

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

3

4 **Timothy M. Eppley^{1,2,3,*}, Julia Watzek⁴, Kathrin H. Dausmann¹, Jörg U. Ganzhorn¹,**
5 **Giuseppe Donati²**

6

7 **1 Biozentrum Grindel, University of Hamburg, Hamburg, Germany**

8 **2 Nocturnal Primate Research Group, Department of Social Sciences, Oxford Brookes**
9 **University, Oxford, United Kingdom**

10 **3 Department of Anthropology, University of Texas, Austin, TX, United States of**
11 **America**

12 **4 Department of Psychology, Language Research Center, Georgia State University, GA,**
13 **United States of America**

14

15 ***Correspondence: Timothy M. Eppley**

16 **Biozentrum Grindel**

17 **University of Hamburg**

18 **Martin-Luther-King Platz 3**

19 **20146 Hamburg**

20 **Germany**

21 **Telephone: +1 (512) 800-0269**

22 **Email: eppleyti@gmail.com**

23

24 **Word Count: 5,162**

25

26 **Abbreviated title: Behavioural thermoregulation in Hapalemur**

27 **Abstract**

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

51 forest as the potential environmental buffering is limited, thus thermoregulatory mechanisms
52 are likely best served by behavioural strategies, i.e., social huddling.

53

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

56

57 **Introduction**

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

71 In contrast, behavioural mechanisms are more varied, and include microhabitat
72 selection (Huey and Pianka 1977; Hill 2006; Willis and Brigham 2007; Kearney et al. 2009;
73 Terrien et al. 2011; Downs et al. 2013), including the utilisation of burrows to avoid harsh
74 environmental conditions (Long et al. 2005), basking and body positioning (Stelzner and
75 Hausfater 1986; Brown and Downs 2007; Warnecke et al. 2010; Kelley et al. 2016), and

76 social thermoregulation (Kauffman et al. 2003; Gilbert et al. 2010; Scantlebury et al. 2010).

77 This last strategy, social thermoregulation (i.e., a behavioural energy conservation
78 mechanism) is the active and close aggregation of animals in order to keep warm and is
79 achieved by adopting hunched and/or curled positions with conspecifics (Hayes 2000; Gilbert
80 et al., 2010). Colloquially, this is referred to as huddling, and has been recorded in numerous
81 avian and mammalian orders (Gilbert et al. 2010). These include birds from the orders
82 Anseriformes (Fortin et al. 2000), Coliiformes (McKechnie and Lovegrove 2001),
83 Coraciiformes (Boix-Hinzen and Lovegrove 1998), Galliformes (Putaala et al. 1995),
84 Passeriformes (Hatchwell et al. 2009; Labisky and Arnett 2006; Burns et al. 2013),
85 Pelecaniformes (Evans 1984), and Sphenisciformes (Gilbert et al. 2008), while mammalian
86 orders include Artiodactyla (Hrupka et al. 2000), Carnivora (Riedman 1990), Chiroptera
87 (Willis and Brigham 2007), Dasyuromorphia (Rhind 2003), Didelphimorphia (Canals et al.
88 1997, 1998), Lagomorpha (Gilbert et al. 2007), Primates (Schino and Troisi 1990; Ostner
89 2002; Donati et al. 2011; Ogawa and Wada 2011), and Rodentia (Hayes et al. 1992; Hayes
90 2000; Kotze et al. 2008). The strategy may improve an individual's (or group's) ability to
91 survive via maintaining optimal T_b and conserving heat (i.e., metabolic energy) by reducing
92 the total body surface area exposed to the environment (Contrera 1984; Hayes et al. 1992;
93 Canals et al. 1989, 1997, 1998; Geiser et al. 2002; Séguy and Perret 2005; Gilbert et al. 2010;

94

95

96 Primates represent a behaviourally and physiologically diverse order of small- and
97 large-bodied endotherms that are distributed throughout various climatic and geographic
98 zones (Lehman and Fleagle 2006). As it is estimated that primates spend approximately half
99 of their lives at sleeping sites, site selection is a vital aspect of an individual's fitness and
100 group's overall performance and behavioural ecology (Cowlshaw 1994; Anderson 1998). In

101 addition to predator avoidance, resting sites are often sought to buffer against environmental
102 variables such as rain and temperature fluctuation (De Vere et al. 2011; Han and Hu 2012;
103 Samson and Hunt 2012), whereby the location and microhabitat variations may optimize
104 physiological processes (Schino and Troisi 1990). For example, in a seasonally harsh
105 environment, black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) select sleeping
106 trees with large diameters at breast height (DBH) and broad crown diameters presumably to
107 provide effective shelter from precipitation and cold exposure (Cui et al. 2006). In fact, many
108 primates are challenged with seasonally harsh environmental conditions, and have exhibited
109 optimal body temperature maintenance via postural changes, e.g., hunched, huddling, and
110 sun-basking positions (Stelzner and Hausfater 1986; Dasilva 1993; Moreland 1993; Hanya et
111 al. 2007; Donati et al. 2011; Ogawa and Wada 2011; Terrien et al. 2011; Danzy et al. 2012;
112 Kelley et al. 2016). Yellow baboons (*Papio cynocephalus*) utilise a hunched position to
113 reduce heat loss during cold weather (Stelzner and Hausfater 1986), while Japanese
114 macaques (*Macaca fuscata*) have been observed to habitually utilise hot springs during cold
115 weather (Zhang et al. 2007). When exposed to low temperatures in environments without the
116 advantage of hot springs, *M. fuscata* huddle and sun-bask during the winter as an effective
117 means of raising T_b (Hanya et al. 2007).

118 The strepsirrhine primates of Madagascar live in an island environment characterised
119 by seasonality and climatic stochasticity, both presumed to have had a major influence on the
120 evolution of lemur life history traits (Wright 1999; Dewar and Richard 2007). So far, all
121 lemurs studied are hypometabolic (Genoud 2002; Simmen et al. 2010), which suggests they
122 rely on behavioural thermoregulatory strategies as an adaptation to scarce and unpredictable
123 resources (Kurland and Pearson 1986; McNab 1986; Morland 1993; Donati et al. 2011). In
124 fact, during the cold and resource deficient austral winter months, many species of
125 Cheirogaleid lemurs (e.g., *Microcebus murinus*, *M. griseorufus*, *Cheirogaleus medius*) reduce

126 their metabolism and enter a temporary state of torpor or prolonged hibernation in order to
127 conserve energy (Dausmann 2005, 2014; Dausmann et al. 2009). Additionally, microhabitat
128 variations such as constructing nests, utilising tree holes or burrowing may reduce the
129 physiological cost of thermoregulation (Kappeler 1998; Schmid 1998; Radespiel et al. 2003;
130 Dausmann et al. 2004; Lutermann et al. 2010; Blanco et al. 2013). Torpor is most often found
131 in mammals with a body mass below 200 g, with reduced energetic savings as body mass
132 increases (Geiser 2004; Heldmaier et al. 2004), potentially providing an explanation why
133 hibernation and torpor are not exhibited by larger, non-Cheirogaleid lemurs (Dausmann et al.
134 2009).

