Received: 6 July 2017 | Revised: 17 January 2018 | Accepted: 18 January 2018

DOI: 10.1002/ajpa.23427

RESEARCH ARTICLE

WILEY American Journal of PHYSICAL ANTHROPOLOGY

Sleep in a comparative context: Investigating how human sleep differs from sleep in other primates

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Funding information
National Science Foundation, Grant/Award Number: BCS-1355902

Abstract

Objectives: Primates vary in their sleep durations and, remarkably, humans sleep the least per 24-hr period of the 30 primates that have been studied. Using phylogenetic methods that quantitatively situate human phenotypes within a broader primate comparative context, we investigated the evolution of human sleep architecture, focusing on: total sleep duration, rapid eye movement (REM) sleep duration, non-rapid eye movement (NREM) sleep duration, and proportion of sleep in REM.

Materials and Methods: We used two different Bayesian methods: phylogenetic prediction based on phylogenetic generalized least squares and a multistate Onrstein-Uhlenbeck (OU) evolutionary model of random drift and stabilizing selection.

Results: Phylogenetic prediction confirmed that humans sleep less than predicted for a primate of our body mass, predation risk, brain size, foraging needs, sexual selection, and diet. These analyses further revealed that humans pack an unexpectedly higher proportion of REM sleep within a shorter overall sleep duration, and do so by reducing NREM sleep (rather than increasing REM). The OU model generally confirmed these findings, with shifts along the human lineage inferred for TST, NREM, and proportion of REM, but not for REM.

Discussion: We propose that the risks and opportunity costs of sleep are responsible for shorter sleep durations in humans, with risks arising from terrestrial sleep involving threats from predators and conspecifics, and opportunity costs because time spent sleeping could be used for learning, creating material objects, and socializing.

KEYWORDS
cognition, human evolution, phylogenetic comparative methods, phylogeny, sleep architecture

1 | INTRODUCTION

All mammals studied thus far sleep, but species vary markedly in the duration of sleep that they exhibit in a typical 24-hr period (McNamara, Capellini, Harris, Nunn, Barton, & Preston, 2008). Elephants, for example, sleep on average 2 hr per day in the wild (Gravett et al., 2017), while some bats sleep nearly 20 hr per day (Zepelin and Rechtschaffen, 1974). Ecological factors are likely to play a role in explaining this variation (Capellini, Barton, McNamara, Preston, & Nunn, 2008a; Lesku, Roth II, Amlaner, & Lima, 2006; Siegel, 2004). For example, sleep might have negative effects on survival by exposing individuals to a greater risk of predation. Across mammals, increased risk of predation at the sleep site is associated with shorter sleep durations (Allison & Cicchetti, 1976; Capellini et al., 2008a; Lesku et al., 2006). Similarly, sleep durations are shorter in species that have high metabolic rates for their body size, consistent with foraging constraints that limit time available for sleep (Capellini, Barton, McNamara, Preston, & Nunn, 2008b). A wide array of functional benefits of sleep have been proposed, including memory consolidation, energy conservation, and maintaining effective immune function (Lesku et al., 2006; Meddis, 1983; Preston, Capellini, McNamara, Barton, & Nunn, 2009; Stickgold, 2005; Zepelin, Siegel, & Tobler, 2005).

Broad comparative studies reveal general patterns that are essential for testing adaptive hypotheses (Harvey & Pagel, 1991; Nunn,

[†]Manuscript for Special Issue from "Primate Sleep Symposium" at IPS 2016

2011). Sleep scientists have appreciated the importance of interspecific comparisons for understanding sleep, with a long-standing set of studies investigating many of the proposed costs and benefits of sleep (Allison & Cicchetti, 1976; Campbell & Tobler, 1984; Elgar, Pagel, & Harvey, 1988; Herculano-Houzel, 2015; McNamara, Barton, & Nunn, 2010). Two research groups (Capellini et al., 2008a; Lesku et al., 2006) have independently investigated the phylogenetic, ecological, and life history drivers of "sleep architecture," which is defined as the quantitative structure and patterning of sleep and includes measures such as total sleep time (TST), durations of rapid eye movement (REM) and non-REM sleep (hereafter, NREM), the cycling of NREM and REM (cycle length), and the distribution of sleep (i.e., monophasic, with one sleep bout, or polyphasic, with multiple sleep bouts) throughout the 24-hr period. In addition to the comparative analyses of predation risk discussed above, these research groups have found that: the proportion of REM sleep covaries positively with brain size (Lesku et al., 2006); counts of circulating immune cells covary positively with sleep durations (Preston et al., 2009); and increasing metabolic rate (relative to body mass) covaries with shorter sleep durations (Capellini et al., 2008b). Within primates, nocturnality was found to be associated with longer sleep durations (Nunn, McNamara, Capellini, Preston, & Barton, 2010).

Comparative research helps to identify the general predictors of some phenotypic characteristics—such as sleep, brain size, or life history—and thus plays a key role in testing adaptive hypotheses (Harvey & Pagel, 1991; Nunn, 2011). However, biologists are also often interested in species that depart strongly in phenotype from other close relatives; examples include seemingly bizarre animals such as the binturong (*Arctictis binturong*, a large-bodied, frugivorous, and arboreal carnivore of Asia), the kakapo (*Strigops habroptilus*, a herbivorous, ground-dwelling parrot of New Zealand that is active at night), or the aye-aye (*Daubentonia madagascarensis*, an insectivorous lemur that appears to fill the niche of woodpeckers, which are absent in Madagascar). Perhaps no single lineage has received as much scientific investigation into "uniqueness" as the lineage separating humans from other primates. Humans have been described as a "spectacular evolutionary anomaly," (Hill, Barton, & Hurtado, 2009; Vitousek, 1997), and one approach to investigating the ways in which humans are unique is through comparative analyses of phenotypic variation (Nunn, 2011).

