus an effective strategy to maintain homeothermy and reduce energy expenditure (Gilbert et al., 2010; Nuñez-Villegas, Bozinovic, & Sabat, 2014; McFarland et al., 2015). This social behaviour, along with decreased interindividual 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 (Donati et al., 2011; Gilbert et al., 2008; Riedman, 1990; Sugita & Ueda, 2013; Yahav & Buffenstein, 1991). 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; Kappeler, Mass, & Port, 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, individuals may experience greater opportunity for social thermoregulation among group mates.

Huddling is not exhibited by all lemurids, however; in fact, ring-tailed lemurs, *L. catta*, and ruffed lemurs (*Varecia* spp.) use sun basking as a warming strategy (Jolly, 1966; Kelley et al., 2016; Morland, 1993; Vasey, 2002). Specifically, they decrease the energetic demands during cold periods by positioning themselves to maximize surface area exposure to sunlight (Terrien et al., 2011). As in *L. catta* (Jolly, 1966; Kelley et al., 2016), this is a strategy commonly used by many mammalian taxa living in arid or semiarid habitats (Brown & Downs, 2007; Danzy et al., 2012; Stelzner & Hausfater, 1986; Terrien et al., 2011; Warnecke et al., 2010). In contrast, *Varecia* spp. are restricted to the humid forests of eastern Madagascar, but sun-bask regardless (Morland, 1993; Vasey, 2002). This is puzzling given that sun-basking behaviour is absent in brown lemurs (*Eulemur* spp.) despite widespread geographical distribution (Donati et al., 2011; Pereira, Strohecker, Cavigelli, Hughes, & Pearson, 1999; Sussman, 1974). *Hapalemur 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, where predation pressure from diurnal raptors would be high (Donati et al., 2011).

Compared to microhabitat rest site selection, huddling appeared to be most important in terms of thermoregulation. Neither of the microhabitat variables (i.e. cover, crown volume) was 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 despite the potential increased buffering effects against environmental variables that larger trees may confer. Our findings are similar to those for big brown bats, *Eptesicus fuscus*, with social thermoregulation being more effective in decreasing energy expenditure than microhabitat rest site selection (Willis & 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 whether inclusion is determined via reciprocal exchange of services.

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References

- Albert, A., Savini, T., & Huynen, M. C. (2011). Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology*, 73, 1222–1230.
- Anderson, J. R. (1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *American Journal of Primatology*, 46, 63–75.
- Anderson, J. R., & McGrew, W. C. (1984). Guinea baboons (*Papio papio*) at a sleeping site. *American Journal of Primatology*, 6, 1–14.
- Angilletta, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience*, 2, 861–881.
- Aujard, F., Perret, M., & Vannier, C. (1998). Thermoregulatory responses to variations of photoperiod and ambient temperature in the male lesser mouse lemur: A primitive or an advanced adaptive character? *Journal of Comparative Physiology B*, 168, 540–548.
- Barnett, A. A., Shaw, P., Spironello, W. R., MacLarnon, A., & Ross, C. (2012). Sleeping site selection by golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian flooded forests. *Primates*, 53, 273–285.
- Barrett, L., Gaynor, D., Rendall, D., Mitchell, D., & Henzi, S. P. (2004). Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *Journal of Human Evolution*, 46, 215–222.
- Bartoń, K. (2016). *MuMIn: Multi-model inference. R package version 1.15.6*. Retrieved from: <http://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Blanco, M. B., Dausmann, K. H., Ranaivoarisoa, J. F., & Yoder, A. D. (2013). Underground hibernation in a primate. *Scientific Reports*, 3, 1768.
- Boix-Hinzen, C., & Lovegrove, B. G. (1998). Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): The influence of huddling. *Journal of Zoology*, 244, 33–41.
- Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*, 51, 676–690.
- Brown, K. J., & Downs, C. T. (2007). Basking behaviour in the rock hyrax (*Procapra capensis*) during winter. *African Zoology*, 42, 70–79.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Burns, D. J., Ben-Hamo, M., Bauchinger, U., & Pinshow, B. (2013). Huddling house sparrows remain euthermic at night, and conserve body mass. *Journal of Avian Biology*, 44, 198–202.
- Campera, M., Serra, V., Balestri, M., Barresi, M., Ravaolahy, M., Randriatafika, F., et al. (2014). Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology*, 35, 957–975.
- Canals, M., Rosenmann, M., & Bozinovic, F. (1989). Energetics and geometry of huddling in small mammals. *Journal of Theoretical Biology*, 141, 181–189.