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

145 Within a degraded habitat, we studied a medium-sized strepsirrhine, the southern
146 bamboo lemur (*Hapalemur meridionalis*), as a model to determine which factor(s) most
147 influenced thermoregulation for resting individuals. As rest site selection may have important
148 fitness consequences (Cowlshaw 1994; Anderson 1998), we first sought to determine what
149 factors most influenced an individual to return to a rest site. We predicted that lemurs would
150 select rest areas of greater environmental protection (e.g., shade, wind protection), whereby

151 individuals would more often return to larger trees with greater crown volumes compared to
152 rest sites only used once. In our second model, we sought to determine which factors
153 maintained thermoregulation via skin temperatures (T_{sk}). We predicted seasonal differences
154 in microhabitat selection, as greater environmental buffering would provide additional
155 thermoregulation during the cool, austral winter. As prolonged social contact during resting
156 bouts (i.e., huddling) is a frequent energy preservation strategy among many mammals and
157 birds (Gilbert et al. 2010), we hypothesized that T_{sk} would increase as a result of increased
158 huddling behaviour. In addition, we predicted that huddling would occur more frequently
159 when T_a is colder. We also predicted that huddling bouts would occur most often at smaller,
160 single-use resting sites that provided limited environmental buffers.

161

162 **Methods**

163 *Ethical note*

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

170

171 *Study Site and Species*

172 Our study was conducted in the protected littoral area of Mandena (24°95'S 46°99'E,
173 0–20 m asl) along the southeast coast of Madagascar. This area consists of 230 ha of
174 fragmented littoral forest and interspersed, seasonally-inundated swamp (Eppley et al.
175 2015a). Littoral forests are characterised as having a relatively low canopy that grows on

176 sandy substrates and occur within 3 km of the coast (Dumetz 1999; Consiglio et al. 2006), yet
177 due to the degree of degradation in Mandena, the vertical structure of this littoral forest is
178 relatively low (Eppley et al. 2015a).

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

184

185 *Climatic data*

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

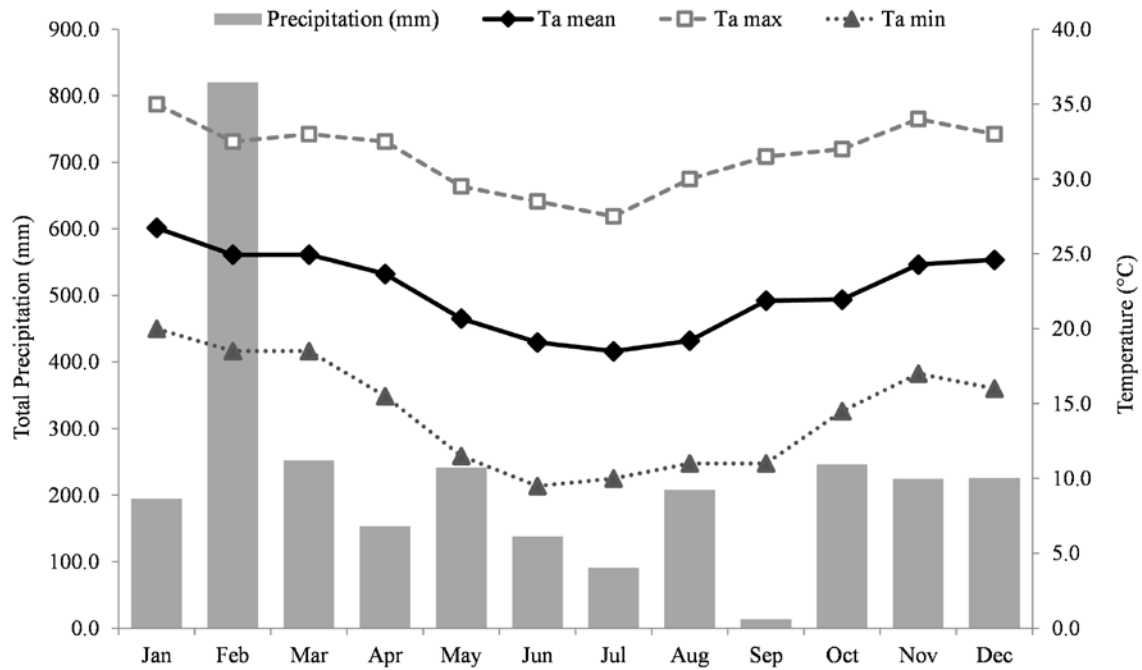


Fig. 1. Monthly total precipitation and mean temperature (including monthly maxima and minima recorded) in Mandena from January to December 2013.

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 (\pm SD) T_{sk} of *H. meridionalis* was $32.8 \pm 2.9^\circ\text{C}$; however, when data-logging tags of individuals registered 0.0% activity, the mean T_{sk} of *H. meridionalis* was $35.8 \pm 1.2^\circ\text{C}$. This fluctuation was due to movement when traveling and foraging, and thus the temperatures recorded while resting with minimal movement are considered accurate.

213 *Behavioural data*

214 From January to December 2013, we conducted behavioural focal follows (from
215 sunrise to sunset) every 5 mins. Data were collected from three social groups, and totalled
216 1,762 h. During the study period, Group 1 consisted of 3-5 individuals (3 adult females, 1
217 adult male), Group 2 consisted of 3-4 individuals (1 adult female, 1 adult male), and Group 4
218 consisted of 8-9 individuals (2 adult females, 2 adult males) (Eppley et al. 2016c).

219 Identification of individuals was made using radio-tracking tags with coloured pendants, with
220 all adult individuals ($N = 10$) from our three focal groups sampled for at least one day each
221 month. As general activity largely influences T_{sk} (Dausmann 2005), our T_{sk} analyses are
222 limited to resting bouts ≥ 15 min.

