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The Human Sleep Paradox: The Unexpected Sleeping Habits of *Homo sapiens*

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Abstract

The human sleep pattern is paradoxical. Sleep is vital for optimal physical and cognitive performance, yet humans sleep the least of all primates. In addition, consolidated and continuous monophasic sleep is evidently advantageous, yet emerging comparative data sets from small-scale societies show that the phasing of the human pattern of sleep–wake activity is highly variable and characterized by significant nighttime activity. To reconcile these phenomena, the social sleep hypothesis proposes that extant traits of human sleep emerged because of social and technological niche construction. Specifically, sleep sites function as a type of social shelter by way of an extended structure of social groups that increases fitness. Short, high-quality, and flexibly timed sleep likely originated as a response to predation risks while sleeping terrestrially. This practice may have been a necessary preadaptation for migration out of Africa and for survival in ecological niches that penetrate latitudes with the greatest seasonal variation in light and temperature on the planet.

INTRODUCTION

Sleep evolved to become one of the most widespread features shared by all life on Earth, with both prokaryotes and eukaryotes exhibiting circadian cycles of rest and activity (Schmidt 2014). Yet the costs of sleep are immense. Organisms must forego fitness-critical tasks such as securing a mate and seeking calories all while increasing the inherent vulnerability brought on by being in an altered state of consciousness. These risks are numerous and include being preyed on, parasitized, and/or impinged by abiotic forces such as inclement weather or natural disaster. Taken together, it is no wonder that researchers such as Rechtschaffen (1971) have noted, "If sleep does not serve an absolute vital function, then it is the biggest mistake the evolutionary process ever made." Sleep, in its ubiquity throughout all life, is not an evolutionary mistake but in fact a fitness-enhancing brain state, physiological process, and behavior.

Here, I outline sleep architecture [the distribution of nonrapid eye movement (NREM) and rapid eye movement (REM) sleep] and how it is measured across mammals. I examine the drivers of sleep patterns among mammals, with a special focus on primates, to assess current models of the evolution of the flexibility in timing and circadian organization of sleep along the human lineage. Specifically, I ask, (*a*) How is sleep architecture defined and measured; (*b*) what is human sleep relative to other species and how does variation manifest both cross-culturally and along urban–rural gradients within *Homo*; and (*c*) is human sleep what we would expect for a primate of our brain and body size, sociality, and dietary breadth? This review demonstrates that, among primates, human sleep is in many ways exceptional, and to explain the evolutionary history of these outlier traits, I propose a model of sleep site sociotechnological niche construction, here called the social sleep hypothesis, as a resolution to the paradoxical nature of human sleep expression.

Sleep Quantified

Sleep is a remarkably complex phenomenon that has been described as a physiological process, a brain state, and a behavior (Webb 1988). Sleep research has historically had a single gold standard for the quantification of brain states: recording electrical activity of the brain. Using electroencephalography (EEG) to detect the brain's electrical activity, neurophysiological signatures can quantitatively discriminate among different states, NREM and REM sleep. NREM sleep is subdivided into two stages: light N2 (NREM stages 1–2) accompanied by electrically detected sleep spindles and a K-complex. The lowest arousal threshold where a sleeping individual is easily awakened is in N2. N3 slow-wave activity (NREM stage 3) is characterized by slow delta rhythms and global cortical oscillations. N3 sleep has a deeper arousal threshold in humans, making it more difficult to stimulate arousal when asleep (Ackermann & Rasch 2014).

REM sleep, driven from bidirectional interactions between the subcortex and cortex, typically shows faster theta rhythms. This sleep stage is complemented by behavioral paralysis (with the exception of myoclonic twitches, which are brief and discrete contractions of muscles) yet paired with a highly active neural pattern comparable to an awake brain. REM sleep can be distinguished by substages known as tonic and phasic REM. The tonic substage is characterized by widespread, low-voltage, fast electrocortical activity, whereas the phasic substage is characterized by both oculomotor activity and cardiorespiratory irregularities (Sallinen et al. 1996).

In summary, sleep research in laboratory and/or captive animal environments using polysomnography (PSG) has revealed three discrete sleep stages: light N2 sleep, deep N3 slow-wave activity, and REM (tonic and phasic) sleep (Vyazovskiy & Delogu 2014), all of which are regulated by homeostatic drive (based on preceding activity history) and circadian rhythm. Given the cumbersome, expensive, and invasive nature of polysomnography (PSG), sleep research was limited to controlled laboratories throughout most of the twentieth century. Thus, until relatively

EEG: electroencephalography

Sleep spindles: a burst of oscillatory brain activity, occurring during stage 2, that is visible on an electroencephalogram consisting of 12–14-Hz waves

K-complex: an electroencephalographic waveform that occurs during stage 2 NREM and serves to suppress cortical arousal and aid sleep-based memory consolidation

Delta rhythm: a high-amplitude brain wave with a frequency oscillation between 0 and 4 Hz that is associated with deep, slow-wave sleep

Theta rhythms: electroencephalographic oscillations in the 4- to 8-Hz frequency range associated with the hippocampus

Myoclonic twitches: brief and discrete contractions of the muscles during REM sleep

Phasic REM: characterized by greater arousal threshold (compared with tonic REM) and associated with distinct oculomotor activity (i.e., rapid eye movements) and cardiorespiratory irregularities

recent developments (such as the use of actigraphy-based biometrics), research in ecologically diverse environments for human and nonhuman animals has been a major methodological challenge (Samson 2020b).