- Canals, M., Rosenmann, M., & Bozinovic, F. (1997). Geometrical aspects of the energetic effectiveness of huddling in small mammals. *Acta Theriologica*, 42, 321–328.
- Canals, M., Rosenmann, M., Novoa, F. F., & Bozinovic, F. (1998). Modulating factors of the energetic effectiveness of huddling in small mammals. *Acta Theriologica*, 43, 337–348.
- Consiglio, T., Schatz, G. E., McPherson, G., Lowry, P. P., Rabenantoandro, J., Rogers, Z. S., et al. (2006). Deforestation and plant diversity of Madagascar's littoral forests. *Conservation Biology*, 20, 1799–1803.

- Contreras, L. C. (1984). Bioenergetics of huddling: Test of a psycho-physiological hypothesis. *Journal of Mammalogy*, *65*, 256–262.
- Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. *Behaviour*, *131*, 293–304.
- Cui, L.-W., Quan, R.-C., & Xiao, W. (2006). Sleeping sites of black-and-white snub nosed monkeys (*Rhinopithecus bieti*) at Baima Snow Mountain, China. *Journal of Zoology*, *270*, 192–198.
- Daniels, H. L. (1984). Oxygen consumption in *Lemur fulvus*: Deviation from the ideal model. *Journal of Mammalogy*, *65*, 584–592.
- Danzon, J., Grobler, J. P., Freimer, N., & Turner, T. (2012). Sunbathing: A behavioral response to seasonal climatic change among South African vervet monkeys (*Chlorocebus aethiops*). *African Primates*, *7*, 230–237.
- Dasilva, G. L. (1993). Postural changes and behavioural thermoregulation in *Colobus polykomos*: The effect of climate and diet. *African Journal of Ecology*, *31*, 226–241.
- Dausmann, K. H. (2005). Measuring body temperature in the field—evaluation of external vs. implanted transmitters in a small mammal. *Journal of Thermal Biology*, *30*, 195–202.
- Dausmann, K. H. (2014). Flexible patterns in energy savings: Heterothermy in primates. *Journal of Zoology*, *292*, 101–111.
- Dausmann, K. H., Glos, J., Ganzhorn, J. U., & Heldmaier, G. (2004). Physiology: Hibernation in a tropical primate. *Nature*, *429*, 825–826.
- Dausmann, K. H., Glos, J., & Heldmaier, G. (2009). Energetics of tropical hibernation. *Journal of Comparative Physiology B*, *179*, 345–357.
- Davis, C. E., Hyde, J. E., Bangdiwala, S. I., & Nelson, J. J. (1986). An example of dependencies among variables in a conditional logistic regression. In S. H. Moolgavkar, & R. L. Prentice (Eds.), *Modern statistical methods in chronic disease epidemiology* (pp. 140–147). New York, NY: Wiley.
- Day, R. T., & Elwood, R. W. (1999). Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: The role of predation risk, proximity to feeding sites, and territorial defence. *Ethology*, *105*, 1035–1051.
- De Vere, R. A., Warren, Y., Nicholas, A., Mackenzie, M. E., & Higham, J. P. (2011). Nest site ecology of the Cross River gorilla at the Kagwene Gorilla Sanctuary, Cameroon, with special reference to anthropogenic influence. *American Journal of Primatology*, *73*, 253–261.
- Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13723–13727.
- Donati, G., Ricci, E., Baldi, N., Morelli, V., & Borgognini-Tarli, S. M. (2011). Behavioral thermoregulation in a gregarious lemur, *Eulemur collaris*: Effects of climatic and dietary-related factors. *American Journal of Physical Anthropology*, *144*, 355–364.
- Downs, C. T., Wimberger, K., & Wilson, A. L. (2013). No effects of huddling on core body temperature in rock hyrax, *Procavia capensis*. *African Zoology*, *48*, 173–176.
- Dumetz, N. (1999). High plant diversity of lowland rainforest vestiges in eastern Madagascar. *Biodiversity and Conservation*, *8*, 273–315.
- Eppley, T. M., Donati, G., & Ganzhorn, J. U. (2016a). Determinants of terrestrial feeding in an arboreal primate: The case of the southern bamboo lemur (*Hapalemur meridionalis*). *American Journal of Physical Anthropology*, *161*, 328–342.
- Eppley, T. M., Donati, G., & Ganzhorn, J. U. (2016b). Unusual sleeping site selection by southern bamboo lemurs. *Primates*, *57*, 167–173.
- Eppley, T. M., Donati, G., Ramanamanjato, J.-B., Randriatafika, F., Andriamandimbarisoa, L. N., Rabehivitra, D., et al. (2015). The use of an invasive species habitat by a small folivorous primate: Implications for conservation. *PLoS One*, *10*, e0140981.
