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# The cost of deep sleep: Environmental influences on sleep regulation are greater for diurnal lemurs

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## Abstract

**Objectives:** Primates spend almost half their lives asleep, yet we know little about how evolution has shaped variation in the duration or intensity of sleep (i.e., sleep regulation) across primate species. Our objective was to test hypotheses related to how sleeping site security influences sleep intensity in different lemur species.

**Methods:** We used actigraphy and infrared videography to generate sleep measures in 100 individuals (males = 51, females = 49) of seven lemur species (genera: *Eulemur*, *Lemur*, *Propithecus*, and *Varecia*) at the Duke Lemur Center in Durham, NC. We also generated experimental data using sleep deprivation for 16 individuals. This experiment used a pair-wise design for two sets of paired lemurs from each genus, where the experimental pair experienced a sleep deprivation protocol while the control experienced normal sleeping conditions. We calculated a sleep depth composite metric from weighted *z* scores of three sleep intensity variables.

**Results:** We found that, relative to cathemeral lemurs, diurnal *Propithecus* was characterized by the deepest sleep and exhibited the most disruptions to normal sleep-wake regulation when sleep deprived. In contrast, *Eulemur mongoz* was characterized by significantly lighter sleep than *Propithecus*, and *E. mongoz* showed the fewest disruptions to normal sleep-wake regulation when sleep deprived. Security of the sleeping site led to greater sleep depth, with access to outdoor housing linked to lighter sleep in all lemurs that were studied.

**Conclusions:** We propose that sleeping site security was an essential component of sleep regulation throughout primate evolution. This work suggests that sleeping site security may have been an important factor associated with the evolution of sleep in early and later hominins.

**KEYWORDS**
activity, lemur, primate evolution sleep intensity, sleep regulation

## 1 | INTRODUCTION

The function of sleep remains a mystery. Sleep is a complex behavior (Vyazovskiy & Delogu, 2014; Webb, 1988) and several functions have been hypothesized, including energy restoration, immunocompetence, brain metabolic homeostasis, neural ontogenesis, and cognitive and emotional processing (McNamara & Auerbach, 2010; Preston, Capellini, McNamara, Barton, & Nunn, 2009; Walker, 2009; Xie et al., 2013). One dimension of sleep involves its architecture, such as the durations of REM and NREM (and the rate of cycling between these states). Numerous studies have investigated how

ecological factors influence these dimensions of sleep among individuals and across species (Campbell & Tobler, 1984; Capellini, Barton, McNamara, Preston, & Nunn, 2008; Lesku et al., 2012; Lesku, Roth, Amlaner, & Lima, 2006; Zepelin, Siegel, & Tobler, 2005). Moreover, recent work has suggested that, relative to nonhuman primates, sleep in humans is evolutionarily exceptional, departing from patterns expected in other primates (Samson & Nunn, 2015; Nunn & Samson, 2018, in this volume). These studies revealed, for example, that humans have the shortest sleep duration but the greatest proportion of that duration dedicated to REM (rapid eye movement) sleep.

Sleep intensity, defined here as compensatory process for too much or too little sleep, is another dimension of sleep that is critical to the homeostatic sleep drive (Borbely, 1982; Borbely & Neuhaus, 1979). The primary measure of sleep intensity is the relative proportion of EEG slow wave activity (SWA; defined as EEG delta waves between 0.5 and 4 Hz) within nonrapid eye movement (NREM). An individual can maintain a relatively constant quota of sleep by having either longer duration sleep or more intense sleep, as found in responses to sleep deprivation in humans (Dijk, Beersma, & Daan, 1987; Feinberg et al., 1985; Werth, Dijk, Achermann, & Borbely, 1996) and nonhuman animals such as mice, hamsters, rats, squirrels and cats (Franken, Dijk, Tobler, & Borbely, 1991; Tobler, 2011), including unihemispheric sleepers such as dolphins (Oleksenko, Mukhametov, Polyakova, Supin, & Kovalzon, 1992). This process of sleep regulation is a homeostatic balance between sleep duration and sleep intensity that aims to maintain a constant species-typical amount of daily sleep necessary for normal, healthy function.

Tobler (2011) notes that definitions of sleep should consider regulatory processes, including the interaction between sleep duration and intensity. Sleep intensity is relevant for understanding sleep in wild animals, where individuals are faced with many risks when sleeping, including increased predation, dangers from inclement weather, social competition, and opportunity costs of foraging, searching for mates, or caring for offspring.

Sleep durations have been observed in most primate studies, yet due to the challenges of measuring intensity (traditionally measured using invasive EEG), few studies have reported variables that target sleep intensity or enable its comparison among species (Nunn, McNamara, Capellini, Preston, & Barton, 2010). When EEG data are lacking, secondary measures rely on behavioral coding of activity threshold, sleep continuity (defined as the frequency of short wake episodes), and motor activity (Tobler, 2011). When compared to short, fragmented sleep epochs, long, consolidated sleep epochs have been demonstrated to exhibit increased recovery power (Vyazovskiy, Achermann, & Tobler, 2007). In response to sleep deprivation, measures of sleep intensity are altered, involving increases in sleep depth that are characterized by decreased frequency of motor movements, and less fragmented sleep (Franken et al., 1991). Although EEG-based measures of sleep intensity are preferred, experimental studies have identified behavioral correlates of sleep intensity. For example, in rodents, the reduction in the number of brief awakenings correlates with increased SWA (Franken et al., 1991; Tobler, Franken, & Jaggi, 1993; Tobler et al., 1996). In sleep-deprived dogs, motor activity measured continuously using actigraphy was reduced up to 40% during recovery (Tobler & Sigg, 1986). Additionally, research has demonstrated a similar reduction in motor activity in sleep-deprived humans (Naitoh, Muzet, Johnson, & Moses, 1973).

