

Sleep and nesting behavior in primates: A review

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Abstract

Sleep is a universal behavior in vertebrate and invertebrate animals, suggesting it originated in the very first life forms. Given the vital function of sleep, sleeping patterns and sleep architecture follow dynamic and adaptive processes reflecting trade-offs to different selective pressures.

Here, we review responses in sleep and sleep-related behavior to environmental constraints across primate species, focusing on the role of great ape nest building in hominid evolution. We summarize and synthesize major hypotheses explaining the proximate and ultimate functions of great ape nest building across all species and subspecies; we draw on 46 original studies published between 2000 and 2017. In addition, we integrate the most recent data brought together by researchers from a complementary range of disciplines in the frame of the symposium "Burning the midnight oil" held at the 26th Congress of the International Primatological Society, Chicago, August 2016, as well as some additional contributors, each of which is included as a "stand-alone" article in this "Primate Sleep" symposium set. In doing so, we present crucial factors to be considered in describing scenarios of human sleep evolution: (a) the implications of nest construction for sleep quality and cognition; (b) the tree-to-ground transition in early hominids; (c) the peculiarities of human sleep.

We propose bridging disciplines such as neurobiology, endocrinology, medicine, and evolutionary ecology, so that future research may disentangle the major functions of sleep in human and nonhuman primates, namely its role in energy allocation, health, and cognition.

KEYWORDS

evolution, great apes, nest building, sleep

1 | INTRODUCTION

Sleep, or sleep-like states, have been investigated for centuries, beginning with observations of the day and night rhythm of Mimosaceae plants (De Mairan, 1729; Du Monceau, 1758), which revealed endogenous pacemakers of activity. Sleep is a universal behavior in vertebrate and invertebrate animals, suggesting it originated with the first organisms (Hartse, 2011; Lesku, Roth, Amlaner, & Lima, 2006; Rattenborg & Amlaner, 2002). In their comprehensive review on the role of sleep in memory, Rasch and Born (2013, p. 681) define sleep "as a natural and reversible state of reduced responsiveness to external stimuli and relative inactivity, accompanied by a loss of consciousness." Reduced responsiveness is risky, however, as animals must respond to life threatening cues such as predators. In addition, this inactivity implies missing out on feeding, caring for young, or socializing; in short, a reduced investment in activities necessary for an individual's fitness. Why has evolution not eradicated sleep?

The increasing body of evidence accumulating from investigations of the many and often mutually nonexclusive hypotheses on the functions of sleep provides answers to this question. Scientists have provided evidence for physiological functions of sleep such as energy saving (Siegel, 2005), tissue repairing (Oswald, 1980), thermoregulation (Parmeggiani, 1986), metabolic regulation (Sharma & Kavuru, 2010), immunological enhancement (Besedovsky, Lange, & Born, 2012), and memory formation (Rasch & Born, 2013).

Behavioral ecology research has looked within and across species to better understand how natural selection has shaped sleep and sleep-related behavior, particularly in the context of predation where vigilance should supplant states of unconsciousness (Lima, Rattenborg, Lesku, & Amlaner, 2005). Such research has covered a wide range of topics including "species-specific" choices of shelter, circadian rhythms affected by the threat of predation, food competitors or food availability, and variations in "sleep architecture." "Sleep architecture" refers to the structural organization of normal sleep, dividing it into non-rapid

eye movement (NREM) and rapid eye movement (REM) sleep, which occur in cycles.