- Eppley, T. M., Ganzhorn, J. U., & Donati, G. (2015). Cathemerality in a small, folivorous primate: Proximate control of diel activity in *Hapalemur meridionalis*. *Behavioral Ecology and Sociobiology*, *69*, 991–1002.
- Eppley, T. M., Ganzhorn, J. U., & Donati, G. (2016c). Latrine behaviour as a multimodal communicatory signal station in wild lemurs: The case of *Hapalemur meridionalis*. *Animal Behaviour*, *111*, 57–67.
- Eppley, T. M., Hall, K., Donati, G., & Ganzhorn, J. U. (2015). An unusual case of affiliative association of a female *Lemur catta* in a *Hapalemur meridionalis* social group. *Behaviour*, *152*, 1041–1061.
- Eppley, T. M., Verjans, E., & Donati, G. (2011). Coping with low-quality diets: A first account of the feeding ecology of the southern gentle lemur, *Hapalemur meridionalis*, in the Mandena littoral forest, southeast Madagascar. *Primates*, *52*, 7–13.
- Eppley, T. M., Watzek, J., Ganzhorn, J. U., & Donati, G. (2017). Predator avoidance and dietary fibre predict diurnality in the cathemeral folivore *Hapalemur meridionalis*. *Behavioral Ecology and Sociobiology*, *71*, 4.
- Evans, R. M. (1984). Some causal and functional correlates of creching in young white pelicans. *Canadian Journal of Zoology*, *62*, 814–819.
- Feilen, K. L., & Marshall, A. J. (2014). Sleeping site selection by proboscis monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia. *American Journal of Primatology*, *76*, 1127–1139.
- Fick, L. G., Kucio, T. A., Fuller, A., Matthee, A., & Mitchell, D. (2009). The relative roles of the parasol-like tail and burrow shuttling in thermoregulation of free-ranging Cape ground squirrels, *Xerus inauris*. *Comparative Biochemistry and Physiology A Molecular & Integrative Physiology*, *152*, 334–340.
- Fortin, D., Gauthier, G., & Larochelle, J. (2000). Body temperature and resting behavior of greater snow goose goslings in the high Arctic. *Condor*, *102*, 163–171.
- Gagge, A. P., & Gonzalez, R. R. (2011). Mechanisms of heat exchange: Biophysics and physiology. In R. Terjung (Ed.), *Comprehensive physiology* (pp. 45–84). New York: John Wiley & Sons, Inc.
- Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology*, *66*, 239–274.
- Geiser, F., Goodship, N., & Pavey, C. R. (2002). Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften*, *89*, 412–414.
- Genoud, M. (2002). Comparative studies of basal rate of metabolism in primates. *Evolutionary Anthropology*, *11*, 108–111.
- Gilbert, C., Blanc, S., Giroud, S., Tralalon, M., Le Maho, Y., Perret, M., et al. (2007). Role of huddling on the energetic of growth in a newborn altricial mammal. *American Journal of Physiology*, *293*, 867–876.
- Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J. M., Giroud, S., Blanc, S., et al. (2010). One for all and all for one: The energetic benefits of huddling in endotherms. *Biological Reviews*, *85*, 545–569.
- Gilbert, C., Robertson, G., Le Maho, Y., & Ancel, A. (2008). How do weather conditions affect the huddling behaviour of emperor penguins? *Polar Biology*, *31*, 163–169.
- Han, J., & Hu, G. (2012). Sleeping behavior of wild Francois' langur (*Trachypithecus francoisi*) at Mayanghe Nature Reserve in summer, Guizhou China. *Acta Theriologica Sinica*, *32*, 362–367.
- Hanya, G., Kiyono, M., & Hayaishi, S. (2007). Behavioral thermoregulation of wild Japanese macaques: Comparisons between two subpopulations. *American Journal of Primatology*, *69*, 802–815.
- Hatchwell, B. J., Sharp, S. P., Simeoni, M., & McGowan, A. (2009). Factors influencing overnight loss of body mass in the communal roosts of a social bird. *Functional Ecology*, *23*, 367–372.
- Hayes, L. D. (2000). To nest communally or not to nest communally: A review of rodent communal nesting and nursing. *Animal Behaviour*, *59*, 677–688.
- Hayes, J. P., Speakman, J. R., & Racey, P. A. (1992). The contributions of local heating and reducing exposed surface area to the energetic benefits of huddling by short-tailed field voles (*Microtus agrestis*). *Physiological Zoology*, *65*, 742–762.