Cathemerality (activity throughout the 24-hr circadian cycle) is common in several lemur species, despite being rare in anthropoid primates (Curtis & Rasmussen, 2006; Halle, 2006; Tattersall, 1987). Lemurs are endemic to Madagascar, an island that is characterized by a hyper-variable environment (Dewar & Richard, 2007). Climactic unpredictability, which can influence the distribution of light, temperature, and circadian variation in predator activity, has been suggested to influence variation in lemur activity patterns (Donati & Borgognini-Tarli, 2006; Wright, 1999). This environmental variation makes lemurs a valuable sytsem in which to investigate sleep regulation in primates. However, seasonal variation in environmental factors masks endogenous circadian rhythms, making it difficult to identify species-typical activity patterns. Masking factors in lemurs include temperature, moonlight, availability of food, and day length (Curtis, Zaramody, & Martin, 1999; Donati, Baldi, Morelli, Ganzhorn, & Borgognini-Tarli, 2009; Donati & Borgognini-Tarli 2006; Eppley, Ganzhorn, & Donati, 2015). Importantly, captive studies provide a method to overcome the challenges of categorizing activity pattern by controlling for environmental variables that influences sleep-wake regulation—thereby providing a complementary approach to determining endogenous activity patterns (Rattenborg et al., 2017).

Recent studies have challenged the historical classification of activity patterns in the Lemuridae. For example, traditionally, cathemeral species have included *Eulemur*, whereas species such as *Varecia rubra*, *V. variegata*, and *L. catta* have been classified as diurnal. At a number of different sites, however, notable variation has been reported in the degree of nocturnal activity in *L. catta*. *L. catta* has been documented to have shown some nocturnal activity at some sites (Donati, Santini, Razafindramanana, Boitani, & Borgognini-Tarli, 2013; LaFleur et al., 2014), while they were more strictly diurnal at several other sites (Sauther et al., 1999; Sussman et al., 2012). Reports of cathemeral behavior in wild *V. variegata* have also been published (Donati & Borgognini-Tarli, 2006). In previous captive work, Bray, Samson, and Nunn (2017) used actigraphy at the Duke Lemur Center (DLC) to generate data on seven lemur species and showed that *Propithecus coquereli* engaged in the least amount of nocturnal activity and that *Varecia* and *Lemur* deviated from the diurnal *Propithecus* pattern. Previous captive work performed on five lemur species at the DLC revealed similar findings (Rea, Figueiro, Jones, & Glander, 2014). Thus, based on these recent findings in this captive environment, we classify *Lemur* and *Varecia* as cathemeral, and compare them specifically to an unequivocally categorized diurnal species—*Propithecus*.

Studying sleep in primates presents several challenges. For example, polysomnography (PSG), a multiparametric test that records both brain and body functions and serves as the standard method for studying sleep in captive mammals, is impractical due to invasive surgical procedures that involve fitting electrodes on the brain's surface (Sri Kantha & Suzuki, 2006). Primary measures in PSG are electroencephalography (EEG) and electromyography (EMG), and their application to captive animals typically involves resource intensive surgery, a significant recovery period, and risk of infection. Moreover, most primates have strong grooming instincts that would result in removal of these devices, especially when animals are housed socially. These negative consequences eliminate the use of EEG in non-research institutions (i.e., zoos and sanctuaries) that have strict guidelines for animal welfare and maintain animals in species-typical social groups.

The limitations of EEG have recently been overcome through technological advances involving cost-effective actigraphy and infrared videography (Andersen, Diaz, Murnane, & Howell, 2013; Barrett et al., 2009; Kantha & Suzuki, 2006; Zhdanova et al., 2002). Here, we used

**TABLE 1** Sleep duration (total sleep time), sample size, and activity pattern classification summary information for the lemur species in this study

| Species | Common name | Mean TST (hr) | N | Sample | Activity pattern and references |
|---|---|---|---|---|---|
| *Eulemur coronatus* | Crowned lemur | 8.96 ± 1.58 | 56 | 9 | Cathemeral (Freed, 1996)[a] (Bray et al., 2017)[b] |
| *Eulemur flavifron* | Blue-eyed black lemur | 8.84 ± 1.72 | 61 | 12 | Cathemeral (Schwitzer et al., 2007)[a] (Bray et al., 2017)[b] |
| *Eulemur mongoz* | Mongoose lemur | 13.68 ± 2.40 | 79 | 11 | Cathemeral (Andriatsarafara, 1998)[a] (Rea et al., 2014)[b] (Bray et al., 2017)[b] |
| *Eulemur* spp. | | 9.96 ± 1.65 | 196 | 32 | |
| *Lemur catta* | Ring-tailed lemur | 11.05 ± 1.68 | 168 | 29 | Moderate cathemerality[a] (Donati et al., 2013)[a] (LaFleur et al., 2014)[a] (Rea et al., 2014)[b] (Bray et al., 2017)[b] |
| *Propithecus coquereli* | Coquerel's sifaka | 10.63 ± 1.92 | 128 | 22 | Diurnal (Erkert & Kappeler, 2004)[a] (Rea et al., 2014)[b] (Bray et al., 2017)[b] |
| *Varecia rubra* | Red ruffed lemur | 9.81 ± 1.85 | 79 | 13 | Moderate cathemerality (Rea et al., 2014)[b] (Bray et al., 2017)[b] |
| *Varecia variegata* | Black-and-white ruffed lemur | 10.90 ± 2.15 | 25 | 4 | Moderate cathemerality (Rea et al., 2014)[b] (Balko in Wright, 1999)[a] (Bray et al., 2017)[b] |
| *Varecia* spp. | | 10.36 h ± 2.00 | 104 | 17 | |

[a]Wild study.
[b]Captive study.
N = the number of 24-hr periods where values were derived for TST. Sample = the number of individuals that contributed to the sample to produce the mean TST values.

actigraphic data and videography to investigate the factors that influence proxies for sleep intensity in seven different species of lemurs at the DLC, including through experimental sleep deprivation in 16 individual of four species. To investigate the links between environmental parameters and sleep, we tested two hypotheses: (1) lemur sleep intensity is influenced by the security of sleeping sites, and (2) more flexibly active cathemeral lemurs show less strict sleep regulation, as compared to more strictly diurnal lemurs. On the basis of the first hypothesis, we predicted that lemurs would exhibit less fragmentation, arousal, and short sleep bouts when they are housed in the safety of less dynamic, indoor enclosures. Based on the second hypothesis, which assumes that sleep flexibility is achieved through a weaker homeostatic drive, we predicted that diurnal lemurs (*Propithecus* sp.) would exhibit less fragmentation, reduced number of arousals, and shorter sleep bouts when compared to cathemeral genera (*Eulemur*, *Lemur*, and *Varecia*). We further predicted that diurnal lemurs would show more deviations from normal (control) activity patterns in response to experimentally induced sleep deprivation.