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

236

237 *Data analyses*

238 To determine which factors influenced the repeated use of resting sites, we fitted
239 Generalized Linear Mixed-effects Models (GLMMs) with preference site as a binomial
240 dependent variable. We define preference sites as those sites that were visited more than once
241 by a focal group. Group was included as a random effect to account for different baseline
242 rates of returning to a rest site. As fixed effects, both as independent terms and in
243 interactions, we included DBH (cm), height (m), crown volume (m³), habitat (littoral forest or
244 swamp), and whether a site was also a feeding site (0/1). We standardized DBH, height, and
245 crown volume, as they were on very different scales of magnitude.

246 To determine which factors influenced lemurs' T_{sk} (a proxy for body temperature), we
247 fitted a Linear Mixed-effects Models (LMMs). As random effects, we included individual
248 identity (nested within groups) to account for different baseline T_{sk} . As fixed effects, both as
249 independent terms and in interactions, we included the focal lemurs' sex (female/male),
250 huddle rate (i.e., proportion of huddling during rest bout), duration of the resting bout (mins),
251 group size, whether the resting site was a preference site (0/1), the crown volume (m³), and
252 cover (the position of the focal, in meters, beneath the tree canopy). In addition, we included
253 climatic variables as fixed effects, specifically temperature (°C), as the mean T_a from the
254 nearest data-logger during the sleeping bout duration, daily total precipitation (mm), and the
255 general season (dry or wet). We standardized huddle rate, duration, and ambient temperature,
256 as they were on very different scales of magnitude.

257 For both the preference site GLMM and the T_{sk} LMM, we used an information-
258 theoretic approach with model averaging to generate a set of candidate models and assess the
259 relative strength of evidence for our hypotheses (Burnham and Anderson 2002). We
260 inspected the Variance Inflation Factors (VIF) of a full model, including all fixed effects, to
261 assess multicollinearity. To obtain unbiased parameter estimates, we did not include collinear
262 terms (VIF > 3) in the same model. Highly related predictors could, however, occur in

263 separate models of the model set. We ranked the models using Akaike's Information
264 Criterion corrected for finite sample sizes (AICc) and defined a subset of top models as those
265 models within two AICc units from the best model ($\Delta_i < 2$). We then computed the model-
266 averaged parameter estimates and the relative importance for each term included in this
267 model set. Importance is the sum of the Akaike weights w_i of all models which include the
268 term in question. As model weights represent the probability of a model to be the best model
269 in the model set and thus reflect model uncertainty, importance can be understood as the
270 likelihood of a term to be included in the best model. We used the lme4 (Bates et al. 2015)
271 and MuMIn (Bartoń 2016) packages in R statistical software version 3.3.2 (R Core Team
272 2016) for these analyses.

273

274 **Results**

275 *Resting sites*

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

283

284

285

286

287

288

289

290

291

292 **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

293 N = total number of sites; Feeding = number of sites used for resting and feeding.

294 *Note that in addition to tree species, unidentified fallen dead trees and the ground
295 (including burrows) were occasionally used by all groups

296

297 *Preferred Resting Sites*

298 From the 430 rest sites, DBH values were missing from 24 sites while two additional

299 sites were found to be outliers for crown volume, thus these were removed from the GLMM.

300 According to our correlation matrix, DBH was positively correlated with height,

301 $r(404) = 0.74$, $P < 0.001$, and crown volume, $r(404) = 0.73$, $P < 0.001$ (Table 2), indicating

302 that trees with larger DBH tended to be taller and tended to have larger crown volumes. Each

303 of these three metrics was a component of at least one model within two AICc of the best-fit

304 model to explain the repeated use of a rest site (Table 3). The two most likely models

305 included only DBH ($\Delta_1 = 0.00$, $w_1 = 0.30$) and only height ($\Delta_2 = 0.39$, $w_2 = 0.25$),

306 respectively, and were supported 2 times and 1.7 times more strongly than the model

307 including only cover (evidence ratios $w_1/w_4 = 0.30/0.15 = 2$, $w_1/w_4 = 0.25/0.15$). Indeed, the

308 estimate for crown volume was imprecise, suggesting that it was not driving resting site

309 selection. Further, whether a resting site also served as a feeding site was 30% likely to be a

310 component of the best model (relative importance of Feed), in addition to either DBH or

311 height. However, the direction of the effect could not be estimated with sufficient confidence,

312 and the more parsimonious models that do not include feeding site were better supported by

313 the data.

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

318

319 **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***	–

320 $N = 404$. * $P < .05$, ** $P < .01$, *** $P < .001$

321

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

Model i	b_0	DBH	HT	CV	Feed	Δ_i	w_i^{323}
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		

324 $N = 404$. Model terms include the intercept (b_0), diameter at breast height (DBH), height
 325 (HT), crown volume (CV), and feeding site (Feed). Columns on the right show the difference
 326 in AICc values between Model i and the model with the lowest AICc, Model 1 (Δ_i) and the
 327 Akaike weight of Model i (w_i). Bottom rows show model-averaged parameter estimates (β),
 328 unconditional standard errors which incorporate model uncertainty (SE), odds ratios, and
 329 relative importance. * $P < .05$, *** $P < .001$.

330

331 *Thermoregulation: huddling vs resting site*

332 Considering all 505 resting bouts, 45.1% involved huddling behaviour. A total of 349
 333 of these resting bouts were observed with radio-collared focal individuals, thus our dataset
 334 was limited to those bouts in which T_{sk} was measured. Similar to the GLMM, incomplete
 335 cases and outliers were excluded from the LMM, leaving 322 resting bouts. Correlation

336 coefficients between our model variables revealed that T_{sk} was higher during the wet season,
 337 for females, at non-feeding rest sites, when T_a was higher, when huddle rates were higher,
 338 and when resting bouts lasted longer (Table 4). Additionally, huddle rates were higher and
 339 resting bouts lasted longer at preference sites, whereas the opposite was seen at dual resting-
 340 feeding sites. Furthermore, the larger the crown volume of the resting site, the deeper below
 341 the canopy the focal individual tended to rest. Our full T_{sk} dataset show that *H. meridionalis*
 342 did not exhibit torpor at any point during the 12-month study, with individuals often wakeful
 343 when resting, occasionally opening their eyes at small disturbances.

344

345 **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***	–

346 $N = 322$. * $P < .05$, ** $P < .01$, *** $P < .001$.