- Heldmaier, G., Ortmann, S., & Elvert, R. (2004). Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory Physiology & Neurobiology*, *141*, 317–329.
- Hill, R. A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology*, *129*, 242–249.
- Hrupka, B. J., Leibbrandt, V. D., Crenshaw, T. D., & Benevenga, N. J. (2000). Effect of sensory stimuli on huddling behavior of pigs. *Journal of Animal Science*, *78*, 592–596.
- Huey, R. B., & Pianka, E. R. (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, *58*, 1066–1075.
- Jolly, A. (1966). *Lemur behavior: A Madagascar field study*. Chicago and London: The University of Chicago Press.
- José-Domínguez, J. M., Asensio, N., García, C. J. G., Huynen, M. C., & Savini, T. (2015). Exploring the multiple functions of sleeping sites in northern pigtailed macaques (*Macaca leonine*). *International Journal of Primatology*, *36*, 948–966.
- Kappeler, P. M. (1998). Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, *46*, 7–33.
- Kappeler, P. M. (2000). Causes and consequences of unusual sex ratios among lemurs. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 55–63). Cambridge, U.K.: Cambridge University Press.
- Kappeler, P. M., Mass, V., & Port, M. (2009). Even adult sex ratios in lemurs: Potential costs and benefits of subordinate males in Verreaux's sifaka (*Propithecus verreauxi*) in the Kirindy Forest CFPF, Madagascar. *American Journal of Physical Anthropology*, *140*, 487–497.
- Kauffman, A. S., Paul, M. J., Butler, M. P., & Zucker, I. (2003). Huddling, locomotor, and nest-building behaviors of furred and furless Siberian hamsters. *Physiology & Behavior*, *79*, 247–256.
- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3835–3840.
- Kelley, E. A., Jablonski, N. G., Chaplin, G., Sussman, R. W., & Kamilar, J. M. (2016). Behavioral thermoregulation in *Lemur catta*: The significance of sunning and huddling behaviors. *American Journal of Primatology*, *78*, 745–754.
- Kosheleff, V. P., & Anderson, C. N. (2009). Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, *139*, 172–181.
- Kotze, J., Bennett, N. C., & Scantlebury, M. (2008). The energetics of huddling in two species of mole-rat (Rodentia: Bathyergidae). *Physiology & Behavior*, *93*, 215–221.
- Labisky, R. F., & Arnett, J. E. (2006). Pair roosting of nesting Carolina wrens (*Thryothorus ludovicianus*). *Wilson Journal of Ornithology*, *118*, 566–569.
- Lehman, S. M., & Fleagle, J. G. (2006). Biogeography and primates: A review. In S. M. Lehman, & J. G. Fleagle (Eds.), *Primate biogeography: Progress and prospects* (pp. 1–58). New York, NY: Springer.
- Long, R. A., Martin, T. J., & Barnes, B. M. (2005). Body temperature and activity patterns in free-living arctic ground squirrels. *Journal of Mammalogy*, *86*, 314–322.
- Lovegrove, G., Kortner, G., & Geiser, F. (1999). The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: Benefits of summer ambient temperature cycles. *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology*, *169*, 11–18.
- Lutermann, H., Verburgt, L., & Rendigs, A. (2010). Resting and nesting in a small mammal: Sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*, *79*, 1211–1219.

- McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., et al. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*, 84, 871–878.
- McKechnie, A. E., & Lovegrove, B. G. (2001). Thermoregulation and the energetic significance of clustering behavior in the whitebacked mousebird (*Colius colius*). *Physiological and Biochemical Zoology*, 74, 238–249.
- McNab, B. K. (1986). The influence of food habits on the energetic of Eutherian mammals. *Ecological Monographs*, 56, 1–19.
- McNab, B. K. (1988). Energy conservation in a tree-kangaroo (*Dendrolagus mitchiei*) and the red panda (*Ailurus fulgens*). *Physiological Zoology*, 61, 280–292.
- Morland, H. S. (1993). Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs. In P. M. Kappeler, & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 193–203). New York, NY: Plenum Press.
- Mzilikazi, N., & Lovegrove, B. G. (2004). Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: A year-long study. *Physiological and Biochemical Zoology*, 77, 285–296.
- Núñez-Villegas, M., Bozinovic, F., & Sabat, P. (2014). Interplay between group size, huddling behavior and basal metabolism: An experimental approach in the social degu. *Journal of Experimental Biology*, 217, 997–1002.
- Ogawa, H., & Wada, K. (2011). Shape of, and body direction in, huddles of Japanese macaques (*Macaca fuscata*) in Arashiyama, Japan. *Primates*, 52, 229–235.
