RESEARCH ARTICLE

Behavioral Thermoregulation in *Lemur catta*: The Significance of Sunning and Huddling Behaviors

ELIZABETH A. KELLEY[1]*, NINA G. JABLONSKI[2,3], GEORGE CHAPLIN[2,3], ROBERT W. SUSSMAN[4], AND JASON M. KAMILAR[5,6]
[1]*Department of Sociology and Anthropology, Saint Louis University, Saint Louis, Missouri*
[2]*Department of Anthropology, The Pennsylvania State University, University Park, Pennsylvania*
[3]*Stellenbosch Institute for Advanced Study [STIAS], Stellenbosch, South Africa*
[4]*Department of Anthropology, Washington University in St. Louis, Saint Louis, Missouri*
[5]*Department of Anthropology, University of Massachusetts, Amherst, Massachusetts*
[6]*Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, Massachusetts*

Regulation of body temperature poses significant problems for organisms that inhabit environments with extreme and seasonally fluctuating ambient temperatures. To help alleviate the energetic costs of autonomic responses, these organisms often thermoregulate through behavioral mechanisms. Among primates, lemurs in Madagascar experience uncharacteristically seasonal and unpredictable climates relative to other primate-rich regions. Malagasy primates are physiologically flexible, but different species use different mechanisms to influence their body temperatures. *Lemur catta*, the ring-tailed lemur, experiences particularly acute diurnal temperature fluctuations in its mostly open-canopy habitat in south and southwest Madagascar. Ring-tailed lemurs are also atypical among lemurs in that they appear to use both sun basking postures and huddling to maintain body temperature when ambient temperatures are cold. To our knowledge, however, no one has systematically tested whether these behaviors function in thermoregulation. We present evidence that ring-tailed lemurs use these postures as behavioral thermoregulation strategies, and that different environmental variables are associated with the use of each posture. Major predictors of sunning included ambient temperature, time of day, and season. Specifically, *L. catta* consistently assumed sunning postures early after daybreak when ambient temperatures were <13°C, and ceased sunning around 10:00a.m., after ambient temperatures approached 26°C. Sunning occurred more often during austral winter months. Huddling was associated with time of day, but not with ambient temperature or season. We conclude that *L. catta* tend to sun, rather than huddle, under cold weather conditions when sunning is possible. However, both sunning and huddling are important behavioral adaptations of *L. catta* that augment chemical thermoregulation and the absence of a dynamic, insulating pelage. Sunning and huddling help to account for the great ecological flexibility of the species, but these adaptations may be insufficient in the face of future changes in protective vegetation and temperature. Am. J. Primatol.   © 2016 Wiley Periodicals, Inc.

INTRODUCTION

Many organisms have evolved behavioral responses to help alleviate the costs of autonomic processes (in terms of energy and water loss) that are needed to maintain optimal body temperature [Boyles et al., 2011; Geiser et al., 2002; Gilbert et al., 2010; Huey & Pianka, 1977; Kearney et al., 2009; Snodgrass et al., 2007; Terrien et al., 2011]. Examples of behavioral thermoregulation strategies include long distance migration, and transferring within the same ecosystem between warmer or cooler localities (e.g. shade-seeking and sun-seeking) [Hill, 2006; Huey & Pianka, 1977; Kearney et al., 2009; Terrien et al., 2011]. Many extant mammals also use

behavioral thermoregulation to save metabolic energy or when generation of metabolic heat is physiologically costly, such as at times of poor resource supply [Geiser et al., 2002; Terrien et al., 2011]. Among primates, there are many examples of species shifting their activity budgets seasonally through adjustments in travel time and length, feeding bout durations, grooming, and resting bouts [Donati et al., 2011; Grueter et al., 2013; Hanya, 2004; Hill, 2006; McFarland et al., 2014; Mendiratta et al., 2009; Moreland, 1993; Nash, 1998; Nowack et al., 2013; Sato, 2012]. Many mammals, including primates, also increase or conserve heat through postural changes, which include hunched and curled positions, huddling, and sun basking [Danzy et al., 2012; Dasilva, 1993; Donati et al., 2011; Hanya et al., 2007; Moreland, 1993; Stelzner & Hausfater, 1986; Terrien et al., 2011].

Lemur catta is a strepsirrhine primate that inhabits the most arid portions of Madagascar's Spiny Thicket Ecoregion in south and southwest Madagascar. Madagascar in general has more seasonal and unpredictable climates relative to other primate-rich regions in the tropics [Wright, 1999]. Southern Madagascar in particular experiences cyclones, frost conditions, exceptionally high intra-annual and inter-annual variability in rainfall and temperature, extreme austral summer solar intensity, and high wind speed [Dewar & Richard, 2007; Kamilar & Muldoon, 2010; Wright, 1999]. Minimum temperatures at known *L. catta* localities can drop as low as 3.7°C, and annual temperatures can range as much as 25.2°C [Kamilar & Muldoon, 2010].

Ring-tailed lemurs are atypical among strepsirrhines in that they appear to use both sun basking postures and huddling to maintain body temperature when ambient temperatures are cold. The only primate within the lemur clade that shares with *L. catta* similar sun basking and huddling behaviors, ostensibly for thermoregulatory purposes, is *Propithecus verreauxi* [Richard, 1978]. *P. verreauxi* is also the only diurnal lemur that often inhabits the same environment as *L. catta*.

Sunning maximizes solar radiation reaching the sparsely haired and darkly pigmented ventral surface of the animal's trunk and limbs, thus, maximizing surface area exposure to the sun [Chaplin et al., 2014]. Sun basking is an important means to gain heat from sunlight and is used as a warming strategy among multiple mammalian groups, many of which also inhabit arid and semi-arid habitats (e.g. marsupials, rock hyraxes, meerkats) [Terrien et al., 2011], including primates outside the lemur clade, such as vervet monkeys [Danzy et al., 2012].