347 Season (dry = 0, wet = 1); Sex (female = 0, male = 1); Duration = length of resting bout

348

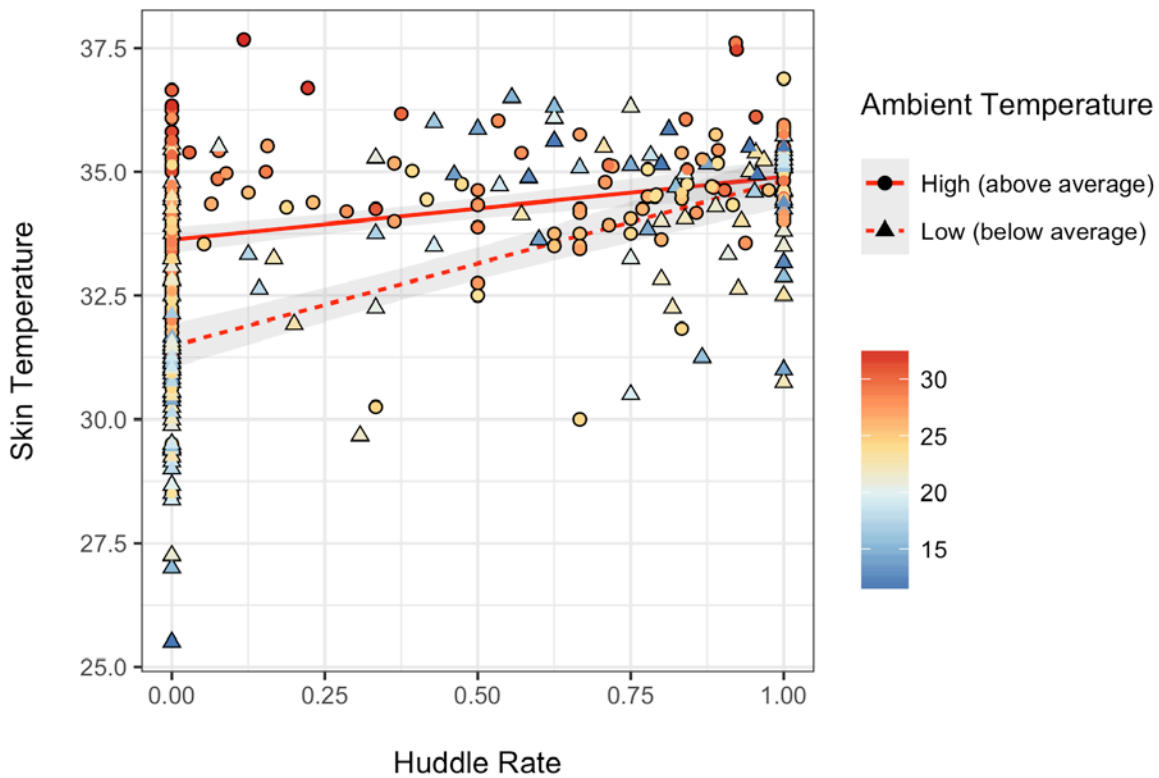
349 **Table 5.** Model-averaged LMM parameters for predicting an increase in *H. meridionalis* T_{sk}

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 \times Dur	-0.26**	0.08	(-0.42, -0.10)	1, 2	1
Hud \times T_a	-0.51**	0.08	(-0.67, -0.36)	1, 2	1
Dur \times T_a	-0.16	0.10	(-0.35, 0.03)	1, 2	1
Hud \times Dur \times T_a	0.24**	0.09	(0.08, 0.41)	1, 2	1

350 $N = 322$. Akaike weights: $w_1 = 0.70$, $w_2 = 0.30$. Difference in AICc values between Model i
 351 and the model with the lowest AICc, Model 1: $\Delta_1 = 0$, $\Delta_2 = 1.68$. Parameters shown are
 352 model-averaged parameter estimates (β), unconditional standard errors which incorporate
 353 model uncertainty (SE), 95% confidence intervals, models that included the term, and relative
 354 importance. * $P < .05$, ** $P < .01$, *** $P < .001$

355

356 The top two models to explain lemurs' T_{sk} both included huddle rate, T_a , and duration,
357 their two-way interactions, and their three-way interaction (Table 5). Model 1 additionally
358 includes group size as a model component and was supported 2.3 times more strongly than
359 Model 2, which does not include group size (evidence ratio $w_1/w_2 = 0.70/0.30$). Specifically,
360 every additional group member was associated with an increase in T_{sk} by 0.13°C . Further, an
361 increase in huddling rate by one standard deviation (0.42) was associated with an increase in
362 T_{sk} by $0.48 - 0.81^\circ\text{C}$. This relationship was stronger when T_a was low (Fig. 2); e.g., for a
363 decrease by one standard deviation in T_a (4.95°C), the slope of huddle rate increased by
364 0.51°C (huddle rate $\times T_a$ interaction). Specifically, in the absence of huddling, lemurs' T_{sk}
365 was lower when T_a was low than when it was high, but that difference vanished at high
366 huddle rates. Finally, the huddle rate $\times T_a \times$ duration three-way interaction indicates that the
367 two-way interaction between huddle rate and T_a changed across different durations. That is,
368 the moderating effect of T_a on the effect of huddle rate on T_{sk} was stronger for short resting
369 bouts than for long ones. Thus, huddling elevated T_{sk} most when T_a was low and resting bouts
370 were short.



371
372

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

377

378 Discussion

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

383

384 *Microhabitat rest site selection*

385 Rest sites in larger trees may confer greater thermoregulatory benefits, such as
386 protection from the direct sun and/or exposure to cold weather. In fact, chimpanzees (*Pan*
387 *troglydytes*) have been observed to become more terrestrial during warm T_a (Takemoto 2004;
388 Kosheleff and Anderson 2009), while chacma baboons (*Papio ursinus*) rest in the shade
389 during midday, taking advantage of thermal microclimates (Hill 2006). Furthermore, both of

390 these species occasionally utilise caves, which provide consistent T_a as well as shelter from
391 extreme weather (Barrett et al. 2004; Pruetz 2007). Moreover, research on Cape ground
392 squirrels (*Xerus inauris*) has shown that using a burrow consistently reduced T_b by 1-2°C
393 (Fick et al. 2009). Similarly, southern bamboo lemurs were occasionally observed to rest on
394 the ground and in terrestrial burrows, an unusual behaviour potentially attributed to increased
395 T_a (Eppley et al. 2016b); however, their overall general selection of larger trees for resting
396 were not shown to confer any thermal benefit. Considering the ecological characteristics of
397 the Mandena littoral forest, large trees are not particularly large compared to less-degraded
398 nearby littoral forests (Campera et al. 2014; Eppley et al. 2015a), so the environmental
399 buffering effect at our site may be potentially limited. Furthermore, microhabitat resting sites
400 selected for thermal characteristics may lack optimal anti-predator protection, or in the case
401 of resources, may lack quick access to food and water (Angilletta et al. 2010).