In contrast to an earlier classification system by Rechtschaffen and Kales (1968), where slow-wave sleep (SWS) was divided into stage 3 and stage 4 sleep, a more recent nomenclature classifies NREM sleep into three stages, with SWS corresponding to N3, and two lighter sleep stages N1 and N2 (Iber, Ancoli-Israel, & Chesson, 2007; Rasch & Born, 2013). A typical eight-hour sleeping bout usually starts with a short and light stage N1, followed by stage N2, which is similarly light, but accounts for about 50% of a sleeping bout and is distributed rather evenly throughout. Waking up during stage N1 or N2 is easy, and on doing so people report thoughts, ideas, and dreams, but with no particular coherence. In contrast, stage N3 sleep, or SWS, is far deeper, having acquired its name because of its slow wave frequency. Here, respiration, heart rate, and blood pressure decrease, rendering waking less likely. SWS usually dominates the first third of a human's sleeping bout. In contrast, REM sleep is characterized by two modes, tonic REM sleep (without actual rapid eye movements) and phasic REM sleep (with acute eye movements but muscle atonia). Human sleepers, when awakened during REM, are able to report coherent dreams with active participation of the dreamer. REM sleep occurs towards the end of a typical sleeping bout (Coolidge & Wynn, 2006; Lima et al., 2005; Samson & Nunn, 2015). "Sleep architecture" seems to be of particular importance when investigating adaptation to potentially lethal environmental constraints, such as predation. Therefore, current research focuses on the role and sequence of each specific phase within sleeping bouts, which show considerable variability within and across species.

Given the vital functions that sleep provides, we should consider it as a constraint influencing life history and resulting in trade-offs similar to those we assess within the framework of optimal foraging theory. Just as for energy intake, individual- and species-specific sleeping patterns and sleep architecture follow dynamic and adaptive processes in response to environmental constraints.

Here, we review the responses in sleep and sleep-related behavior to environmental constraints across primate species, investigating both proximate and ultimate benefits. We integrate the most recent data brought together by researchers from a complementary range of disciplines, such as primatology, behavioral ecology, and evolutionary anthropology, many of whom contribute their findings in this compilation of papers from the 26th Congress of the International Primatological Society (Chicago, August 2016) "Burning the midnight oil: Great ape nocturnal activity and the implications for the understanding of human evolution" symposium, and comprising orangutan (*Pongo pygmaeus*; MacKinnon, 1974), gorilla (*Gorilla gorilla*; Casimir, 1979), chimpanzee (*Pan troglodytes*; van Lawick-Goodall, 1968), and bonobo (*Pan paniscus*; Kano, 1992). Special attention is given to great ape nest-building behavior by updating our knowledge presented in an earlier review by Fruth and Hohmann (1996). We update our understanding of the implications of nest construction and the role it may have played in hominin evolution, and investigate the relevance of the tree-to-ground transition, as well as some peculiarities of human sleep, to human evolution.

2 | HISTORICAL ASPECTS OF SLEEP RESEARCH

The origin of chronobiology dates back to the 17th century (Barrera-Mera & Barrera-Calva, 1998). Since then, the discipline has influenced sleep research in both animal and human studies (Aschoff & Wever 1981; Dunlap, Loros, & DeCoursey, 2004; Kleitman, 1963).

Research subsequently expanded from the study of sleep distribution across a 24-hr period into describing the distribution of stages of sleep within sleeping bouts. In 1924, Hans Berger, a German psychiatrist, was the first to record a human electroencephalogram and succeeded in identifying different brain wave patterns that reflect states of sleep and wakefulness (Millett, 2001). This led the way to a better understanding of the different qualities of sleep and the specific roles of different sleep states.

Primates exhibit a vast array of different sleeping behaviors. Timing of sleeping patterns varies quite markedly; some species are considered nocturnal, such as the African and Asian strepsirrhine prosimians (Reinhardt & Nekaris, 2016) and the South American genus, *Aotus* (Wright, 1989). Most primates, however, are diurnal, although a few species, such as the owl monkey, *Aotus azarai*, and several Malagasy strepsirrhines (e.g., *Eulemur* spp., *Hapalemur* sp., *Lemur catta*), exhibit cathemerality (Curtis & Rasmussen, 2006). It is difficult to tease apart the multiple influences on variation in sleeping patterns; for example, the activity patterns of some lemurs could be attributed to phylogeny and niche differentiation of different genera (Dammhahn & Kappeler, 2014), whilst certain African lorisiformes show variable sleep patterns even within species (Svensson et al., 2018). New technologies, such as remote-operated camera traps and acoustic sensors, have recently revealed previously undocumented nocturnal wakefulness and activity in wild great apes; a phenomenon that is now hypothesized to occur in many primates (Piel, 2018; Tagg et al., 2018). Increasing evidence reveals cathemeral and fragmented sleeping patterns in many species to be a response to factors such as light, food, predator or human imposed constraints (Colquhoun, 2007; Engqvist & Richard, 1991; Eppley, Ganzhorn, & Donati, 2015; Kümpel, Milner-Gulland, Rowcliffe, & Cowlishaw, 2008).

