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Sleep influences cognitive performance in lemurs

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Abstract

Primates spend almost half their lives asleep, yet little is known about how sleep influences their waking cognition. We hypothesized that diurnal and cathemeral lemurs differ in their need for consistent, non-segmented sleep for next-day cognitive function—including long-term memory consolidation, self-control, foraging efficiency, and sociality. Specifically, we expected that strictly diurnal *Propithecus* is more reliant on uninterrupted sleep for cognitive performance, as compared to four other lemur species that are more flexibly active (i.e., cathemeral). We experimentally inhibited sleep and tested next-day performance in 30 individuals of 5 lemur species over 960 total nights at the Duke Lemur Center in Durham, North Carolina. Each set of pair-housed lemurs experienced a sleep restriction and/or deprivation protocol and was subsequently tested in a variety of fitness-relevant cognitive tasks. Within-subject comparisons of performance on these tasks were made by switching the pair from the experimental sleep inhibited condition to a normal sleep environment, thus ensuring cognitive equivalency among individuals. We validated effectiveness of the protocol via actigraphy and infrared videography. Our results suggest that 'normal' non-disrupted sleep improved memory consolidation for all lemurs. Additionally, on nights of normal sleep, diurnal lemurs performed better in foraging efficiency tasks than cathemeral lemurs. Social behaviors changed in species-specific ways after exposure to experimental conditions, and self-control was not significantly linked with sleep condition. Based on these findings, the links between sleep, learning, and memory consolidation appear to be evolutionarily conserved in primates.

Keywords Lemur · Activity · Sleep · Cognition · Primate evolution

Introduction

Sleep is a complex behavior found widely throughout the animal kingdom (Basner et al. 2013; Siegel 2009; Vyazovskiy and Delogu 2014; Webb 1988) with probable functions that include brain and body metabolic homeostasis, glymphatic clearance, memory consolidation, and emotional processing and self-control (Albrecht 2012; Capellini et al. 2009; McNamara and Auerbach 2010; Meldrum et al. 2015; Nishida et al. 2009; Xie et al. 2013). In humans, a growing body of evidence demonstrates the importance of sleep duration and continuity of sleep to achieve adaptive levels of waking cognitive performance and multiple dimensions of neurobehavioral effectiveness, including executive function, working memory, attention, and emotional regulation (Durmer and Dinges 2005; Goel et al. 2009). Despite some initial studies on the links between sleep and cognition in non-human species, such as mice (Halassa et al. 2009; Nair et al. 2011) and apes (Martin-Ordas and Call 2011; Shumaker et al. 2014), the specific relationships between sleep and cognition remain a mystery in most mammals.

Primate sleep is characterized by several unique features. In a comparative study, Nunn et al. (2010) found that (1) nocturnal primates sleep longer than diurnal primate species, (2) primates show increased sleep intensity, i.e., deeper sleep staging with greater arousal threshold, and (3) primates

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generally consolidate sleep into a single inactive period. Similarly, in a study of captive lemurs, Samson et al. (2018) discovered that sleep-site security and comfort were linked with sleep depth in a diurnal species. In humans, sleep architecture shows several evolutionarily derived characteristics. Compared to other primates, for example, humans sleep less and have an unexpectedly high proportion of REM sleep within an overall shorter sleep duration (Nunn and Samson 2018; Samson and Nunn 2015). Subsequent analyses also revealed that the unique sleep architecture characterized by humans was the result of elimination of NREM (non-rapid eye movement), whereas REM (rapid eye movement) duration has remained constant even in the face of evolutionary pressure to reduce total sleep times (Nunn and Samson 2018).

Within primates, lemurs provide an important model system to investigate the linkage between activity pattern, sleep, and cognition because of high interspecies variation in each of these domains. Research on this subject is made all the more relevant due to recent studies that have challenged the historical classification of lemur activity patterns. For example, traditionally, species such as *Varecia rubra*, *V. variegata*, and *L. catta* have been classified as diurnal cathemeral species whereas *Eulemur* has been classified as cathemeral. Yet, *L. catta* has been documented to have shown some nocturnal activity at some research sites (Donati et al. 2013; LaFleur et al. 2014), in contrast to more strictly expressed diurnality at other sites (Sauther et al. 1999). Additionally, cathemeral behavior in wild *V. variegata* has been reported (Donati and Borgognini-Tarli 2006). In previous captive work, Bray et al. (2017) showed that *Propithecus coquereli* engaged in the least amount of nocturnal activity and that *Varecia* and *Lemur* deviated from the diurnal *Propithecus* pattern, which corroborated with previous captive work performed on five lemur species at the DLC (Rea et al. 2014). Based on these emerging findings, we classify *Lemur* and *Varecia* as cathemeral, and compare them specifically to *Propithecus*—an unequivocally diurnal species.