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

413

414 *Huddling behaviour*

415 Our results suggest that huddling confers an immediate effect as a thermoregulatory
416 mechanism, and assists in maintaining an optimal T_b during longer duration resting bouts.
417 Huddling has been shown to confer higher and more constant T_b than solitary resting, thus, it
418 is an effective strategy to maintain homeothermy and reduce energy expenditure (Gilbert et
419 al. 2010; Nuñez-Villegas et al. 2014; McFarland et al. 2015). This social behaviour, along
420 with decreased inter-individual distances, has been shown to increase in colder weather
421 conditions (i.e., lower T_a), and as such, is a typical behavioural response to thermal stress
422 (Riedman 1990; Yahav and Buffenstein 1991; Gilbert et al. 2008; Donati et al. 2011; Sugita
423 and Ueda 2013). Unlike most endothermic birds and mammals, many lemurid species display
424 an unusual trait by exhibiting even or male-biased adult sex ratios, which may lead to
425 potential benefits (Kappeler 2000, 2009). One proposed benefit for having surplus adult
426 males in a group is for increased energy conservation via social thermoregulation (Morland
427 1993); however, this is not always the case (Ostner 2002). Furthermore, increased social links
428 have been shown to lead to energy conservation advantages in gregarious vervet monkeys
429 (*Chlorocebus pygerythrus*; McFarland et al. 2015). Nevertheless, bamboo lemur groups in
430 Mandena are typically limited to small family units with one adult male and one to two adult
431 females, and in fact, only one of our three studied groups had a surplus adult male (Eppley et
432 al. 2016c). Thus, it is unlikely that this peculiar lemurid trait confers a thermoregulatory
433 benefit among *H. meridionalis*. Southern bamboo lemur group size, however, did
434 significantly predict an increase in T_{sk} . It is possible that with larger groups sizes, individuals
435 may experience greater opportunity for social thermoregulation among group mates.

436 Huddling is not exhibited by all lemurids, however; in fact, both ring-tailed lemurs
437 (*Lemur catta*) and ruffed lemurs (*Varecia* spp.) use sun-basking as a warming strategy (Jolly
438 1966; Morland 1993; Vasey 2002; Kelley et al. 2016). Specifically, they decrease the
439 energetic demands during cold periods by positioning themselves to maximize surface area

440 exposure to sunlight (Terrien et al. 2011). Similar to *L. catta* (Jolly 1966; Kelley et al. 2016),
441 this is a strategy commonly used by many mammalian taxa living in arid or semi-arid habitats
442 (Stelzner and Hausfater 1986; Brown and Downs 2007; Warnecke et al. 2010; Terrien et al.
443 2011; Danzy et al. 2012). On the contrary, *Varecia* spp. are restricted to the humid forests of
444 eastern Madagascar, but sun-bask regardless (Morland 1993; Vasey 2002). This is perplexing
445 given that sun-basking behaviour is absent in brown lemurs (*Eulemur* spp.) despite
446 widespread geographic distribution (Sussman 1974; Pereira et al. 1999; Donati et al. 2011).
447 *H. meridionalis* was never observed to sun-bask at any period during our study. It has been
448 postulated that this behaviour within humid forests would only be possible on the emergent
449 portion of the canopy, thus predation pressure from diurnal raptors would be high (Donati et
450 al. 2011).

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

459

460 **Conclusion**

461 Both microhabitat resting site selection and behavioural positioning (e.g., huddling,
462 sun-basking, etc.) have been shown to play a large role in the thermoregulation of a multitude
463 of endothermic birds and mammals. While rest site selection and the microhabitat may confer
464 thermoregulatory benefits to individuals, our data only supported huddling among the

465 southern bamboo lemurs to help increase T_b on cold days. This is potentially due to the
466 increasing degradation and fragmented state of Mandena, whereby relatively few large trees
467 exist and lemurs must adjust behaviourally to cope within increasingly anthropogenic
468 landscapes. Furthermore, this leads us to question whether huddling in a small group is a
469 cooperative benefit conferred to all group members, or if inclusion is determined via
470 reciprocal exchange of services.

471

472 **References**

473 Albert A, Savini T, Huynen MC. 2011. Sleeping site selection and presleep behavior in wild
474 pigtailed macaques. *American Journal of Primatology* 73:1222-1230.

475

476 Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their
477 significance. *American Journal of Primatology* 46:63-75.

478

479 Anderson JR, McGrew WC. 1984. Guinea baboons (*Papio papio*) at a sleeping
480 site. *American Journal of Primatology* 6:1-14.

481

482 Angilletta MJ, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal
483 physiology in endotherms. *Frontiers in Bioscience* 2:861-881.

484

485 Aujard F, Séguy M, Terrien J, Botalla R, Blanc S, Perret M. 2006. Behavioral
486 thermoregulation in a non human primate: effects of age and photoperiod on temperature
487 selection. *Experimental Gerontology* 41:784-792.

488

489 Barnett AA, Shaw P, Spironello WR, MacLarnon A, Ross C. 2012. Sleeping site selection by
490 golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian
491 flooded forests. *Primates* 53:273-285.

492

493 Barrett L, Gaynor D, Rendall D, Mitchell D, Henzi SP. 2004. Habitual cave use and
494 thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *Journal of Human*
495 *Evolution* 46:215-222.

496

497 Bartoń K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. Retrieved from
498 <http://CRAN.R-project.org/package=MumIn>.

499

500 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using
501 lme4. *Journal of Statistical Software* 67:1-48.

502

503 Blanco MB, Dausmann KH, Ranaivoarisoa JF, Yoder AD. 2013. Underground hibernation in
504 a primate. *Scientific Reports* 3:1768.