Comparative methods make it possible to rigorously investigate evolution along a single branch on phylogeny (McPeek, 1995; Nunn & Zhu, 2014; Revell, 2008), including the human lineage (Jaeggi et al., 2017; Nunn, 2011; Organ, Nunn, Machanda, & Wrangham, 2011; Vining & Nunn, 2016). Some of these methods, for example, integrate interspecific variation and phylogeny to predict human phenotypes, and then test whether observed human phenotypes depart from this expectation (Nunn & Zhu, 2014). This type of analysis involves phylogeny-based prediction followed by an "outlier test" to determine whether human phenotypes differ from what is predicted based on evolutionary variation across species. While this general approach has long been used, for example by detecting whether humans depart from allometric relationships (e.g., Harcourt, Harvey, Larson, S. G., & Short, 1981; Martin & Harvey 1985), newer versions of the method incorporate phylogeny into both the estimation of allometric relationships and the prediction of the human phenotype by using phylogenetic generalized least squares (PGLS, Martins & Hansen, 1997; Symonds & Blomberg, 2014). Other new methods enable the investigation of adaptive regimes on a phylogeny (Uyeda & Harmon 2014), with changes in these regimes consistent with major shifts, including on terminal branches of the tree (e.g., Vining & Nunn 2016). This type of analysis fits an Ornstein-Uhlenbeck (OU) model of evolution, which incorporates both stabilizing selection and drift (Butler & King, 2004; Hansen, 1997).

Previously, we conducted an outlier analysis of sleep evolution along the human lineage (Samson & Nunn, 2015). Using the phylogenetic prediction method (Nunn & Zhu, 2014), our analyses used variation in body mass, interbirth interval, activity period, endocranial volume (ECV), and phylogeny to predict the duration of human sleep. We found that humans sleep substantially less than predicted based on these characteristics in primates, suggesting that additional, unmodeled factors are involved in the evolution of human sleep, such as predation risk at the sleep site or foraging needs (Capellini et al., 2008a; Lesku et al., 2006). Additional analyses using the same general approach further revealed that humans exhibit a higher proportion of REM sleep. From these analyses, we proposed that human sleep has been shaped by risks and opportunity costs, with risks involving increased predator and conspecific threats from sleeping on the ground, and opportunity costs of sleep involving time lost for building and maintaining social bonds, and fewer opportunities for individual or social learning (Samson & Nunn, 2015).

Here, we significantly extend the initial analyses of Samson and Nunn (2015) in the following ways. First, we investigate a broader set of predictor variables and additional primate species (Samson, Bray, & Nunn, in press), as this may disentangle the factors that led to changes in sleep duration along the human lineage, and thus enable us to better predict human sleep duration based on ecological factors that are shared with other primates (rather than being unique to humans). For example, if greater predation risk in terrestrial settings is the primary driver of shorter human sleep, then incorporating this ecological variable into the statistical model should lead to better prediction of human sleep. Second, we investigate the evolution of REM and NREM sleep durations, as it was unclear if the increased percentage of REM sleep in humans that was found previously (Samson & Nunn, 2015) is due to increased REM duration, decreased NREM duration, or some combination thereof. We therefore use the expanded data to predict sleep characteristics involving TST, proportion of TST in REM, and the durations of NREM and REM. Third, we implement better assessment of the predictive models by applying PGLS phylogenetic prediction to all species in the dataset. If most primates are identified as exceptional based on these analyses, this would indicate that the model itself is not very robust, and would significantly devalue our efforts to make inferences in humans. Finally, by additionally using the OU model to investigate the evolution of sleep, we provide better understanding of evolutionary changes throughout primate evolution, including on the human lineage.

2 | MATERIALS AND METHODS

2.1 | Data on sleep, ecology, behavior, and morphology

As measures of sleep, we compiled data on TST, NREM, REM, and proportion of REM for primates. Data primarily come from the Phylogeny of Sleep database (https://www.bu.edu/phylogeny/, McNamara et al., 2008), which has been used in previous comparative research (Capellini et al., 2008a; Capellini, Nunn, McNamara, Preston, & Barton, 2008c; Nunn et al., 2010). We used species level means of sleep quotas from only adult aged nonhuman primates, and used the "high-quality" subset of data in Capellini et al. (2008a). To these data, we added staging of sleep in the orangutan (*Pongo pygmaeus*) based on videography (Samson & Shumaker, 2013), and data on TST in six species of lemurs based on actigraphy (Samson et al., in press, this issue). For analyses of sleep stages—that is, REM and NREM—we did not use estimates based on actigraphy. We do include estimates of REM and NREM for the orangutan in our main analyses, but repeated those analyses after omitting this species, given that sleep stage data for the orangutan were not obtained using EEG. We further note that all sleep data come from captive primates, which might influence sleep duration due to lack of predation and food stress or increased social stress; however, the consistency of human sleep across different environments (see below), coupled with good evidence for phylogenetic signal in sleep phenotypes across species (Capellini et al., 2008a), suggests that species typical sleep durations can be obtained from captive data, which is also currently the only way to obtain data on REM and NREM sleep. The data on sleep phenotypes is provided in Table 1, with the complete dataset, including ecological and phenotypic variables, available in the Online Supporting Information Materials.

In terms of variables investigated in the PGLS, we include: dietary variables (folivory and number of dietary components), body mass, and day journey length to assess whether animals with greater foraging needs sleep less (e.g., a folivorous, larger-bodied or omnivorous primate may need more foraging time, and body mass covaries with life history traits that may influence sleep, Capellini et al., 2008a); occupation of an open or terrestrial habitat, as a measure of increased predation risk that is expected to reduce sleep durations; group size as a variable that increases or decreases sleep through its reduction in predation risk (increasing sleep) and/or through night time disruption from conspecifics (reducing sleep, Capellini et al., 2008a); activity period, based on previous findings that nocturnal species sleep less (Nunn et al., 2010); ECV as a proxy for neurological needs for sleep (Capellini et al., 2008a; Lesku et al., 2006); and sexual size dimorphism (SSD) as a variable that captures competition for mates, with increasing competition expected to reduce sleep times (e.g., Lesku et al., 2012). While some hypotheses have considered the importance of developmental mode in sleep architecture (especially REM, see Capellini et al., 2008a), we do not have appropriate data on juvenile sleep and brain growth for testing these hypotheses. We provide more details on the data in what follows.