## 2 | METHODS

### 2.1 | Study subjects

We generated actigraphic data from seven lemur species totaling 100 individuals with a nearly equal sex ratio (male *n* = 51, female *n* = 49; see Table 1). Complete biographic information is available in Bray et al. (2017). Subjects were housed at the DLC in Durham, NC. *Eulemur* species were generally housed in adult pairs along with any dependent

offspring (Colquhoun, 2006; Tattersall, 1975), while *Lemur catta* (Jolly, 1966; Sauther et al., 1999), *Propithecus coquereli* (Richard et al., 1991), and *Varecia* species (Britt, 2000; Vasey, 2007) were typically housed in multimale-multifemale groups. All animals had unlimited access to water and received fresh fruit, vegetables, and Purina monkey chow daily. All animal use and methods were approved by the Duke University Institutional Animal Care and Use committee (Protocol #: A236-13-09) and the DLC Research Committee.

### 2.2 | Data collection

The baseline study was conducted over 11 months from January 2014 to November 2014. Daily activity was continuously recorded using MotionWatch 8 (CamNtech) tri-axial accelerometers generating a dataset totaling 596 days. These actigraphic sensors are lightweight (7g), and attached to standard nylon pet collars. Animals were monitored to ensure no adverse reactions to the collar; subjects acclimated to the collars within 2 hr. Most subjects wore the collars between 6 and 8 days, although a small subset of *L. catta* subjects were collared for 68–73 days to generate longitudinal data. Housing (i.e., the sleeping site environment) was recorded for each night of sampling (indoor only, indoor and outdoor enclosure access, and free-range forest access). Each day's recording was indexed by several independent variables: day length (the difference between sunrise and sunset times), moonphase (continuously between 1 = full moon and 0 = new moon), and mean nighttime temperature (°C).

Dependent variables were generated from processed activity logs recorded at one-minute epochs. The sensor sampled movement once a

SAMSON ET AL.

American Journal of
PHYSICAL
ANTHROPOLOGY
The Official Journal of the American Association of Physical Anthropologists

WILEY 581

second at 50 Hz and accumulated data (which outputs on a ratio scale), ultimately assigning an activity value per 1-min epoch. Recent advances in scoring algorithms have increased accuracy in detecting wake-sleep states and total sleep times (Stone & Ancoli-Israel, 2011). Using actigraphy data, we generated total average sleep times for each species. As in previous studies quantifying sleep in primates (Andersen et al., 2013; Barrett et al., 2009; Kantha & Suzuki, 2006; Zhdanova et al., 2002), we used the definition of sleep in actigraphy as the absence of any force in any direction during the measuring period (i.e., one minute epoch) (Campbell & Tobler, 1984).

Kawada (2013) notes that actigraphy is not a substitute for sleep measures generated by polysomnography, which directly quantifies brain activity, and cautions that actigraphy can overestimate sleep given the lack of sensitivity for arriving at sleep-wake differentiation. In addition to these general limitations of actigraphy, sleep-wake algorithms have been developed and validated for humans, but not for nonhuman primates. We arrived at a cutoff value for sleep-wake determination based on ground-truthed validation that used infrared videography (AXIS P3364-LVE Network Camera) to determine that animals were consistently at rest (i.e., sustained quiescence in a species-specific posture) when actigraphy values were less than four. We performed this videographic analysis randomly throughout the night and for each species. Observing the range of values from all epochs in our dataset, we noted a clear break, with values from one to three being absent. Confirming the validity of this break, video recordings of epochs with values of zero were clearly inactive, whereas values of four or more showed small-scale behavior such as subjects visually scanning their environment.

To assess measures of inferred sleep intensity, the following variables were derived from nighttime recordings: sleep motor activity is the number of motor activity bouts per hour; this value was derived by assigning each epoch either a "0" or "1" based on whether there was activity (raw activity counts > 4) scored during the epoch (assigning a 1) or not (assigning a 0), and was assigned to only single epochs of activity preceded and followed by inactivity. Sleep fragmentation is the number of awakenings greater or equal to two minutes of consecutive activity per hour. Short sleep bouts are the number of brief inactive episodes per hour, lasting only one epoch and preceded and followed by activity. To provide a measure of underlying inferred sleep intensity, a sleep depth composite (SDC) score was calculated (by first transforming raw scores into $z$ scores and then generating a sum each categorical $z$ score) using the unit-weighted $z$ scores (Ackerman & Cianciolo, 2000) of the three sleep intensity variables. For sleep intensity measures, we used previous methods for studying sleep in primates (Barrett et al., 2009; Zhdanova et al., 2002). We analyzed recorded variables from 12-hr periods between 18:00 and 06:00 (following the DLC lights-off/staff away time period). Definitions for sleep intensity variables follow those outlined in previous work (Samson & Shumaker, 2015).