The Drivers of Mammalian Sleep–Wake Regulation

To understand contemporary human sleep, a thorough comparative examination of the drivers that influence sleep durations across mammals and primates is necessary. This comparative perspective can help uncover to what extent the function of sleep is limited by the brain (e.g., memory consolidation) or ecology (e.g., diet and trophic level). Since the late twentieth century, researchers have provided insight into the comparative patterns of mammalian sleep (Tobler 1989); here I summarize recent research, applied by two independent research groups (Capellini et al. 2008a; Lesku et al. 2006, 2008), that used more sophisticated statistical-phylogenetic methods (Nunn 2011). These analyses have included not only the duration of REM and NREM sleep, but also important variables such as the duration of the NREM–REM cycle and distribution of sleep through the circadian cycle into monophasic or polyphasic sleep periods. Major hypotheses regarding the function of sleep range broadly in three categories: ecology, neurobiology, and physiology. These studies, which span more than 127 different mammalian species representing 46 families across 17 orders (Capellini et al. 2008a), have revealed that, after controlling for evolutionary relatedness, the primary drivers of sleep architecture are predation, metabolism, immune function, gestation length, brain mass, and neuroanatomical regions such as the amygdala (see **Table 1**).

Predation risk across mammals is mediated by stability and safety of sleep site, with longer reported sleep times associated with lower predation risk; animals at high trophic levels (e.g., carnivores) sleep longer than lower trophic levels (e.g., herbivores). Metabolism mediates sleep duration (with and without control for body mass) as faster basal metabolic rates have a negative association with sleep durations; thus, there appears to be an evolutionary advantage for species with greater metabolisms shortening and polyphasically fragmenting their sleep (Phillips et al. 2010). Although relative brain mass fails to show an association with sleep durations, it is linked with the increased percentage of REM sleep across mammals. Neuroanatomy is especially limited by sample size (owing to a low number of species with numerous regions of the brain mapped out across broad phylogenetic categories), yet the size of the amygdala has shown a positive covariance with NREM sleep (Capellini et al. 2009). Mammals with longer gestation lengths, after correcting for body mass, sleep less (Capellini et al. 2008a,b). In addition, species with more sleep have higher

Polysomnography: a multiparametric measure of EEG brain activity, electrooculography eye movement, and electromyography skeletal muscles

Circadian rhythm: an endogenous and entrainable 24-h oscillating process that regulates the sleep–wake cycle

Actigraphy: a noninvasive method that measures gross motor activity and monitors rest–activity cycles using a small actimetry sensor

Polyphasic sleep: a behavior of multiphase sleep periods, usually more than two (biphasic sleep) or one consolidated bout (monophasic sleep), throughout the circadian period

Table 1   The ecological, physiological, and neuroanatomical drivers of mammalian sleep architecture

Driver of sleep architecture	Supported functional hypothesis	Reference(s)
Predation and trophic level	Animals at lower trophic levels, such as herbivores under greater predation risk, sleep less than carnivores at higher trophic levels.	Capellini et al. 2008a,b; Lesku et al. 2006, 2008
Brain mass and neuroanatomy	Relative brain mass is positively associated with the proportion of REM sleep, and the amygdala (associated with processing emotional information) covaries with sleep architecture.	Capellini et al. 2009
Metabolism	Metabolism has a negative association with sleep duration in that lower metabolic needs favor more total sleep time.	Capellini et al. 2009
Immune strength	Species that sleep more are characterized by fewer parasites and higher white blood cell counts.	Preston et al. 2009
Gestation	Species with longer gestation lengths sleep less.	Capellini et al. 2008a

Abbreviation: REM, rapid eye movement.

white blood cell counts and fewer parasites (Preston et al. 2009). Finally, REM and NREM total sleep durations covary positively, suggesting an important general mammalian trend—typically, the ecological conditions that permit more sleep increase both REM and NREM (McNamara et al. 2010).

The fact that NREM and REM covary and increase given the right conditions highlights a critical point: There exists a fundamental trade-off between circadian activity and sleep versus the functional benefits inherent to sleep. On the one hand, as noted by Nunn and colleagues (2016, p. 233), "This 'tradeoff' perspective is highly relevant to understanding the short duration of human sleep: they suggest that if an animal has something 'better' to do than sleep (such as forage, court potential mates, or watch for predators), natural selection will favor shorter sleep durations." On the other hand, because brain mass and amygdala size have been associated with sleep staging, natural selection may increase a sleep stage to grant specific neurological benefits, a finding that is consistent with the modern captive rodent and human models of the functional benefits of sleep (Carskadon & Dement 2017).

