

Sleep Intensity and the Evolution of Human Cognition

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Over the past four decades, scientists have made substantial progress in understanding the evolution of sleep patterns across the Tree of Life.^{1,2} Remarkably, the specifics of sleep along the human lineage have been slow to emerge. This is surprising, given our unique mental and behavioral capacity and the importance of sleep for individual cognitive performance.^{3–5} One view is that our species' sleep architecture is in accord with patterns documented in other mammals.⁶ We promote an alternative view, that human sleep is highly derived relative to that of other primates. Based on new and existing evidence, we specifically propose that humans are more efficient in their sleep patterns than are other primates, and that human sleep is shorter, deeper, and exhibits a higher proportion of REM than expected. Thus, we propose the sleep intensity hypothesis: Early humans experienced selective pressure to fulfill sleep needs in the shortest time possible. Several factors likely served as selective pressures for more efficient sleep, including increased predation risk in terrestrial environments, threats from intergroup conflict, and benefits arising from increased social interaction. Less sleep would enable longer active periods in which to acquire and transmit new skills and knowledge, while deeper sleep may be critical for the consolidation of those skills, leading to enhanced cognitive abilities in early humans.

Sleep occupies approximately one-third of a typical human life span. Deviations from this standard are linked to cognitive impairment and negative health consequences. For

example, sleep is critical for working memory, attention, decision-making, and visual-motor performance.⁷ Sleep loss, driven by access to artificial lighting, shift-work, and increased

international travel, has societal costs, ranging from decreases in workplace productivity to fatal accidents. Occupations that demand high-level cognitive function during shift work or that restrict sleep are particularly relevant.⁸ Humans in the developed world sleep in vastly different ways than our hominin ancestors slept.³ These differences may have important consequences for global health and treatment of sleep disorders.^{4,9}

Understanding human sleep also has implications for understanding human evolution,⁵ which is the focus of our paper. To synthesize current understanding of human sleep ecology and evolution, we turn to the ethnographic and historical literatures and recent studies to synthesize findings related to sleep in small-scale, subtropical, noncontraceptive human populations that lack ready access to artificial light (henceforth called traditional populations). In addition, using new phylogenetic comparative methods, we investigate primate sleep and identify unique aspects of human sleep. Building on recent ideas concerning the importance of the tree-to-ground transition in hominin sleep and cognition,^{5,10} we argue that the transition to obligate terrestrial environments may have been a consequence of allometric scaling. This transition may explain resulting physiological and techno-cultural adaptations, such as beds, shelters, controlled use of fire, variation in chronotypes (see glossary), and large social groups that gave early members of the genus *Homo* the advantage of deep, efficient sleep. We suggest that changes

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Key words: comparative study; human uniqueness; human evolution; allometry; evolutionary mismatch

GLOSSARY

Actigraphy — a noninvasive method that measures gross motor activity and, using a small actimetry sensor, monitors rest-activity cycles.

Chronotype — a behavioral propensity to sleep during a particular phase during a circadian period, often described as “owls” or “eveningness” (delayed sleep period) versus larks or “morningness” (advanced sleep period).

Delta-rhythm — a high-amplitude brain wave with a frequency oscillation between 0–4 hertz and associated with deep, slow-wave sleep.

K-complexes — an electroencephalographic waveform that occurs during stage 2 NREM and serve to suppress cortical arousal and aid sleep-based memory consolidation.

Phasic REM — a state of REM sleep characterized by greater arousal threshold compared to

tonic REM and associated with distinct oculomotor activity (that is, rapid eye movements) and cardio-respiratory irregularities.

Polyphasic sleep — a behavior of multi-phase sleep periods, usually two (biphasic sleep).

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

Sleep fragmentation — the number of awakenings greater or equal to two minutes per hour of sleep time.

Sleep intensity — a homeostatic mechanism that regulates sleep depth. Greater sleep intensity, and therefore sleep depth, varies in the course of sleep and usually occurs shortly after sleep onset.

Sleep motor activity — The number of motor activity movements per hour of sleep time.

Sleep spindles — burst of oscillatory brain activity occurring during stage 2 sleep; it is visible on an EEG consisting of 12–14 hertz waves.

Theta rhythms — Electroencephalographic oscillations associated with the hippocampus in the 4–8 hertz frequency range.

Tonic REM — A state of widespread, low-voltage, fast electrocortical activity associated with a lower arousal threshold than phasic REM and hippocampal theta, a decrease in neck and chin electromyogram amplitude, and brain temperature elevation.

in sleep were central to the fabric of human evolution even though, to date, the study of sleep in traditional societies and nonhuman primates has received remarkably little attention.^{3,11–13}

INVESTIGATING UNIQUE ASPECTS OF HUMAN SLEEP

Sleep can be viewed as a brain state, a process, and a behavior;^{14,15} it is an emergent property of the brain that serves several purposes, including energy restoration, immunocompetence, brain metabolic homeostasis, neural ontogenesis, and cognitive and emotional processing.^{16–18} Sleep is regulated by homeostatic¹⁹ and circadian mechanisms.²⁰ Consequently, the more we go without it the more we need it (homeostatic drive). Similarly, as night falls, physiological mechanisms such as melatonin release are activated in diurnal animals to facilitate sleep (the circadian drive).

When asleep, the brain shifts between qualitatively and quantitatively different states, nonrapid eye

movement (NREM) and rapid eye movement (REM) sleep.²¹ NREM sleep is subdivided into two important stages. Light N2 (NREM stages 1–2) is accompanied by sleep spindles and K-complexes and is associated with the lowest arousal threshold; that is, a sleeper is most easily awakened from this stage. The second stage of NREM sleep is deep N3 slow-wave activity (SWA) (NREM stage 3), characterized by delta rhythms and slow, global cortical oscillations. Deep N3 sleep, as compared to light sleep, is associated with a high arousal threshold, making it is more difficult to awaken a sleeper from this stage.^{22,23}

REM sleep, in contrast, has an electroencephalographic (EEG) pattern that, despite its association with complete behavioral paralysis, indicates brain activity that is similar to an awake state. In general, EEGs during REM sleep show faster theta rhythms, which arise from bidirectional subcortical, hippocampal, and cortical network interactions.^{24,25} REM sleep can be subclassified into two modes, tonic and phasic. Tonic

REM sleep refers to the state of widespread theta rhythms, whereas phasic REM is characterized by actual rapid eye movements (REMs) associated with ponto-geniculoccipital (PGO) waves.²⁶ Importantly, as noted by Ermis and colleagues²⁷ external stimuli are heavily inhibited during phasic REM, which they describe as a state, “with maximal environmental shielding (disconnection from the external world), [and] hence a most vulnerable phase of sleep.” In summary, modern human sleep research has revealed three discrete sleep stages: Light N2 sleep, deep N3 slow wave activity, and REM (tonic and phasic) sleep.^{14,27}

Is Human Sleep Flexible?

Perspectives promoted by sleep hygiene (that is, behaviors that are conducive to habitually sleeping well) largely focus on the importance of consolidated sleep at consistent intervals from one 24-hour period to the next.²⁸ Yet we all have experience with staying up too late, and

TABLE 1. Hominoid Sleep Ecology: Overview of Ape, Human Hunter-gatherer, and Post-industrial Sleep Environments^a

	Great ape	Hunter-gatherer	Post-industrial
Chronology	18-14 mya to present	1.8 mya to present	Nineteenth century to present
Sleeping platform	Arboreal sleeping platforms made of foliage	Foliage, animal hide	Padded bed, profuse sleeping accoutrements
Sleep group size ^a	5	26	1-2
Diurnal inactivity	Fluid	Fluid	Rigid
Fire	Absent	Present	Absent
Sleep onset	Rigid (sunset)	Fluid	Scheduled
Wake onset	Rigid (sunrise)	Rigid (sunrise)	Scheduled
Lux	Dark/dim (source: moonlight)	Fire, moonlight	Artificially controlled
Acoustics	Dynamic (fauna, conspecifics)	Fire ambient noise; dynamic (fauna, group members)	Silent, environmentally buffered
Security	Arboreal platforms, group size, insect repellent/odor masking properties of nests	Fire, group size, defensive structures, sentinels, males in prone position closest to potential threats, mother-infant co-sleeping	Environmentally buffered through complex domicile construction
Thermoregulation	Sleep platform complexity, foliage; mother-infant co-sleeping	Fire, shelter, mother-infant co-sleeping, group sleep during temperature nadir	Closed domicile, temperature regulation via blankets and modification of ambient temperature.