Data on ECV were taken mainly from Isler et al. (2008). We used the same value for both species of ruffed lemurs (*Varecia*), and also for brown lemurs (*Eulemur macaco*), and black lemurs (*E. flavifrons*), as these pairs of sister species are closely related and were not subdivided in Isler et al. (2008). For sifakas (*Propithecus coquereli*), we used an average from all *Propithecus spp*. available in Isler et al. (2008). ECV for *Homo sapiens* comes from Robson and Wood (2008). For most species, we obtained mean male and female body mass estimates from Smith and Jungers (1997). For *Eulemur macacao*, *E. flavifrons*, Guinea baboons (*Papio papio*), fork-marked lemurs (*Phaner spp*.), and *Varecia spp*., values were taken from primary sources listed in Rowe and Meyers (2011), due to missing data or taxonomic uncertainty in Smith and Jungers (1997). To quantify sexual size dimorphism, we followed the two-step

TABLE 1 Data on sleep phenotypes used in the analyses

Species	TST	REM duration	NREM duration
Aotus trivirgatus	16.97	1.82	15.15
Callithrix jacchus	9.5	1.61	7.9
Chlorocebus aethiops	9.77	0.65	9.044
Erythrocebus patas	10.9	0.86	9.99
Eulemur coronatus	8.96		
Eulemur flavifrons	8.84		
Eulemur macaco	9.65	0.84	8.81
Eulemur mongoz	11.9	0.72	11.16
Homo sapiens	7	1.56	5.41
Lemur catta	11.05		
Macaca arctoides	9	1.38	7.65
Macaca fascicularis	10.46	1.71	8.74
Macaca mulatta	10.23	2.05	8.19
Macaca nemestrina	9.88	0.99	8.89
Macaca radiata	9.1	1.05	8.06
Macaca sylvanus	11.74	1.07	10.68
Microcebus murinus	15.36	0.99	14.37
Pan troglodytes	9.67	1.45	8.22
Papio anubis	9.84	1.39	8.45
Papio hamadryas	9.83	1.27	8.61
Papio papio	10.07	1.06	9.01
Perodicticus potto	11		
Phaner furcifer	11.5		
Pongo pygmaeus	9.11	1.11	8
Propithecus coquereli	10.63		
Saguinus oedipus	13.18		
Saimiri sciureus	9.72	1.77	7.8
Theropithecus gelada	10.91		
Varecia rubra	9.81		
Varecia variegata	10.9		

Note: Blank cells indicate that no data were available.

ratio recommended by Smith (1999). This index is symmetrical around 1, with values <1 if females are the larger sex and >1 if males are the larger sex. In species with larger males, this index is calculated as the ratio of male and female mass, and as 2 – (female mass/male mass) when females are the larger sex.

Group size data were taken from several sources, as follows. First, we consulted a database that was independently compiled by Alexander Harcourt from the published literature (personal communication 2015, hereafter "Harcourt database"). Group size for *Pan troglodytes* was obtained from Nunn and van Schaik (2002), while group size for humans was from Marlowe (2010). Inferring group size for these two species presents challenges due to their hierarchical societies; here, we use data at the level of the local group ("camp") for warm-climate foragers from Marlowe (2010) and at the community level for chimpanzees. For bushbabies (*Galago*), *Propithecus*, *Varecia*, vervets (*Chlorocebus*), and *Eulemur*, we obtained mean group sizes from primary references given in Rowe and Myers (2011). We acknowledge that group size exhibits striking variation in primates (Patterson, Sandel, Miller, & Mitani, 2014). Given that the methods used here do not incorporate intraspecific variation, and that intraspecific variation was not found to impact statistical findings in a previous study of group size and brain size (Sandel et al., 2016), we do not investigate intraspecific variation in this context.

For diet, we used the Harcourt database. If leaves were recognized as a substantial and important component of a species' diet, this database codes "folivory" as 1 (otherwise folivory is set to zero). Other dietary categories in this database included frugivory, insectivory, carnivory, seeds, gums, and flowers. We obtained a dietary breadth metric that summed these dietary categories. Median values for genera were obtained from the Harcourt database for *Papio*, *Propithecus*, and *Varecia*. We assigned a score of 4 to *Homo sapiens*, to represent leaves, fruits, meat, and seeds/nuts. For day journey length, we obtained data from the Harcourt database. Due to lack of data, day journey lengths for *Aotus spp*., *Galago senegalensis*, *Macaca arctoides*, *M. radiata*, *M. sylvanus*, *Papio spp*., and *Saimiri sciureus* were taken from Nunn & van Schaik (2002). For *Microcebus* and *Phaner*, we consulted Rowe and Myers (2011), and obtained primary sources for *Microcebus berthae* and *Phaner pallescens*, which were congeneric with the species in our dataset. We also obtained day journey length for *Eulemur*, *Perodicticus*, and *Varecia* genera from primary references in Rowe and Myers (2011). We obtained data on habitat, coding species into whether they are terrestrial and whether they live in an "open" habitat, using the Harcourt database and Nunn and van Schaik (2002).

We coded activity period with two variables. One variable, "nocturnality," codes species into whether they are primarily nocturnal or diurnal; all cathemeral lemurs were coded as diurnal in this case. Another variable, "cathemerality," indicated whether species were cathemeral (Tattersall, 1987). For this, we used recent findings presented in Bray, Samson, & Nunn, (2017), with *Varecia spp*., *Eulemur spp*., and ring-tailed lemurs (*Lemur catta*) coded as cathemeral. We included cathemerality as a separate variable because of the possibility that circadian flexibility in these species might affect sleep architecture, for example by leading to shorter TST.

Our methods also require that we quantify sleep architecture for humans. For TST, we used a value of 7 hr, based on a variety of sources from Western and non-Western populations, as follows. In non-Western populations, our previous research on both Malagasy agriculturalists and Hadza foragers suggests that 7 hr is conservative, with these studies estimating human sleep at 6.5 and 6.25 hr, respectively (Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017b; Samson, Manus, Krystal, Fakir, Yu, & Nunn, 2017c). This also corresponds to findings from a recent study of three subsistence societies without electricity that also included the Hadza (Yetish et al., 2015). Similarly, a study of a Haitian nonelectric population revealed a TST duration of 7 hr (Knutson, 2014), and a meta-analysis of Western populations revealed an average TST of 7 hr (Ohayon, Carskadon, Guilleminault, & Vitiello, 2004). We report on the sensitivity of the outlier tests to using 7 hr for TST in humans. For NREM and REM, values were also taken from the meta-analysis of Ohayon et al. (2004). To account for the differences in sleep stages by age in Ohayon et al. (2004), we derived the human mean by averaging a cross-section of sleep architecture values from seven postreproductive "adult" ages. Specifically, from the ages of 15–45 years, we averaged the values from 5-year intervals by measuring the proportion of each sleep stage from the graphical output provided in the meta-analysis.