Primate Sleep in a Comparative Context

Only 7% of primate species (∼30 species) have had their sleep architecture quantified; despite this dearth of data, researchers have reported a wide variation in how sleep is expressed in the primate order. In general, primate sleep differs from general mammalian patterns in several critical ways. Primates have (*a*) consolidated, monophasic sleep to achieve greater sleep quality; (*b*) reduced sleep times among diurnal primate species; and (*c*) increased sleep intensity (i.e., the depth of sleep) (Nunn et al. 2010). The influence of allometric scaling and evolutionary ecology of ancestral primate sleep sites has been detailed in other works (Nunn et al. 2016, Samson & Nunn 2015), but I briefly recap here to contextualize the evolution of primate sleep architecture.

The small-bodied ancestral primate was likely a solitary, nocturnal, and arboreal animal that often used tree holes to avoid predation, thermoregulate, and care for young (Kappeler 1998). Paleocene and Eocene primates' body size steadily increased through time (Fleagle & Kay 1985), driving primate body mass beyond the capacity of most fixed-point nests. The loss of secure fixed-point sleep sites likely altered the dynamics of the sleep environments of evolving larger-bodied primates, which may explain why, when compared with apes, monkeys have less sleep efficiency. For example, direct comparisons between the sleep quality of an orangutan and that of a baboon showed that the comfortable positional behaviors characteristic of ape sleep sites facilitate longer and higher-quality sleep (Samson & Shumaker 2015). The sophisticated alteration of sleep sites is a universal behavior in apes that was phylogenetically reconstructed sometime between 18 and 14 mya (Duda & Zrzavy 2013). Thus, the challenge of finding an arboreal sleep site that could secure a massive proto-ape body was overcome by constructing a sleeping platform.

Recent phylogenetic generalized least squares (PGLS) analyses within the primate order have revealed a significant improvement in the scientific understanding of how ecology, morphology, and behavior influence sleep architecture in primates (Nunn & Samson 2018). As I describe in detail in the next section, humans represent an extreme as the shortest sleepers (typically sleeping an average of only seven hours per circadian period), whereas the "marathon sleepers," such as mouse lemurs, cotton-top tamarins, and owl monkeys, range in sleep duration from 13 to 17 h (Samson & Nunn 2015). One of the most powerful drivers of primate sleep duration is nocturnality. In the PGLS model, nocturnality increased sleep duration by 1.31 h per diel cycle. The benefits of foraging when natural predators are least equipped to hunt in the few hours of true darkness (with minimal residual ambient light from the sun or moon) appears to be the most likely explanation for this substantial effect (Nunn & Samson 2018). Thus, because only a few hours per day are needed to perform fitness-relevant tasks, more time is allotted to sleep.

Sleep intensity: a homeostatic mechanism that regulates sleep depth, arousal threshold, and functional benefits of differing sleep stages

Sleep efficiency: the total time spent asleep divided by the total time spent in a sleeping environment

Diel: denoting or involving a period of 24 h

Although nocturnality was a positive driver of both NREM and REM duration, cathemeral species were characterized by less REM. Notably, REM (specifically phasic REM) is tethered to the greatest sleep arousal threshold. Animals in phasic REM are extremely vulnerable and are perceptually disconnected from the dangers in their environments. This state would be disadvantageous in unpredictable environments and may explain why cathemerality is a common activity pattern found in the primates of Madagascar (Wright 1999). Furthermore, the model also revealed that both folivery and sexual size dimorphism negatively covaried with REM. One interpretation for folivery-driving reductions in REM is that low-quality food may not be sufficient to fuel the additional energetic demands of a REM active brain. Additionally, increased sexual size dimorphism may have driven reductions in REM (for both sexes) owing to increased sex-specific competition for access to mates that could have increased the overall need for vigilance.

In summary, primate sleep architecture is driven by several factors, most notably activity pattern, diet, and sexual size dimorphism (Nunn & Samson 2018). Yet the most powerful predictor is activity pattern. With respect to activity pattern, primates have adopted three general sleep phenotypes, and each has had trade-offs in terms of the distribution of sleep architecture throughout the circadian cycle. (*a*) The nocturnal phenotype, where species perform fitness-critical actions in the cover of darkness and cryptically conceal themselves while inactive, has substantially increased sleep durations and extended both NREM and REM. (*b*) With the cathemeral phenotype, species capitalize on activity in both photoperiod and scotoperiod as an adaptation to unpredictable environments at the cost of reducing REM sleep owing to the dangers associated with a high arousal threshold. (*c*) The diurnal phenotype, where species have consolidated sleep into monophasic periods, reduced total sleep times and, in general, increased sleep intensity (deep slow-wave sleep and REM). We turn next to humans—a classically classified diurnal species—where many of these trends are either expressed in their extreme or upended altogether.