^aAveraged great ape group size⁷¹ and hunter-gatherer group size¹⁰⁹

many people have sleep disorders that affect the quality of sleep and next-day performance.²⁹ Are these patterns of late nights and disrupted sleep typical only of modern humans or are they characteristic of all humans and throughout human evolution? In other words, are today's sleep patterns a case of evolutionary mismatch to ancestral environments or actually characteristic of the selective pressures on human sleep? The study of small-scale modern human forager populations living in adaptively relevant habitats is essential for addressing these questions.

Information on human sleep in settings without artificial (that is, electrically produced) light is accessible from historical and ethnographic records,^{4,30,31} along with a handful of more recent studies that more directly quantify sleep patterns.^{13,32} Worthman and Melby³ argued that, compared to their postmodern industrial counterparts, traditional societies are characterized by strikingly different sleep ecology and behavior. As summarized in Table 1, equatorial hunter-gatherer sleep environments are characterized by a pattern that is more similar to that

of other primates: co-sleeping, in which individuals sleep within close enough proximity to monitor each other using two or more senses;³³ daytime napping, often during the daily extremes in temperature; audio conditions that are acoustically dynamic and often noisy; and lighting conditions that are generally dim or dark. Security from large hunting predators and smaller blood-sucking arthropods is achieved by sleeping socially and through use of fire.

Arguably, the most significant behavioral facilitator of sleep quality is the environment where the individual sleeps; sleep sites encompass extremes in temperatures, noise, and sleepers' familiarity with their surroundings.^{34,35} Modern equatorial hunter-gatherer sleeping platforms include organic substrates and covers to facilitate thermoregulation and, provide a better quality of sleep.³⁶ These substrates may take the form of piles of vegetation constructed from branches, lianas, leaves, and grasses, which are sometimes interwoven and usually accompanied by animal hides.³⁷ In addition to fire, hunter-gatherers display a variety of anti-predation defenses, including

semi-permanent shelter structures and earthworks dug into the ground to form concealed concavities in which to sleep.^{3,38,39} Although early studies showed Australian aboriginal populations to be characterized by greater metabolic tolerance to body cooling,⁴⁰ it still is not known how these adaptations help cope with the stresses of dynamic terrestrial sleep environments.

Hunter-gatherer sexual partners generally co-sleep. Accordingly, the male may gain increased opportunity for care of nearby offspring and reduce opportunities for infidelity by his mate; in turn, females may gain increased paternal care, including protection of offspring.^{41,42}

In addition, evidence exists of a genetic underpinning to variation in human chronotypes.⁴³ Relative to other mammals, human sleep timing is highly variable and these extremes are measured by the timing of sleep onset, which informs chronotype (colloquially dubbed morning "larks" versus evening "owls").⁴⁴ Natural sentinels could also increase the group survival of terrestrial sleepers. The elderly exhibit less slow-wave sleep, lower thresholds for

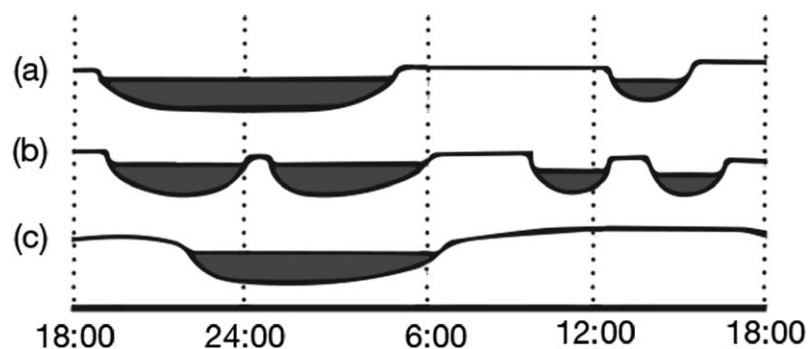


Figure 1. Is human sleep flexible? (A, B) Polyphasic sleep phasing, compared to (C), the relatively consolidated monophasic sleep characterized by populations living in postindustrial developed economies. Compared to traditional populations, recent work points to a surprising convergence in the consolidation of “modern” sleep phasing with inferred ancient patterns.

awakening, and more awakenings during a single sleep period.⁴⁵ Children and adults with attention deficit hyperactivity disorder (about 3%-5% of a population) may also have a lower threshold and greater frequency of awakenings.⁴⁶ Variability in chronotype, resulting in sleep sentinels, could have led to increased night-time vigilance and survivability, possibly via group selection, as a way of countering predation or defending against night raids by rival groups.

The question of “normal” human sleep phasing has received attention from both empirical and historical researchers. Ekirch⁴⁷ used historical records as the basis for his proposal that biphasic sleep was common in European civilizations before the Industrial Revolution. In addition, experiments suggested that humans from Western populations can revert to a biphasic sleep pattern under conditions of long nights.⁴⁸ From Wehr’s⁴⁸ research emerges the “human sleep flexibility hypothesis,” according to which humans show circadian rhythms and behavioral strategies that facilitate flexible, polyphasic sleep patterns. The alternative sleep consolidation hypothesis forwards the idea that a single, integrated sleep period, with a low frequency of daytime napping, best characterizes traditional populations (Fig. 1) and therefore represents “normal” ancestral sleep.

In support of the sleep consolidation hypothesis, Yetish and colleagues¹³ recently used actigraphy to quantify natural sleep patterns in

three traditional populations in Tanzania, Namibia, and Bolivia. Strikingly, these populations exhibited similar sleep parameters, with an average duration of 5.7-7.1 hours. Typically, sleep onset would occur several hours after sunset, with after-hours activity facilitated by firelight. However, wake onset, which was associated with sunrise, was less variable. The sleep efficiency in these three traditional populations was between 81% and 86%, and thus comparable to that in industrial populations. Sleep consistently occurred during the period of night with the lowest temperature and individuals slept longest during the times of year with the coolest temperatures. These findings highlight the role of environmental factors in sleep patterns. In summary, with temperature proposed as a major regulator of sleep duration and timing, data generated in these equatorial populations supports the hypothesis that ancient humans’ sleep was consolidated into one major sleep bout per 24 hours.

Multiple approaches exist to investigate the phasing of human sleep more quantitatively. First and foremost, more data are needed on sleep patterns in humans that lack access to artificial light. This includes not only hunter-gatherers and small-scale agriculturalists who live in equatorial habitats, but also populations in high-latitude arctic areas characterized by long summer daylight hours with moderate temperatures and long, cold winters with extremely low light exposure or no

light exposure. In addition, populations in developing countries, which experience emerging “evolutionary mismatch” situations, in which their rapidly changing environments differ radically from ancestral environments, may exhibit sleep phasing that differs from that in traditional and/or postindustrial populations.

Similarly, more research is needed on natural patterns of variation in ape sleep, especially activity at night. Sleep research on apes has recently gained traction because data-logging equipment and infrared cameras can record vocalizations and activity around great ape sleep sites in both wild^{49,50} and captive sites.⁵¹ Comparative approaches are also needed to rigorously measure sleep intensity in a broad set of primates and to place humans in that comparative context. We next turn to an example of use of this comparative approach to determine different aspects of human sleep architecture.

Sleep Duration, Depth, and Percentage of REM in Comparative Perspective

Human sleep, when compared on a gross level to that of other primates, appears to be characterized by several unique traits. Based on a 7.0-hour sleep duration estimated in multiple populations over 66 studies, with these populations cross-sectioned at five-year intervals from the ages of 15 through 45 years,^{32,45} human sleep duration is the shortest recorded among primates (Fig. 2A). This is in stark contrast to the primate “marathon sleepers” (for example, owl monkeys, cotton-top tamarins, and mouse lemurs), which have total sleep times ranging from 13-17 hours.¹¹ The human REM to NREM ratio (22:78) is the highest proportion of REM to NREM of all primates (Fig. 2B).