Temperature is another environmental factor that has been shown to influence pattern and quality of sleep in lemurs (Samson, Bray, & Nunn, 2018). and chimpanzees (Pruetz, 2018). While the external drivers mentioned above may trigger nocturnal activity in diurnal great apes, internal factors, such as the need to defecate (K. Zamma, pers. comm.), may contribute as well. This taxon-wide behavioral flexibility in the amount and timing of sleep raises numerous questions, and shows how species may adapt their sleep patterns to cope with the challenges of environmental and anthropogenic stressors.

3 | PRIMATE SLEEPING SITES

With a total of around 410 primate species predominantly inhabiting the tropical belt of our planet (Mittermeier, Rylands, & Wilson, 2013), it is natural that we find a fascinating array of niche differentiation in the distribution of activity patterns and sleeping site locations across species.

Arboreal sites are common; some small monkeys sleep solitarily or in small groups using tree holes (Kappeler, 1998), while many larger primates sleep on bare branches, even when predominantly terrestrial at times of activity (Anderson, 2000; Fruth & McGrew, 1998). In addition, some large-bodied primates sleep terrestrially on bare ground or on cliffs, such as group-sleeping baboons (*Papio* spp.) (Hamilton, 1982), or individually sleeping great apes (Fruth & Hohmann, 1996; Tagg, Willie, Petre, & Haggis, 2013). Of particular interest in the study of primate sleep is nest-building behavior, which has evolved independently six to eight times in primates (Kappeler, 1998). Great apes universally build nests in which to sleep at night and sometimes during day. Nest building is a habitual behavior in great apes, constructions are built for short periods only and never serve as a shelter for caching young. Structures are commonly built within trees, although ground nests built with terrestrial vegetation are common in gorilla and ground-nesting is likely present at low rates across all species and subspecies (Tagg et al., 2013). These structures attracted the attention of early explorers such as Du Chaillu (1861), Hornaday (1879), and Savage and Wyman (1843–1844). When these structures came to scientific attention about 100 years later, they were named “sleeping platform,” “nest,” or “bed.”

Nest building in great apes is a phylogenetically conservative behavior likely to have evolved in the Miocene (Fruth & Hohmann, 1996), somewhere between 18 and 14 mya (Duda & Zrzavý, 2013). Nest building may have been an evolutionary response to cope with the allometric effect of the increasing body size of apes, which would “have benefited from more resilient and stable sleeping substrates to reduce both physical stress on the body and the probability of lethal falls” (Samson & Nunn, 2015, p. 231).

Nest building was originally thought to be innate until Bernstein (1962), and later Videan (2006), showed that captive-reared chimpanzees did not know how to build good nests, even when their mothers were wild born. Nest-building behavior is now known to be acquired throughout the ape’s ontogeny, starting with attempts by infants to construct day nests. Early on, nest building was discussed in the context of the cognitive modification of the physical environment or tool use. While nest building was considered separately from tool use by some authors (Beck, 1980; Tuttle, 1986), others tended to subsume it under this category (Galdikas, 1982; McGrew, 1992). Recently, Shumaker, Walkup, and Beck (2011) redefined tool use in such a way as to incorporate nest use and argued it is the most pervasive form of material culture in great apes. Nest construction reflects the great apes’ ability for environmental problem solving; an ability that forms the basis of skilled object manipulation of which all apes are capable, and is considered to have been crucial for hominization (McGrew, 1992).