505

- 506 Boix-Hinzen C, Lovegrove BG. 1998. Circadian metabolic and thermoregulatory patterns of
507 red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *Journal of*
508 *Zoology* 244:33-41.
- 509
- 510 Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive thermoregulation in
511 endotherms may alter responses to climate change. *Integrative and Comparative Biology*
512 51:676-690.
- 513
- 514 Brown KJ, Downs CT. 2007. Basking behaviour in the rock hyrax (*Procavia capensis*)
515 during winter. *African Zoology* 42:70-79.
- 516
- 517 Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical
518 information-theoretic approach. New York: Springer.
- 519
- 520 Burns DJ, Ben-Hamo M, Bauchinger U, Pinshow B. 2013. Huddling house sparrows remain
521 euthermic at night, and conserve body mass. *Journal of Avian Biology* 44:198-202.
- 522
- 523 Campera M, Serra V, Balestri M, Barresi M, Ravaolahy M, Randriatafika F, Donati G. 2014.
524 Effects of habitat quality and seasonality on ranging patterns of collared brown lemur
525 (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology* 35:957-
526 975.
- 527
- 528 Canals M, Rosenmann M, Bozinovic F. 1989. Energetics and geometry of huddling in small
529 mammals. *Journal of Theoretical Biology* 141:181-189.
- 530
- 531 Canals M, Rosenmann M, Bozinovic F. 1997. Geometrical aspects of the energetic
532 effectiveness of huddling in small mammals. *Acta Theriologica* 42:321-328.
- 533
- 534 Canals M, Rosenmann M, Novoa FF, Bozinovic F. 1998. Modulating factors of the energetic
535 effectiveness of huddling in small mammals. *Acta Theriologica* 43:337-348.
- 536
- 537 Consiglio T, Schatz GE, Mcpherson G, Lowry PP, Rabenantoandro J, Rogers ZS,
538 Rabevohitra R, Rabehevitra D. 2006. Deforestation and plant diversity of Madagascar's
539 littoral forests. *Conservation Biology* 20:1799-1803.
- 540
- 541 Contreras LC. 1984. Bioenergetics of huddling: test of a psycho-physiological
542 hypothesis. *Journal of Mammalogy* 65:256-262.
- 543
- 544 Cowlshaw G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131:293-
545 304.
- 546
- 547 Cui L-W, Quan R-C, Xiao W. 2006. Sleeping sites of black-and-white snub nosed monkeys
548 (*Rhinopithecus bieti*) at Baima Snow Mountain, China. *Journal of Zoology* 270:192-198.
- 549
- 550 Daniels HL. 1984. Oxygen consumption in *Lemur fulvus*: deviation from the ideal
551 model. *Journal of Mammalogy* 65:584-592.
- 552
- 553 Danzy J, Grobler JP, Freimer N, Turner T. 2012. Sunbathing: a behavioral response to
554 seasonal climatic change among South African vervet monkeys (*Chlorocebus aethiops*).
555 *African Primates* 7:230-237.

- 556
557 Dasilva GL. 1993. Postural changes and behavioural thermoregulation in *Colobus polykomos*:
558 the effect of climate and diet. *African Journal of Ecology* 31:226-241
559
- 560 Dausmann KH. 2005. Measuring body temperature in the field—evaluation of external vs.
561 implanted transmitters in a small mammal. *Journal of Thermal Biology* 30:195-202.
562
- 563 Dausmann KH. 2014. Flexible patterns in energy savings: heterothermy in primates. *Journal*
564 *of Zoology* 292:101-111.
565
- 566 Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G. 2004. Physiology: hibernation in a
567 tropical primate. *Nature* 429:825-826.
568
- 569 Dausmann KH, Glos J, Heldmaier G. 2009. Energetics of tropical hibernation. *Journal of*
570 *Comparative Physiology B* 179:345-357.
571
- 572 Day RT, Elwood RW. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus*
573 *midas midas*: The role of predation risk, proximity to feeding sites, and territorial defence.
574 *Ethology* 105:1035-1051.
575
- 576 De Vere RA, Warren Y, Nicholas A, Mackenzie ME, Higham JP. 2011. Nest site ecology of
577 the Cross River gorilla at the Kagwene Gorilla Sanctuary, Cameroon, with special reference
578 to anthropogenic influence. *American Journal of Primatology* 73:253-261.
579
- 580 Dewar RE, Richard AF. 2007. Evolution in the hypervariable environment of Madagascar.
581 *Proceedings of the National Academy of Sciences, USA* 104:13723-13727.
582
- 583 Donati G, Ricci E, Baldi N, Morelli V, Borgognini-Tarli SM. 2011. Behavioral
584 thermoregulation in a gregarious lemur, *Eulemur collaris*: Effects of climatic and
585 dietary-related factors. *American Journal of Physical Anthropology* 144:355-364.
586
- 587 Downs CT, Wimberger K, Wilson AL. 2013. No effects of huddling on core body
588 temperature in rock hyrax, *Procavia capensis*. *African Zoology* 48:173-176.
589
- 590 Dumetz, N. 1999. High plant diversity of lowland rainforest vestiges in eastern
591 Madagascar. *Biodiversity & Conservation* 8:273-315.
592
- 593 Eppley TM, Verjans E, Donati G. 2011. Coping with low-quality diets: a first account of the
594 feeding ecology of the southern gentle lemur, *Hapalemur meridionalis*, in the Mandena
595 littoral forest, southeast Madagascar. *Primates* 52:7-13.
596
- 597 Eppley TM, Donati G, Ramanamanjato J-B, Randriatafika F, Andriamandimbiarisoa LN,
598 Rabehevitra D, Ravelomanantsoa R, Ganzhorn JU (2015a) The use of an invasive species
599 habitat by a small folivorous primate: implications for conservation. *PLoS ONE*
600 10:e0140981.
601
- 602 Eppley TM, Hall K, Donati G, Ganzhorn JU (2015b) An unusual case of affiliative
603 association of a female *Lemur catta* in a *Hapalemur meridionalis* social group. *Behaviour*
604 152:1041-1061.
605