The sun basking behaviors of *L. catta* and *P. verreauxi* are notable in that the lemurs face the sun with arms and legs extended, faces turned sideways, and with ventrums exposed prominently to the sun [Jolly, 1966]. Group members will often sun synchronously, and it is common for individuals to maintain the posture without moving for over an hour [Jolly, 1966; Kelley, 2011]. The only other lemur that has a similar sunning posture is *Varecia*. However, the basking behaviors of this species appear to be different, as sun basking with *Varecia* occurs opportunistically rather than as a regular part of the daily activity budget [Vasey, 2002, 2004; Vasey, pers comm].

A second commonly observed behavior of *L. catta* is huddling. Huddling occurs when individuals rest in hunched and curled positions in contact with one or more of their groupmates [Gilbert et al., 2010]. Among *L. catta*, huddling sometimes occurs for clear social benefits, such as to obtain access to infants during the birth season, and to facilitate male–male affiliation [Gabriel et al., 2014; Kelley, 2011]. However, *L. catta* may also huddle to reduce individual heat loss when ambient temperatures are low [Gilbert et al., 2010; Pereira et al., 1999].

Many mammals maintain warmth and limit heat loss by adopting hunched and curled positions. These positions minimize heat dissipation by reducing the animals' total body surface contact to air, and by conserving lost body heat in the concealed ventral area [Gilbert et al., 2010; Terrien et al., 2011]. Among primates, baboons predictably use hunched positions to adjust to cooler ambient temperatures, especially during the early morning hours when ambient temperatures have fallen as low as 6°C [Kummer, 1997; Stelzner & Hausfater, 1986]. Within Lemuridae (*Eulemur* sp.), redfronted lemurs regularly form huddling groups once temperatures fall below 15°C [Ostner, 2002], and collared lemurs both curl and huddle more often during the colder seasons [Donati et al., 2011].

Morphologically, ring-tailed lemurs have an average body mass of 2 kg [Kelley, 2011], have high surface to volume ratios, and share with all examined strepsirrhines an absence of *musculi arrectores pilorum* (MAP) and functional piloerection on the trunk and limbs [Chaplin et al., 2014; Montagna, 1962]. Physiologically, *L. catta* have poorly developed sweat glands similar to the conditions of *Eulemur* sp. [Montagna, 1962], but are different from *Eulemur* in that they have comparably lower water flux rates and field metabolic rates (FMR) [Simmen et al., 2010]. Unlike *Eulemur*, *L. catta* can relatively successfully inhabit semi-arid environments that lack sources of fresh water [Ellwanger & Gould, 2011; Goodman et al., 2006; Kelley, 2011; Simmen et al., 2010]. While the thermoneutral zone of *L. catta* has never been calculated [Curtis, 2006], the thermoneutral zone for *Eulemur* is estimated to range from 22°C to 30°C [Daniels, 1984]. "Neutral temperatures" for semi free-ranging *L. catta* in North America are between 23°C and 28°C [Murray, 2014; Digby, pers comm].

Here, we test the idea that *L. catta* has two thermoregulatory postures—sunning and huddling—to mitigate the dangers of hypothermia under cold weather conditions. We propose two primary hypotheses. (H1) *L. catta* has evolved a specialized and finely tuned behavioral response, namely sunning, to maximize the benefits of sun exposure in open habitats. (H2) *L. catta* uses huddling as a second thermoregulatory response to maximize heat retention, especially when sunning is not possible. We predicted that sunning and huddling would be more common in the early morning hours, when ambient temperatures are low. We also tested to see whether wind speed, season, and age predicted one or both behaviors.

METHODS

Study Site

Cap Sainte–Marie (CSM) is located in the Androy region of Madagascar at the southernmost end of the island, 25°35.459′ S, 45°8.534′ E. Although the region is bounded by major river systems, the focal groups of this study ranged >33 km away from any of these water sources. Daylight hours vary from 10.4 hr in June to 13.6 hr in December [Lee, 2010]. Rainfall and ambient temperature ranges at CSM are similar to those of semi-arid desert biomes [Noy-Meir, 1973; Rauh, 1995]. Daytime maxima can reach 46.7°C, with daytime highs during the austral winter closer to 24°C, and wind speeds of 20–25 km/hr [Kelley, 2011; Vincelette et al., 2008]. Nighttime lows rarely fall under 13°C. During this 12-month study, the area experienced 686 mm of rain [Kelley, 2011, 2013] (Fig. 1). However, it rained a total of only 57 days, and 150 mm of the year's total rainfall occurred on a single day [Kelley, 2013]. Most of the rain occurred during the month of February and

coincided with cyclones [Kelley, 2011, 2013] (Fig. 1). Kelley [2011, 2013] provides detailed descriptions of the region, including its vegetation.

Study Population

Very few endemic mammals inhabit the CSM area, and the estimated density of *L. catta*, 0.017 individuals/ha, is very low relative to all other study sites for the species [Kelley, 2011]. The habitat at CSM is a mosaic of scrub vegetation known as Didiereaceae–*Euphorbia* bush forest [Rauh, 1995], introduced *Opuntia* sp., and small plot agricultural fields. These fields are tended by villagers in the area of the Antandroy ethnic group [Kelley, 2011, 2013]. Zebu herds and goats also roam the area, as zebu herding is the main economic activity in the area.