2.2 | Phylogenetic comparative methods

In all phylogeny-based analyses, we used 200 dated primate phylogenies from 10kTrees version 3 (Arnold, Matthews, & Nunn, 2010), which provides a posterior distribution of trees from a Bayesian phylogenetic analysis. A consensus tree is provided in the electronic Supporting Information (Figure S1).

We used two methods to investigate sleep architecture along the human lineage in a comparative context. The first method—phylogenetic prediction—was based on PGLS, with the following statistical model: $\text{Sleep Phenotype} = \text{ECV} + \text{Female Body Mass} + \text{SSD} + \text{Folivory} + \text{Dietary Categories} + \text{Open Habitat} + \text{Terrestrial} + \text{Day Journey Length} + \text{Group Size} + \text{Nocturnal} + \text{Cathemeral}$, with all quantitative metrics except for proportion REM $\log_{10}$ transformed. We used a Bayesian framework for model fitting, implemented in BayesModelS (Nunn & Zhu, 2014) in the statistical software R (R Development Core Team, 2014). BayesModelS uses Markov Chain Monte Carlo (MCMC) to generate a posterior probability distribution of regression coefficients, along with Bayesian model selection procedure to assess the probability that a coefficient should be included in the model. When a coefficient is included often and is more consistently positive or negative (rather than centered on zero), this indicates greater support for a predictor variable in the model.

We also estimated λ and κ, which scale the phylogeny to better meet the underlying assumptions of phenotypic change under a Brownian motion model of evolution (Nunn, 2011). The parameter λ (Freckleton, Harvey, & Pagel, 2002) multiplies the internal branches by a value ranging from 0 to 1, with 0 equivalent to a star phylogeny (Felsenstein, 1985) and, thus, indicative of no phylogenetic signal. The parameter κ raises branches to the value κ (Pagel, 1999). Fitting of this

model has been used to assess whether a "speciational" model of evolutionary change occurs, that is, with evolutionary change occurring at diversification points on the tree of extant taxa (Garland et al., 1993; Nunn, 2011; Pagel, 1999). Here, we use the λ and κ parameters to improve the fit of the model, rather than for investigating tempo and mode of evolutionary change.

In our MCMC analyses, we ran analyses with a burnin of 100 iterations and sampled the MCMC chain every 50 iterations (thin rate), producing a posterior probability distribution of 1000 samples for estimating regression coefficients, the probability of including coefficients in the statistical model (model selection), λ versus κ, and estimates of λ or κ. To ensure adequate burnin and thin rate (i.e. sampling from a stable distribution of likelihoods with low correlation across neighboring samples), we checked that a plot of likelihoods had stabilized and showed low autocorrelation.

We assessed support for coefficients as: (1) the proportion of MCMC samples that included its coefficient in the model (vs. assuming it is zero), with support between 10 and 30% as "weak," between 30 and 50% indicative of "support," and 50% or more as "strong support"; and when the coefficient was included in the model, (2) the proportion of regression coefficients from the MCMC sample that were positive or negative, based on predictions identified above, with weak support indicated by 85% to just under 90% of MCMC samples in the predicted direction, while 90% to just under 95% indicated "support" and >95% indicated "strong support." These criteria are intended only to help operationalize results, and ultimately, readers should interpret the probabilities of support we provide and make their own assessments. Note that if a coefficient is included in the posterior distribution 30% of the time, this means that it is used when predicting sleep architecture in 30% of the posterior samples; hence, it can have a meaningful impact on the predicted distribution even at low support levels. To make inferences about whether the coefficient is positive or negative, we present estimates for model coefficients from the MCMC sample in which it was estimated (rather than excluded from the model and thus set to zero).

We considered humans to depart from other primates if less than 5% of the posterior distribution is smaller than or larger than the value in humans, which is equivalent to using a 90% credible interval (i.e., 5% on each tail of the posterior distribution), but as with support levels for coefficients from the model just noted, we provide actual probabilities so that readers can make their own assessments. To assess the performance of model prediction in humans, we repeated the process for all primates in the analysis, that is, by dropping that species out, fitting the model, predicting the sleep phenotype in that species, and then comparing the observed value to that posterior probability distribution of predictions. We identify other primates that lie outside the 90% credible interval.

Our second approach was based on modeling adaptive regimes across a phylogeny for each of the groups in our study using an OU model. We especially focused on the lineage leading to humans, and tested whether a shift in the selection regime was inferred on this branch. Under the OU model, species evolve through various selection regimes that map to branches on the phylogeny. The goal is to characterize the regimes across the tree, and to assess whether a shift in selection regime occurred on the branch connecting *Homo* to the other primates. As evidence for "support" for a change in adaptive regime on a branch, we required that two conditions be met: at least 20% of the MCMC chain had to infer a change along that branch, and 80% or more of those changes had to be in a consistent direction. We identify branches that meet these support criteria graphically, while also providing more detailed statistics for shifts along the human lineage.

To implement this approach, we used the R package bayou (Uyeda & Harmon, 2014), which is a Bayesian implementation of OU model fitting. We ran two chains and ensured convergence by graphical inspection of the output, calculation of Gelman's R for key parameters of the model, and by comparing the magnitude of shifts across branches in the two runs, aiming for strong correlations in branch shift probabilities across runs. The first 10% of samples were dropped from each chain as burnin, and the chains were combined for all further analyses and plotting.

3 | RESULTS

3.1 | Total sleep time

Humans were predicted to sleep 9.55 hr, which is 36% >7 hr of TST used as the human value in this analysis. Indeed, only 1.8% of the posterior predicted distribution of TST was below the observed sleep time for humans, indicating that humans are a phylogenetic outlier in terms of TST, with less sleep observed in humans than predicted based on variation across primates (Figure 1). Humans would remain an outlier even if average human TST was 7.50 hr, based on the support levels we used for determining outlier status.