WHAT IS HUMAN SLEEP?

The question "What is natural human sleep?" has been of central focus to the study of human sleep ecology. Pioneering efforts by Worthman and colleagues (Worthman 2008, Worthman & Brown 2013) placed human sleep within an anthropological and ecological framework, and McKenna and colleagues (Gettler & McKenna 2011; McKenna 1986; McKenna et al. 1994, 1999) provided much needed evolutionary framing to the importance of arrangements of mother–infant co-sleeping. Until the publication of these groundbreaking works, sleep scarcely figured in the human evolutionary biology literature.

Papua New Guinea was the fieldsite of the first quantitative anthropological study of sleep (Siegmund et al. 1998). Yet the widespread use of actigraphy in human biology research did not take hold until after a study by Knutson (2014) in rural farmers in Haiti. Notably, many human sleep ecology studies have been published since, including investigations of sleep in small-scale societies in the Toba/Qom horticulturalists (de la Iglesia et al. 2015), research among small-scale agriculturalists with no access to electricity (Samson et al. 2017d), reports of the first ever comparative study of equatorial hunter-gatherers (Samson et al. 2017a,b; Yetish et al. 2015), and the first publication on the sleep of agropastoralists in the Himba of Namibia (Prall et al. 2018). Numerous independent groups are performing sleep research in field locations across the globe (Beale et al. 2017, Moreno et al. 2015, Pilz et al. 2018, Smit et al. 2019). Yetish & McGregor (2019) provide a comprehensive review of these works within an ecological framework, where they describe small-scale subsistence societies (hereafter termed 4S) as populations of modern humans living in ecological niches and subsistence conditions that more closely resemble those of late Pleistocene appropriate (LPA) hunter-gatherers (foragers that are mobile, share food, hunt large mammals, and live within bands and camps in relatively egalitarian social systems).

Cathemeral: rather than being restricted to the light or dark portions of the 24-h period, cathemeral activity is distributed over both in the diel cycle

Photoperiod: the phase of light or absence of darkness throughout the circadian period

Scotoperiod: the phase of darkness or absence of daylight throughout the circadian period

Small-scale subsistence societies (4S): the umbrella term 4S refers to small-scale subsistence societies where the product of adult work is primarily not money but food

Table 2 Key environmental variables to control for in models where sleep has been recorded in the field

Drivers of human sleep in field environments	General description	Reference(s)
Dusk/dawn/photoperiod	Light is a primary circadian entrainment factor. In particular, sunrise times prove to be predictive of wake times in multiple small-scale societies.	Samson et al. 2017a, Yetish et al. 2015
Temperature	Because temperatures drop significantly during the night, and individuals tend to have little environmental buffering, increased temperature typically increases sleep duration.	Samson et al. 2017a
Lux	Greater exposure to lux appears to reduce sleep duration.	Samson et al. 2017a
WBGT	WBGT is a measure of the apparent or "real feel" temperature of the environment and is calculated by combining measurements of ambient air temperature, black globe temperature, and relative humidity as a percentage. Evidence suggests that sleep onset and offset times may be regulated by WBGT.	P. Manger, personal communication; Yetish et al. 2015
Lunar phase	Lunar phase has shown to be a driver of nighttime sleep–wake activity in a hunter-gatherer population.	Casiraghi et al. 2021, Samson et al. 2018
Rainfall	Increased rainfall appears to reduce sleep duration.	McKinnon et al. 2021
Ambient noise	Typically, continuous measures of activity are positively associated with increased activity throughout the circadian period; specifically, a pattern shown in one small-scale agricultural population demonstrates that high dB values are related to nighttime increases in activity.	Samson et al. 2017a

Table adapted from Samson (2020b).

Abbreviation: WBGT, wet bulb global temperature.

These 4S sleep studies have proven invaluable to assess cross-cultural variation in sleep that has, throughout the twentieth century, been dominated by Western, clinical, and laboratory-based polysomnography. The data generated from these studies has been instrumental in ascertaining a cross-culturally derived value of human sleep duration generated within an ecologically informed context. This work has discovered several ecological factors that have been shown to drive sleep duration and quality in 4S societies (**Table 2**), which should be modeled and controlled for in future studies. Furthermore, investigators can now apply Bayesian approaches to predict LPA ancestral sleep durations for equatorial African populations from the three hunter-gatherer studies among the BaYaka (5.94 h), Hadza (6.25 h), and San (6.97 h). Using a large and methodologically mixed data set that includes 59 studies using both actigraphy and PSG-generated sleep durations, Samson (2020a) predicted a human sleep duration mean of 7.04 ± 0.11 h, with a credible interval of 6.86–7.23 h. Specifically, hunter-gatherers—compared with postindustrial agriculturalists (which include economically developed countries in the Global North, such as the United States, Canada, Europe, Japan, and Australia) and small-scale developing market economies—were the shortest sleeping subsistence group, with a predicted Gaussian mean and standard deviation of 6.56 ± 0.39 h, with a credible interval equaling 5.93–7.18 h in sleep duration.