We observed two of the five groups that lived within a 10 km radius of the CSM area. The first group (B) ranged in size from 11 to 15 individuals and resided on the coastal land of Bevaro Moravato village at 25°29.665′ S, 45°7.687′ E. The second group (T) declined from nine to six individuals during the study, mainly through multiple deaths [Kelley, 2011]. Its range spanned two smaller villages, Tsankalamanga and Andafambola. The ranging area of this group was closer inland at 25°26.799′ S, 45°8.272′ E [Kelley, 2011]. At their closest point, the two groups' ranges were separated by a distance of 5.5 km [Kelley, 2013].

All adults and weaned young were included in the study. In May 2007, a veterinary team collared 14 adult individuals with either radio collars or nylon "safe cat" identification collars while collecting health data for a related project [Kelley, 2011, 2013]. From May to June 2007, EK conducted a pilot study to practice data collection techniques and to learn to identify the remaining adults and weaned young through distinguishing characteristics.
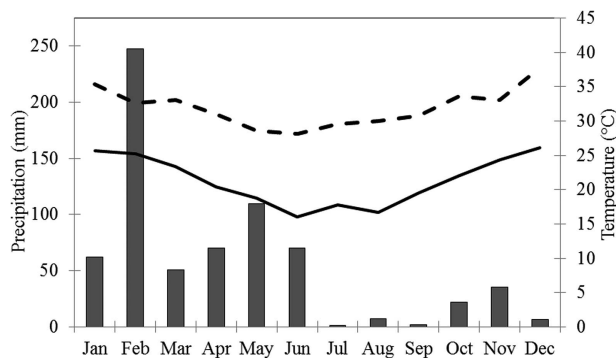

Fig. 1. Total monthly precipitation and daily minimum and maximum ambient temperatures averaged by month from August 2007 to July 2008. Bars equal total monthly precipitation in millimeters. Rainfall data are from a rain gauge at CSM Reserve. Dotted line equals maximum ambient temperature averages and solid line equals minimum ambient temperature averages in °C. Ambient temperature readings came from the Bevaro Moravato group ranging area, with data collected every hour with an average of 8.48 hr per day, 1.94 days per week. $N = 679$.

Field Methods

Data collected for this study are from a broader study on the groups' ecology, ranging, health, and nutrition [Kelley, 2011, 2013]. EK collected the behavioral and climate data described below from August 2007 to July 2008.

EK collected behavioral data for approximately 7–9 hr a day, 1–2 days a week per group, using focal animal sampling [Martin & Bateson, 1993]. EK changed the focal animal every hour, and collected data on all group animals through randomly ordered predetermined rotations. EK used 1 min instantaneous recording to document the following activity categories: sunning (the specialized basking posture we described in the introduction), resting (inactivity with eyes open, daytime sleep, self-groom), huddling (differentiated from solitary "hunched" resting by physical contact between individuals), travel, and

active social activity (grooming including two or more partners, play) [Altmann, 1974; Gould, 1994; Hall, 1965; Martin & Bateson, 1993]. EK was not always able to reach the sleeping site of group T before the start of morning activity. This group was far from camp (~13 km), and ceased to be detectable through radio collar technology early in the study [Kelley, 2011].

EK measured ambient temperature (°C) and wind speed (km/hr) 3–5 m away from the focal subjects and typically at the animals' height. EK did not collect humidity and solar radiation data, which we acknowledge may also influence the temperature experienced by the animals [Hill, 2006]. Ambient temperatures never fell low enough to create wind chill [Bluestein & Zecher, 1999]. EK collected microclimate data (i.e. ambient temperature and wind speed) approximately every hour, at the change of the focal individual, with a hand-held Kestrel 2000 Wind Meter. There are no wind data for the months of May to July because of equipment failure. EK recorded rainfall data using a rain gauge that the Madagascar forestry (ANGAP) officials managed at the CSM Special Reserve campsite. EK collected rain gauge data several times a week and immediately after rainfall.

EK conducted this research through IACUC approval from the Saint Louis Zoo and Washington University in St. Louis (#20100116, #20060089), and through approval from the University of Antananarivo, Madagascar. The research also adhered to the ASP Principles for the Ethical Treatment of Non-Human Primates.

Analytical Methods

In total, we used 47,245 instantaneous samples over 82 days and from 25 individuals in our data analyses. This was equivalent to 2,064 hr of observation across all individuals and days. We only included samples that contained data for all variables.

We analyzed the data using generalized linear mixed models (GLMM) with a binomial distribution and a logit link function [Bolker et al., 2009] using the glmer function in the lme4 [Bates et al., 2014] and lmerTest [Kuznetsova et al., 2013] packages for R [R Development Core Team, 2014]. We used each observation hour per individual per day as a data point in the models. Each GLMM included two random effects, Animal ID and Day, because we measured each individual multiple times throughout the study period, and collected multiple focal samples each day. We included seven fixed effects, ambient temperature, wind speed, time of day, sex, age, month of the year, and group. We used group as a "control" variable to account for possible differences between the groups that we did not quantify but that could affect the results. We included months of the year in the models to account for the effects of

seasonality. We quantified months of the year on a circular scale [Bachelet, 1981], to account for the fact that consecutive months are more similar to each other then would be the case if each month was assigned a linear numeric value. For example, month 1, January is more similar to month 12, December, than it is to month 4, April. To generate monthly values on a circular scale, we multiplied each month of the year by 30 to represent the degrees of a circle. For example, we assigned month 1, January, a value of 30, and month 6, June, a value of 180. We then calculated the cosine of that value for each month. The warmest months of the year were December and January, and the coolest months were June and July. We chose December and June as the zero degree and 180 degree markers (choosing January and July yielded nearly identical results). Therefore, calculating the cosine of these degrees yielded a value of 1 for December and −1 for June. The months between these two extremes were associated with intermediate values, for example, March and September were both associated with a value of zero, indicating similar climatic conditions. We should note that one possible drawback of this method is that cosine transformed values are not always equidistant between months, for example, September is associated with zero, October with 0.5, and November with 0.867. Therefore, we examined the sensitivity of our models to this quantification of seasonality by running another set of models using categories to quantify seasonality. We constructed four categories each comprising 3 months of the year (Dec–Feb, Mar–May, Jun–Aug, Sep–Nov). Using categories to represent seasonality yielded nearly identical results, so we present only the models using the circular statistics. Because we included month in the model, our time of day variable should account for time since sunrise, as well as seasonal shifts in sunrise.