While these patterns are intriguing, a more quantitative phylogenetic approach is needed to assess the degree to which human sleep differs from that of other primates.⁵² We used such an approach – an evolutionary outlier analysis – to assess whether human sleep is extraordinary as compared to variation

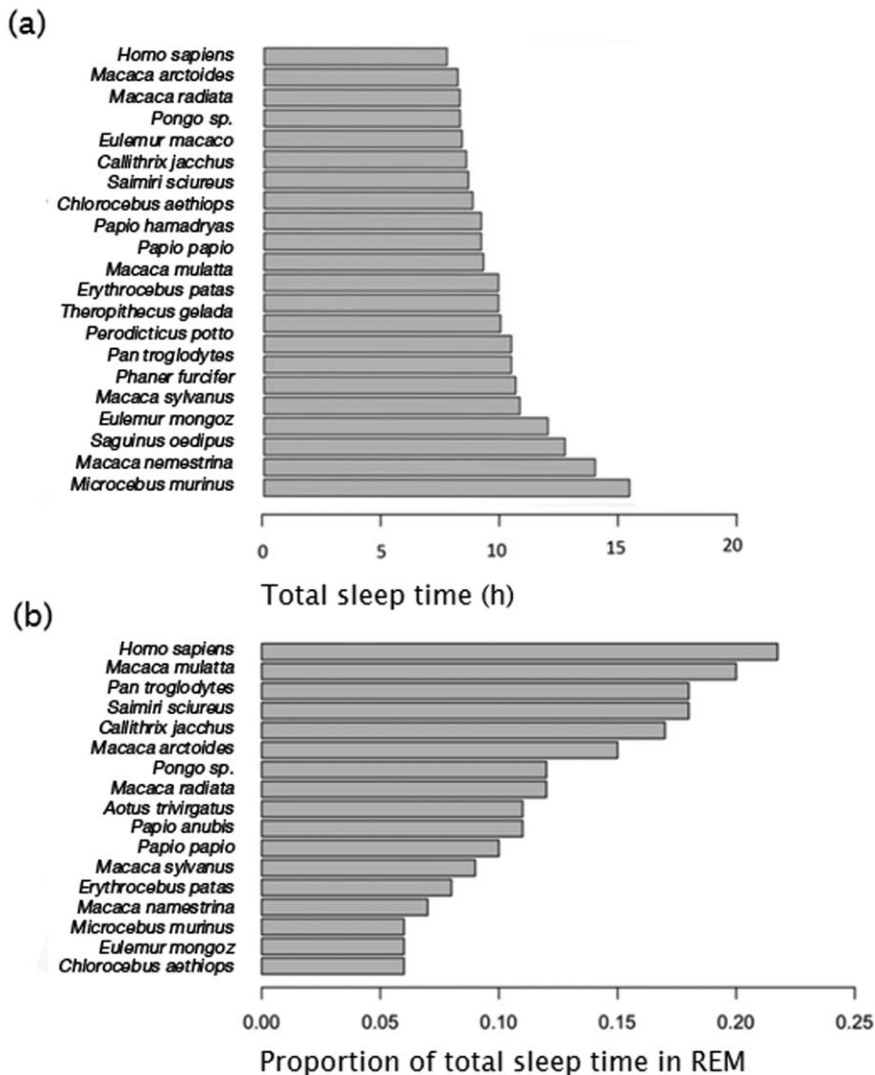


Figure 2. Human sleep relative to that of nonhuman primates. Humans have (A) the shortest total sleep times and (B) the greatest proportion of REM relative to total sleep time. We investigate these patterns phylogenetically and quantitatively in Box (see Figs. 3 and 4).

among primates in general.^{53,54} This analysis combines phylogeny with data on predictor variables to make a phylogenetically informed prediction of a response variable for a particular species on the phylogeny (Box 1). As shown in Box 1, our analyses demonstrated that humans have exceptionally short sleep (Fig. 3) with a greater proportion of REM (Fig. 4) than would be predicted for a primate of similar phenotypic characteristics.

Because of the challenges of using invasive EEG with endangered species, only 7% of primate species have had their sleep architecture quanti-

fied.⁵⁵ Even fewer have had detailed descriptions of sleep environment and species-specific sleeping postures documented. Specifically, there is a dearth of data recording the full range of critical sleep measures – light N2 sleep, deep N3 sleep, and REM – and behavioral variables such as sleep efficiency, sleep motor activity, and sleep fragmentation (see Glossary). Therefore, variables that are critically important for understanding sleep intensity are currently lacking for primates. As we will discuss, given the link between sleep homeostasis and motor activity,⁵⁶ several variables drawn from actigra-

phy may serve as behavioral proxies for deep sleep, thus opening the door for future studies of these variables and their correlates.

ALLOMETRIC SCALING AND ECOLOGY OF SLEEP SITES

Humans are also characterized by sleeping terrestrially, which is unusual among primates. Other primates will occasionally sleep terrestrially, or some individuals in some populations will show more regular ground sleeping. For example, where predation is regionally low for chimpanzees, a small proportion of males has been observed to sleep on the ground.⁵⁷ Similarly, physically massive male gorillas that live in predator-poor environments often sleep on the ground.⁵⁸ But it is only in humans that all age and sex classes habitually sleep terrestrially.

As suggested by these examples of gorilla and chimpanzee male sleep patterns, physical characteristics and ecology are important in predicting primate sleep sites. Indeed, a consideration of allometry helps shed light on some aspects of primate sleep site patterns. In a simple geometric model, the doubling of the length of an animal corresponds to disproportionate increases in area and volume.⁵⁹ The exponential increase in volume relative to stature creates physical limits on where a primate can successfully obtain the benefits of sleep.⁶⁰

To investigate allometric scaling of sleep-site use, we have identified four major sleep-site categories that primates use to overcome the challenges of finding security and comfort (Box 2): fixed-point nests, tree branches, arboreal sleeping platforms, and terrestrial beds (Fig. 5). Each of these is related to what we call a “sleep-scaling threshold” as a way to overcome the exponential increase in body volume.

The ancestral primate was likely arboreal,⁶¹ a way of life that presents major challenges to most primates in locating comfortable and secure sleep sites. Small-bodied primates often use tree-holes or circular leaves that mesh together to avoid predators and mosquito vectors that spread parasites, as well as to thermoregulate, provision, and care for young.^{62–64}

Box 1. Phylogenetic Outlier Analysis

A major challenge for comparative methods is to investigate change in a quantitative trait along a single branch of a phylogeny, as one might wish to do for humans, while also controlling for variation in factors that explain variation in the trait of interest.⁵² A standard way to achieve this is by regressing a response variable on other traits and testing whether humans are “outliers,” as has been done in studies of brain size.¹⁰⁵ It is important in this context also to control for phylogeny, in terms of both the underlying regression model and assessing whether humans are outliers.¹⁰⁶ For example, if apes lie above the regression line, we might expect that humans do, too, suggesting that it is something about apes (not just humans) that differs from other primates.

We used recent Bayesian phylogenetic methods⁵³ for statistical modeling of sleep durations in primates, then used the statistical model to predict sleep duration in humans. Sleep durations were used only if they passed the minimum requirements for data quality as detailed in previous work that compiled sleep quotas for phylogenetic analysis.^{107,108} By comparing actual sleep duration in humans to the predicted outcomes from the model, we can investigate whether humans are a typical primate (our observed sleep duration⁴⁵ falls within the predicted interval) or a “phylogenetic outlier” (our sleep duration falls outside the

predicted interval). More specifically, we estimated regression coefficients and the degree of phylogenetic signal in the data using Markov chain Monte Carlo (MCMC) approaches and implemented Bayesian model selection, which includes predictor variables in the statistical model in proportion to their posterior probability (body mass was forced into the model at all iterations in the MCMC chain).⁵³ When phylogenetic signal in the residuals from the statistical model is high (estimated with the scaling parameters λ and κ),⁵² the human value is shifted based on phylogeny to reflect values of sleep duration in our close phylogenetic relatives. We used a Bayesian posterior probability distribution of models and phylogenies to generate a Bayesian posterior prediction distribution, which is what would be predicted in a primate with phenotypic characteristics similar to those of humans. We determined that humans are exceptional if the observed human value falls outside the 95% credible interval.

Analyses of sleep duration showed that humans are exceptionally short sleepers, with the human value (shown as a line in Figure 3) substantially below the 95% credible interval of predicted sleep durations (only 1 of 500 samples from the posterior prediction was more extreme than observed). In fact, however, most of the coefficients relating these traits to total sleep time in primates were not different

from zero, and often not included in the model. Our predictions take into account that uncertainty about which variables to include in the model, along with uncertainty about primate phylogeny. We also found good evidence of phylogenetic signal; the branch length scaling parameter λ for total sleep time had a mean of 0.69 (SD = 0.28).