## 2.3 | Experimental procedure

The experimental procedure was conducted over 2 months from September to October 2015. In a pair-wise experimental design (focusing on cathemeral *Eulemur* and diurnal *Propithecus*) two sets of paired lemurs (total $n = 4$ from each species) underwent 2 weeks of simultaneous testing. During the same night, the experimental pair experienced a sleep deprivation procedure while the other pair (housed in a different wing) experienced normal sleeping conditions. To achieve sleep deprivation, the lemurs experienced 10 hr (from 18:00 to 04:00) of audio playbacks of <30-s duration every five minutes; the following day, the pairs were switched and the experimental pair became the control pair and vice versa. The audio stimuli included the following noises randomly emitted playbacks: cage doors closing, dishes falling, general daytime DLC ambient noise, and inclement weather. We used four different sound sequences per category for 16 total possible playbacks. The playbacks dB level ranged from 60 to 100 dB. In addition to actigraphy data, we used infrared videography to determine whether animals were awakened by sounds. Using videography, we also determined species-specific responses to playback to ensure animal welfare. The typical response to playback was an opening of the eyes and a more upright body posture. We monitored post nighttime period behavior for increased aggression or signs of distress, which were not observed by us or DLC staff that also monitored the animals.

## 2.4 | Data analysis

We generated descriptive statistics characterizing the nightly distribution of total sleep time and sleep intensity among lemurs by individual, species, sex, and activity pattern. Activity patterns were assessed in a companion study (Bray et al., 2017), which corroborates recent studies showing that *Propithecus* is diurnal (Erkert & Kappeler, 2004) and *Eulemur* spp. cathemeral (Donati et al., 2013; LaFleur et al., 2014), and further suggesting that *Varecia* spp. And *L. catta* demonstrate moderate expression of cathemerality (see above, and also Rea et al., 2014).

Statistical analyses were conducted using *R* version 3.1.3 (R Core Team, 2016) and IBM SPSS 22. To assess total sleep times, we used the *accelerometry* package (Van Domelen, 2015) to process 24-hr periods of actigraphy. Averaged nightly sleep intensity variables were checked for normality with Kolmogorov-Smirnov tests. Because of non-normal distributions of data, we used Spearman's rank correlation coefficients to examine relationships among activity patterns and sleep intensity.

To assess the predictors of sleep intensity, we built a linear mixed effects model for the SDC using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). Species was used as a fixed-effect as a proxy for activity pattern, and comparisons were made to *Propithecus* (the only unambiguously diurnal species) as the reference taxon. Other fixed effects in the model were sex as well as nighttime temperature, day length, and housing access. Two interactions were assumed in the model: (1) temperature and housing access and (2) temperature and daylength. To control for repeated measures, we included "subject" as random effects. We obtained parameter estimates using optimization of the log-likelihood. We averaged statistical models with $\Delta AIC < 10$, and we used the *MuMIn* package (Bartoń, 2015). Statistical inferences were made using standardized coefficient estimates with shrinkage and 95% confidence intervals.

*American Journal of* PHYSICAL ANTHROPOLOGY *The Official Journal of the American Association of Physical Anthropologists* SAMSON ET AL.

**TABLE 2** Descriptive statistics characterizing baseline lemur sleep intensity by species.

| Variable | Genus | N | Mean | SE | Range |
|---|---|---|---|---|---|
| Sleep motor activity (per hour) | E. coronatus | 19 | 23.0 | 0.73 | 9.7–18.0 |
| | E. flavifron | 49 | 20.4 | 0.69 | 11.4–31.8 |
| | E. mongoz | 55 | 16.5 | 0.62 | 9.6–27.3 |
| | Eulemur spp. | 123 | 20.0 | 0.68 | |
| | L. catta | 145 | 18.3 | 0.36 | 0.0–26.7 |
| | P. coquereli | 81 | 14.3 | 0.50 | 6.8–24.3 |
| | V. rubra | 16 | 23.5 | 1.98 | 14.1–41.3 |
| | V. variegata | 9 | 20.2 | 1.23 | 12.4–25.4 |
| | Varecia spp. | 25 | 21.9 | 1.6 | |
| Sleep fragmentation (per hour) | E. coronatus | 19 | 2.8 | 0.17 | 1.3–3.8 |
| | E. flavifron | 49 | 2.6 | 0.09 | 1.5–4.3 |
| | E. mongoz | 55 | 2.2 | 0.06 | 1.3–3.3 |
| | Eulemur spp. | 123 | 2.5 | 0.11 | |
| | L. catta | 145 | 2.9 | 0.07 | 0.0–5.3 |
| | P. coquereli | 81 | 2.5 | 0.12 | 1.0–5.6 |
| | V. rubra | 16 | 3.1 | 0.32 | 1.8–6.2 |
| | V. variegata | 9 | 3.8 | 0.23 | 2.5–4.5 |
| | Varecia spp. | 25 | 3.5 | 0.28 | |
| Short sleep bout (per hour) | E. coronatus | 19 | 1.6 | 0.12 | 0.6–2.6 |
| | E. flavifron | 49 | 1.2 | 0.07 | 0.5–3.2 |
| | E. mongoz | 55 | 1.1 | 0.04 | 0.6–2.3 |
| | Eulemur spp. | 123 | 1.3 | 0.08 | |
| | L. catta | 145 | 1.2 | 0.05 | 0–3.1 |
| | P. coquereli | 81 | 1.3 | 0.07 | 0.2–3.0 |
| | V. rubra | 16 | 1.6 | 0.30 | 0.4–4.4 |
| | V. variegata | 9 | 1.8 | 0.10 | 1.5–2.45 |
| | Varecia spp. | 25 | 1.7 | 0.20 | |
| Sleep depth composite | E. coronatus | 19 | −0.88 | 0.30 | −3.1–2.8 |
| | E. flavifron | 49 | −0.07 | 0.18 | −3.1–5.7 |
| | E. mongoz | 55 | 0.79 | 0.13 | −3.5–4.3 |
| | Eulemur spp. | 123 | −0.58 | 0.20 | |
| | L. catta | 145 | −0.05 | 0.11 | −5.4–4.3 |
| | P. coquereli | 81 | 0.57 | 0.21 | −4.8–12.7 |
| | V. rubra | 16 | −1.16 | 0.72 | −4.0–9.3 |
| | V. variegata | 9 | −1.56 | 0.34 | −3.3–2.8 |
| | Varecia spp. | 25 | −1.36 | 0.53 | |

Higher sleep depth composite (SDC) values indicate deeper sleep. To remove the confounds of temperature and dynamic sleep environments on sleep intensity, free ranging sleep environments and extreme nighttime temperatures >20°C were removed from this sample. N = the number of 24-hr periods where values were derived for sleep intensity variables.