Thus, the goals of this study are (1) to assess the importance of sleep for lemur cognition, and (2) to investigate differences among species in the links between sleep and cognition for fitness-relevant metrics of cognitive performance, especially in relation to activity period. To pursue these goals, we inhibited sleep in different species of lemurs using either a sleep restriction (i.e., inhibiting sleep over a subset of a normally inactive period) or sleep deprivation protocol (i.e., a total inhibition of sleep throughout the normal inactive period). We then assessed next-day cognitive performance for concurrently tested lemurs along several axes of fitness-related tasks involving memory, self-control, foraging efficiency, and social behavior.

We tested two hypotheses. First, as found in humans (Bonnet and Arand 2005; Miller et al. 2008), we hypothesized that reduced sleep impacts multiple dimensions of cognition in lemurs. Thus, we predicted that sleep-restricted and/or -deprived diurnal lemurs would have (1) impaired memory, (2) reduced self-control, (3) impaired foraging efficiency, (4) reduced focus, and (5) exhibit a greater frequency of agonistic behaviors, as compared to lemurs experiencing concurrent, normal sleep. Second, we hypothesized that diurnal species rely on consolidated and high-quality nocturnal sleep for normal cognitive function, as compared to lemurs that show evidence for cathemerality. Thus, we predicted that the strictly diurnal sifakas (*Propithecus* sp.) would show greater impairments in cognitive functions following sleep restriction or deprivation, as compared to all the other species in our dataset, which show variable evidence for cathemeral activity.

Materials and methods

Husbandry and general methods

Throughout the study, we performed cognitive experiments and generated actigraphic data from five lemur species totaling 30 individuals, with a nearly equal sex ratio (males = 14, females = 16; see Supplemental Table 1). Most but not all of the same individuals were used for testing in both years; to deal with variable availability of animals, we controlled for *season* and *individual* in our statistical models (see below). Additionally, all rewards were species-appropriate foods established by previous research performed at the Duke Lemur Center (Rosati et al. 2014).

Activity was continuously recorded using MotionWatch 8® (CamNtech) tri-axial accelerometers, generating a dataset totaling 960 days (see Supplemental Table 1 for a summary of lemur species and number of lemurs per species that participated in the study). These actigraphic sensors are lightweight (7 g) and were attached to standard nylon pet collars. Subjects were monitored to ensure no adverse reactions to wearing the collar with the device; all individuals successfully acclimated to the collars within 2 h. Subjects wore the collars for 7–14 days, depending on season (2014 or 2015). Actigraphy was generated at 1-min epochs. Complete biographic information and details (such as age of the lemurs) on actigraphy protocol are available in Bray et al. (2017).

Using recent advances in accuracy in detecting sleep–wake states with actigraphy data (Stone and Ancoli-Israel 2011), we generated total sleep times for each species, similar to previous studies quantifying sleep in primates (Andersen et al. 2013; Barrett et al. 2009; Kantha and Suzuki 2006; Zhdanova et al. 2002). Specifically, the MotionWatch 8® classified each minute epoch as either active or inactive. With infrared videography, we assessed the actual behavior associated with various integer values

using video recorded from an AXIS® P3364-LVE Network Camera (Axis Communications, Lund, Sweden). Using a previously validated cutoff at integer value 4—with values of 0 clearly showing inactivity, whereas values of 4 or greater displaying wakeful activity—we classified epochs with an actigraphy value under 4 as sleep. Finally, we used infrared videography to confirm that our experimental protocols at night were effective at disrupting sleep; videography followed previous protocols used at the Duke Lemur Center (Bray et al. 2017).

For the duration of the study, adult individuals of each species were housed in sex-balanced, pair-bonded groups. All animals had unlimited access to water, and they received fresh fruit, vegetables, and Purina monkey chow daily. Cognitive tasks were performed in the morning prior to feeding to ensure individuals were food motivated for task completion. 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.