We next examined the proportion of REM sleep across primates to assess whether humans are a phylogenetic outlier in this regard as well. Analyses of the proportion of REM sleep also showed that humans are a striking outlier (Fig. 4), with the human REM proportion substantially above the 95% credible interval of predicted REM proportion (only 2 of 500 samples in the posterior probability distribution were greater than the observed value for humans). Again, we found good evidence of phylogenetic signal based on the finding that the branch-length scaling parameter λ for REM proportion had a mean of 0.59 (SD = 0.27).

In summary, taking phylogeny and primate ecology into account, human sleep differs substantially from that of other primates: We are exceptionally short sleepers and we pack a higher proportion of REM sleep into our short sleep durations. It appears that evolution has whittled away sleep durations along our lineage, just as access to electricity and lighting continues to do in the present day.

Evolutionary reconstruction of primate life-history traits points to an ancestral sleep state that most likely resembled that of extant galagos, a solitary, nocturnal animal that produces a single offspring provisioned in a fixed-point nest.⁶³ Early nest-like sleeping shelters may primarily have protected against predation and biting insects,⁶⁴ conferred a thermoregulatory buffer, and increased overall safety by reducing the risk of falling from arboreal sleep sites.⁶⁵ These val-

uable sites, especially tree-holes, would have required time to locate and potentially secure from other animals or, in the case of leaves and branches, to construct or parasitize. Open nests may provide some of these benefits but, when closed sites are available, they considerably enhance these benefits.

Paleocene and Eocene primates' body size, like that of many other mammals, steadily increased through time.^{66,67} As primate body mass

expanded beyond the capacity of most fixed-point nests, a major transition occurred from fixed-point nest sleep to tree-branch sleep. Abandonment of the fixed-point nest sleep-site strategy in divergent primate lineages may also have been a result of the change from nocturnal to diurnal activity patterns, which resulted in larger social groups as a defense against diurnal predators.⁶⁸ From the measurements of postural behavior of the few primates that have been

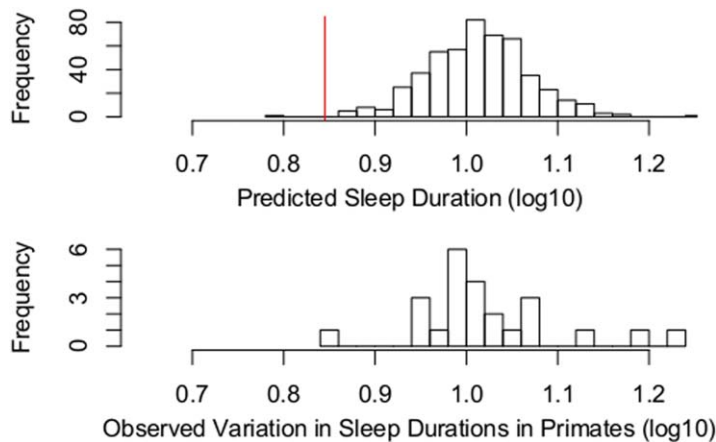


Figure 3. We conducted a Bayesian analysis to predict total sleep duration based on phylogeny, body mass, activity period, endocranial volume, percentage of leaves in the diet, interbirth interval, and foraging group size. The distribution (top) reflects the posterior probability for predicted sleep duration relative to the observed variation in sleep durations (bottom); the vertical line represents the observed human value. Because the observed value falls outside the 95% credible interval, we conclude that human sleep length is different from what one would predict for a primate with our traits and phylogenetic position. In other words, humans, relative to other primates, have extremely short total sleep durations. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

recorded during sleep bouts, it is observed that they typically huddle together in a guarded position. This dynamic and precarious sleep environment may explain why, as compared to apes, monkeys have less efficient, lighter sleep.⁶⁹

Great apes are characterized by a universal behavior that has helped them solve the challenge of sleeping securely and comfortably in the trees in spite of their massive bodies. They construct a “nest” or sleeping platform.^{70,71} Great apes build a new

sleeping platform each night, specifically selecting trees for their firm, stable, and resilient biomechanical properties.^{72–74} In contrast, the lesser apes, the gibbons, do not build sleeping platforms; instead, they follow the ancestral primate pattern of sleeping on tree branches, typically lying or sitting on what is available without altering their local environment.⁷⁵ Arboreal platforms provide several benefits to sleepers, including keeping individuals out of range of terrestrial predators,^{76–78} repelling blood-sucking arthropods and/or masking individual insect-attracting odors,^{64,79–81} providing added insulation to keep warm,^{65,81} and providing a more stable and secure environment.⁷²

Phylogenetic reconstruction places the emergence of nest building sometime between 18–14 mya.⁸² The innovation of ape nest construction, coinciding with the evolution of body mass over the 30 kg threshold (Fig. 6), suggests that larger body mass made sleeping on branches less advantageous for apes. At this size, apes would have benefited from more resilient and stable sleeping substrates to reduce both physical stress on the body and the probability of lethal falls. This evolutionary event could have then established the prerequisite adaptations to alter sleep architecture within the Hominidae.

In addition to the challenges of a larger-bodied animal sleeping on branches, cognitive demands in great apes may have favored nest-building. In particular, more stable sleeping sites provide physical support for large-bodied hominoids to maintain deep and sustained sleep,^{60,83} which may be linked to enhanced cognitive function in the great apes.⁷¹ This idea has become known as the sleep-quality hypothesis. The alternative “engineering hypothesis” switches causality to suggest that the greater cognitive performance of great apes enables them to build nests.⁸³ Rather than viewing these two hypotheses as mutually exclusive, it could be that increased complexity in sleeping platform construction could have positively affected cognition, which then enhanced nest building potential, resulting in a positive feedback loop.

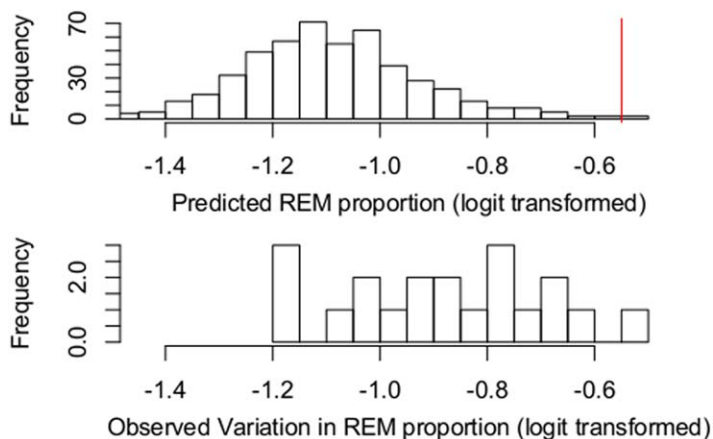


Figure 4. We conducted a Bayesian analysis to predict REM proportion based on phylogeny, body mass, activity period, endocranial volume, percentage of leaves in the diet, interbirth interval, and foraging group size. The distribution (top) reflects the posterior probability for predicted REM proportion relative to the observed variation in REM proportion (bottom); the vertical line represents the observed human value. Because the observed value falls outside the 95% credible interval, we conclude that human REM is different from what one would predict for a primate with our traits and phylogenetic position. In other words, humans, relative to other primates, have an extremely long proportion of REM to total sleep time. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

Box 2. Sleep Sites and Body Mass

A primary driver of primate sleep-site selection is circumscribed not only by mass but also volume (as an allometric scaling function of body length), relative to local ecological pressure and functional morphology. Large-bodied primates must position themselves on relatively smaller sup-

ports. Even if larger primates positioned themselves on geometrically proportional supports, stress on the body increases disproportionately. As body length increases, weight increases at a cube length, whereas the surface of the body supporting weight increases at only a square.

Thus, large primates disproportionately stress the skin, connective tissue, and skeleton when lying horizontally. More importantly, the relatively constant size of supporting branches would no longer be appropriate for the task of securing a sleep site (Figs. 5 and 6).