Of the predictor variables, we investigated, only nocturnality was consistently entered into the PGLS model across MCMC chains (67% of samples, "strong support", see Table 2). Among these samples,

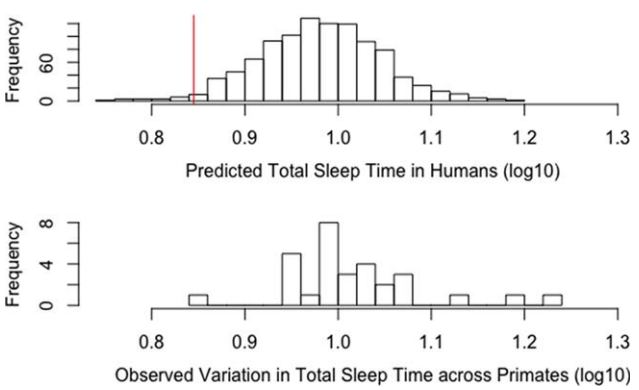

FIGURE 1 Predicted human TST and the distribution of TST across primates. The top panel provides the posterior probability distribution of predicted TST, with the red line indicating the observed value for humans. The bottom panel provides a histogram of sleep durations across primate species. These analyses reveal that human sleep is much shorter than predicted for a primate of our phenotypic characteristics and phylogenetic placement (top panel), and is the shortest of all primates (bottom panel)

TABLE 2 Predictors of TST in primates (PGLS analysis)

Variable	Coefficient	SE	% Support	% Positive
Intercept	1.019	0.002	NA	100
ECV	−0.063	0.01	10	26.5
Body Mass	−0.019	0.001	NA	25.9
SSD	0.001	0.007	4	48.9
Folivore	0.032	0.003	5	94
Diet categories	0.027	0.002	9	93.6
Open habitat	−0.013	0.006	2	50
Terrestriality	0.01	0.005	4	65.1
Day journey length	−0.01	0.006	4	36.8
Group size	0.018	0.003	4	78.4
Nocturnal	0.117	0.002	67	99.3
Cathemeral	−0.022	0.01	6	30.4

$N = 30$ species; results are presented for the model that excluded humans. Shading indicates variables that had at least weak predictive capacity, based on the combination of the two criteria given in the Methods for support levels, with darker shading indicating greater support.

99.3% of the coefficients for "nocturnality" were positive (again, "strong support"). Dietary variables were commonly positive (>90%), but rarely entered in the model (<10%). The phylogenetic scaling parameters λ and κ were approximately equally favored (56.3% probability of λ), with evidence of weak phylogenetic signal in model residuals (mean $\lambda = 0.20$). When predicting sleep for all primates, only two (of 30) other species were identified as outliers: *Callithrix jacchus* was identified as a negative outlier (i.e., sleeping less than predicted, like *Homo*), while *Aotus trivirgatus* was identified as a positive outlier (i.e., sleeping more than predicted).

In OU modeling in bayou, we found evidence for a negative shift in the adaptive regime along the branch leading to *Homo*, along with four other shifts in selective regime on other branches on the phylogeny (Figure 2). The lineage to *Homo* was inferred as having a shift on 29.2% of the iterations of the MCMC chain, with the clear majority of these (98.3%) constituting negative shifts toward lower TST.

3.2 | Proportion of REM

Humans were predicted to spend 13.8% of their TST in REM. The observed value was 22.3% and fell in the upper tail of the posterior probability distribution of predictions, with only 3.1% of the distribution larger than what was observed (Figure 3). Thus, humans are a positive outlier in the proportion of time spent in REM sleep, and would remain so even if only 21.3% of TST was spent in REM sleep, based on our support criteria. Thus, outlier status for proportion of REM is supported in this analysis, but not as strong as for TST. We re-ran analyses that removed *Pongo* from the dataset, given that the sleep architecture for this species was not obtained using EEG (see Materials and Methods). This reanalysis produced largely similar results, with only 4.5% of the distribution larger than observed.

As shown in Table 3, being a folivore or consuming more dietary categories tended to depress the proportion of REM sleep (i.e., a negative coefficient received "strong" support for both variables, with 97.8% of "folivory" coefficients being negative, and 99.4% of "number

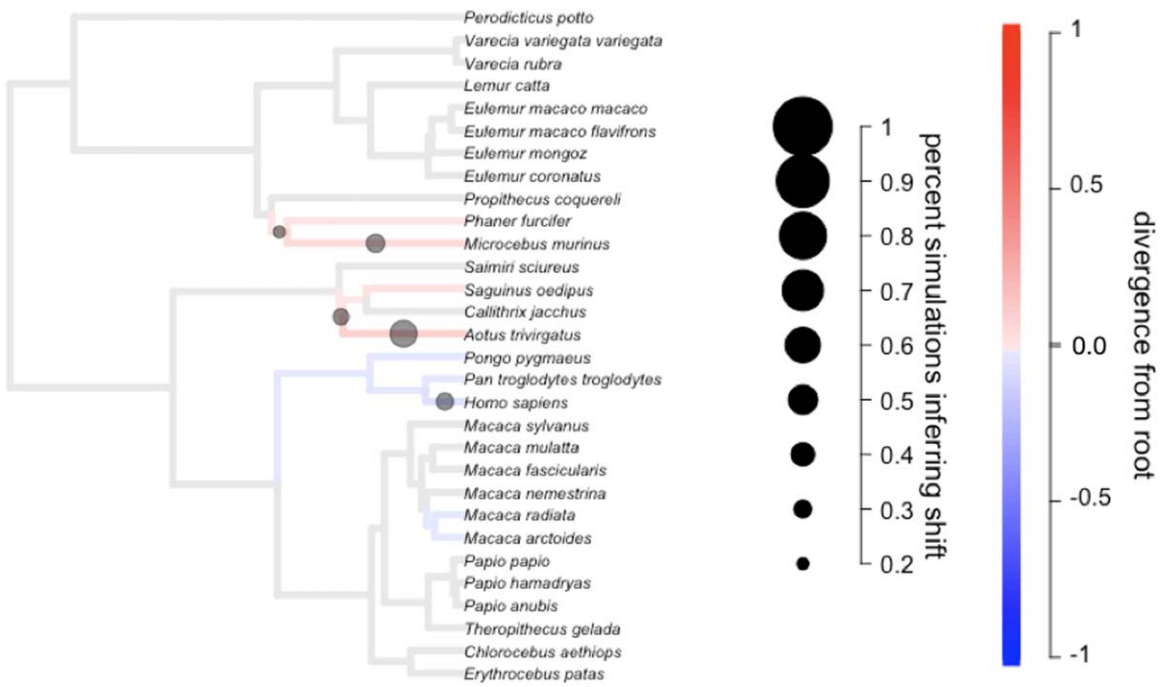

FIGURE 2 Phylogenetic modeling of TST using an Ornstein Uhlenbeck model. We map onto primate phylogeny inferred transitions in the adaptive regime, based on support criteria provided in the text. The figure also shows deviations of the inferred adaptive regime from the root of the tree, with redder colors indicating increases in TST, and bluer colors indicating decreases in TST colors