Sleep restriction and deprivation

For the sleep restriction protocol, we used an experimental design counter-balancing two sets of paired lemurs (total $n = 4$ from each species) that underwent 2 weeks of simultaneous testing. During the same night, the experimental pair experienced a sleep restriction or deprivation protocol, while the other pair (housed in a different wing) experienced normal sleeping conditions. The experimental condition in the sleep restriction phase lasted for 1 week; in the sleep deprivation phase, the experimental condition lasted for 2 days. After the completion of a week of cognitive tasks, the pair's sleeping conditions were then switched the following Monday. Thus, the previous pair of lemurs that slept in the experimental conditions for week one switched to normal conditions in week two (and vice versa). The purpose of this counter-balanced design was to ensure that individuals experienced both conditions, thus allowing generation of within-subject (i.e., baseline) data and to ensure cognitive equivalency among individuals.

The sleep restriction protocol was used in season one (September–November 2014). In this phase, lemurs experienced 4 h (from 20:00 to 00:00) of audio playbacks of < 15 s duration. Every 15 min, the subjects were exposed to a pool of 16 random playbacks (range = 60–100 dB) that included sounds familiar to the animals, such as daytime DLC ambient noise, falling food dishes, cage doors closing, and inclement weather.

The sleep deprivation protocol was used in season two (September–November 2015). For this more extreme form of sleep interruption, lemurs experienced 10 h (from 20:00 to 06:00) of audio playbacks of < 30 s duration played every 5 min. The additional protocol was added to increase the intensity of experimental stimulus to capture the degree to which altered sleep influences lemur cognition. The playback categories were identical to the sleep restriction procedure.

In addition to actigraphy, animals were monitored via infrared videography and sound pressure data loggers. This was done to ensure that the stimuli were effective in keeping animals awake throughout the time of sampling, and to monitor adverse behavioral responses when exposed to the stimulus over time. Sleep restriction was performed for no longer than four consecutive nights. Sleep deprivation was performed for no longer than two consecutive nights, thus we reduced the experiment from 2 (during season one) to 1 week (in season two).

Behavioral assessment

The goal of the behavioral analysis was to observe subjects for 90 min during the day following a night of sleep restriction or normal sleep. Specifically, we comparatively examined the difference in frequency of aggressive and affiliative behaviors relative to experimental condition. The observational sessions were performed in season one in sleep restriction and normal sleep conditions.

Memory, foraging, and self-control tasks

The goal of the memory problem was for the subject to remember where a reward (preferred food item) was hidden after experiencing either sleep restriction (i.e., experimental condition) or normal sleep (i.e., control condition). Specifically, we used a previously published testing paradigm (Rosati et al. 2014). In this protocol, the animals observe the location of a food source, and then are tested on their memory of this location 4 days later. We implemented this protocol on a blue T-shaped platform (136-cm-long entry wing; 122-cm cross-wing; 72 cm high). Affixed to the cross-wings were opaque cups (6 cm deep) that were baited with food rewards. A subject first learned that one wing of a T-shaped platform (Fig. 1a; see supplemental for detailed information on the memory task) always provided food. The test session followed after four nights of consecutive sleep restriction or four nights of normal sleep, where we examined whether lemurs would recall which location had previously been baited on the platform.

For the foraging task, we examined the ability of the lemurs to discriminate between objects they could forage on a rock-board (i.e., a surface analogous to a wild, obstacle environment; Fig. 2b). The primary goal of the task was to assess the subject's ability to recover three high-value food rewards, over alternative low-value food rewards (chow) and false food rewards (i.e., wads of paper of similar size and color to the high-value food reward). As subjects