A few recent studies have begun to investigate how nests and sleep enhance cognitive performance in nonhuman great apes. First, Samson and Shumaker⁸⁴ provided captive orangutans with different materials to construct a night nest. They quan-

tified the sleeping platform complexity each night, measuring it as an index of the number of material items available to construct a bed, and found that complexity covaried positively with reduced night-time motor activity, less fragmentation, and

greater sleep efficiency. Second, in captive apes undergoing experimental cognitive testing, sleep has been shown to stabilize and protect memories from interference.⁸⁵ Future research could investigate these questions with similar approaches,



Figure 5. (A) Fixed-point nests are used to avoid predators, stay within optimal temperatures, and store resources and offspring (photo accredited to Manfred Eberle). (B) Tree branches are used to avoid predators, but are less stable than other sleep sites. (C) Sleeping platforms are universally used by large-bodied great apes as stable and secure sleep sites that are warm and confer resistance to biting insects and arboreal predators (photo accredited to Kathelijne Koops). Terrestrial beds are used by massive apes (male chimpanzees and gorillas) and humans (photo of Hadza hunter accredited to Mathiew Paley/paleyphoto.com). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

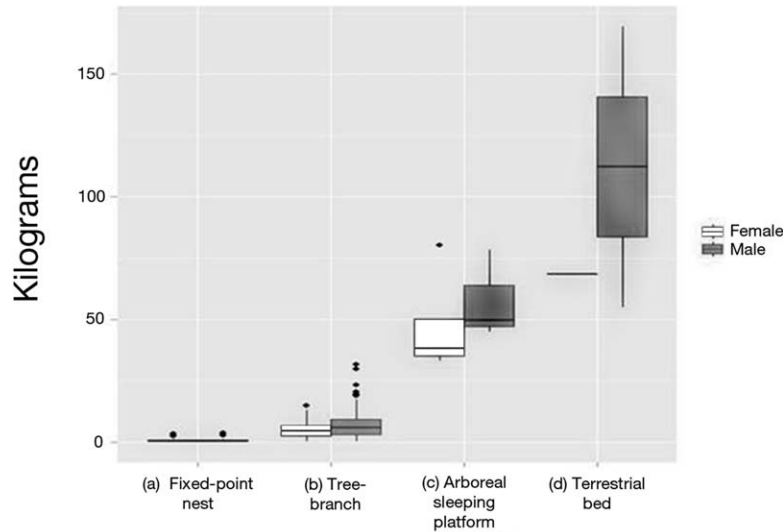


Figure 6. The effect of allometric scaling illustrated by body mass (y-axis) and sleep-site category (x-axis), and accounting for sex (white = female, grey = male), shows how primates have adapted their sleep environments relative to evolutionary increases in body mass. Data from species' averages in Smith and Jungers.¹¹⁰

combined with quantitative measures of sleep depth and quality.

EARLY HUMAN SLEEP ECOLOGY

Given the dramatic morphological changes and exponentially increasing body volume that took place during the *Australopithecus-Homo* transition, inferential evidence supports *H. erectus* as the first fully terrestrial ground-sleeping hominin. *Homo's* predecessor, *Australopithecus*, shares several anatomical features (such as a narrow scapula and long, curved phalanges) with the great apes; these features reduced structural fatigue and are clear indicators of arboreal adaptation.⁸⁶ In contrast, it is generally accepted that *H. erectus* is the first obligate biped,⁸⁷ with resulting mass and stature estimates (*H. erectus* males = 1.8 m, 66 kg; females = 1.6 m, 56 kg) that are comparable to those of modern humans.^{88–90} Therefore, with limb proportions that would make it difficult to facilitate arboreal sleep, *Homo* was likely the first full-time ground sleeper.

Regardless of the specific timing of the transition to the ground, a critical question remains: Once on the ground, how did our ancestors cope without arboreal sleeping sites and the benefits they confer? As noted, arboreal platforms provide

many benefits that would have been lost when sleeping on the ground. Thus, one might predict that movement from tree to ground sleep would have increased risks from predation by large-bodied animals such as leopards, hyenas and saber-toothed cats;⁹¹ disease transmission by blood-sucking arthropods such as terrestrially hunting mosquitoes;⁹² and reduced thermoregulatory homeostasis when in contact with the conductive properties of the earth's relatively cooler temperature.

Thus, to make the terrestrial sleep transition, early hominins would likely have evolved numerous behavioral adaptations to counteract these risks and the loss of benefits of arboreal platforms. With respect to early hominin sleep ecology, possession of fire has been proposed as essential for enabling sleep in terrestrial environments.¹⁰ It has been proposed that the first of our hominin ancestors to use fire was *H. erectus*,⁹³ and although the claim remains uncertain because of fragmentary archeological evidence, it has been argued that fire was necessary for the transition to obligate terrestriality.⁹⁴ Fire at night would have helped deter predators,⁹⁴ kept individuals warm during cold nights, and fumigated sleep sites with smoke to deter biting insects^{3,4} (Table 1). Moreover, fire may have increased

group cohesion and promoted meditation.⁹⁵ Possible costs in the habitual use of fire may have included increased rates of respiratory disease⁹⁶ and attraction of intraspecific competitors.

The details of this transition are difficult to pin down in the archeological record. There is evidence of the use of smoke to repel malaria vectors in Amazonian societies.⁹⁷ Tests aimed at investigating the use of fire in relation to controlling biting insects could be one way forward. Additional data obtained by experimentally manipulating access to fire in an outdoor environment, alongside mobile polysomnography and insect-trap measures, could directly test fire's role in sleep safety and quality. Finally, similar data generated with hunter-gatherers could clarify the frequency with which fires are used and the benefits obtained for thermoregulation and predator avoidance.

SLEEP INTENSITY HYPOTHESIS

Building on these and other emerging findings in evolutionary anthropology and sleep biology, we propose the "sleep intensity hypothesis", which postulates that early humans sleeping in novel terrestrial environments had characteristic sleep architecture that fulfilled homeostatic need in the shortest time possible. Such a shift in sleep ecology could explain the unique characteristics of human sleep, resulting in an overall pattern of efficient sleep expression with subsequent cognitive and behavioral advantages emerging from high-quality sleep and increased net hours of activity along the human lineage. We present this idea by first providing some additional background on sleep biology, then consider selective pressures on human sleep.

Vyazovskiy and Delogu¹⁴ advance the theory that NREM and REM work in a complementary system, with NREM enabling information processing, synaptic plasticity, and cellular maintenance during a general "recovery phase" and REM enabling periodic excursions into an activated brain, identifying networks that have undergone recovery from

the previous NREM period, thus performing a “selection phase.” In other words, REM “tags” which parts of the brain are sufficiently stabilized, differentiating them from those that need more SWA processing.

The net result of NREM-REM cycling is an efficient process. It ensures that functional requirements for current cognitive demands are met in the shortest possible time.²² Indeed, Halász and colleagues⁹⁸ note, “It may be that the full-blown development of these synergetic regulations is a human-specific trait which was necessary due to the vulnerability of the cognitive functions of the frontal neocortex.”⁹⁸ In full-time terrestrial environments, hominins, sleeping in large, sentineled groups on stable ground beds protected by fire, would have been uniquely positioned to capitalize on the adaptive advantage of deeper, more intense, REM-dominated sleep.

The terrestrial sleep transition would have eliminated the significant dangers of arboreal activity for a diurnal animal at night, one of the most important being the danger of lethal falls by large-bodied individuals. In this situation, early humans could have dedicated a greater proportion of time to behaviorally vulnerable, yet highly consolidated, sleep states with high arousal thresholds, such as N3 (SWS) and REM sleep, with less time in light N2 (NREM stages 1-2). This would have increased the relative proportion of deep sleep versus light sleep, while shortening the total time individuals needed to be inactive. Moreover, early humans may have been the first primates to exhibit a single integrated sleep period with a greater proportion of deep sleep characterized by a major initial period of N3 (SWS) and coupled bouts of proportionately longer REM sleep.

In addition, with the use of fire, cooking would have reduced the time invested in chewing from 4-7 hours a day to about 1 hour.⁹⁴ Indeed, one study has found that, relative to other primates, humans are evolutionary outliers in their chewing time,⁵⁴ spending only 4.7% of the active day feeding, whereas *Pan* spends 37.5% of the day doing so. Including the reduction in time spent chewing from the

Pan average (270 minutes) to a human average (35 minutes⁵⁰) and a release from the obligate inactivity of arboreal sleep sites (720 minutes) to a human average (420 minutes), the net gain of activity in 24 hours could have amounted to approximately 8.9 hours. Moreover, fire may have increased the “artificial day,” since early human activity may have been extended past dusk by access to controllable light. In sum, the innovations of fire and high-quality sleep sites on the ground could have increased early *Homo* waking activity by 37% in a 24-hour period.