Our first model used the number of minutes sunning per hourly focal follow as a binary dependent variable (weighted by the total number of observation minutes during the hour). One of these models was a null model, using Group, our control variable, as a fixed effect and the two random effects (another null model only using random effects produced nearly identical results). We tested the performance of our full model by comparing it to the null model (with only the control variable and random effects) using a likelihood ratio test [anova function in R; R Development Core Team, 2014].

We examined a second model in which the number of minutes huddling per hour was the binary dependent variable (weighted by the total number of minutes observed during the hour). Similar to the sunning models, we used a likelihood ratio test to compare this model to a null model. In addition, four of our fixed effects—ambient temperature, wind speed, time of day, and month—were log base10

transformed. This was necessary because running the full model with the raw data resulted in an error related to the scaling of the fixed effects. Using transformed data remedied this problem.

For both models, we treated fixed effects as statistically significant predictors of sunning or huddling if they exhibited a two-tailed *P*-value <0.05.

We also examined the relationship among the fixed effects by constructing a correlation matrix associated with each full model. This matrix included all of the fixed effects in each model. If the correlation matrix yielded pairs of variables that were highly correlated $(r > 0.75)$, then we re-ran the model without one of these variables.

Finally, we calculated variance inflation factors (VIF) to quantify the degree of colinearity among the predictors in our mixed models. We used the R code posted on the weblog of the Human Language Processing Lab [2011] at the University of Rochester (Available online at: https://hlplab.wordpress.com/2011/02/24/diagnosing-collinearity-in-lme4/) as we did not find any other published methods for calculating VIFs from lme4 objects (i.e. mixed models).

RESULTS

Predicting Sunning Behavior

Based on our GLMM, we found that temperature, time of day, wind speed, and month were the best predictors of sunning behavior in ring-tailed lemurs (Table I). All four variables related negatively to sunning, that is, sunning behaviors were less common when ambient temperature was high, times were later in the day, wind speed was low, and during the austral summer months. Specifically, all animals in a group on a given day would stop sunning as ambient temperatures approached 26°C (Fig. 2), and sunning behavior often ceased by 10:00a.m. (Fig. 3).
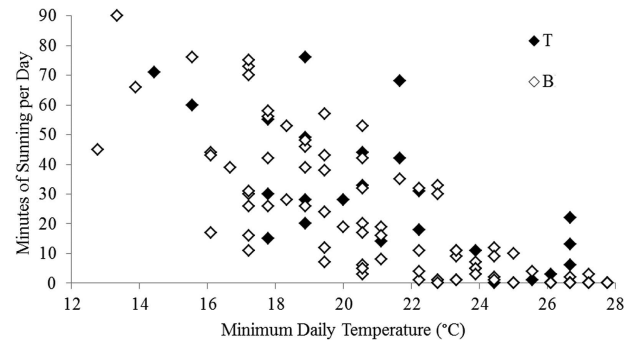

Fig. 2. Scatterplot of minimum daily ambient temperature in °C, in comparison to minutes per day that the focal groups spent in sunning activity. Each point represents all animals in a group on a given day. For the B group, minimum daily temperature data typically reflect the ambient temperature at the site before sunrise. $N = 79$. For the T group, minimum daily temperature data typically reflect the ambient temperature at the site between 7:30 and 8:30 in the morning. $N = 56$.

The full model predicted sunning behavior significantly better than the null model (Likelihood ratio test: $\chi^2 = 3907$, $P < 0.0001$, df = 6). As is depicted in Table II, none of the variables reached our correlation threshold of 0.75. The variables that were most closely associated were temperature and time of day $(r = -0.729)$. We found that colinearity was not problematic in our sunning models, with all variables associated with VIF values below 2.8.

Predicting Huddling Behavior

The GLMM predicting huddling behavior included three significant predictors: wind speed, time of day, and age category (Table III). Low wind speeds and early morning hours were associated with more huddling. In addition, juveniles huddled more often than adults did; this included both juvenile–adult huddling and juvenile–juvenile huddling. The full model predicted huddling significantly better than the null model ($\chi^2 = 532.3$, $P < 0.0001$, df = 6). Similar

TABLE I. Generalized Linear Mixed Model (GLMM) Including All Fixed Effects and Sunning Behavior as the Dependent Variable

Fixed effects[a]	Coeff.	Std. error	CI$_{95}$	*z*-value	*P*
(Intercept)	43.268	1.793	39.75, 46.78	24.135	<0.0001
Temperature (°C)	−21.586	1.085	−23.71, −19.46	−19.901	<0.0001
Wind speed (km/hr)	−0.783	0.236	−1.25, −0.32	−3.315	0.001
Time of day	−5.468	0.343	−6.14, −4.80	−15.955	<0.0001
Group[b]	1.401	1.233	−1.02, 3.82	1.136	0.256
Sex[c]	−0.236	0.220	−0.67, 0.19	−1.075	0.282
Age category[d]	−0.300	0.229	−0.75, 0.15	−1.308	0.191
Month/season[e]	−1.973	0.875	−3.69, −0.26	−2.254	0.024