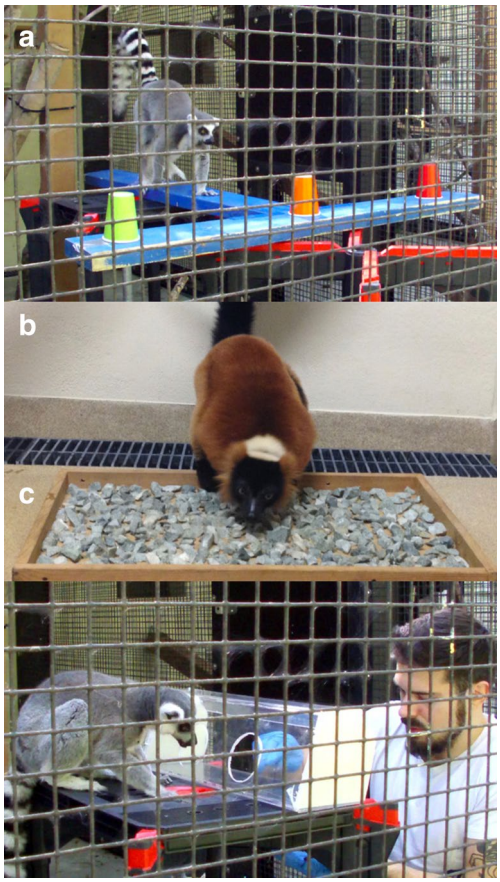

Fig. 1 Apparatus for each task. **a** The memory apparatus with a *L. catta* subject. **b** The foraging efficiency apparatus with a *V. rubra* subject. **c** The self-control apparatus with a *L. catta* subject

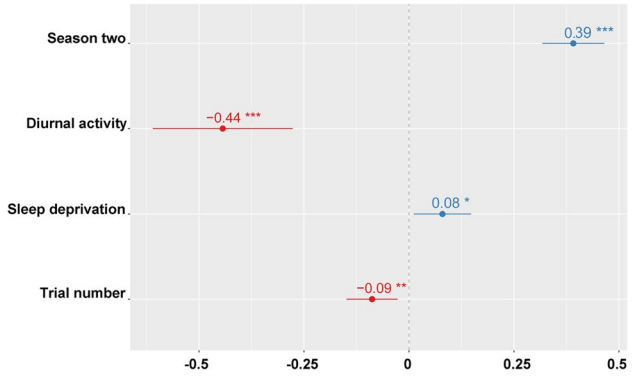

Fig. 2 A standardized fixed effects plot (with the number of search attempts needed to finish the task) illustrating the negative influence of poor sleep on lemurs. Sleep restriction/deprivation (vs. normal sleep) and the 2015 season two (vs. 2014 season 1) are positive predictors (right of zero) of overall less efficient foraging (i.e., greater number of search attempts). In contrast, trial number and diurnal activity patterns are negative predictors (left of zero) of overall foraging efficiency. Asterisks indicate level of significance (*$p < 0.05$–0.01, **$p < 0.01$–0.001, ***$p < 0.001$)

foraged, the number of total foraging events was observed and recorded until task completion when all three high-value food rewards were obtained (see supplemental for detailed information on foraging task). The test sessions were performed the morning after nights where they either experienced normal, restricted (season one), and deprived sleep (season two).

The self-control task assessed the ability of the lemurs to inhibit a prepotent motor response using a previously published paradigm (Diamond 1990; MacLean et al. 2014). Specifically, the subject was required to successfully retrieve a food reward that was placed behind a plexiglass wall; this wall contained two holes for accessing the reward (Fig. 1c; see supplemental for detailed information on the self-control task). To succeed, the subject must inhibit the impulse to reach for the food directly—thereby bumping into the plexiglass—in favor of a detour response to retrieve the item successfully from behind the wall using one of the two holes. The test sessions were performed the morning after nights in which subjects experienced normal sleep, restricted sleep (season one), or deprived sleep (season two).

Data analysis

Statistical analyses on this longitudinal study were conducted using R version 3.1.3 (Team, 2016), with a sample size of 960 days (i.e., circadian periods) for analysis. To assess species-specific behavioral responses relative to sleep restriction/deprivation, we used X^2 analyses. Specifically, we determined the frequency of aggressive and affiliative behaviors in both the sleep-limited and normal sleep conditions for each genus, and compared the expected values (i.e., the null hypothesis) between the observed values.

To assess the influence of sleep restriction protocols on lemurs, we used functional linear modeling (FLM) with the *actigraphy* package (Shannon et al. 2015) to assess deviations from normal (control) activity patterns before and after the switch between sleep restriction/deprivation and normal sleep. 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 assess differences in sleep–wake activity between normal sleep and sleep-limited (experimental) groups. Analyses were conducted within species using a 24-h cycle. At time points where the observed F statistic was above the threshold of significance, it was concluded that the experimental and control groups differed in mean circadian activity patterns. The number of times the groups differed (termed here as a deviation from the normal sleep condition) were summed to assess intra-specific responses to the experimental sleep condition.