Increased sleep intensity conferred at least three cognitive benefits on early

In full-time terrestrial environments, hominins, sleeping in large, sentineled groups on stable ground beds protected by fire, would have been uniquely positioned to capitalize on the adaptive advantage of deeper, more intense, REM-dominated sleep.

humans. The first of these involves threat priming. By way of the phenomenological content of sleep (dreaming), REM primes sleepers by rehearsing likely threatening events or social scenarios that may occur in their waking environments.⁹⁹ Increased innovation is a second benefit of increased sleep intensity. In particular, REM sleep and its contents may have allowed for a wider networking of ideation, resulting in greater frequency of creativity, insight, and innovation.¹⁰⁰ Moreover, increased sleep intensity likely enhanced memory consolidation. Clear evidence exists regarding the role of SWS and REM sleep in processing daily information into long-term memory stores. For example, SWS has been

associated with the consolidation of procedural memories (for example, visuospatial locations and stone-knapping skills)¹⁰¹ and the processing of emotionally valent declarative and episodic memories.¹⁷ It is worth noting that Walker and Stickgold¹⁰² proposed a homeostatically driven demand on sleep-dependent memory consolidation that reciprocally enhances sleep depth; in other words, sleep enhances learning and, in turn, learning enhances sleep.

With the increase in potential activity budget, significant group-level social activity could have been expanded to the night time. This could have had important consequences for hominin socioecology by increasing the total time available to bond communities,¹⁰³ transmit cultural information, and augment waking cognitive abilities. In turn, with a reduction in total sleep time and increase in sleep intensity, there may have been selective pressure for the cognitive and behavioral benefits of improved memory consolidation, increased creativity, and social intelligence, all of which would plausibly improve survival in challenging novel terrestrial environments.

KEY PREDICTIONS AND FUTURE DIRECTIONS

In exploring primate sleep ecology and physiology, we presented a novel hypothesis that attempts to explain how modern human sleep architecture evolved. While some existing data led us to this hypothesis, future research should test specific predictions arising from it. First, generating descriptive statistics on sleep architecture in previously unrecorded captive and wild primates is essential. Our ability to test these hypotheses is limited because of the dearth of nonhuman primate sleep studies. As noted earlier, such studies are difficult because of the invasive nature of EEGs and EMGs. However, cost-effective technology to test such hypotheses is now becoming available (Table 2). Key species to generate further data to test the sleep intensity hypothesis are lemurs (for example, *Lemur catta*, *Propithecus* spp., and *Eulemur* spp.), the

TABLE 2. Recording Primate Sleep: Current Cost-Effective Technology That Can Expand Primate Sleep Datasets

Technology	Gross Measure	Specifics	Invasive
Actigraphy	Active/nonactive states	Can measure activity at 1-sec interval resolution; in humans, algorithms may generate NRME/REM states at 90% efficacy	No
Videography/ Eularian magnification	Behavioral signatures	Can measure respiration and gross body motor movement; in apes, shown to differentiate between NREM/REM states at 80% efficacy	No
Piezoelectric	Active/nonactive states	Automatically records data; can measure breathing rhythms	No
EEG	Gold standard "brain wave activity"	Automatically records data; can differentiate between NREM/REM states and measure delta and theta wave states	Yes

New World Cebidae, the Old World colobines, and the apes.¹¹ Moreover, sleep expression encompasses more than just NREM and REM distribution; to effectively move forward, research should also quantify behavioral measures such as sleep efficiency, motor activity, and sleep fragmentation, which can be measured in primates via actigraphy and infrared videography.

As data accumulate for more species, phylogenetic comparative methods can be applied to reanalyze key hypotheses and infer ancestral states to assess characteristics of sleep in extant taxa, including humans. Several questions could be targeted using comparative data on NREM, REM, sleep depth, and their correlates: Across mammals, how do evolutionary transitions to various kinds of sociality influence sleep? Do ecological variables associated with sleep ecology correlate with sleep architecture? Specifically, do animals with fixed-point nests or arboreal sleeping platforms have different sleep characteristics than do those that sleep on branches? Do rates of innovation and social learning covary with specific types of sleep architecture (more REM coupled with less total sleep)? We predict that the mechanisms that facilitate differences in sleep intensity and depth will be functionally related to sleep environments, particularly dis-

crete parameters that augment security and comfort in sleep sites.

A critical test of the sleep intensity hypothesis will come from sleep data generated in traditional human populations characterizing normal sleep patterns in varying climates and latitudes. The hypothesis would be disproved if traditional populations were characterized by longer than average sleep durations. A critical test of the sleep intensity hypothesis was recently reported: Research that generated sleep durations of 5.7-7.1 hours for traditional populations¹³ discovered even shorter durations than the standard human average used in our phylogenetic analysis. This finding supports the sleep intensity hypothesis. Furthermore, the sleep intensity hypothesis would be disproved by comparative data showing that human sleep is less efficient than that of our closest phylogenetic relatives when sleeping is done in similar conditions. However, even if we found that sleep across apes is largely similar, modern human reliance on high quality sleep is critical. Increased attention to sleep along the ape lineage may give a clearer understanding of why we sleep.

CONCLUSIONS

As Rechtschaffen¹⁰⁴ noted, "If sleep does not serve an absolute vital function, then it is the biggest mis-

take the evolutionary process ever made." We advanced the hypothesis that human sleep has unique characteristics and that those characteristics are intimately intertwined with other features that have made humans so successful. We also proposed that the four known primate sleep environments are linked to the allometric sleep-scaling threshold, and that these discrete categories lend support to *H. erectus* having been the first full-time terrestrial sleeper among the primates.

These considerations led us to articulate the sleep intensity hypothesis, which states that evolutionary shifts in human sleep environments have allowed sleep quality to improve by permitting deeper sleep. This evolutionary model of early hominin sleep builds on previous contributions⁵ and dovetails with current hypotheses related to the importance of fire⁹⁴ and group cohesion¹⁰⁴ in human evolution. For early humans, a unique sleep architecture promoting information consolidation by way of highly efficient, secure, and comfortable sleep environments could have resulted in high degrees of cognitive and behavioral plasticity.

Empirical sleep research in anthropology is in its infancy. That being said, the window of possibility to test many of the relevant hypotheses that could answer the greater questions of sleep's role in human evolution may be coming to a close. Wild populations of great apes are among the most endangered in the world, and hunter-gatherer cultures remain extremely vulnerable to massive shifts in subsistence strategy and cultural norms, given increased (often hostile) exposure to larger nation states. Therefore, generating sleep data in an ecologically relevant context is acutely urgent.