$N = 2,064$ observation hours.
[a]Two random effects were included in the model: Individual ID and Day.
[b]Group T was the reference category for Group.
[c]Male was the reference category for Sex.
[d]Juvenile was the reference category for Age category.
[e]Austral summer months (e.g. Dec–Jan) were coded with positive values and austral winter months (e.g. Jun–Aug) were coded with negative values.
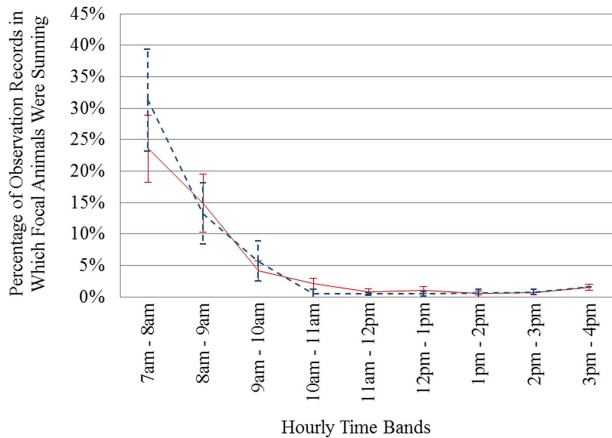
Fig. 3. Percentage of observation records in which focal animals were sunning by hour band throughout the year. Solid red line equals B group, dotted blue line equals T group. N of activity records for each hourly band = 2,137–3,581 for B group, 764–2,771 for T group. Error bars represent standard errors.

to the sunning model, none of the fixed effects in the huddling model was highly correlated with each other (Table IV). We found that colinearity among our predictor variables was low, with all VIFs being less than 1.8.

DISCUSSION

The results support our first hypothesis that *L. catta* sun as a primary behavioral strategy to regulate homeostasis under cold weather conditions. Specifically, sunning in *L. catta* is independently associated with ambient temperature, time of day, and season. With both groups, sunning behavior ceased once temperatures approached 26°C (Fig. 2). Most sunning occurred in the morning soon after sunrise (before 7:00a.m.), and ended around 10:00a.m. (Fig. 3). Season was also independently associated with sunning, with more sunning occurring during the austral winter months. In these months, the lemurs' diets were largely monotonous (i.e. consisted largely of *Opuntia* fruit) [Kelley, 2011, 2013], and there were large fluctuations in daily ambient temperature readings. For example,

average daily ambient temperatures fluctuated by 13.3°C in August versus 6.0°C in April for group B; while average daily ambient temperatures fluctuated by 14.6°C in July versus 7.4°C in February for group T. The association between increased sunning and factors associated with seasonality (i.e. decreased food availability and low ambient temperatures) occurs widely among mammals, from marsupials to haplorhine and strepsirrhine primates, in environments that range from subalpine to tropical forests [Hanya et al., 2007; Moreland, 1993; Terrien et al., 2011]. Notably, body temperature readings in other primate species indicate that body temperature changes coincide with patterns observed in ambient temperature readings. For example, while daily body temperatures tend to be lowest during the morning in baboons [Brain & Mitchell, 1999], daily average body temperatures vary significantly more in the winter months than in the summer months in vervet monkeys [Lubbe et al., 2014].

As with sunning, time of day was a significant predictor of huddling, with more huddling occurring prior to nighttime sleep and before sunrise. Huddling behavior among *L. catta* at CSM was common, with huddling composing 16.5% and 17.0% of group B's and group T's total yearly activity budgets respectively [Kelley, 2011]. While the average huddle consisted of three animals for both groups, there were times when all members of the group huddled together [Kelley, unpublished data]. Yet in contrast to sunning, ambient temperature and season had little predictive power on the huddling behavior of *L. catta* at CSM. This finding differs from research on the closely related *Eulemur*, where huddling is an important thermoregulatory behavior in response to these variables [Donati et al., 2011; Ostner, 2002]. Our results appear to suggest that huddling behavior among *L. catta* is not used to mitigate heat loss from exposure to daytime low ambient temperatures nor to mitigate the physiological costs associated with seasonal stress. However, *L. catta* at CSM are extremely social relative to other studied *L. catta* groups, and the huddling they use in social bonding may obscure the way that huddling relates to environmental variables that predict the need to

TABLE II. Fixed Effects Correlation Matrix Associated With GLMM in Table I

Variable	Time of day	Temperature	Wind speed	Group	Sex	Age category
Time of day	1					
Temperature	−0.729	1				
Wind speed	−0.190	0.02	1			
Group	0.036	−0.037	−0.068	1		
Sex	0.036	−0.037	−0.008	0.016	1	
Age category	0.009	−0.018	−0.011	−0.018	0.085	1
Month/season	0.248	−0.231	−0.34	0.056	0.014	0.006

N = 2,064 observation hours.