- Ostner, J. (2002). Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). *Folia Primatologica*, 73, 175–180.
- Pereira, M. E., Strohecker, R. A., Cavigelli, S. A., Hughes, C. L., & Pearson, D. D. (1999). Metabolic strategy and social behavior in Lemuridae. In B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn, & S. M. Goodman (Eds.), *New directions in lemur studies* (pp. 93–118). New York, NY: Plenum Press.
- Pruetz, J. D. (2007). Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: Implications for thermoregulatory behavior. *Primates*, 48, 316–319.
- Putaala, A., Hohtola, E., & Hissa, R. (1995). The effect of group-size on metabolism in huddling grey partridge (*Perdix perdix*). *Comparative Biochemistry and Physiology B*, 111, 243–247.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from: <http://www.R-project.org>.
- Radespiel, U., Ehresmann, P., & Zimmermann, E. (2003). Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus*, *M. ravelobensis*) in northwestern Madagascar. *American Journal of Primatology*, 59, 139–151.
- Reichard, U. (1998). Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *American Journal of Primatology*, 46, 35–62.
- Rhind, S. G. (2003). Communal nesting in the usually solitary marsupial, *Phascogale tapoatafa*. *Journal of Zoology*, 261, 345–351.
- Riedman, M. (1990). *The pinnipeds, seals, sea lions, and walruses*. Berkeley, CA: University of California Press.
- Samson, D. R., & Hunt, K. D. (2012). A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *American Journal of Primatology*, 74, 811–818.
- Scantlebury, M., Bennett, N. C., Speakman, J. R., Pillay, N., & Schradin, C. (2006). Huddling in groups lead to daily energy savings in free-living African four-striped grass mice, *Rhabdomys pumilio*. *Functional Ecology*, 20, 166–173.
- Schino, G., & Troisi, A. (1990). Behavioral thermoregulation in long-tailed macaques: Effect on social preference. *Physiology & Behavior*, 47, 1125–1128.
- Schmid, J. (1998). Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in Madagascar: Insulation capacities and energetic consequences. *International Journal of Primatology*, 19, 797–809.
- Schmid, J., & Ganzhorn, J. U. (1996). Resting metabolic rates of *Lepilemur ruficaudatus*. *American Journal of Primatology*, 38, 169–174.
- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., et al. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343, 842–843.
- Séguy, M., & Perret, M. (2005). Factors affecting the daily rhythm of body temperature of captive mouse lemurs (*Microcebus murinus*). *Journal of Comparative Physiology B*, 175, 107–115.
- Simmen, B., Bayart, F., Rasamimanana, H., Zahariev, A., Blanc, S., & Pasquet, P. (2010). Total energy expenditure and body composition in two free-living sympatric lemurs. *PLoS One*, 5, e9860.
- Stelzner, J. K., & Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow baboons. *Primates*, 27, 449–463.
- Sugita, N., & Ueda, K. (2013). The role of temperature on clustering behavior and mating opportunity in Bonin flying foxes. *Mammalian Biology*, 78, 455–460.
- Sussman, R. W. (1974). Ecological distinctions in sympatric species of Lemur. In R. D. Martin, G. A. Doyle, & A. C. Walker (Eds.), *Prosimian biology* (pp. 75–108). London, U.K.: Duckworth.
- Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology*, 124, 81–92.
- Terrier, J., Perret, M., & Aujard, F. (2011). Behavioral thermoregulation in mammals: A review. *Frontiers in Bioscience*, 16, 1428–1444.
- Vasey, N. (2002). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: II. Intraspecific patterns. *American Journal of Physical Anthropology*, 118, 169–183.
- Warnecke, L., Schleucher, E., & Geiser, F. (2010). Basking behaviour in relation to energy use and food availability in one of the smallest marsupials. *Physiology & Behavior*, 101, 389–393.
- Westman, W., & Geiser, F. (2004). The effect of metabolic fuel availability on thermoregulation and torpor in a marsupial hibernator. *Journal of Comparative Physiology B*, 174, 49–57.
- Willis, C. K., & Brigham, R. M. (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology and Sociobiology*, 62, 97–108.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*, 42, 31–72.
- Yahav, S., & Buffenstein, R. (1991). Huddling behavior facilitates homeothermy in the naked mole rat *Heterocephalus glaber*. *Physiological Zoology*, 64, 871–884.
- Zhang, P., Watanabe, K., & Eishi, T. (2007). Habitual hot-spring bathing by a group of Japanese macaques (*Macaca fuscata*) in their natural habitat. *American Journal of Primatology*, 69, 1425–1430.