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REFERENCES

- Zepelin H, Siegel J, Tobler I. 2005. Mammalian sleep. In: Kryger MH, Roth R, Dement WC, editors. Principles and practice of sleep medicine. Philadelphia, PA: Elsevier Saunders. p 91–100.
- Lesku JA, Roth TC, Lima SL, et al. 2006. Sleep architecture in birds: an avian perspective on Zepelin and Rechtschaffen (1974). *Sleep* 29:A35–A35.
- Worthman CM, Melby MK. 2002. Toward a comparative developmental ecology of human sleep. In: Carskadon MA, editor. Adolescent sleep patterns: biological, social, and psychological influences. Cambridge, MA: Cambridge University Press. p 69–117.
- Worthman CM. 2008. After dark: the evolutionary ecology of human sleep. In: Trevathan WR, Smith EO, McKenna JJ, editors. Evolutionary medicine and health. Oxford: Oxford University Press. p 291–313.
- Coolidge FL, Wynn T. 2006. The effects of the tree-to-ground sleep transition in the evolution of cognition in early *Homo*. *Before Farming* 4:1–18.
- Siegel JM. 2001. The REM sleep: memory consolidation hypothesis. *Science* 294:1058–1063.
- Durmer JS, Dinges DF. 2005. Neurocognitive consequences of sleep deprivation. *Semin Neurol* 25:117–129.
- Drummond SPA, Gillin JC, Brown GG. 2001. Increased cerebral response during a divided attention task following sleep deprivation. *J Sleep Res* 10:85–92.
- McNamara P, Auerbach S. 2010. Evolutionary medicine of sleep disorders: toward a science of sleep duration. In: McNamara P, Barton RA, Nunn CL, editors. Evolution of sleep: phylogenetic and functional perspectives. Cambridge: Cambridge University Press. p 107–122.
- Coolidge FL, Wynn T. 2009. The rise of *Homo sapiens*: the evolution of modern thinking. West Sussex, UK: Wiley-Blackwell.
- Nunn CL, McNamara P, Capellini I, et al. 2010. Primate sleep in phylogenetic perspective. In: McNamara P, Barton RA, Nunn CL, editors. Evolution and sleep: phylogenetic and functional perspectives. New York: Cambridge University Press. p 123–145.
- Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am J Primatol* 46:63–75.
- Yetish G, Kaplan H, Gurven M, et al. 2015. Natural sleep and its seasonal variations in three pre-industrial societies. *Curr Biol* 25:1–7.
- Vyazovskiy VV, Delogu A. 2014. NREM and REM sleep: complementary roles in recovery after wakefulness. *Neuroscientist* 20:203–219.
- Webb WB. 1988. Theoretical presentation: an objective behavioral model of sleep. *Sleep* 11:488–496.
- Kavanau JL. 1997. Memory, sleep and the evolution of mechanisms of synaptic efficacy maintenance. *Neuroscience* 79:7–44.
- Walker MP. 2009. The role of sleep in cognition and emotion. *Ann NY Acad Sci* 1156:168–197.
- Xie L, Kang H, Xu Q, et al. 2013. Sleep drives metabolite clearance from the adult brain. *Science* 342:373–377.
- Achermann P, Dijk DJ, Brunner DP, et al. 1993. A model of human sleep homeostasis based on EEG slow-wave activity: quantitative comparison of data and simulations. *Brain Res Bull* 31:97–113.
- Fisher SP, Foster RG, Peirson SN. 2013. The circadian control of sleep. *Exp Pharmacol* 217: 157–83.
- Saper CB, Fuller PM, Pedersen NP, et al. 2010. Sleep state switching. *Neuron* 68:1023–1042.
- Ackermann S, Rasch B. 2014. Differential effects of non-REM and REM sleep on memory consolidation? *Curr Neurol Neurosci* 14:1–10.
- Vyazovskiy VV, Harris KD. 2013. Sleep and the single neuron: the role of global slow oscillations in individual cell rest. *Nat Rev Neurosci* 14:445–453.
- Huber R, Deboer T, Tobler I. 2000. Effects of sleep deprivation on sleep and sleep EEG in three mouse strains: empirical data and simulations. *Behav Brain Res* 857:8–19.
- Nishida M, Pearsall J, Buckner RL, et al. 2009. REM sleep, prefrontal theta, and the consolidation of human emotional memory. *Cereb Cortex* 19:1158–1166.
- Sallinen M, Kaartinen J, Lyytinen H. 1996. Processing of auditory stimuli during tonic and phasic periods of REM sleep as revealed by event-related brain potentials. *J Sleep Res* 5: 220–228.
- Ermis U, Krakow K, Voss U. 2010. Arousal thresholds during human tonic and phasic REM sleep. *J Sleep Res* 19:400–406.
- Morin CM. 2011. Psychological and behavioral treatments for insomnia I: approaches and efficacy. In: Kryger MH, Roth T, Dement WC, editors. Principles and practice of sleep medicine, 5th ed. St. Louis, MO: Elsevier Saunders. p 866–883.
- Thorpy MJ. 2011. Classification of sleep disorders. In: Kryger MH, Roth T, Dement WC, editors. Principles and practice of sleep medicine, 5th ed. St. Louis, MO: Elsevier Saunders. p 680–693.
- Ekirch AR. 2006. At day's close: night in times past. New York, NY: WW Norton.
- Everett DL. 2009. Don't sleep, there are snakes: life and language in the Amazonian jungle. New York: Vintage.
- Knutson KL. 2014. Sleep duration, quality, and timing and their associations with age in a community without electricity in Haiti. *Am J Hum Biol* 26:80–86.
- McKenna JJ, McDade T. 2005. Why babies should never sleep alone: a review of the co-sleeping controversy in relation to SIDS, bed-sharing and breast feeding. *Paediatr Respir Rev* 6:134–52.
- Epstein R, Herer P, Tzischinsky O, et al. 1997. Changing from communal to familial sleep arrangement in the Kibbutz: effects on sleep quality. *Sleep* 20:334–339.
- Libert JP, Bach V, Johnson LC, et al. 1991. Relative and combined effects of heat and noise exposure on sleep in humans. *Sleep* 14:24–31.
- Reynolds B. 1968. The material cultures of the peoples of the Gwembe valley. New York: Praeger.
- Turnbull CM. 1962. The forest people. New York: Simon and Schuster.
- Wobber V, Hare B, Wrangham R. 2008. Great apes prefer cooked food. *J Hum Evol* 55: 340–348.
- Wrangham RW, Jones JH, Laden G, et al. 1999. The raw and the stolen: cooking and the ecology of human origins. *Curr Anthropol* 40: 567–594.
- Hammel HT, Elsner RW, Lemessurier DH, et al. 1959. Thermal and metabolic responses of the Australian aborigine exposed to moderate cold in summer. *J Appl Phys* 14:605–615.
- Gray PB. 2013. Evolution and human sexuality. *Am J Phys Anthropol* 152:94–118.
- Hewlett BS. 2014. Hunter-gatherers of the Congo Basin: cultures, histories, and biology of African pygmies. New Brunswick, NJ: Transaction Publishers.
- Randler C. 2014. Sleep, sleep timing and chronotype in animal behaviour. *Anim Behav* 94:161–166.
- Viola AU, Archer SN, James LM, et al. 2007. PER3 polymorphism predicts sleep structure and waking performance. *Curr Biol* 17:613–618.
- Ohayon MM, Carskadon MA, Guilleminault C, et al. 2004. Meta-analysis of quantitative sleep parameters from childhood to old age in healthy individuals: developing normative sleep values across the human lifespan. *Sleep* 27: 1255–1273.
- Owens JA. 2004. Sleep in children: cross-cultural perspectives. *Sleep Biol Rhythms* 2: 165–173.
- Ekirch AR. 2001. Sleep we have lost: pre-industrial slumber in the British isles. *Am Hist Rev* 106:343–386.
- Wehr TA. 1992. In short photoperiods, human sleep is biphasic. *J Sleep Res* 1:103–107.
- Zamma K. 2014. What makes wild chimpanzees wake up at night? *Primates* 55:51–57.
- Krief S, Cibot M, Bortolamiol S, et al. 2014. Wild chimpanzees on the edge: nocturnal activities in croplands. *Plos One* 9:1–11.
- Videan EN. 2006. Sleep in captive (*Pan troglodytes*): the effects of individual and environmental factors on sleep duration and quality. *Behav Brain Res* 169:187–192.
- Nunn CL. 2011. The comparative approach in evolutionary anthropology and biology. Chicago: University of Chicago Press.
- Nunn C, Zhu L. 2014. Phylogenetic prediction to identify “evolutionary singularities.” In: Garamszegi LZ, editor. Modern phylogenetic comparative methods and their application in evolutionary biology. Berlin: Springer. p 481–514.
- Organ CL, Nunn CL, Machanda Z, et al. 2011. Phylogenetic rate shifts in feeding time during the evolution of *Homo*. *Proc Natl Acad Sci USA* 108:14555–14559.
- Sri Kantha S, Suzuki J. 2006. Sleep quantitation in common marmoset, cotton top tamarin and squirrel monkey by non-invasive actigraphy. *Comp Biochem Phys* 144:203–210.
- Tobler I. 2005. Phylogeny of sleep regulation. In: Kryger MH, Roth R, Dement WC, editors. Principles and practice of sleep medicine. Elsevier Saunders. Philadelphia, PA. p 77–90.
- Koops K, Humle T, Sterck EHM, et al. 2007. Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: environmentally or socially determined? *Am J Primatol* 69:407–419.
- Yamagiwa J. 2001. Factors influencing the formation of ground nests by eastern lowland gorillas in Kahuzi-Biega National Park: some