TABLE III. Generalized Linear Mixed Model (GLMM) Including All Fixed Effects and Huddling Behavior as the Dependent Variable

Fixed Effects[a]	Coeff.	Std. error	CI$_{95}$	z-value	P
(Intercept)	−0.984	0.985	−2.92, 0.95	−0.999	0.318
Temperature	−0.362	0.552	−1.44, 0.72	−0.656	0.512
Wind speed	−0.768	0.104	−0.97, −0.57	−7.419	<0.001
Time of day	−0.394	0.146	−0.68, −0.11	−2.694	0.007
Group[b]	0.452	1.380	−2.25, 3.16	0.328	0.743
Sex[c]	−0.129	0.174	−0.47, 0.21	−0.747	0.455
Age category[d]	0.490	0.180	0.14, 0.84	2.717	0.007
Month/season[e]	0.389	0.783	−1.14, 1.92	0.497	0.619

$N = 2,064$ observation hours.
[a]Two random effects were included in the model: Individual ID and Day.
[b]Group T was the reference category for Group.
[c]Male was the reference category for Sex.
[d]Juvenile was the reference category for Age category.
[e]Austral summer months (e.g. Dec–Jan) were coded with positive values and austral winter months (e.g. Jun–Aug) were coded with negative values.

thermoregulate. At CSM for example, rates of male–male and male–female affiliative behavior are much higher across all reproductive seasons when compared with other studied *L. catta* groups [Gabriel et al., 2014]. In addition, individuals who are highly affiliative with one another include combinations of all age/sex classes [Kelley, 2011, 2012]. CSM groups also differ from comparative groups in that dispersal opportunities are limited, and many of the males (and females) appeared to be relatively young, natal residents [Kelley, 2011]. Juveniles, which have some of the strongest affiliative bonds in these groups with various partners (other juveniles, adults of both sexes), express affiliation through both grooming and huddling behavior [Kelley, 2011, 2012]. Huddling behavior among juveniles may also explain why age was a predictor of huddling but not sunning in this study.

In addition to time of day, wind speed was the only other variable that predicted both sunning and huddling, and both behaviors increased as wind speed decreased. Since wind speed lowers the feel of ambient temperature [Hill, 2006], these results may at first seem counterintuitive. However, sunning is less effective when wind speed is high because it

exposes an animal's thinly furred ventrum to wind penetration [Stelzner & Hausfater, 1986]. Huddling, however, can mitigate heat loss through wind exposure, and in fact, yellow baboons react to high wind speed by hunching their bodies and turning their backs to the wind [Stelzner & Hausfater, 1986]. It is unclear why *L. catta* at CSM did not consistently adopt a similar pattern of behavior. One possibility is that these lemurs had access to *Opuntia* hedges, which have large interiors that create microenvironments with little to no wind [Kelley, unpublished data]. Access to these hedges may at least partly explain the seemingly counterintuitive association between low wind speed and huddling with *L. catta* at this site.

Although sunning is necessarily a daytime activity, the first mammals to rely on the thermal benefits of sunning were likely nocturnal [Geiser et al., 2002]. Sunning can double the rewarming rate of small heterothermic mammals, especially among small mammals emerging from torpor [Geiser et al., 2002]. Early mammals may have needed this external source of heat to rewarm quickly after nocturnal activity so that they could save energy through sleep during the day [Geiser et al., 2002]. Notably, *L. catta* are sometimes active at night

TABLE IV. Fixed Effects Correlation Matrix Associated With GLMM in Table III

Variable	Time of day	Temperature	Wind speed	Group	Sex	Age category
Time of day	1					
Temperature	−0.615	1				
Wind speed	−0.312	0.112	1			
Group	0.019	−0.020	−0.030	1		
Sex	0.014	−0.021	−0.004	0.004	1	
Age category	−0.004	0.000	0.001	−0.020	0.099	1
Month/season	0.131	−0.139	−0.201	0.053	0.003	0.000

$N = 2,064$ observation hours.

[Donati et al., 2013; LaFleur et al., 2014; Parga, 2011], and the ancestral activity pattern for lemurids may have been cathemeral [Donati et al., 2013; Griffin et al., 2012]. However, *L. catta* are highly active during the day relative to other Lemuridae, that is, *Eulemur fulvus* in the few forests where the two are naturally sympatric [Sussman, 1972]. We propose that, unlike other Lemuridae, *L. catta* has evolved sunning as an adaptation to maximize the thermoregulatory benefits of intense solar radiation that is abundant during the day in semi-arid open habitats. This sunning behavior has enabled *L. catta* (and anecdotally *P. verreauxi*) to inhabit some of the most seasonal climates of any diurnally active living lemur [Kamilar & Muldoon, 2010; Wright, 1999].

Yet sunning alone may not be sufficient for maintaining homeostasis with this species; huddling and other social behaviors may also be important. In Barbary macaques, for example, the number of social partners and time spent feeding have been significant predictors of survival for groups that suffered multiple losses during a particularly cold and snowy winter [McFarland & Majolo, 2013]. In vervet monkeys, females with many social partners tend to be less heterothermic during the winter season than females who are less socially integrated, which may be associated with the females' abilities to secure social partners for huddling [McFarland et al., 2015]. In our study, five of the six deaths that we observed in group T occurred in the months of June to August [Kelley, 2011]. At least one and possibly two individuals died just days or weeks after the death of a primary huddling partner (i.e. an old male with a young adult female, and a young adult male with an adult female)[Kelley, 2011]. In addition, two male siblings that frequently played together also died within weeks of each other [Kelley, 2011]. In fact, the only individuals in T that survived belonged to a matriline consisting of the highest-ranking female, her two daughters, one natal male, and two newly integrated nonresident adult males [Kelley, 2011]. While we could not determine causes of death, hypothermia and loss of affiliative partners may have been contributing factors.