These discoveries shed light on sleep in postindustrial societies. Sleep deprivation in developed economies [i.e., WEIRD (western, educated, industrialized, rich, democratic) nations] (Henrich et al. 2010) is argued to have been on the rise for the past five decades and to be reaching epidemic levels (Van Cauter & Knutson 2008). The disruption has been attributed to growing technological innovation and the 24-7 demands of the job market. This trend has led some public health officials to argue that sleepers in these societies are experiencing a sleep epidemic and has led to concerns for the general public. Yet the evidence in support of said public belief is scarce and contradictory (Lamote de Grignon Pérez et al. 2019), and comparative data being generated by sleep

anthropologists indicate that humans sleeping in modern, economically developed environments do not appear to be experiencing a sleep epidemic. The discovery that human forager sleep is especially short and fragmented has critical implications for understanding modern human sleep and for human health and well-being, which must be considered within a comparative, evolutionary lens.

THE HUMAN SLEEP PARADOX

Despite substantial progress in understanding the evolution of sleep, surprising and paradoxical results remain (Nunn & Samson 2018, Samson & Nunn 2015). Consider one such paradox: Humans rely on sleep for fitness-critical traits that include immune function (Irwin 2015), efficient metabolism (Schmidt 2014), and cell maintenance and repair (Vyazovskiy & Harris 2013); in addition, sleep is also vital for many cognitive functions such as memory consolidation (Stickgold et al. 2000, Walker & Stickgold 2004), creativity and innovation (Wagner et al. 2004), and emotional regulation (Walker 2009), all of which are crucial for reproductive success in humans. Yet, despite needing sleep for critical physiological and cognitive functions, humans sleep the least of any primate.

Moreover, desynchronization in circadian rhythms and/or chronic sleep deprivation increases the risks for obesity, hypertension, heart disease, and immune system dysfunction, which may increase the risks for infection, inflammation, and several cancers. Thus, human sleep is linked not only to enhanced fitness but also to the optimization of basic health (Nunn et al. 2016). As noted above, modern sleepers in industrialized settings appear to have longer sleep duration than 4S sleepers. This finding leads to the provocative idea that urban sleepers may be experiencing a trade-off where their secure, temperature-regulated, and light-regulated sleep sites may be costing them synchronized circadian rhythms (i.e., inconsistent, fragmentated, and low-amplitude rhythms). Several poor mental and physical outcomes have been associated with misaligned circadian rhythms. Circadian misalignment impairs autonomic function and increases cardiovascular risk, insulin sensitivity, and inflammation, and these processes are relatively independent of sleep duration (Grimaldi et al. 2016). This trade-off may explain why the developed world has a high rate of sleep disorders.

The sleep intensity hypothesis (SIH), introduced by Samson & Nunn (2015, p. 233), postulates that "early humans sleeping in novel terrestrial environments had characteristic sleep architecture that fulfilled homeostatic need in the shortest time possible," resulting in a reorganization of 24-h activity patterns that led to the occupation of a novel adaptive regime. Ultimately, if supported, the SIH implies that short and deep sleep was a critical preadaptation underpinning a suite of typical human traits. These include significant increases in group-level social activity extended into the nighttime, thereby increasing the total time available to strengthen group bonds, improve waking cognition, and transmit cultural information.