For each task, we built a linear mixed effects model for our response variables using the *lme4* package (Bates et al. 2015). For the memory task, we assessed the predictors of two response variables: (1) *correct answers* (choosing the cup with the reward on the test trail) and (2) *focus* (total duration to trial completion from start to finish). We used the natural log of the focus data, due to its non-normal distribution. As a fixed effect in the model, we used *trial number* to control for repeated measures of the same subjects' *activity pattern* (diurnal *Propithecus* or cathemeral for all other lemurs) and *experimental condition* (normal sleep or sleep restricted). To determine whether the relationship between activity pattern and cognition was different between normal and sleep restriction states, we included an interaction effect between activity pattern and experimental condition. The foraging efficiency task and the self-control task used identical response and predictor variables, except that as a fixed effects in the model, we used *season* as a fixed effect in these models because (unlike the memory task) we had multiple seasons, and the fixed effect captured differences in the intensity of sleep limitation across seasons (i.e., season one involved sleep restriction and season two used sleep deprivation). For all models, we included *subject* as a random effect, and we used the *MuMIn* package to conduct conditional model averaging for all models with $\Delta\text{AIC} < 10$ (Bartoń 2015). Statistical inferences were made using 95% confidence intervals on standardized coefficient estimates with shrinkage, focusing on those coefficients with confidence intervals that excluded zero.

Results

Sleep manipulation and activity patterns

Based on the actigraphic FLM analysis, the sleep restriction protocol revealed that sleep-restricted *Propithecus* were characterized by the greatest number of significant circadian deviations compared to normal sleep conditions, suggesting that disruptions to sleep in this diurnal species were most impactful on activity periods. In other words, when diurnal lemurs were compared between the control (normal) and experimental (restricted) sleep conditions, they demonstrated a greater number of periods that significantly differed in activity. For an illustration of baseline, regular species–species circadian activity, see our previous work (Bray et al. 2017). *Eulemur* experienced one significant alteration to their normal pattern, whereas *Propithecus* experienced five significant alterations. *Lemur* experienced three significant alterations and *Varecia* experienced two significant alterations from the normal sleep conditions. Moreover, daytime periods after sleep deprivation, particularly between 07:00 and 08:00, showed a recovery period of less overall activity in diurnal *Propithecus*, whereas we found no evidence for a recovery period in cathemeral *Eulemur*, *Lemur*, and *Varecia*. Thus, sleep restriction protocols affected post-protocol sleep–wake activity in all subjects but these effects were expressed in species-specific ways.

The sleep deprivation experiment revealed similar, but more extreme, patterns. Sleep-deprived diurnal *Propithecus* were characterized by the greatest number of significant deviations from normal sleep conditions. By the maximum critical value threshold, FLM analysis revealed that *Eulemur* experienced one significant alteration to their normal pattern, whereas *Propithecus* experienced three significant alterations. *Lemur* experienced one significant alteration and *Varecia* experience no significant alterations from the 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 periods in cathemeral *Eulemur*, *Lemur*, and *Varecia*. In sum, both the sleep restriction and sleep deprivation altered circadian patterns in lemurs, but to different extents, with the deprivation protocol having a more profound impact on circadian activity (Supplemental Table 2).

Sleep and behavior

Overall, the Pearson's X^2 test data showed a significant association between aggressive behavior frequency and sleep restriction ($X^2 = 12.02$, $df = 3$, $p = 0.007$), with sleep restriction leading to more aggression. However, we found no significant association between affiliative behaviors and sleep restriction ($X^2 = 5.30$, $df = 3$, $p = 0.15$). Within-species comparison of aggressive behaviors (Fig. 3) revealed that only *Eulemur* showed no significant difference between experimental conditions ($X^2 = 1.8$, $df = 3$, $p = 0.18$), whereas *Lemur* ($X^2 = 19.3$, $df = 3$, $p < 0.001$) and *Propithecus* ($X^2 = 9.2$, $df = 3$, $p = 0.002$) were less aggressive after sleep-restricted nights and *Varecia* ($X^2 = 3.8$, $df = 3$, $p = 0.05$) was more aggressive after sleep-restricted nights. Within-species comparisons of affiliative behaviors revealed that only *Lemur* showed less affiliative behavior after sleep-restricted nights ($X^2 = 16.00$, $df = 3$, $p < 0.001$), whereas *Eulemur* ($X^2 = 2.6$, $df = 3$, $p = 0.10$), *Propithecus* ($X^2 = 1.6$, $df = 3$, $p = 0.12$) and *Varecia* ($X^2 = 0.20$, $df = 3$, $p = 0.67$) did not demonstrate a significant difference in affiliative behavior between the experimental conditions.