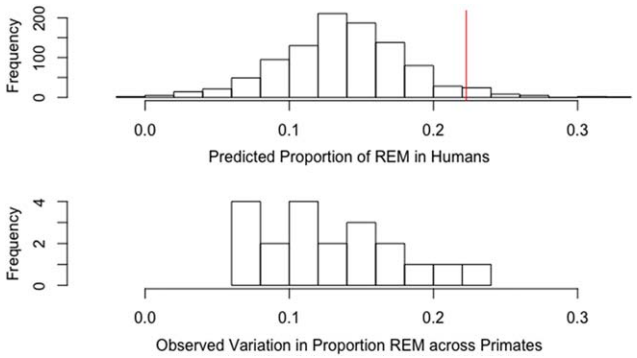

FIGURE 3 Predicted percentage of REM in humans and its distribution across primates. The top panel provides the posterior probability distribution of predicted percentage of REM, with the red line indicating the observed value for humans. The bottom panel provides a histogram of percentage of REM across primate species. These analyses reveal that humans have a higher than predicted REM percentage for a primate of our phenotypic characteristics and phylogenetic placement (top panel), and is the highest percent among all primates (bottom panel)

of diet categories" coefficients being negative). No other variables were influential in this analysis (Table 3). All models favored the κ model, with a mean κ estimate of 0.38. Among the 20 species for which data were available, no other primate hit the threshold of being an outlier, although *Macaca mulatta* approached the 90% credible interval as having a higher than predicted percentage of REM sleep.

Our bayou analysis of proportion of REM revealed a similar pattern, with the lineage leading to *Homo* being one of four branches meeting our support criteria (Supporting Information Figure S2). Support for a shift in adaptive regime along the human lineage was 25.5%,

TABLE 3 Predictors of percentage of REM sleep in primates (PGLS analysis)

Variable	Coefficient	SE	% Support	% Positive
Intercept	0.12	0.002	NA	97.7
ECV	0.003	0.012	11	49.5
Body mass	0.006	0.001	NA	58.5
SSD	−0.03	0.004	7	23.5
Folivore	−0.036	0.001	23	2.2
Diet categories	−0.023	0.001	16	0.6
Open habitat	0.002	0.005	2	70
Terrestriality	−0.004	0.006	2	50
Day journey length	0.014	0.005	4	68.4
Group size	0.02	0.004	2	84
Nocturnal	−0.037	0.004	9	17.4
Cathemeral	−0.048	0.008	8	24

$N = 20$ species; results are presented for the model that excluded humans. Shading indicates variables that had at least weak predictive capacity, based on the combination of the two criteria given in the Methods for support levels.

and was substantially more often positive than negative (95.1% of the time positive). The mean magnitude of the positive shift was ~10 times larger than the mean magnitude of the 4.9% of the shifts inferred as negative. Similar results were obtained in bayou when *Pongo* was removed from the analysis.

The inferred increase in the proportion of REM along the human lineage raises the question of whether this arises from a lower total duration of NREM, a higher total duration of REM, or some combination thereof. The next analyses aim to disentangle those possible patterns.

3.3 | Duration of NREM

In phylogenetic prediction of NREM sleep duration, we found evidence that humans are negative outliers, with only 0.8% of the posterior distribution being less than observed (Figure 4). The model predicted that humans would exhibit 8.42 hr of NREM, whereas the observed value was only 5.41 hr. Based on our outlier criteria, humans would remain an outlier even if, on average, they spent 6.45 or fewer hours in NREM. Similar results were obtained when analyzing the data without *Pongo*, with only 1.1% of the distribution being less than observed.

The analyses also identified a larger set of predictors for NREM sleep (Table 4), including greater NREM in species that are not strictly diurnal and in species that consume resources from more dietary types. For branch length scaling parameters, κ was again favored over λ (97%), with a mean κ of 0.43. When predicting NREM for the 20 primates with NREM data, we found two additional species that were identified as outliers: *Eulemur mongoz* exhibited more NREM than predicted, while *Callithrix jacchus* exhibited less NREM than expected.

In OU modeling in bayou, we found strong support for a shift along the human lineage (46.0%, Supporting Information Figure S3), with a clear majority of inferred changes involving a reduction in NREM (98.7%). Several other shifts occurred, including a strongly

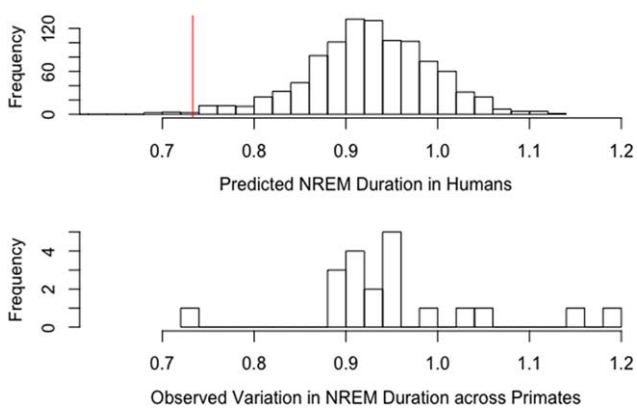

FIGURE 4 Predicted NREM in humans and its distribution across primates. The top panel provides the posterior probability distribution of NREM, with the red line indicating the observed value for humans. The bottom panel provides a histogram of percentage of REM across primate species. These analyses reveal that humans have a lower than predicted NREM duration for a primate of our phenotypic characteristics and phylogenetic placement (top panel)

TABLE 4 Predictors of NREM sleep in primates (PGLS analysis)

Variable	Coefficient	SE	% Support	% Positive
Intercept	0.957	0.004	NA	100
ECV	−0.162	0.009	25	12.3
Body mass	0.05	0.002	NA	79
SSD	−0.016	0.007	6	35.1
Folivore	0.022	0.008	2	68.2
Diet categories	0.035	0.001	37	99.5
Open habitat	0	0.006	3	51.9
Terrestriality	0.007	0.006	4	54.3
Day journey length	0.01	0.007	4	70.3
Group size	0.017	0.006	3	69.2
Nocturnal	0.242	0.002	99	100
Cathemeral	0.093	0.005	19	88.9

N = 20 species; results are presented for the model that excluded humans. Shading indicates variables that had at least weak predictive capacity, based on the combination of the two criteria given in the Methods for support levels.