Sleep research in hunter-gatherers has been critical for testing evolutionary hypotheses related to human sleep ecology. One prediction stemming from the SIH is that comparative models that account for primate phylogeny and species-specific phenotypic traits will demonstrate not only shorter-than-expected sleep durations in humans, but also a reorganization of sleep architecture toward deeper stages. Nunn & Samson (2018) used phylogenetic modeling methods to predict human sleep, which included body mass, predation risk, brain size, foraging needs, sexual selection, and diet. The analysis revealed that among the 30 primates in which sleep architecture has been recorded, humans sleep the least. In fact, the model predicted human sleep duration to be 9.55 h—well above the value typical of hunter-gatherers or any other group measured. In addition, the analysis discovered that within this overall shorter sleep duration, humans undergo a higher
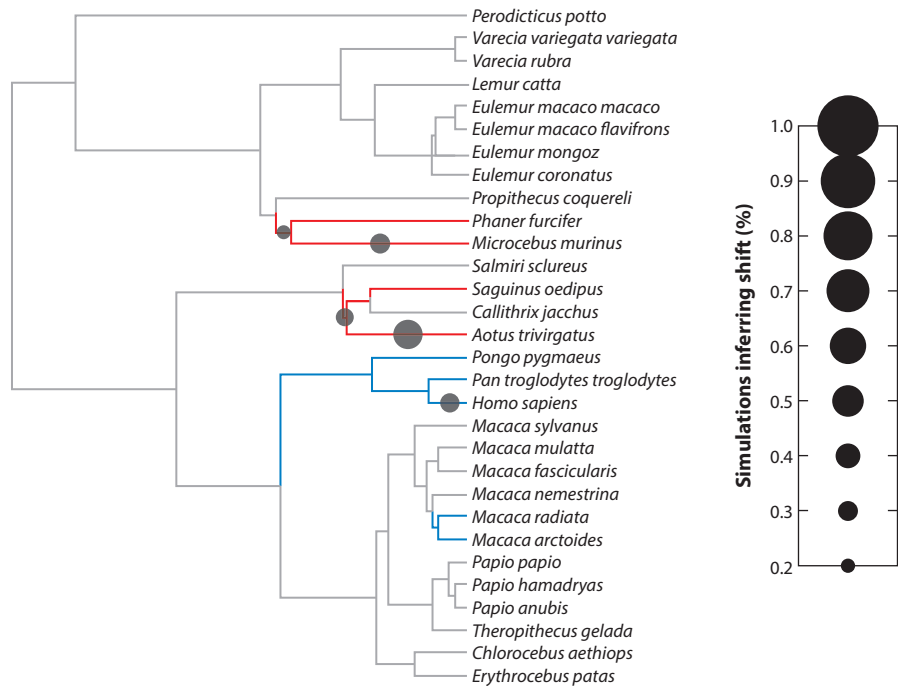
Figure 1

An Ornstein–Uhlenbeck (OU) model of total sleep time. The model inferred primate phylogeny transitions in the adaptive regime and shows deviations of the inferred adaptive regime from the root of the tree. Red color indicates increases in total sleep time, and blue color indicates decreases in total sleep time. Figure adapted with permission from Nunn & Samson (2018).

proportion of REM sleep, which was achieved by reducing NREM instead of increasing REM sleep. Finally, using a multistate Ornstein–Uhlenbeck (OU) evolutionary model, the findings support the idea that human sleep is derived. Specifically, the human lineage is inferred to have deviated from the ancestral adaptive regime sometime after the split with the common ancestor of chimpanzees and humans (**Figure 1**). Overall, the evolutionarily novel adaptive sleep regime expressed by modern humans changed throughout the evolution of *Homo* by way of reduced total sleep time and NREM sleep stages, while protecting REM.

Mounting evidence indicates that, in addition to demonstrating a shortening of total sleep duration and an increase in sleep quality, humans flexibly express sleep behavior throughout the diel more so than other diurnal primates. Thus, another paradox of human sleep is concerned with not just sleep duration and quality but also the timing of our sleep–wake activity. In 1965, after the original test of circadian rhythmicity in humans, Aschoff noted, "By nature, man belongs to the group of light-active organisms" (Aschoff 1965). Yet recent 4S investigations among human foragers (see above) suggest that significant nighttime activity may have been a feature of ancestral human populations and is not simply an invention of artificial light and postindustrial shift work.

Empirical and historical sources have contributed to an increasing awareness of the inherent variation in human sleep–wake activity patterns in order to answer the fundamental question, What is the normative human activity pattern? Laboratory-based experimental studies in humans have shown that biphasic sleep patterns are typical under long scotoperiods (Wehr 1992, 1999). Descriptions of "first and second sleep" have been shown to be ubiquitous throughout both

European and non-Western historical records (Ekirch 2016, 2018). The growing contributions from sleep anthropologists in 4S settings have empirically verified what ethnologists have known for decades: that human sleep ecology is dynamic and bustling with activity and the reasons are myriad for this predictably unpredictable sleep onset (Worthman & Melby 2002).

Human forager activity throughout the diel cycle appears to be comparable with species traditionally defined as cathemeral. Variation in genes related to chronotype could have been selected for under several circumstances: (*a*) frequency-dependent selection where individuals with rare chronotypes in a population are favored under circumstances where they are awake when others are asleep (Ayala & Campbell 1974); (*b*) sexual selection could enhance variability in chronotype, exemplified perhaps by reproductive success among varied chronotypes in Western populations (Randler et al. 2012) and cultural practices such as with the Himba, where evidence indicates that sleep durations may vary as a function of reproductive efforts related to cultural norms that protect nighttime extrapair partnerships (Prall et al. 2018); and (*c*) group and/or kin selection could favor groups of individuals that show more chronotype variation (Marshall 2011, Nowak et al. 2010). Therefore, contrary to the long-standing view that humans evolved a circadian system with little plasticity, chronotype variation and human sleep architecture (which includes nocturnal activity) in modern populations may represent a legacy of natural selection that reduced the inherent danger and vulnerability represented by sleep (Samson et al. 2017a). Thus, a major avenue of future research should empirically test the assumption that humans are diurnal.