Sleep, memory, foraging, and self-control

Memory task *focus* (time to completion of the trial) was not found to be influenced by any of the predictor variables, although sleep restriction ($\beta \pm \text{SE} = 0.11 \pm 0.08$, $Z = 1.33$, $\text{CI} = -0.344$ to 0.122) was the most important variable in

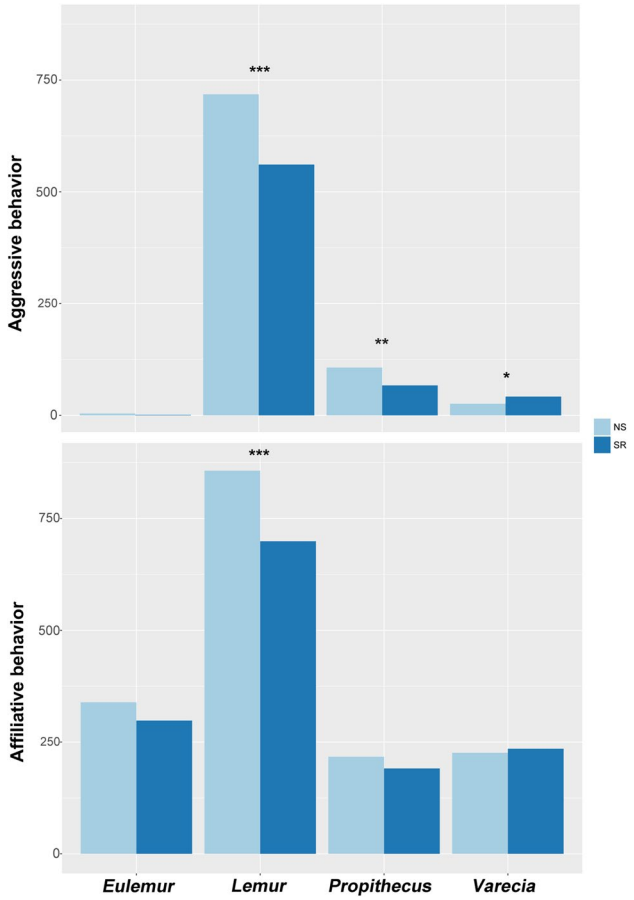

Fig. 3 Sleep and behavior in lemurs. Within-species comparisons of aggressive and affiliative behavior between normal sleep and sleep-restricted conditions showed that only *Lemur* was less affiliative after sleep restriction (*$p < 0.05$–0.01, **$p < 0.01$–0.001, ***$p < 0.001$; light bars show behavior after normal sleep, i.e. NS, while darker bars show behavior after sleep-restricted nights, SR)

the model (importance = 0.56). Based on the standardized coefficient in the model, *correct answers* were significantly impaired by sleep restriction for all lemurs (Table 1). Moreover, *sleep restriction* was the most important predictive factor of *correct answers* (importance = 0.96) in the model.

Foraging task *focus* (time to completion to the trial) improved (i.e., was found to be shorter) by *trial number* ($\beta \pm SE = -0.21 \pm 0.03$, $Z = 6.04$, CI = −0.276 to −0.141). In contrast, *focus* was found to be positively influenced by *season two*, when the more intense sleep intervention took place ($\beta \pm SE = 0.10 \pm 0.04$, $Z = 2.20$, CI = 0.011–0.182), that is, time to completion of the task was longer in duration during the second season but shorter in duration with greater numbers of performed trials. *Trial number* was the variable that was best supported in the models (importance = 1). Based on the standardized coefficient in the foraging efficiency model, *foraging efficiency* was significantly better with greater *trial number* and by diurnal lemurs, but impaired by sleep restriction/deprivation and in the second season (Table 2). After controlling for experimental condition, the coefficient for *diurnal activity pattern* had confidence intervals that did not include zero, indicating that activity pattern influenced foraging efficacy for *Propithecus.* Foraging efficiency was impaired by sleep restriction and deprivation. Moreover, this impairment was especially significant for diurnal lemurs, as they exhibited decreased foraging efficiency after nights where they were sleep deprived (Fig. 2).