4 | GREAT APE NESTING BEHAVIOR AND PROXIMATE FUNCTIONS OF GREAT APE NESTS

Goodall (1962) provided the first detailed description of chimpanzee nest-building behavior. Nests of all great apes are similarly constructed, despite interspecies differences in habitat and social organization. When in trees, nest-builders usually select horizontal side branches for

the foundation, over which they bend and break adjacent branches. The rim of these platforms is formed by bending, breaking and occasionally interweaving additional smaller branches from the outer to the inner surfaces, resulting in a circular or oval, bowl-shaped structure. The center of this “bowl” is often lined with detached leafy twigs. When nests are built on the ground, nonwoody vegetation is often used. Average arboreal nest heights range from 10 to 20 m, and construction types range from sturdy nests on side branches or in single treetops to nests integrating several adjacent trees, sometimes so flexible that the “bowl” resembles a hammock.

An ape will usually build a new nest each evening and, despite lack of systematic investigation, is assumed to use it for rest from dusk until dawn (but see Tagg et al., 2018; Piel, 2018, Pruetz, 2018; Stewart, Piel, Azkarate, & Pruetz, 2018; in this volume). Occasionally, nests are also built during the day, usually for rest, but have also been observed to serve functions of grooming, play, sex, nursing, and giving birth. Nests are usually not constructed in isolation from each other but in groups, reflecting differences in the social organization and social structure of the species (Fruth, 1995; Schaller, 1963; van Lawick-Goodall, 1968). For species living in a fission-fusion social organization, aggregation at night has been suggested to allow information transfer on the quality of food patches visited during day (Fruth & Hohmann, 1994a).

Nests are built by each weaned individual great ape independent of sex and age, and take between 1 and 7 min to construct. Time of construction depends on season, weather, and light conditions, and social opportunities or requests. Tree choice is highly selective and may be influenced by seasonal availability of building material, quality, flexibility, and strength of wood, as well as leaf size and phytochemical properties (Samson & Hunt, 2014; van Casteren et al., 2012). Nest reuse has been reported for all studied populations and, although frequencies differ, it likely depends on the availability of nesting locations and material for construction. Sex differences are reported for all species and concern nest height and frequency, with females on average constructing their nests higher and more often producing day nests than males.

In an extensive review, Fruth and Hohmann (1996) compiled data on nest building in all great ape species and most subspecies, investigating 31 published studies and complementing these with the answers to 21 questionnaires through which field primatologists contributed their unpublished data. Overall, there was considerable variation in physical parameters such as nest height, not only across, but also within great ape species. Variation is influenced by environmental parameters (e.g., rainfall, temperature, habitat structure, availability of material, predator presence), demographic (e.g., sex or age class), and social factors (e.g. socially transferred habits). Variation within species exceeded variation across species.

For this review, we consulted 46 original studies published between 2000 and 2017 investigating great ape nest construction in all species and subspecies (Table 1). Our main focus was on studies conducted in the wild, and we did not consider those using nests as a tool for calculating density estimations. Overall, the picture that emerged in the original review still persists. In addition, an increasing number of studies systematically investigate hypotheses concerning nest function. Table 1 shows these studies and their foci.

TABLE 1 Behavioral aspects and proximate hypotheses of great ape nest construction investigated in original studies published between 2000 and 2017

Genus	Gorilla		Pan		Pongo	
	<i>beringei</i>	<i>gorilla</i>	<i>trogodytes</i>	<i>elliotti</i>	<i>paniscus</i>	<i>pygmaeus</i>
Species	<i>beringei</i>	<i>gorilla</i>	<i>versus</i>	<i>trogodytes</i>	<i>paniscus</i>	<i>pygmaeus</i>
Subspecies	<i>graueri</i>	<i>diehli</i>	spp. ^a	<i>schweinfurthii</i>	spp. ^a	spp. ^a
Nesting Behavior						
Innate or learned					1 ^b	
Arboreal/terrestrial	1 ^c	1 ^g	1 ^h	1 ^o	2 ^{p,q}	1 ^r
Group size					2 ^{s,t}	
Sex bias					1 ^u	1 ^v
Reuse		1 ^g		1 ^x		2 ^{y,v}
Selectivity						
Site	1 ^z	2 ^{aa,bb}	2 ^{z,cc}	1 ^k	1 ^{bb}	5 ^{x,ee,ff,gg,hh}
Food resources		1 ^w				4 ^{ii,jj,kk,ll}
Material	1 ^c	3 ^{w,e,pp}	1 ^z	2 ^{jk}		1 ^{ll}
Height				4 ^{jj,rr}		2 ^{mm}
						1 ^{mm}
						2 ^{vv}
Nest function hypotheses						
Thermoregulation		1 ^f	1 ^g	3 ^{jj,mm}	1 ^o	3 ^{qs,ss}
Predator avoidance		1 ^d	1 ^z	1 ^{jj,rr}	1 ⁿ	4 ^{uu,rr,pp,q}
Parasite avoidance				2 ^{jm}		2 ^{gg,hh}
Comfort				2 ^{mtt}		2 ^{ss,uu}
						1 ^{mm}
						1 ^r