To conclude, our research indicates that *L. catta* tend to sun, rather than huddle, under cold weather conditions. However, we believe that both sunning and huddling are important behavioral adaptations of *L. catta* that augment chemical thermoregulation and the absence of a dynamic, insulating pelage. Sunning maximizes the abundant source of solar energy that is available in the highly seasonal but open habitats of Madagascar where this species lives, for example, gallery forests, rocky montane outcrops, spiny forests, and semi-desert scrub [Gould, 2006]. Huddling maintains body heat among cohuddlers, with huddling occurring most often overnight and prior to morning sunning. The aggregation of hunched individuals reduces the surface area-to-volume ratios of the huddlers, preventing heat loss to the environment from radiation, conduction, and convection [Terrien et al., 2011]; and if one animal has a lower body temperature, it can draw heat from its companion [Gilbert et al., 2010]. These combined behaviors may partly explain why *L. catta* is an ecologically flexible species. However, major threats to the lemurs today include poaching and habitat destruction [LaFleur, 2013], while environmental threats in the region include predictions of unsustainable habitat loss through increased heavy and erratic rainfall punctuated with periods of prolonged drought [Dyoulgerov et al., 2011]. Thus, what has yet to be determined is how vulnerable *L. catta* will be to the effects of climate change and habitat alteration, and whether differences in survival relate to meeting thermoregulatory needs.

REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

Bachelet E. 1981. Circular statistics in biology. London: London Academic Press. p 371.

Bates D, Maechler M, Bolker B. 2014. lme4: Linear mixed-effects models using S4 classes. Version R package version 1.1-7. Available online at: http://CRAN.R-project.org/package=lme4

Bluestein M, Zecher J. 1999. A new approach to an accurate wind chill factor. Behavioral Modeling and Simulation 80:1893–1900.

Bolker BM, Brooks ME, Clark CJ, et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. Integrative and Comparative Biology 51:676–690.

Brain C, Mitchell D. 1999. Body temperature changes in free-ranging baboons. International Journal of Primatology 20:585–598.

Chaplin G, Jablonski NG, Sussman RW, Kelley EA. 2014. The role of piloerection in primate thermoregulation. Folia Primatologica 85:1–17.

Curtis DJ. 2006. Cathemerality in lemurs. In: Gould L, Sauther ML, editors. Lemurs: ecology and adaptation. New York: Springer. p 133–157.

Daniels HL. 1984. Oxygen consumption in *Lemur fulvus*: deviation from the ideal model. Journal of Mammalogy 65:584–592.

Danzy J, Grobler JP, 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 GL. 1993. Postural changes and behavioral thermoregulation in *Colobus polykomos*: the effect of climate and diet. African Journal of Ecology 31:226–241.

Dyoulgerov M, Bucher A, Zermoglio F. 2011. Vulnerability, risk reduction, and adaptation to climate change: Madagascar. In: Dyoulgerov M, editor. Country profiles. Washington D.C.: The World Bank Group. p 15.

Dewar RE, Richard AF. 2007. Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences 104:13723–13727.

Donati G, Ricci E, Baldi N, Morelli V, Borgognini-Tarli SM. 2011. Behavioral thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic and dietary-related factors. American Journal of Physical Anthropology 144:355–364.

Donati G, Santini L, Razafindramanana J, Boitani L, Borgognini-Tarli SM. 2013. (Un-) expected nocturnal acitivity in "diurnal" *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. American Journal of Physical Anthropology 150:99–106.

Ellwanger N, Gould L. 2011. Variations in behavioral patterns between *Lemur catta* groups living in different forest types: implications for conservation. Endangered Species Research 14:259–270.

Gabriel DN, Gould L, Kelley EA. 2014. Seasonal patterns of male affiliation in ring-tailed lemurs (*Lemur catta*) in diverse habitats across southern Madagascar. Behavior 151:935–961.

Geiser F, Goodship N, Pavey CR. 2002. Was basking important in the evolution of mammalian endothermy? Naturwissenschaften 89:412–414.

Gilbert C, McCafferty D, Le Maho Y, et al. 2010. One for all and all for one: the energetic benefits of huddling in endotherms. Biological Reviews 85:545–569.

Goodman S, Rakotoarisoa S, Wilmé L. 2006. The distribution and biogeography of the ringtailed lemur (*Lemur catta*) in Madagascar. In: Jolly A, Sussman R, Koyama N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p 3–15.

Gould L. 1994. Affiliation in male *Lemur catta* (Doctoral dissertation). Washington University in St.Louis.

Gould L. 2006. Lemur catta ecology: what we know and what we need to know. In: Gould L, Sauther ML, editors. Lemurs: ecology and adaptation. New York: Springer. p 255–274.

Griffin RH, Matthews LJ, Nunn CL. 2012. Evolutionary disequilibrium and activity period in primates: a Bayesian phylogenetic approach. American Journal of Physical Anthropology 147:409–416.

Grueter CC, Li D, Ren B., Li M. 2013. Overwintering strategy of Yunnan snub-nosed monkeys: adjustments in activity scheduling and foraging patterns. Primates 54:125–135.

Hall K. 1965. Experiment and quantification in the study of baboon behavior in its natural habitat. In: Jay P, editor. Primates: studies in adaptation and variability. New York: Holt, Rinehart, and Winston. p 32–119.

Hanya G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. American Journal of Primatology 63:165–177.

Hanya G, Kiyono M, Hayaishi S. 2007. Behavioral thermoregulation of wild Japanese macaques: comparisons between two subpopulations. American Journal of Primatology 69:802–815.

Hill RA. 2006. Thermal constraints on activity scheduling and habitat choice in baboons. American Journal of Physical Anthropology 129:242–249.

Huey RB, Pianka ER. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal kalahari lizards. Ecology 58:1066–1075.

Human Language Processing Lab. 2011. Diagnosing collinearity in mixed models from lme4. Available online at: https://hlplab.wordpress.com/2011/02/24/diagnosing-collinearity-in-lme4/

Jolly A. 1966. Lemur behavior: a Madagascar field study. Chicago and London: The University of Chicago Press. p 187.

Kamilar JM, Muldoon KM. 2010. The climatic niche diversity of Malagasy primates: a phylogenetic perspective. PLoS ONE 5:e11073.