Self-control task *focus* (time to completion to the trail) improved (i.e., was found to be shorter) by *trial number* ($\beta \pm SE = -0.21 \pm 0.03$, $Z = 6.02$, CI = −0.275 to −0.140), *normal sleep* ($\beta \pm SE = -0.08 \pm 0.04$, $Z = 2.13$, CI = −0.157 to −0.007), and *season two* ($\beta \pm SE = -0.18 \pm 0.05$, $Z = 3.47$, CI = −0.291 to −0.081), that is, all of the aforementioned predictor variables decreased *focus*, with *season two* and *trial number* being ranked most important (importance = 1). Based on the standardized coefficient in the self-control model, *self-control* was significantly improved by *season* and by *trial number* but not by *experimental condition* or *activity pattern* (Table 3). Specifically, *diurnal activity pattern* and *normal sleep* confidence intervals included zero and, therefore, did not influence *self-control* outcomes.

Discussion

Our primary questions were (1) whether sleep deprivation has a demonstrable effect on subsequent sleep–wake patterns and (2) whether lemur sleep restriction and sleep deprivation cause significant behavioral changes and cognitive impairment in diurnal lemurs. In general, we found that sleep deprivation had the most significant effects, and these effects

Table 1 The effect of predictor variables on long-term memory

Predictor	Estimate and SE	Confidence interval	Importance
Experimental condition	−1.11 (0.39)	(−1.890, −0.321)	1st = 0.96
Activity	0.14 (0.65)	(−1.164, 1.441)	3rd = 0.33
Trial number	− 0.51 (0.38)	(−1.257, 0.235)	2nd = 0.47
Activity × experimental condition	0.18 (0.54)	(−0.896, 1.260)	4th = 0.08

Cathemeral is the reference category for *activity* and *normal sleep* is the reference category for *experimental condition*. Positive coefficients indicate increased correct answers

Table 2 The effect of predictor variables on foraging efficiency

Predictor	Estimate and SE	Confidence interval	Importance
Season two	0.40 (0.04)	(0.327, 0.482)	1st = 1
Sleep restriction	0.07 (0.03)	(0.004, 0.137)	3rd = 0.82
Diurnal	− 0.46 (0.08)	(− 0.624, − 0.293)	1st = 1
Trial number	− 0.09 (0.03)	(− 0.148, − 0.026)	2nd = 0.95
Activity × experimental condition	− 0.05 (0.05)	(− 0.140, 0.041)	4th = 0.32

Cathemeral is the reference category for *activity* and *normal sleep* is the reference category for *experimental condition*. Positive coefficients indicate greater number of search attempts and thus less foraging efficiency

were more profound on diurnal lemurs' sleep–wake activity, that is, *Propithecus*' circadian patterns were more strongly affected than the other species' and they were the only species to show a recovery period, with downstream effects on cognition (i.e., see foraging efficiency below). Specifically, we found support for the first hypothesis in some (but not all) cognitive dimensions tested in this study. For example, we found that long-term memory was impaired by sleep restriction for all lemurs, a result that was independent of activity pattern (Table 1). Additionally, foraging efficiency was influenced both by sleep restriction and deprivation. Yet, counter to the predictions, self-control was not significantly influenced by sleep restriction and deprivation (Table 3). In support of the second hypothesis (that diurnal species rely on less interrupted, high-quality nocturnal sleep for normal cognitive function), we found that foraging efficiency outcomes were strongest for diurnal *Propithecus* (Table 2 and Fig. 2) compared to cathemeral species. Finally, behavior was influenced by sleep restriction, but in species-specific ways. *Varecia* displayed a greater frequency of aggressive behaviors after sleep restriction, while *Lemur* and *Propithecus* exhibited a lower frequency of aggressive behaviors; additionally, *Lemur* displayed a greater number of affiliative behaviors after normal sleep (Fig. 3).

Given the length and complexity of both the study and working with captive primates, there were limitations to this study. As noted above, some subjects took part in one season but not the other. We attempted to have the same individuals in both seasons, but this was not possible due to DLC practice of cycling lemurs to different environments; as noted in "Materials and methods", to address the potential for 'practice effects' to influence the outcomes, we included trial number as a factor in the models. Moreover, although EEG (electroencephalography) is the 'gold standard' for measuring sleep, it presents ethical challenges due to the invasive nature of implanting electrodes on the surface area of the brain and the strong autogrooming instinct that prohibits electrodes being placed on the skin; therefore, we used non-invasive actigraphy as an ethical and scientifically validated alternative. Finally, with respect to sample size, we acknowledge that lack of significance for some main effects, such as sociality, may reflect limited number of individuals or species.