**TABLE 3** The effect of predictor variables on the sleep depth composite (SDC)

| Predictor | β | SE | Confidence interval | z | Importance |
|---|---|---|---|---|---|
| Day length | 0.18 | 0.14 | (−0.098, 0.449) | 1.26 | 0.93 |
| Outdoor access | −0.20 | 0.10 | (−0.396, −0.001) | 1.96 | 0.92 |
| Temperature | −0.38 | 0.56 | (−1.467, 0.716) | 0.68 | 0.96 |
| Male | −0.18 | 0.08 | (−0.341, −0.025) | 2.28 | 0.82 |
| Temperature × housing | 0.30 | 0.15 | (−0.001, 0.603) | 1.95 | 0.62 |
| Temperature × day length | 0.99 | 0.70 | (−0.395, 2.374) | 1.40 | 0.47 |
| *Eulemur coronatus* | −0.02 | 0.09 | (−0.195, 0.150) | 0.25 | 0.20 |
| *Eulemur flavifron* | 0.03 | 0.09 | (−0.137, 0.201) | 0.41 | 0.20 |
| *Eulemur mongoz* | −0.18 | 0.09 | (−0.364, −0.014) | 2.11 | 0.20 |
| *Lemur catta* | −0.17 | 0.10 | (−0.362, 0.021) | 1.73 | 0.20 |
| *Varecia rubra* | 0.05 | 0.10 | (−0.136, 0.246) | 0.56 | 0.20 |
| *Varecia variagata* | −0.02 | 0.08 | (−0.176, 0.134) | 0.27 | 0.20 |

*Female* is the reference category for sex, *indoor access* is the reference category for housing, and outgroup diurnal *Propithecus* is the reference category for *species*. Positive coefficients indicate deeper sleep, while negative coefficients indicate lighter sleep. After correcting for fixed effects, outdoors access negatively influenced sleep depth.

Finally, to experimentally assess the influence of security of sleeping site on sleep intensity, we performed a within species (*L. catta*) linear mixed effects model for SDC (see above protocol) on one male and female for a total of 144 nights. The fixed effect was housing access and we include "subject" as a random effect. The sample was balanced for indoor/outdoor vs. free-range sleep environments (i.e., Monday to Thursday, subjects slept indoor/outdoor; Friday to Sunday they slept in the free ranging environment).

Functional linear modeling (FLM) was used to assess deviations from normal (control) activity patterns. The FLM approach, specifically designed for actigraphy time-series data analysis, measures raw, activity counts within and between samples, and can overcome problems when summary statistics mask differences across groups (Wang et al., 2011). FLM was used to compare activity patterns, on the 24-hr cycle (with Fourier smoothed averages), within species to assess the differences in sleep-wake activity between normal sleep and sleep-deprived
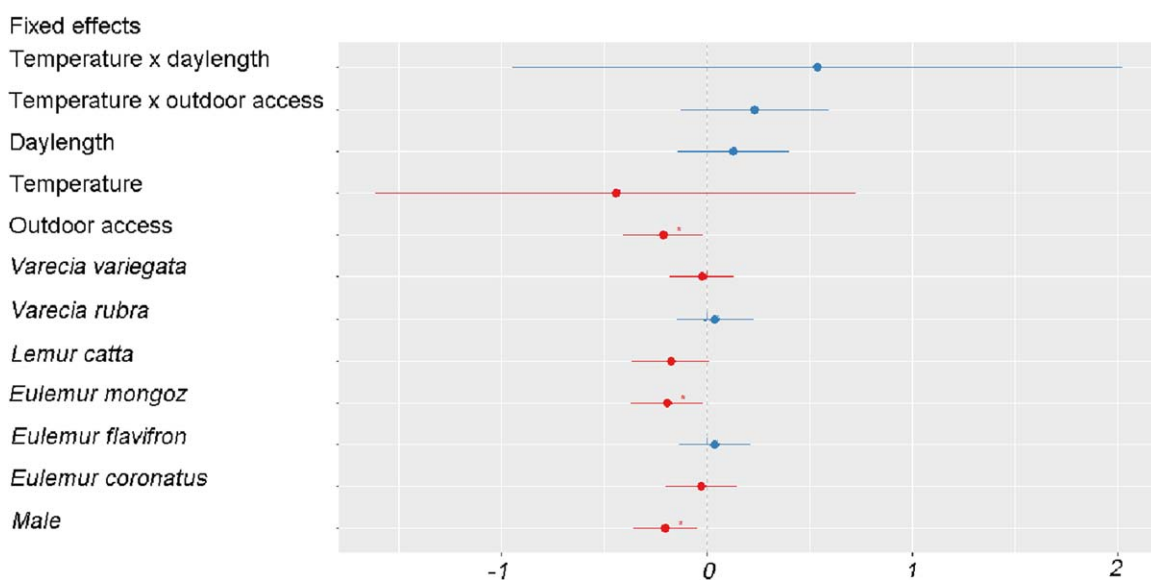