Kearney M, Shine R, Porter WP. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences 106:3835–3840.

Kelley EA. 2011. *Lemur catta* in the region of Cap Sainte–Marie, Madagascar: introduced cacti, xerophytic didiereaceae–euphorbia bush, and tombs (Doctoral dissertation). Washington University in St. Louis.

Kelley EA. 2012. The social organization of *Lemur catta* in the region of Cap Sainte–Marie, Madagascar. American Journal of Physical Anthropology 54:179.

Kelley EA. 2013. The ranging behavior of *Lemur catta* in the region of Cap Sainte–Marie, Madagascar. American Journal of Physical Anthropology 150:122–132.

Kummer H. 1997. In quest of the sacred baboon: a scientist's journey. New Jersey: Princeton University Press. p 337.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2013. lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). Version R package version 2.0-25. Available online at: http://cran.r-project.org/web/packages/lmerTest/

LaFleur M. 2013. Madagascar's most famous lemur facing big threats. Mongabay.com. Available online at: http://news.mongabay.com/2013/1218-lafleur-ringtailed-lemurs.html

LaFleur M, Sauther M, Cuozzo F, et al. 2014. Cathemerality in wild ring-tailed lemurs (*Lemur catta*) in the spiny forest of Tsimanampetsotsa national park: camera trap data and preliminary behavioral observations. Primates 55:207–217.

Lee K, editor. 2010. C UNL Astronomy education. Available online at: http://astro.unl.edu

Lubbe A, Hetem RS, McFarland R, et al. 2014. Thermoregulatory plasticity in free-ranging vervet monkeys, *Chlorocebus pygerythrus*. Journal of Comparative Physiology B 184:799–809.

Martin P, Bateson PPG. 1993. Measuring behavior: an introductory guide, second edition. Cambridge: Cambridge University Press. p 222.

McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP. 2014. Behavioral flexibility of vervet monkeys in response to climatic and social variability. American Journal of Physical Anthropology 154:357–364.

McFarland R, Fuller A, Hetem RS, et al. 2015. Social integration confers thermal benefits in a gregarious primate. Journal of Animal Ecology 84:871–878.

McFarland R, Majolo B. 2013. Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. Biology Letters 9:20130428.

Mendiratta U, Kumar A, Mishra C, Sinha, A. 2009. Winter ecology of the Arunachal macaque *Macaca munzala* in Pangchen Valley, western Arunachal Pradesh, northeastern India. American Journal of Primatology 71:939–947.

Montagna W. 1962. The skin of lemurs. Annals of the New York Academy of Sciences 102:190–209.

Moreland H. 1993. Seasonal behavioral variation and its relationship to thermoregulation. In: Kappeler P, Ganzhorn J, editors. Lemur social systems and their ecological basis. New York and London: Plenum Press. p 193–203.

Murray R. 2014. The effects of age on behavioral thermoregulation in *Lemur catta* and *Propithecus coquereli* (Distinction thesis). Duke University.

Nash LT. 1998. Vertical clingers and sleepers1: seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. Folia Primatologica 69:204–217.

Nowack J, Wippich M, Mzilikazi N, Dausmann KH. 2013. Surviving the cold, dry period in Africa: behavioral adjustments as an alternative to heterothermy in the African Lesser Bushbaby (*Galago moholi*). International Journal of Primatology 34:49–64.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology, Evolution, and Systematics 4:25–51.

Ostner J. 2002. Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). Folia Primatologica 73:175–180.

Parga JA. 2011. Nocturnal ranging by a diurnal primate: are ring-tailed lemurs (*Lemur catta*) cathemeral? Primates 52:201–205.

Pereira M, Strohecker R, Cavigelli S, Hughes C, Pearson D. 1999. Metabolic strategy and social behavior in Lemuridae. In: Rasamimanana H, Ganzhorn J, Goodman S, editors. New directions in lemur studies. New York: Kluwer Academic/Plenum Publishers. p 93–118.

R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available online at: http://www.R-project.org/

Rauh W. 1995. Succulent and xerophytic plants of Madagascar, volume 1. California: Strawberry Press. p 342.

Richard A. 1978. Behavioral variation: case study of a Malagasy lemur. New Jersey: Associated University Presses. p 213.

Sato H. 2012. Diurnal resting in brown lemurs in a dry deciduous forest, northwestern Madagascar: implications for seasonal thermoregulation. Primates 53:255–263.

Simmen B, Bayart F, Rasamimanana H, et al. 2010. Total energy expenditure and body composition in two free-living sympatric lemurs. PLoS ONE 5:e9860.

Snodgrass JJ, Leonard WR, Robertson ML. 2007. Primate bioenergetics: an evolutionary perspective. In: Ravosa MJ, Dagosto M, editors. Primate origins: adaptations and evolution. New York: Springer. p 703–737.

Stelzner JK, Hausfater G. 1986. Posture, microclimate, and thermoregulation in yellow baboons. Primates 27:449–463.

Sussman R. 1972. An ecological study of two Madagascan primates: *Lemur fulvus rufus* (Audebert) and *Lemur catta* (Linnaeus) (Doctoral dissertation). Duke University.

Terrien 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.

Vasey N. 2004. Circadian rhythms in diet and habitat use in red ruffed lemurs (*Varecia rubra*) and white-fronted brown lemurs (*Eulemur fulvus albifrons*). American Journal of Physical Anthropology 124:353–363.

Vincelette M, Dumouchel J, Giroux J, Heriarivo R. 2008. The Tolagnaro (Fort Dauphin) region: a brief overview of the geology, hydrology, and climatology. SI/MAB Series 11:9–18.

Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. American Journal of Physical Anthropology 110:31–72.