A number of studies have investigated sleep and cognitive performance in humans (Durmer and Dinges 2005; Goel et al. 2009; Hobson and Pace-Schott 2002; Walker and Stickgold 2006) and in captive lab animals (Gruart-Masso et al. 1995; Smith et al. 1998; Youngblood et al. 1999). From these studies, a general process of learning and behavioral modification is emerging. Newly attained information is not immediately stored at the time of learning in its final form, as memories undergo a series of transformations over time; during this time, they are integrated into a pre-existing set of mnemonic representations, or pruned to be eliminated. This process is known as memory consolidation, and sleep has been implicated as a critical factor in time-dependent processes of memory consolidation (Peigneux et al. 2001). Sleep's role in memory consolidation has been demonstrated in a wide variety of taxa, suggesting that it is evolutionarily conserved across species (Walker and Stickgold 2004). For example, rodent studies have provided evidence in support of hippocampus-dependent tasks that are conditioned forms of learning (Ambrosini et al. 1993; Beaulieu and Godbout 2000; Datta 2000), while another study found that memory was stabilized in captive apes undergoing experimental cognitive testing after periods of sleep (Martin-Ordas and Call 2011). This previous body of work is consistent with our results showing that, despite activity pattern, sleep influences memory in lemurs.

Table 3 The effect of predictor variables on self-control

Predictor	Estimate and SE	Confidence interval	Importance
Season two	− 0.93 (0.25)	(− 1.426, − 0.436)	1st = 1
Experimental condition	0.09 (0.19)	(− 0.292, 0.471)	3rd = 0.33
Activity	0.46 (0.33)	(− 0.189, 1.111)	2nd = 0.51
Trial number	− 0.66 (0.18)	(− 1.019, − 0.298)	1st = 1
Activity × experimental condition	− 0.25 (0.27)	(− 0.779, 0.272)	4th = 0.07

Cathemeral is the reference category for *activity* and *normal sleep* is the reference category for *experimental condition*. Positive coefficients indicate increased self-control

MacLean et al. (2014) showed that absolutely larger brains confer greater cognitive advantages than relatively larger brains, suggesting that as the total number of neurons increases so too does modularization, thus facilitating new cognitive networks. These authors also found that anthropoid primates were the best performing species in the self-control cylinder task identical to this study. Although an important aspect of our understanding of comparative cognition, we found that self-control was not influenced by sleep restriction or deprivation in lemurs. It may be that the primate reliance on sleep quality to regulate self-control originated after the origin of anthropoids—with larger absolute brain size—specifically with the advent of the Catarrhini approximately 31.6 mya (Perelman et al. 2011).

Inhibition influences the expression of agonistic and affiliative behaviors, and sleep in humans has been implicated in emotional regulation (Walker 2009). Our results suggest interesting links between normal sleep and experimentally restricted sleep in behavioral outcomes for lemurs. Interestingly, *L. catta* and *Propithecus* showed reduced aggressive behaviors, which we interpret as species-specific fatigue responses to sleep restriction. However, *L. catta*, the most social of species given the largest group sizes in the wild (Sauther et al. 1999), behaved more affiliatively after normal sleep nights. *Varecia* was the only species that confirmed predictions that sleep restriction would increase aggressive behaviors.

Cathemeral behavior in wild lemurs has been proposed to provide several ecological advantages to hyper-variable patterns of temperature and precipitation (Donati and Borgognini-Tarli 2006; Wright 1999), reduced predation risk (Colquhoun 2006), and reduced competition from sympatric species (Curtis and Rasmussen 2006; Curtis et al. 1999). A potential cost associated with cathemerality involves the sensory and morphological adaptations that are needed to navigate both diurnal and nocturnal environments. Unlike cathemeral lemurs that forage in either the day or night, diurnal *Propithecus* would be particularly reliant upon high-quality, non-segmented nocturnal sleep periods due to the temporal restriction of foraging having to take place during the diurnal circadian period. This may explain why the effect of the normal sleep condition had the strongest positive influence on *Propithecus*' foraging efficiency.

In summary, evidence for the importance of sleep in primate cognition is an underexplored topic (Nunn et al. 2010; Samson and Nunn 2015), and based on this research we maintain that it has important implications for primate evolution. We propose that (1) uninterrupted, non-segmented sleep is particularly important for diurnal primates when foraging, but less so for other lemurs, (2) reliance on sleep for memory consolidation is a conserved trait characterized by lemurs in general, and (3) self-control has not been demonstrated to be linked to sleep in lemurs but affiliative and agonistic behavior is influenced by sleep.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed in the study involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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