**FIGURE 1** A longitudinal experiment to assess sleep security and sleep intensity in *L. catta*. Individuals (one male and one female) slept more deeply when within secure indoor/outdoor enclosure compared to when they slept in dynamic free range environments. The effect was similar for both the male and female, with the male characterized by greater sleep
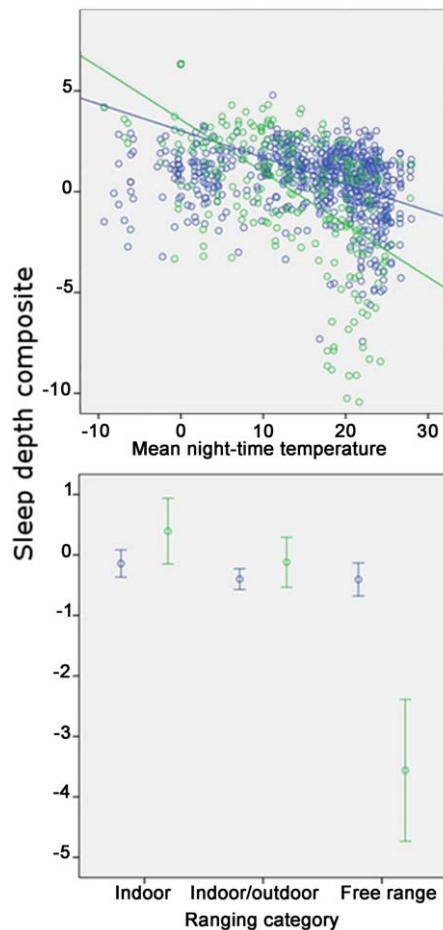
**FIGURE 2** Activity pattern and sleep intensity. *Propithecus* characterized by a dirunal activity pattern (green) are more sensitive to fluctuations in the environment than cathemerals (blue). Specifically, diurnals are more sensitive (exhibiting lighter sleep) to temperature fluctuation (left: diurnal slope, $y = -2.62 + 0.26^*x$, $R^2 = 0.38$; cathemeral slope, $y = -2.06 + 0.13^*x$, $R^2 = 0.27$) and environmental security (top panel). Housing status influenced lemur SDC, but more so for diurnal lemurs (ANOVA $F = 4.64$, $df = 188$, $p = 0.032$; bottom panel)

(experimental) groups. All reported errors are standard deviations and all significance tests were set at the level of $P \leq 0.05$.

## 3 | RESULTS

Table 1 provides average total sleep times for seven lemur species, based on 596 total days of actigraphy. Six of these are new reports for species that had not previously been studied. Averaged or summed by genus, total sleep durations (within a 24-hr period) were longest in *Lemur* (11.05 hr ± 1.68), second longest in *Propithecus* (10.63 hr ± 1.92), third longest in *Varecia* (10.36 hr ± 2.00) and shortest in *Eulemur* (9.96 ± 1.65). A correlation matrix revealed that sleep intensity variables show significant positive linear relationships with one another (range of correlation matrix: $r = 0.42$–$0.89$, $N = 100$, $p < 0.01$),

revealing that they make suitable variables with which to calculate a sleep depth composite score (Ackerman & Cianciolo, 2000). SDC was averaged for each genus to provide a baseline genus-specific measure of sleep intensity. *Varecia* showed the least sleep intensity (1.36), whereas *Propithecus* showed the greatest sleep intensity. *Eulemur* (0.05) and *Lemur* (0.05) were characterized by moderate sleep intensity (Table 2).

Lemur sleep intensity was influenced by security of sleeping sites (Table 3). Based on the confidence intervals that excluded zero in the model, lemurs were characterized by greater SDC when sleeping indoors (Figure 1). Male lemurs were characterized by lower SDC. Of all the species compared to the *Propithecus* reference taxon, *Eulemur*
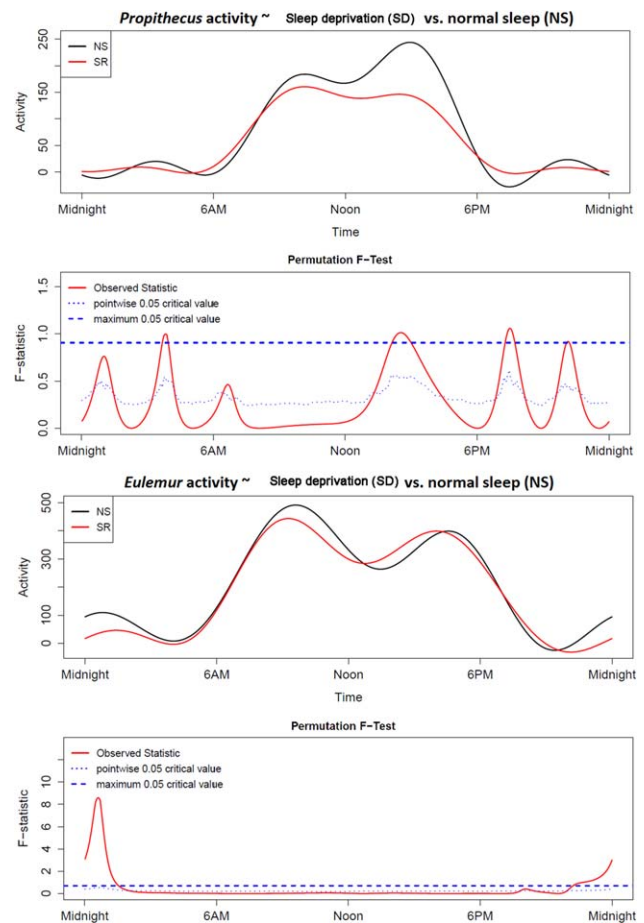