Overall, opportunity costs appear to mediate sleep–wake regulation (Yetish et al. 2018). Several costs—such as social and individual learning and technological innovation—have been lauded as critical to human evolutionary success (Hill et al. 2009). In essence, by shortening human sleep duration and making its expression more flexible throughout the diel cycle, ancestral humans had more time to develop skills, enhance knowledge, vie for mates, support offspring, and craft alliances. Among primates, human sleep architecture differs in profound ways from predictions of what would be found in our species if we were a typical primate.

A UNIFYING EVOLUTIONARY THEORY OF HUMAN SLEEP EXPRESSION: THE SOCIAL SLEEP HYPOTHESIS

Human sleep is a unique constellation of traits that has resulted in short, flexible, and circadian activity patterns. As a consequence of human evolution, a number of sleep activity–related outlier traits emerge that defy typical trends exhibited by other animals: (*a*) Despite relying on sleep for physical and cognitive performance, humans sleep the least of any primate; (*b*) despite having unusually low thermal tolerance compared with similar-sized mammals (with associated weak circadian rhythms), humans are characterized by strong circadian rhythms (Hazlerigg & Tyler 2019) and have adapted to ecological niches that penetrate latitudes with the greatest seasonal variation in light and temperature on the planet; and (*c*) despite the apparent benefits to consolidated sleep (Bonnet 1989, Stampi 1992), humans are characterized by significant adaptive plasticity in phasing of sleep–wake activity. I propose that these paradoxes can be resolved under one model: Humans can withdraw anytime throughout the diel cycle, removing themselves from the immediate challenges of their local ecology—and in any environment worldwide—through social and technological security procured by sleep niche construction. I refer to this model as the social sleep hypothesis.

The adoption of camp- and band-level societies by early humans was one of the adaptations most critical to our species' survival (Apicella et al. 2012, Boehm 2012, Fu et al. 2012, Hill et al. 2009). Just as a snail carries its physical environment—a protective shell—on its back, human groups carry their social environments with them wherever they move (Rosenquist et al. 2011).

Of all the primates, only humans are habitual ground sleepers, with the rare exceptions of male chimpanzees where predation is low (Koops et al. 2012) and male gorillas who have few natural predators.

To help explain how early *Homo* overcame risks arising from the transition to terrestrial sleep, the social sleep hypothesis puts forward the idea that early humans engaged in a type of sociotechnological niche construction that enabled short and flexibly timed, high-quality sleep. Thus the capacity for flexibly timed, high-quality sleep was permitted by the extended structure of camp- and band-level social groups that emerged approximately 1.8 mya (Domínguez-Rodrigo et al. 2019) and by the technologies, such as fire (Gowlett 2006) and sheltered dwellings, that supported early humans' survival and increased fitness. Specifically, the sleep site secured by sentinels (i.e., a few individuals who are awake and vigilant during the most vulnerable sleep period for the majority of individuals in a sleeping group) and environmentally buffering domiciles produced an exophenotype that was a highly mobile location within which to withdraw from immediate ecological challenges and attain deep, restorative sleep. Moreover, once established, secure sleep sites may have supported in-group prosociality and intragroup coalitional alliance building. For example, poor sleep acts as a social contagion that can drive social isolation (Simon & Walker 2018), and social networks with stronger ties tend to augment sleep (Li et al. 2019); it stands to reason that this positive feedback loop of better sleeping and more cooperative ancestral camps and bands would have led to increased fitness. On the basis of this hypothesis, I predict (*a*) that social networks, the size of sleeping groups, temperature, and protection are drivers of short, high-quality, and flexible sleep in apes and humans with few environmental buffers; and (*b*) that quality sleep drives prosociality and coalitionary alliance building.

Several lines of evidence derived from sleep studies of hunter-gatherers and great apes support predictions of the social sleep hypothesis. First, modern hunter-gatherers use simple and mobile technologies (i.e., flexible branches stuffed and lined with grass and animal hide) and the controlled use of fire to reduce thermal stress and increase the security of their sleep environments (Samson et al. 2017b). Second, synchronous sleep in the Hadza is extremely rare, resulting in naturally sentineled sleep environments, where one or more adult individuals were reported awake during 99.8% of sampled epochs between when the first person went to sleep and the last person awoke (Samson et al. 2017c). Therefore, asynchronous periods of wakefulness provide an opportunity for vigilance when sleeping in groups. Mechanistically, this chronotype variation was driven by age, resulting in group-level asynchronous sleep throughout the nocturnal period. Third, simulations of wakefulness dynamics in relation to group size demonstrate that incorporating chronotype variation into the model substantially increases the mean number of individuals who are awake at night for groups, thereby resulting in a reduction in the duration of a time span when all individuals are in a vulnerable sleep state. Fourth, several 4S sleep studies have shown that supplemental napping throughout the day is common (Prall et al. 2018; Samson et al. 2017a,c; Smit et al. 2019); from forager camps and nomadic pastoralists to small-scale horticultural and agricultural societies, the ability to withdraw throughout any time in the 24-h period to a secure, temperature-regulated sleep site would enable short, flexible sleep expression. Last, experimental evidence describing another advantage to group sleep has been demonstrated in wild chimpanzees, where the encounter-dilution effect reduced the risk of insect exposure among individuals sleeping in groups (Samson et al. 2019).