- evolutionary implications of nesting behavior. *J Hum Evol* 40:99–109.
- 59 Fleagle JG. 1999. Primate adaptation and evolution. 2nd ed. San Diego: Academic Press.
- 60 Samson DR. 2012. The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. *Primates* 53:357–364.
- 61 Covert HH. 1995. Locomotor adaptations of Eocene primates: adaptive diversity among the earliest prosimians. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark; the nocturnal prosimians*. New York: Plenum Press. p 495–509.
- 62 Mooring MC, Hart BL. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123:173–193.
- 63 Kappeler PM. 1998. Nests, tree holes, and the evolution of primate life histories. *Am J Primatol* 46:7–33.
- 64 Nunn CL, Heymann EW. 2005. Malaria infection and host behaviour: a comparative study of Neotropical primates. *Behav Ecol Sociobiol* 59:30–37.
- 65 McGrew WC. 2004. *The cultured chimpanzee: reflections on cultural primatology*. New York: Cambridge University Press.
- 66 Fleagle JG, Kay R. 1985. The paleobiology of catarrhines. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Alan R. Liss. p 23–36.
- 67 Baker J, Meade A, Pagel M. 2015. Adaptive evolution towards larger size in mammals. *Proc Natl Acad Sci USA* 112:5093–5098.
- 68 van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102:915–941.
- 69 Samson DR, Shumaker WR. 2015. Orangutans (*Pongo spp.*) have deeper, more efficient sleep than baboons (*Papio papio*) in captivity. *Am J Phys Anthropol* 157:421–427.
- 70 Goodall JM. 1962. Nest building behavior in the free ranging chimpanzee. *Ann NY Acad Sci* 102:455–467.
- 71 Fruth B, Hohmann G. 1996. Nest building behavior in the great apes: the great leap forward? In: Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 225–240.
- 72 Samson DR, Hunt KD. 2014. Chimpanzees preferentially select sleeping platform construction tree species with biomechanical properties that yield stable, firm, but compliant nests. *PLoS One* 9:1–8.
- 73 van Casteren A, Sellers WI, Thorpe SKS, et al. 2012. Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proc Natl Acad Sci USA* 109:6873–6877.
- 74 van Casteren A, Sellers WI, Thorpe SKS, et al. 2013. Factors affecting the compliance and sway properties of tree branches used by the sumatran orangutan (*Pongo abelii*). *PLoS One* 8:1–9.
- 75 Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hyllobates lar*). *Am J Primatol* 46:35–62.
- 76 Anderson JR. 1984. Ethology and ecology of sleep in monkeys and apes. *Adv Stud Behav* 14:165–229.
- 77 Pruett JD, Fulton SJ, Marchant LF, et al. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401.
- 78 Stewart FA, Pruett JD. 2013. Do chimpanzee nests serve an anti-predatory function? *Am J Primatol* 75:593–604.
- 79 Herman N. 2010. Nest site selection in Bornean orangutans (*Pongo pygmaeus wurmbii*): the role of microclimatic factors and mosquito avoidance strategies. PhD dissertation, University of Zurich.
- 80 Samson DR, Muehlenbein MP, Hunt KD. 2013. Do chimpanzees (*Pan troglodytes schweinfurthii*) exhibit sleep related behaviors that minimize exposure to parasitic arthropods? A preliminary report on the possible anti-vector function of chimpanzee sleeping platforms. *Primates* 54:73–80.
- 81 Stewart FA. 2011. Brief communication: why sleep in a nest? Empirical testing of the function of simple shelters made by wild chimpanzees. *Am J Phys Anthropol* 146:313–318.
- 82 Duda P, Zrzavy J. 2013. Evolution of life history and behavior in Hominidae: towards phylogenetic reconstruction of the chimpanzee-human last common ancestor. *J Hum Evol* 64:424–446.
- 83 Baldwin PJ, Sabater Pi J, McGrew WC, et al. 1981. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* 22:474–486.
- 84 Samson DR, Shumaker RS. 2013. Documenting orang-utan sleep architecture: sleeping platform complexity increases sleep quality in captive *Pongo*. *Behaviour* 150:845–861.
- 85 Martin-Ordas G, Call J. 2011. Memory processing in great apes: the effect of time and sleep. *Biol Lett* 7:829–832.
- 86 Hunt KD. 1996. The postural feeding hypothesis: an ecological model for the evolution of bipedalism. *S Afr J Sci* 92:77–90.
- 87 Wood B, Collard M. 1999. Anthropology: the human genus. *Science* 284:65–71.
- 88 McHenry HM, Coffing K. 2000. *Australopithecus* to *Homo*: transformations in body and mind. *Ann Rev Anthropol* 29:125–146.
- 89 McHenry HM. 1991. Body size and proportions in early hominids. *Am J Phys Anthropol* 84:407–431.
- 90 Anton SC, Snodgrass JJ. 2012. Origins and evolution of genus *Homo*: new perspectives. *Curr Anthropol* 53:S479–S496.
- 91 Werdelin L, Lewis ME. 2005. Plio-Pleistocene carnivora of eastern Africa: species richness and turnover patterns. *Zool J Linn Soc Lond* 144:121–144.
- 92 Bodker R. 2003. Relationship between altitude and intensity of malaria transmission in the Usambara Mountains, Tanzania. *J Med Entomol* 40:706–717.
- 93 Gowlett JAJ, Wrangham RW. 2013. Earliest fire in Africa: towards the convergence of archaeological evidence and the cooking hypothesis. *Arch Res Afr* 48:5–30.
- 94 Wrangham R, Carmody R. 2010. Human adaptation to the control of fire. *Evol Anthropol* 19:187–199.
- 95 Rossano M. 2006. The religious mind and the evolution of religion. *Rev Gen Psychol* 10:346–364.
- 96 Kurmi OP, Lam KBH, Ayres JG. 2012. Indoor air pollution and the lung in low- and medium-income countries. *Eur Respir J* 40:239–254.
- 97 Moore SJ, Hill N, Ruiz C, et al. 2007. Field evaluation of traditionally used plant-based insect repellents and fumigants against the malaria vector *Anopheles darlingi* in Riberalta, Bolivian Amazon. *J Med Entomol* 44:624–630.
- 98 Halász PB, Bódizs R, Parrino L, et al. 2014. Two features of sleep slow waves: homeostatic and reactive aspects from long term to instant sleep homeostasis. *Sleep Med* 15:1184–1195.
- 99 Revonsuo A. 2000. The reinterpretation of dreams: an evolutionary hypothesis of the function of dreaming. *Behav Brain Sci* 23:793–1121.
- 100 Wagner U, Gais S, Haider H, et al. 2004. Sleep inspires insight. *Nature* 427:352–355.
- 101 Peigneux P, Laureys S, Fuchs S, et al. 2004. Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron* 44:535–545.
- 102 Walker MP, Stickgold R. 2004. Sleep-dependent learning and memory consolidation. *Neuron* 44:121–133.
- 103 Dunbar RIM, Gowlett JAJ. 2014. Fireside chat: the impact of fire on hominin socioecology. In: Dunbar RIM, Gamble C, Gowlett JAJ, editors. *Lucy to language: the benchmark papers*. Oxford: Oxford University Press. p 277–293.
- 104 Rechtschaffen A. 1971. The control of sleep. In: Hunt WA, editor. *Human behaviour and its control*. Cambridge, MA: Schenkman. p 75–92.
- 105 Sherwood CC, Bauernfeind AL, Bianchi S, et al. 2012. Human brain evolution writ large and small. In: Hofman M, Falk D, editors. *Evolution of the primate brain: from neuron to behavior*. New York: Elsevier. p 237–254.
- 106 Gardlan T, Ives AR. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am Nat* 155:346–364.
- 107 Capellini I, Barton RA, McNamara P, et al. 2008. Phylogenetic analysis of the ecology and evolution of mammalian sleep. *Evol* 6:1764–1776.
- 108 McNamara P, Capellini I, Harris E, et al. 2008. The phylogeny of sleep database: a resource for sleep scientists. *Open Sleep J* 1:11–14.
- 109 Marlowe F. 2010. *The Hadza: hunter-gatherers of Tanzania*. Berkeley: University of California Press.
- 110 Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *J Hum Evol* 32:523–559.