**FIGURE 3** Functional linear modeling comparison between normal sleep and sleep-deprived lemurs. *Propithecus* (a diurnal lemur) showed greater deviations from normal activity patterns than cathemeral lemurs when exposed to the experimental sleep deprivation condition. When exposed to sleep deprivation, *Propithecus* is characterized by depressed daytime activity and lower amplitude activity at night. The panel illustrates both the maximum critical value (a conservative $p$ value threshold) and point-wise critical value (less conservative $p$ value); the blue hashed and dotted lines are the proportion of all permutation $F$ values at each time point at the significance level of 0.05. When the observed $F$-statistic (solid line) is above the hashed or dotted line, it is concluded that the two groups have significantly different mean circadian activity patterns at those time points
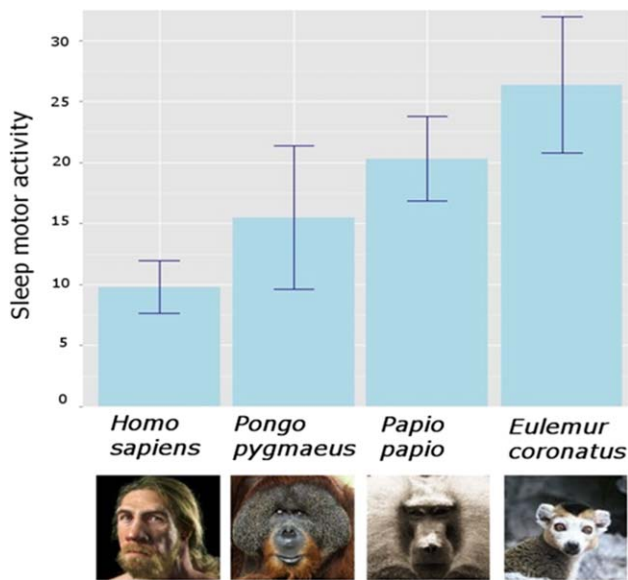
**FIGURE 4** Sleep motor activity as a measure of sleep intensity across primates. Few studies have generated sleep intensity values in primates, thus the sample size is not yet large enough for a formal statistical analysis. Sleep motor activity is a measure of sleep intensity and can be recorded noninvasively using infrared videography. Descriptive statistics shown here suggest that sleep motor activity, and thus sleep depth, may be a derived trait in humans, with a trend of more light sleep being characteristic of phylogenetically distant primates. Sleep intensity values derived from unpublished data and integrated with data from this study

*mongoz* was characterized by lower SDC. The confidence interval on the estimates for the other variables overlapped with zero, suggesting that these factors have weaker or less consistent effects on sleep intensity. The experimental intraspecies (*L. catta*) mixed model that controlled for repeated measures of subjects showed that nights spent in the indoor/outdoor enclosures were characterized by deeper sleep compared to nights when they had access to forest enclosures (SDC: $\beta \pm SE = -0.19 \pm 0.09$, $p = 0.04$, C.I. = 0.054, 0.358), where security of sleeping site is expected to be lower.

Diurnal *Propithecus'* normal sleep-wake patterns were more sensitive to fluctuations in the environment than the other lemurs. Relative to other lemurs, *Propithecus* sleep was more disturbed (i.e., a lower SDC value) on nights when they had outside access and when temperatures were higher (see Figure 2). Additionally, the sleep deprivation experiment revealed that sleep-deprived diurnal *Propithecus* was characterized by the greatest number of significant deviations from normal sleep conditions. Moreover, daytime periods after sleep deprivation show a recovery period of less overall activity in diurnal *Propithecus*; but show no such recovery period in *Lemur* and *Varecia* and *Eulemur* species that deviate from traditional diurnality. By the conservative maximum critical value threshold, FLM analysis showed that *Eulemur* experienced one significant alteration to their normal pattern, whereas *Propithecus* experienced three significant alterations (see Figure 3). *Lemur* experienced one significant alteration and *Varecia*

experienced no significant alterations from the normal sleep conditions.

## 4 | DISCUSSION

This study investigated sleep intensity in lemurs in relation to the security of sleeping sites. We found two lines of evidence supporting the hypothesis that lemur sleep intensity is influenced by the security of sleeping sites. First, our linear mixed model (Table 3 and Figure 1) revealed that a strong predictor for SDC was housing conditions. That is, subjects that had access to the outside enclosure exhibited lighter sleep than subjects with indoor access only; additionally, the interaction between housing and temperature indicated that sleep was lighter on nights when subjects were outside and temperature was greater, as compared to nights when subjects had indoor access only. Second, *L. catta* in the longitudinal condition followed a similar trend, with lighter sleep (lower SDC) on nights without access to secure indoor environments. Sleeping indoors provides an environmental buffer from noise, rainfall, temperature extremes, exposure to moonlight, and perceived predation threats, and thus may serve as a mediating factor that increases depth of sleep. Collectively, these findings show that deep sleep in lemurs is significantly influenced by the perceived security of local sleep environments.

In support of the hypothesis that more flexibly active cathemeral lemurs show less strict sleep regulation, as compared to more strictly diurnal *Propithecus*, we found that diurnal lemurs are characterized by deeper sleep and greater activity pattern disruption following exposure to dynamic or stimulating environments. Not only did diurnal *Propithecus* show marked differences (compared to cathemeral lemurs) in sleep intensity in response to outdoor environments (Figure 2), but experimental evidence showed that sleep deprivation alters diurnal more than cathemeral activity patterns (Figure 3). Hence, cathemeral lemur activity patterns may be less vulnerable to environmental fluctuation, or it may be that transitions to and from a sleep state are less costly given they can "rebound" anytime throughout the circadian cycle.

Until recently, sleep quotas—the basic parameters of sleep expression—were available for only 20 of the 350 or so recognized extant primate species (McNamara et al., 2008). The sleep intensity data presented in this study also augment the data on this variable for non-human primates (Table 2). The only other primate species with recorded values for sleep intensity are *Papio* and *Pongo* (Samson & Shumaker, 2015), *Macaca* (Kaemingk & Reite, 1987), *Saimiri* (Erny, Wexler, & Moore-Ede, 1985) and humans (Naitoh et al., 1973). Some hints of potentially interesting patterns emerge from this small sleep intensity dataset. For example, it appears that one measure of sleep intensity—motor activity—may show a phylogenetic signal, with *Homo sapiens* being characterized by the least nighttime motor activity and *Eulemur coronatus* (in our study) being characterized by the most (see Figure 4). This hypothesis awaits sample sizes large enough to perform formal phylogenetic tests.