Finally, the social sleep hypothesis provides an explanation for how ancestral human populations dispersing out of Africa could have maintained high-quality sleep in highly variable environments. The dispersal of early humans from Africa that led to the expansion of their geographical range occurred 1.75 mya (Carbonell et al. 2008). This range encompassed Mediterranean habitats, savannas, and tropical forests and, until recently, was thought to be confined to regions

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Exophenotype: the nonincidental effect that genes have outside the body, specifically made to its social surroundings in order to improve its likelihood for survival and reproduction

below 45°N. More recent evidence from Happisburgh (Norfolk, United Kingdom) shows that Early Pleistocene hominins were surviving at the southern edge of the boreal zone (e.g., conifer-dominated forest) as early as 0.78 mya (Parfitt et al. 2010). The presence of Early Pleistocene humans in these northern latitudes may well be explained by a social-sleep model given a so-ciotechnologically constructed niche by which our ancestors could withdraw. Sentineled sleep sites, technological innovation in clothing, the use of complex shelters, and/or the control of fire would have been essential to survival in high-latitude winter environments.

In sum, if novel data support the social sleep hypothesis, it brings to bear the possibility that socially secured sleep is a direct driver of typical forager camp sizes and a critical preadaptation for human success in dispersal across the globe. Specific data that would be helpful in testing this hypothesis include a comprehensive description of primate sleeping group sizes and social network composition as well as detailed observations of sleep site alterations that provide protection and thermoregulatory buffering of environments.

HOMO SAPIENS SLEEP: NEW FRONTIERS IN THE EXPLORATION OF THE EVOLUTION OF HUMAN UNIQUENESS

The specifics of sleep along the human lineage have been remarkably slow to emerge. In this re-view, I attempt to reconcile numerous disparate phenomena associated with the evolution of sleep within the primate order. The anthropology of sleep is an open area ripe for scientific exploration. Key factors, such as predation, geography (i.e., latitude and longitude), lunar phase, and recent hu-man evolutionary phenomena (e.g., linguistic communication, domestication, social networking, and life history), all influence the timing, quality, and duration of human sleep.

In the future, several critical comparative questions can be targeted by sleep anthropolo-gists; other than a few key studies looking at mother–infant co-sleeping (Crittenden et al. 2018, Vitzthum et al. 2018), adults have been the primary focus of field research. Thus efforts are needed to provide an integrated anthropology of infant and adolescent sleep (Ball et al. 2018, 2019). The influence of lunar phasing on human physiology is a hotly debated topic (Cajochen et al. 2013, Foster & Roenneberg 2008), yet most work has been in a WEIRD context; the first analysis of lunar phase on sleep–wake activity in foragers demonstrated that moonlight is linked with sleep expression in the Hadza (Samson et al. 2018) and the Toba/Qom (Casiraghi et al. 2021). Under-lying sex differences of sleep architecture as measured by EEG have not proven to be significant (Dijk et al. 1989). However, sleep research with the Himba (Prall et al. 2018) reported extremely short male sleep durations (4.78 h versus a female average of 5.92 h), demonstrating that socioe-cological contexts can evoke strong sex-related effects in sleep–wake regulation. In addition, the kind of social network analyses pioneered by Christakis & Fowler (2014) may be critical to illus-trating how social relationships influence sleep. Domestication of animals by humans began with Late Pleistocene dogs (Larson et al. 2012), and one proposed adaptive function of the coevolu-tion between both species was the guarding function of dogs (Larson & Fuller 2014); quantitative studies assessing the relationship between dogs and human sleep remain unexplored. Finally, turn-ing toward the future of our species, a critical need in space exploration programs is research that focuses on optimizing human environments to maintain peak performance levels (Caddick et al. 2017). An anthropology of space approach will be critical to understanding the underlying psy-chosocial factors that will enhance and optimize sleep as humans migrate to the Moon and Mars (Caddick et al. 2018, Flynn-Evans et al. 2016).

In conclusion, sleep engages with a central question in biological anthropology: In what way are humans unique compared with other animals? We live in large social networks, persist in inhospitable places, communicate complex thoughts by way of language, and domesticate an

unprecedented number of flora and fauna. Despite our bodies being relatively feeble, humans have become the most dominant predator alive. Sleep may be one of the most critical functions of all life, and it stands to reason that, in large part, what makes humans exceptional (even when compared with our primate relatives) is our cognition and resulting cultural complexity. Research continues to reveal a fascinating, interdependent relationship between the kind of sleep we experience and our ability to think. Thus, human-specific sleep patterns proved to be a foundational preadaptation that has been critical to the unparalleled evolutionary success of our species.

DISCLOSURE STATEMENT

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