^aSpecies was unknown in captive research studies; ^bVidean, 2006; ^cRothman et al., 2006; ^dYamagiwa, 2001; ^eBrugiere & Sakom, 2001; ^fMehlman and Doran, 2002; ^gSunderland-Groves et al., 2009; ^hLukas et al., 2003; ⁱPruetz et al., 2008; ^jKoops et al., 2012; ^kCarvalho et al., 2015; ^lKoops et al., 2007; ^mStewart, 2011; ⁿLast and Muh, 2013; ^oTagg et al., 2013; ^pFuruichi and Hashimoto, 2000; ^qSamson and Hunt, 2014; ^rSamson and Shumaker, 2015; ^sHernandez-Aguilar et al., 2013; ^tChancellor et al., 2012; ^uBrownlow et al., 2001; ^vRayadin and Saitoh, 2009; ^wIwata and Ando, 2007; ^xHernandez-Aguilar, 2009; ^yAncrenaz et al., 2004; ^zDe Vere et al., 2011; ^{aa}Haurez et al., 2014; ^{bb}Morgan et al., 2006; ^{cc}Funwi-Gabga and Mateu, 2012; ^{dd}Weiche and Anderson, 2006; ^{ee}Hakizimana et al., 2015; ^{ff}Ogawa et al., 2007; ^{gg}Krief et al., 2012; ^{hh}Samson et al., 2015; ⁱⁱMulawwa et al., 2010; ^{jj}Inogwabini et al., 2012; ^{kk}Serckx et al., 2016; ^{ll}Serckx et al., 2014; ^{mm}Cheyne et al., 2013; ⁿⁿSpehar and Rayadin, 2017; ^{oo}Basabose and Yamagiwa, 2002; ^{pp}Willie et al., 2014; ^{qq}Stanford and O'Malley, 2008; ^{rr}Stewart and Pruetz, 2013; ^{ss}Samson, 2012; ^{tt}Stewart et al., 2007; ^{uu}Samson and Hunt, 2013.

In the following sections, we outline these hypotheses, incorporating recent results from published literature, including this symposium set.

4.1 | Comfort

The comfort hypothesis assumes that increased body size in primates may have constrained relaxed sleep. Comfort, defined as “things that contribute to physical ease and well-being” (Oxford Living Dictionaries, 2017), here translates into the construction of platforms that evolved, not for reasons of survival, but simply because freshly built, soft and warm nests allow for a more comfortable sleep (Baldwin, Pi, McGrew, & Tutin, 1981; Nissen, 1931). This hypothesis found support by Stewart, Pruetz, & Hansell (2007), who showed that chimpanzee nests at Fongoli, Senegal, vary in complexity and comfort, with more highly complex nests being more comfortable. This is in line with findings from Sumatran orangutans (*Pongo abelii*; van Casteren et al., 2012). In a recent study, Cheyne, Rowland, Höing, and Husson (2013) investigated nests of Southern Bornean orangutans (*P. pygmaeus wurmbii*), showing that they sought protection from wind and rain rather than protection from predators. In line with the climatic drivers of the use of nests, Samson and Hunt (2012) investigated the physical comfort levels of chimpanzee tree versus ground nests, and reported various advantages of ground nests, such as reduced energy expenditure and homeostatic microclimate. All authors agreed that additional functions may be of major importance.