TABLE 5 Predictors of REM sleep in primates (PGLS analysis)

Variable	Coefficient	SE	% Support	% Positive
Intercept	0.182	0.01	NA	76.7
ECV	−0.195	0.022	29	29.8
Body mass	0.077	0.006	NA	69.2
SSD	−0.135	0.008	20	12.2
Folivore	−0.089	0.005	16	7.1
Diet categories	−0.043	0.004	8	10.5
Open habitat	−0.008	0.012	8	46.8
Terrestriality	−0.098	0.009	12	14.4
Day journey length	0.069	0.011	11	70.4
Group size	0.047	0.009	9	69.6
Nocturnal	0.091	0.011	15	78.8
Cathemeral	−0.252	0.011	31	9.3

N = 20 species; results are presented for the model that excluded humans. Shading indicates variables that had at least weak predictive capacity, based on the combination of the two criteria given in the Methods for support levels.

supported increase in NREM along the lineage leading to genus *Aotus*. Similar results were obtained in analyses the removed *Pongo* from the dataset.

3.4 | Duration of REM

Human REM duration of 1.56 hr was only moderately larger than the mean of the posterior distribution of predictions (1.29 hr) from PGLS analyses (Figure 5). Indeed, 30.6% of the posterior distribution was larger than the observed value, suggesting that human REM duration is not notably different from expectations based on phenotypic variation in other primates. Results were similar in analyses that omitted *Pongo*, with 36% of the posterior distribution being larger than the observed value.

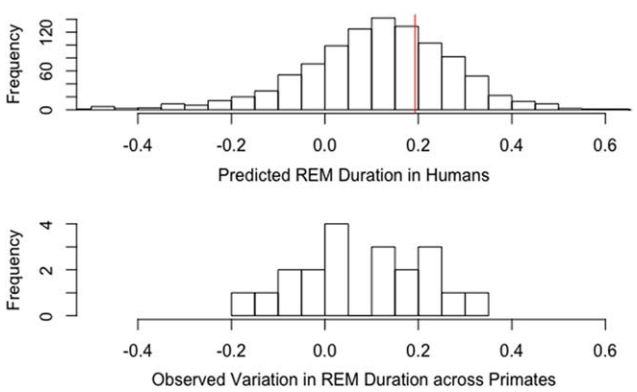

FIGURE 5 Predicted REM in humans and the distribution of REM durations across primates. The top panel provides the posterior probability distribution of REM, with the red line indicating the observed value for humans. The bottom panel provides a histogram of REM across primate species. These analyses do not support humans as having an unusually high total REM duration (top panel)

Several phenotypic and ecological variables predicted REM duration, but only weakly; these included negative effects of SSD, folivory, and cathemeral activity pattern, (Table 5). For branch length-scaling parameters, κ was again highly favored over λ (99.2%), with a mean κ of 0.347. Looking across the other 20 species with sufficient data for these analyses, we found no phylogenetic outliers, although *Chlorocebus aethiops* nearly met conditions for being a negative outlier and *Macaca mulatta* was nearly a positive outlier.

In bayou analyses, we found a shift involving a reduction in REM on the branch leading to *Homo* and *Pan*, but not on the human lineage itself (Supporting Information Figure S4). On that internal ape lineage, the probability of the shift occurring was 23%, with 82% being positive shifts. Five other shifts in the adaptive regime were inferred elsewhere on the tree, some with greater support than found in the apes. Similar results were found when removing *Pongo* from the bayou analysis.

4 | DISCUSSION

The analyses presented here represent the most in-depth comparative analysis of sleep in primates to date, with a special focus on the terminal branch leading to humans. Based on comparative patterns in primates and phylogeny, we found strong evidence that human TST is much shorter than predicted, confirming an initial analysis of this possibility in Samson and Nunn (2015) with an expanded dataset and improved methodology. Specifically, our updated phylogenetic prediction analyses revealed that humans are outliers, and would remain so by our criteria even if we assigned humans a TST of 7.5 hr, which exceeds values

from recent studies of traditional populations (reviewed in the Methods). In addition, a more sophisticated model of evolutionary change, which explicitly models both stabilizing selection and drift (the OU model), infers a shift in the selective regime for TST along the human lineage. Looking at a subset of primates for which we had data on REM and NREM, we also found that humans reached outlier status for the percentage of time spent in REM, also confirming findings presented in Nunn and Samson (2015). While this finding clearly met our criteria for support, the analyses were not as strong as those for TST, with only 3.1% of the distribution being larger than the observed value. Evolutionary analysis using an OU model also revealed support for a shift in the percentage of REM along the human lineage.

A shift toward a higher proportion of REM could arise from a shift toward more REM, a shift toward less NREM, or a combination of these two shifts. Our analyses of REM and NREM durations revealed that NREM is the major driver of the reduction in TST in humans. With a reduction in predicted NREM of 3 hr, this negative change could more than compensate for the reduction of 2.55 hrs of TST from predictions. Humans may also have experienced a mild increase in REM sleep, which is hinted at in our modeling (an increase of 0.3 hr, but not reaching our *a priori* support levels), and may be harder to detect given that REM is a small proportion of TST. Such an effect on increased REM might be detectable in future models that have access to larger sample sizes, but it seems clear from our analyses that the increase in the proportion of REM is mainly due to a substantial reduction in NREM rather than an increase in REM. It is intriguing to think that, even with such a large decrease in TST, humans may have expanded REM; research on human subjects suggests that REM is critical for memory consolidation (Stickgold, 2005), emotional regulation (Nishida, Pearsall, Buckner, & Walker, 2009; Simon et al., 2015), threat rehearsal (Revonsuo 2000), and potentially also insight (Wagner et al. 2004). Future research could investigate the specific stages of NREM that shifted over evolutionary time. Based on recent evidence that variability in human chronotype may have increased group level vigilance during nighttime periods by way of sentinel-like behavior (Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017a), we predict that the lightest stages of NREM sleep (stage 1 and 2, where arousal threshold is low) proportionally decreased relative to deep NREM slow wave sleep (stage 3, where arousal threshold is high).