- 606 Eppley TM, Ganzhorn JU, Donati G (2015c) Cathemerality in a small, folivorous primate:
607 proximate control of diel activity in *Hapalemur meridionalis*. Behavioral Ecology and
608 Sociobiology 69:991-1002.
609
- 610 Eppley TM, Donati G, Ganzhorn JU (2016a) Determinants of terrestrial feeding in an
611 arboreal primate: the case of the southern bamboo lemur (*Hapalemur meridionalis*).
612 American Journal of Physical Anthropology 161:328-342.
613
- 614 Eppley TM, Donati G, Ganzhorn JU (2016b) Unusual sleeping site selection by southern
615 bamboo lemurs. Primates 57:167-173.
616
- 617 Eppley TM, Ganzhorn JU, Donati G (2016c) Latrine behaviour as a multimodal
618 communicatory signal station in wild lemurs: the case of *Hapalemur meridionalis*. Animal
619 Behaviour 111:57-67.
620
- 621 Eppley TM, Watzek J, Ganzhorn JU, Donati G (2017) Predator avoidance and dietary fibre
622 predict diurnality in the cathemeral folivore *Hapalemur meridionalis*. Behavioral Ecology
623 and Sociobiology 71:4.
624
- 625 Evans RM. 1984. Some causal and functional correlates of creching in young white pelicans.
626 Canadian Journal of Zoology 62:814-819.
627
- 628 Feilen KL, Marshall AJ. 2014. Sleeping site selection by proboscis monkeys (*Nasalis*
629 *larvatus*) in West Kalimantan, Indonesia. American Journal of Primatology 76:1127-1139.
630
- 631 Fick LG, Kucio TA, Fuller A, Matthee A, Mitchell D (2009) The relative roles of the parasol-
632 like tail and burrow shuttling in thermoregulation of free-ranging Cape ground squirrels,
633 *Xerus inauris*. Comparative Biochemistry and Physiology A-Molecular & Integrative
634 Physiology 152:334-340.
635
- 636 Fortin D, Gauthier G, Larochelle J. 2000. Body temperature and resting behavior of greater
637 snow goose goslings in the high Arctic. Condor 102:163-171.
638
- 639 Gagge AP, Gonzalez RR. 2011. Mechanisms of heat exchange: biophysics and physiology. In
640 R. Terjung (Ed.). *Comprehensive Physiology* (pp. 45-84). New York: John Wiley & Sons,
641 Inc.
642
- 643 Geiser F. 2004. Metabolic rate and body temperature reduction during hibernation and daily
644 torpor. Annual Review of Physiology 66:239-274.
645
- 646 Geiser F, Goodship N, Pavey CR. 2002. Was basking important in the evolution of
647 mammalian endothermy? Naturwissenschaften 89:412-414.
648
- 649 Genoud M. 2002. Comparative studies of basal rate of metabolism in primates. Evolutionary
650 Anthropology 11:108-111.
651
- 652 Gilbert C, Blanc S, Giroud S, Trabalon M, Le Maho Y, Perret M, Ancel A. 2007. Role of
653 huddling on the energetic of growth in a newborn altricial mammal. American Journal of
654 Physiology 293:867-876.
655

- 656 Gilbert C, Robertson G, Le Maho Y, Ancel A. 2008. How do weather conditions affect the
657 huddling behaviour of emperor penguins? *Polar Biology* 31:163-169.
658
- 659 Gilbert C, McCafferty D, Le Maho Y, Martrette JM, Giroud S, Blanc S, Ancel A. 2010. One
660 for all and all for one: the energetic benefits of huddling in endotherms. *Biological Reviews*
661 85:545-569.
662
- 663 Han J, Hu G. 2012. Sleeping behavior of wild Francois' langur (*Trachypithecus francoisi*) at
664 Mayanghe Nature Reserve in summer, Guizhou China. *Acta Theriologica Sinica* 32:362-367.
665
- 666 Hanya G, Kiyono M, Hayaishi S. 2007. Behavioral thermoregulation of wild Japanese
667 macaques: comparisons between two subpopulations. *American Journal of Primatology* 69:
668 802-815.
669
- 670 Hatchwell BJ, Sharp SP, Simeoni M, McGowan A. 2009. Factors influencing overnight loss
671 of body mass in the communal roosts of a social bird. *Functional Ecology* 23:367-372.
672
- 673 Hayes LD. 2000. To nest communally or not to nest communally: a review of rodent
674 communal nesting and nursing. *Animal Behaviour* 59:677-688.
675
- 676 Hayes JP, Speakman JR, Racey PA. 1992. The contributions of local heating and reducing
677 exposed surface area to the energetic benefits of huddling by short-tailed field voles
678 (*Microtus agrestis*). *Physiological Zoology* 65:742-762.
679
- 680 Heldmaier G, Ortman S, Elvert R. 2004. Natural hypometabolism during hibernation and
681 daily torpor in mammals. *Respiratory Physiology & Neurobiology* 141:317-329.
682
- 683 Hill RA. 2006. Thermal constraints on activity scheduling and habitat choice in baboons.
684 *American Journal of Physical Anthropology* 129:242-249.
685
- 686 Hrupka BJ, Leibbrandt VD, Crenshaw TD, Benevenga NJ. 2000. Effect of sensory stimuli on
687 huddling behavior of pigs. *Journal of Animal Science* 78:592-596.
688
- 689 Huey RB, Pianka ER. 1977. Seasonal variation in thermoregulatory behavior and body
690 temperature of diurnal Kalahari lizards. *Ecology* 58:1066-1075.
691
- 692 Jolly A. 1966. Lemur behavior: a Madagascar field study. Chicago and London: The
693 University of Chicago Press.
694
- 695 José-Domínguez JM, Asensio N, García CJG, Huynen MC, Savini T. 2015. Exploring the
696 multiple functions of sleeping sites in northern pigtailed macaques (*Macaca leonine*).
697 *International Journal of Primatology* 36:948-966.
698
- 699 Kappeler PM. 1998. Nests, tree holes, and the evolution of primate life histories. *American*
700 *Journal of Primatology* 46:7-33.
701
- 702 Kauffman AS, Paul MJ, Butler MP, Zucker I. 2003. Huddling, locomotor, and nest-building
703 behaviors of furred and furless Siberian hamsters. *Physiology & Behavior* 79:247-256.
704