4.2 | Antipredation

Animals are vulnerable when asleep, as their ability to detect predators is reduced. Sleeping in trees is a solution; however, large-bodied apes need a surface that allows both loss of muscle tone and maintained security when asleep (Samson & Hunt, 2012). Comparing nest height and density between Fongoli and Mt Assirik, Senegal, two chimpanzee sites with different predation pressures, Pruetz et al. (2008) supported the antipredation hypothesis by demonstrating that nests were built higher and in closer proximity to each other at Mt Assirik, the site with higher predation pressure. Similarly, Stewart and Pruetz (2013) compared physical characteristics of nesting trees between Issa, Tanzania, and Fongoli, Senegal; here, Issa is the relatively predator-rich site. As expected, chimpanzees in Issa were observed to select taller trees with higher lowest branches over other suitable trees (Hernandez-Aguilar, 2006), and nested higher and more at the distal branch extremities than did chimpanzees in Fongoli (Stewart & Pruetz, 2013). Data from Koops, McGrew, de Vries, and Matsuzawa (2012), who investigated chimpanzee nesting at Seringbara, Nimba Mountains, Guinea, where predators are thought to be absent, are in line with those from Fongoli. In summary, the construction of platforms allowing safe and comfortable sleep can be considered to offer a two-fold benefit through improving sleep and avoiding predation (Koops et al., 2012; Stewart & Pruetz, 2013).

4.3 | Thermoregulation

When temperature is low, particularly during the night, the costs of physiological thermoregulation increase. In savanna-woodland habitats

like Fongoli, where temperature extremes may range between highs of 45°C during the day and lows of 7°C at night, nests provide considerable insulation (Stewart, 2011). Nest use can thus be considered a form of behavioral thermoregulation. In addition, vertical nest site choice may be driven by microclimatic patterns, such as relative humidity (Samson & Hunt, 2012). At Seringbara, Koops et al. (2012) found chimpanzee nest height increased with increasing humidity. Temperature during the day can also affect great ape sleeping patterns at night, as shown in Fongoli by Pruetz (2018), whereby increased nocturnal activity appeared to be the result of compensating for thermal stress experienced during the day. Evidence provided in this issue suggests that chimpanzees adjust nest shape and architecture in response to local weather conditions (Stewart, Piel, Azkarate, & Pruetz, 2018).

4.4 | Antipathogen

Disease vectors, such as mosquitoes, have a vertical distribution and may therefore influence nest site choice. While avoidance of annoyance by biting insects could be a proximate influence on nest site choice, avoidance of disease vectors may ultimately offer an evolutionary advantage over exposed conspecifics (Koops et al., 2012; Samson, Muehlenbein, & Hunt, 2013). So far, pathogenicity of transmitted parasite infections, such as malaria, are unknown, although *Plasmodium* spp. have been detected in great apes (Krief et al., 2010; Liu et al., 2010, 2014). Koops et al. (2012) found no difference in densities of potential disease vectors at different heights of the forest canopy, concluding that mosquito densities at their site could not be identified as a significant selection pressure influencing nest building. However, tree choice at other sites does hint at insect avoidance as an influencing factor; for example, in Semliki, another savanna site, experimental mosquito capture was lower in proximity to a highly preferred tree species (Samson et al., 2013), and at Tuanan in Central Kalimantan, Indonesia, orangutans (*Pongo pygmaeus wurmbii*) selected naturally mosquito-repellent tree species when mosquito density was high (Largo, Bastian, & Van Schaik, 2009).

5 | EVOLUTION OF GREAT APE NEST CONSTRUCTION AND USE AND IMPLICATIONS FOR SLEEP

Traces of nests within trees remain visible over generations, with broken branches recovering and continuing to grow into their altered direction. They are living artefacts allowing investigation of distribution and reuse, accumulation, and enabling an enhanced understanding of their associated patterns. In paleoanthropology, artefacts are used to reconstruct early hominin ranging behavior and the formation of hominin archeological sites. Nest sites therefore contribute to a better understanding of the evolution of human shelter; these primitive ape platforms provide analogues to the earliest home-bases of hominins (Fruth & Hohmann, 1994b; Hernandez-Aguilar, 2009; McGrew, 1992, 2004; Sept, 1998; Sept et al., 1992).