Our PGLS model fitting also offers a chance to understand how ecology, morphology, and behavior influence sleep architecture in primates. For TST, our analyses confirmed earlier findings (based on different methods and less data) that nocturnality covaries strongly with longer sleep durations in primates (Nunn et al. 2010). Using coefficients from our model, we estimate that nocturnality increases TST by 1.31 hr per 24 hr, which is a substantial effect. Several factors could account for this effect, as nocturnal and diurnal primates exhibit many striking differences in ecology, morphology, and sociality. However, we think the most plausible explanation is that nocturnal species may prefer to forage in maximal darkness to reduce predation risk; hence, they may benefit from becoming active only after full darkness has been reached. This would effectively give them more time for sleep, and they appear to be taking that evolutionary route based on our analyses. In addition, nocturnal species often live in smaller groups (or solitarily), and often have concealed sleep sites that may reduce predation during both day and night, thus relaxing predation risk at the sleep site and favoring more sleep (Capellini et al., 2008a; Lesku et al., 2006). We did not find an effect of cathemerality in analyses of TST.

We also investigated the predictors of REM, NREM, and the proportion of REM sleep. These analyses revealed that the number of dietary categories covaries positively with more NREM (Table 4), and this appears to cut into the proportion of REM sleep (Table 3) rather than simply lengthening TST (Table 2, i.e., this variable was impactful on TST). Nocturnality was positively associated with both NREM and REM durations, suggesting that both contribute to increased TST in nocturnal lineages, while cathemeral species had substantially less REM sleep. This association between cathemerality and less REM may occur because REM (and particularly phasic REM) is associated with the greatest arousal threshold of any sleep state. Thus, animals in this sleep stage are maximally disconnected from their external environment and are therefore exceptionally vulnerable, particularly in unpredictable environments, which characterizes the ecology of Madagascar where cathemerality is most commonly found (Donati & Borgognini-Tarli, 2006; Wright, 1999). We also found evidence for SSD and folivory having a negative association with REM. Thus, our analyses revealed some new effects on sleep architecture that had not been documented in previous work on primate sleep (Nunn et al., 2010), although many of these effects were weak.

Our analyses support general conclusions from our previous, smaller analysis that revealed the intriguing pattern that humans sleep substantially less than predicted for a primate with our phylogenetic position, ecology, and phenotypic characteristics (Samson & Nunn, 2015). In that previous study, we proposed that both risks and opportunity costs produce the shorter sleep durations found in humans. Some risks may arise from a more terrestrial lifestyle, including sleeping on the ground. This lifestyle would have exposed early humans to greater predation risk, and potentially to greater threats from hostile conspecifics, who would have been able to locomote more effectively on the ground at night (as compared with primates moving arboreally at night in the trees). Importantly, our proxies for predation risk, involving terrestriality and living in an "open" habitat, were not predictive of TST (Table 2), suggesting that additional factors are important for humans, or that early humans experienced a higher level of risk from terrestrial sleep that is not captured by these proxies, and would result in lower predicted sleep time if these factors could be effectively incorporated into the statistical models.

Opportunity costs of sleep may be more important for understanding human sleep. Some of these opportunity costs also relate directly to unique aspects of human evolution, in this case involving the importance of learning—both individually and socially—and the importance of technology and material culture for reproductive success. As we all know from our own lives, sleep reduces the opportunities for productive activities, which importantly include learning new skills and applying them to generate objects, new knowledge, or teaching our allies, spouses, and children. We propose that the importance of these activities in human evolution has contributed to the shortening of human

sleep that we document, perhaps more so than risks from sleeping on the ground. Further support for this hypothesis comes from the findings that humans have largely achieved shorter sleep through less NREM, with some hints that REM has increased modestly despite the huge decrease in TST. As REM is known to be involved in memory consolidation (Peigneux, Laureys, Delbeuck, & Maquet, 2001; Stickgold, 2005; Stickgold, James, & Hobson, 2000) and rehearsal of stressful situations or problems (Revonsuo, 2000; Valli & Revonsuo, 2009), these findings further suggest that our material culture has played a major role in shaping human sleep.

Our findings may be limited by the use of captive animals for obtaining measures of sleep, where potential ecological drivers of sleep are more controlled, including food availability and predation. At present, however, it is only possible to obtain estimates of sleep stages in captivity, using either EEG or visual methods. Regarding these methodological differences in estimating sleep architecture, we demonstrated that our main conclusions were insensitive to including sleep stages from the orangutan in our analyses, which were obtained with videography rather than EEG (Samson & Shumaker, 2013). We also acknowledge that individuals vary in their sleep durations, and that different primate populations exhibit variation in group size, diet and other socioecological variables. At present, we lack data to assess these sources of variation, although recent research suggests that the effects of intraspecific variation may be minor (Sandel et al., 2016).

In conclusion, our analyses provide new insights into the evolution of primate sleep, including in humans. We find that human sleep architecture differs greatly from predictions of what would be found in a typical primate, based on our phenotypic, phylogenetic, and ecological characteristics and how these characteristics influence sleep in other primates. These results have importance for human evolution, and for understanding human health (McNamara & Auerbach, 2010; Nunn, Samson, & Krystal, 2016; Worthman, 2008). For example, short human sleep could account for why humans appear to be uniquely susceptible to Alzheimer's disease (Nesse, Finch, & Nunn, 2017). Future research could investigate the hypotheses for drivers of short sleep by studying sleep in different human populations, including in relation to risks, activities at night, demands on time budgets, and cultural transmission and evolution.

ACKNOWLEDGMENTS

The authors thank the organizers for inviting us to contribute to this special issue, Ian Miller for comments, edits and statistical advice, two anonymous reviewers and the Associate Editor for comments, and Isabella Capellini and Alexander Harcourt for assistance with data. They acknowledge the National Science Foundation for funding (BCS-1355902).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Nunn CL, Samson DR. Sleep in a comparative context: Investigating how human sleep differs from sleep in other primates. *Am J Phys Anthropol*. 2018;00:1–12. https://doi.org/10.1002/ajpa.23427