- 705 Kearney M, Shine R, Porter WP. 2009. The potential for behavioral thermoregulation to
706 buffer “cold-blooded” animals against climate warming. *Proceedings of the National*
707 *Academy of Sciences, USA* 106:3835-3840.
708
- 709 Kelley EA, Jablonski NG, Chaplin G, Sussman RW, Kamilar JM. 2016. Behavioral
710 thermoregulation in *Lemur catta*: The significance of sunning and huddling behaviors.
711 *American Journal of Primatology* 78:745-754.
712
- 713 Kosheleff VP, Anderson CN. 2009. Temperature's influence on the activity budget,
714 terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American*
715 *Journal of Physical Anthropology* 139:172-181
716
- 717 Kotze J, Bennett NC, Scantlebury M. 2008. The energetics of huddling in two species of
718 mole-rat (Rodentia: Bathyergidae). *Physiology & Behavior* 93:215-221.
719
- 720 Kurland JA, Pearson JD. 1986. Ecological significance of hypometabolism in nonhuman
721 primates: allometry, adaptation, and deviant diets. *American Journal of Physical*
722 *Anthropology* 71:445-457.
723
- 724 Labisky RF, Arnett JE. 2006. Pair roosting of nesting Carolina wrens (*Thryothorus*
725 *ludovicianus*). *The Wilson Journal of Ornithology* 118:566-569.
726
- 727 Lehman SM, Fleagle JG. 2006. Biogeography and primates: a review. In SM Lehman, JG
728 Fleagle (Eds.), *Primate biogeography: progress and prospects* (pp. 1-58). New York:
729 Springer.
730
- 731 Long RA, Martin TJ, Barnes BM. 2005. Body temperature and activity patterns in free-living
732 arctic ground squirrels. *Journal of Mammalogy* 86:314-322.
733
- 734 Lovegrove G, Kortner G, Geiser F (1999) The energetic cost of arousal from torpor in the
735 marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *Journal of*
736 *Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 169:11-18.
737
- 738 Lutermann H, Verburgt L, Rendigs A. 2010. Resting and nesting in a small mammal:
739 sleeping sites as a limiting resource for female grey mouse lemurs. *Animal*
740 *Behaviour* 79:1211-1219.
741
- 742 McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015.
743 Social integration confers thermal benefits in a gregarious primate. *Journal of Animal*
744 *Ecology* 84:871-878.
745
- 746 McKechnie AE, Lovegrove BG. 2001. Thermoregulation and the energetic significance of
747 clustering behavior in the whitebacked mousebird (*Colius colius*). *Physiological and*
748 *Biochemical Zoology* 74:238-249.
749
- 750 McNab BK. 1986. The influence of food habits on the energetic of eutherian mammals.
751 *Ecological Monographs* 56:1-19.
752
- 753 McNab BK. 1988. Energy conservation in a tree-kangaroo (*Dendrolagus matschiei*) and the
754 red panda (*Ailurus fulgens*). *Physiological Zoology* 61:280-292.

755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804

Morland HS. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs. In: PM Kappeler, JU Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp 193-203). New York: Plenum Press.

Mzilikazi N, Lovegrove BG. 2004. Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiological and Biochemical Zoology* 77:285-296.

Nuñez-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 ME, Strohecker RA, Cavigelli SA, Hughes CL, Pearson DD. 1999. Metabolic strategy and social behavior in Lemuridae. In: B Rakotosamimanana, H Rasamimanana, JU Ganzhorn, SM Goodman (Eds), *New directions in lemur studies* (pp.93-118). New York: Plenum Press.

Pruetz JD. 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. *Primates* 48:316-319.

Putala 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.

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.

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>.

Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *American Journal of Primatology* 46:35-62.

Rhind SG. 2003. Communal nesting in the usually solitary marsupial, *Phascogale tapoatafa*. *Journal of Zoology* 621:345-351.

Riedman M. 1990. *The Pinnipeds. Seals, Sea Lions, and Walruses*. Berkeley: University of California Press.

Samson DR, Hunt KD. 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.

- 805 Scantlebury M, Bennett NC, Speakman JR, Pillay N, Schradin C. 2006. Huddling in groups
806 lead to daily energy savings in free-living African four-striped grass mice, *Rhabdomys*
807 *pumilio*. *Functional Ecology* 20:166-173.
808
- 809 Schino G, Troisi A. 1990. Behavioral thermoregulation in long-tailed macaques: effect on
810 social preference. *Physiology & Behavior* 47:1125-1128.
811
- 812 Schmid J. 1998. Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in
813 Madagascar: insulation capacities and energetic consequences. *International Journal of*
814 *Primateology* 19:797-809.
815
- 816 Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, et al. 2014. Averting lemur
817 extinctions amid Madagascar's political crisis. *Science* 343:842-843.
818
- 819 Séguy M, Perret M. 2005. Factors affecting the daily rhythm of body temperature of captive
820 mouse lemurs (*Microcebus murinus*). *Journal of Comparative Physiology B* 175:107-115.
821
- 822 Simmen B, Bayart F, Rasamimanana H, Zahariev A, Blanc S, Pasquet P. 2010. Total energy
823 expenditure and body composition in two free-living sympatric lemurs. *PLoS ONE* 5:e9860.
824
- 825 Stelzner JK, Hausfater G. 1986. Posture, microclimate, and thermoregulation in yellow
826 baboons. *Primates* 27:449-463.
827
- 828 Sugita N, Ueda K. 2013. The role of temperature on clustering behavior and mating
829 opportunity in Bonin flying foxes. *Mammalian Biology* 78:455-460.
830
- 831 Sussman RW. 1974. Ecological distinctions in sympatric species of Lemur. In: RD Martin,
832 GA Doyle, AC Walker (Eds). *Prosimian biology* (pp. 75-108). London: Duckworth.
833
- 834 Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to
835 microclimate in the tropical forest. *American Journal of Physical Anthropology* 124:81-92.
836
- 837 Terrien J, Perret M, Aujard F. 2011. Behavioral thermoregulation in mammals: A
838 review. *Frontiers in Bioscience* 16:1428-1444.
839
- 840 Vasey N. 2002. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: II.
841 Intraspecific patterns. *American Journal of Physical Anthropology* 118:169-183.
842
- 843 Warnecke L, Schleucher E, Geiser F. 2010. Basking behaviour in relation to energy use and
844 food availability in one of the smallest marsupials. *Physiology & Behavior* 101:389-393.
845
- 846 Westman W, Geiser F. 2004. The effect of metabolic fuel availability on thermoregulation
847 and torpor in a marsupial hibernator. *Journal of Comparative Physiology B* 174:49-57.
848
- 849 Willis CK, Brigham RM. 2007. Social thermoregulation exerts more influence than
850 microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology and*
851 *Sociobiology* 62:97-108.
852
- 853 Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment.
854 *Yearbook of Physical Anthropology* 42:31-72.

855

856 Yahav S, Buffenstein R. 1991. Huddling behavior facilitates homeothermy in the naked mole
857 rat *Heterocephalus glaber*. *Physiological Zoology* 64:871-884.

858

859 Zhang P, Watanabe K, Eishi T. 2007. Habitual hot-spring bathing by a group of Japanese
860 macaques (*Macaca fuscata*) in their natural habitat. *American Journal of Primatology*

861 69:1425-1430.