As another example of general patterns to investigate, our analyses of lemurs suggest that body mass may explain variation in sleep

586 | WILEY *American Journal of* PHYSICAL ANTHROPOLOGY
*The Official Journal of the American Association of Physical Anthropologists*

SAMSON ET AL.

intensity for other primates. One factor may be the ability to sleep in a concealed and safe sleep site. For example, although wild *Propithecus* has a substantial range of variation in body mass—the smallest being *P. verreauxi* at 2.8 kg (Richard et al., 2002) to largest *P. diadema* at 6.5–6.9 kg (Powzyk, 1997)—the species in this study (*P. coquereli*) exhibits a body mass of 3.3–4.6 kg (Hartstone-Rose & Perry, 2011). Although comparable to *Varecia* at 3.0–4.5 kg (Vasey, 2002), this was larger than *Eulemur* at 1.48–2.47 kg (Terranova & Coffman, 1997) and *Lemur* at 2.2 kg (Sussman, 1991). Therefore, *Propithecus* may generally find it more difficult to locate cryptic sleeping sites, such as in lianas, suggesting the existence of a tradeoff between body mass and flexibility in sleep timing and continuity. This interpretation would explain the increased environmental sensitivity that we documented in *Propithecus*.

Another aspect of primate sleep evolution involves use of arboreal sleeping platforms, which are often called "nests." Phylogenetic reconstruction estimates the innovation of ape nest construction sometime between 18 and 14 million years ago (Duda & Zrzavy, 2013). Nest building, coinciding with the evolution of increased body mass over the 30 kg threshold, suggests that larger body mass made sleeping on branches less viable for these large-bodied apes (Samson, 2012; Samson & Nunn, 2015). Arboreal sleeping platforms likely served multiple functions (McGrew, 2004), including predation avoidance (Stewart & Pruetz, 2013), thermoregulatory buffering (Stewart, 2011), reduced insect and disease vector exposure (Samson, Muehlenbein, & Hunt, 2013; Stewart, 2011), and improved sleep quality (Samson & Shumaker, 2015) and comfort (Stewart, Pruetz, & Hansell, 2007). The transition from tree-branch to arboreal sleeping platform would have been a stepwise improvement in the overall quality of sleeping sites (Fruth & Hohmann, 1996). The next significant improvement in sleeping site could have been the tree-to-ground transition, which likely occurred with early *Homo* given the dramatic morphological changes that took place during the *Australopithecus-Homo* transition (Coolidge & Wynn, 2009). This evolutionary event could have then established the prerequisite adaptations to alter early hominin sleep architecture, where hominins would have benefited from more stable and less thermodynamically stressful sleeping sites (Samson & Hunt, 2012), and could have combined shelter and bedding technology (Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017b) and group level social cohesion, promoting sentinel-like behavior (Samson, Crittenden, Mabulla, & Mabulla, 2017c) to improve sleep intensity as a result of greater comfort and security at sleeping sites.

Greater quality sleeping environments may have been linked to changes to cognitive ability (Fruth & Hohmann, 1996; Samson & Nunn, 2015). This hypothesis has garnered recent support through research that investigated the link between sleep environment and cognitive performance in nonhuman great apes. For example, captive orangutan sleeping platform complexity, measured as an index of the number of material items available to construct a bed, covaried positively with reduced nighttime motor activity, less fragmentation, and greater sleep efficiency (Samson & Shumaker, 2013). In another study of captive apes undergoing experimental cognitive testing, sleep was shown to stabilize and protect memories from interference (Martin-Ordas & Call,

2011). Future research should investigate the relationship between cognition and sleep intensity and quality in more phylogenetically distant primates. If a link was established between cognition and sleep intensity in lemurs, for example, and not just humans and apes, it would suggest that the importance of sleep to cognition was an evolutionarily conserved trait within primates.

Sleep is a time of great risk for animals, potentially resulting in selection of safe sleep sites and greater vigilance when a safe site is unavailable (Nunn et al., 2010). We see signatures of this risk in our data, with lower sleep intensity when animals sleep outside, as compared to greater sleep intensity when sleeping indoors where it is safer. Lower sleep intensity in outdoor-sleeping lemurs may have been a result of abiotic (e.g., inclement weather, variation in temperature, and lunar phase) and biotic stimuli (e.g., calls from predatory animals). Our data suggest that wild lemurs would benefit from deeper, more intense sleep if they were to locate and use secure sleep sites, where they would be more protected from these threats. Therefore, we propose that sleeping site security is an essential component for regulation of sleep in lemuriformes Evidence for the importance of sleeping sites for sleep quality has been investigated in hominoids (Koops, McGrew, de Vries, & Matsuzawa, 2012; Samson & Hunt, 2012, 2014; Stewart, 2011; Stewart & Pruetz, 2013; Stewart et al., 2007) and cercopithecoids (Bert, Balzamo, Chase, & Pegram, 1975). This conclusion suggests that behaviors that influence sleeping site selection, thereby augmenting sleep quality, are evolutionarily conserved in primates and may be critically important for primates with diurnal activity patterns.

Humans appear to be characterized by deeper sleep than phylogenetically distant primates, but they may share with lemurs the flexibility in sleep phase. For example, controlled laboratory studies revealed that, when exposed to a short photoperiod, human sleep becomes unconsolidated (Wehr, 1999). Ethnographic work has demonstrated that a variety of cultures (across subsistence regimes) often exhibit nighttime activity and daytime napping (Worthman & Melby, 2002). Historical records document a segmented sleep pattern associated with European and equatorial preindustrial populations (Ekirch, 2016). Sleep measured in a small scale traditional equatorial agricultural society in Madagascar, without access to electricity, has been described as "segmented" or nocturnally biphasic with common noon-time napping (Samson et al., 2017d) and Hadza hunter-gatherer sleep has been demonstrated to be flexibly expressed in different social and ecological contexts (Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017a). These studies support the notion that ancestral human sleep was more flexible than typically experienced today by Western populations, suggesting perhaps even a biphasic, or polyphasic, pattern. This suggests that as sleeping site security increased, early hominins may have been permitted greater sleep intensity and flexibility in timing of sleep periods—which could have been a critical event marked by changes in sleep architecture, cognition, and waking performance.

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