Furthermore, great ape nesting and its implications for sleep are relevant to understanding the evolution of human sleep patterns. Due

to the presence of this behavior in all extant great ape species, it was likely present in their last common ancestor (LCA) living around 14 million years ago (MYA), and in the *Pan-Homo* LCA living around 7 MYA. Fruth and Hohmann (1996) framed a scenario whereby in the mid- to late-Miocene, nest building began as a by-product of great ape feeding behavior and represented a selective advantage over quickly radiating and better-adapted monkeys. Fruth and Hohmann (1996) hypothesized that nests had their origins in feeding competition rather than the need for rest. These “proto-nests” may have led to the “feeding nests” that can be regularly observed in great apes (Basabose & Yamagiwa, 2002; Fruth & Hohmann 1993). Feeding nests may then have turned into resting platforms, providing support for the increasing body weight of apes. According to Fruth and Hohmann (1996), these originally proximate functions of early nests may have brought about an improvement in the quality of sleep. This improved sleep quality is hypothesized to have resulted in a sleep architecture that allows not only the essential metabolic processes, such as the release of growth hormones and physiological recuperation, but above all, enhanced cognition.

Samson and Nunn (2015) formalized this evolutionary scenario by postulating a positive feedback loop that merges two previously exclusive hypotheses: namely the “sleep quality hypothesis,” which assumes that improved sleep led to an increase in cognitive abilities, and the alternative “engineering hypothesis,” which assumes that the increasing cognitive performance of great apes enabled them to build nests. In addition, they supported this scenario through developing and subsequently testing the “sleep intensity hypothesis.” They showed that early humans “experienced selective pressure to fulfill sleep needs in the shortest time possible” (p. 225). In this volume, Nunn and Samson (2018) extend their previous analyses of Samson and Nunn (2015) by including more relevant ecological variables and additional primate species, and investigate how human sleep differs from other primate species, thus proposing a certain uniqueness of human sleep.

6 | TREE-TO-GROUND SLEEP TRANSITION AND ITS IMPLICATIONS FOR HUMAN EVOLUTION

Whilst nest construction likely contributed to the “great leap forward” in the evolution of great ape cognition, the tree-to-ground transition may have resulted in a similar leap in hominins (Coolidge & Wynn, 2006). Despite habitually exhibiting sleep, ingestion of food, and locomotion as arboreal behaviors, all great apes are terrestrial to varying degrees during the day (Doran, 1996; Loken et al., 2013). However, the proportion of nests at lower heights and on the ground increases in areas with lower or absent predation pressure. Tagg et al. (2013) showed that all subspecies of chimpanzee sometimes build night nests on the ground. To what extent these findings allow reconsideration of the advantages and disadvantages of a tree-to-ground transition, however, needs careful evaluation.

Can we date the tree-to-ground transition for sleep in hominin evolution? Fossil evidence shows many early hominins to have ape-like anatomical adaptations that likely allowed them to climb trees [*Ardipithecus ramidus* (White et al., 2009); *Australopithecus afarensis*

(Alemseged et al., 2006); *A. africanus* (Berger & Tobias, 1996); *Homo habilis* (Richmond, Aiello, & Wood, 2002; Ruff, 2009)]. Despite a lack of the requisite morphological traits for tree climbing in the newly discovered Australopithecine, *A. sediba* (Berger et al., 2010), the more arboreal-adapted, less habitual bipeds such as *Ardipithecus ramidus*, *Australopithecus afarensis*, and *A. africanus* (cited above), suggest a transition to terrestriality occurred in the more committed bipeds, such as *Homo erectus* (Ruff, 2009). Although Berger et al. (2010) postulated this transition to have occurred in a ‘mosaic fashion,’ it is possible that early hominins continued to sleep in trees, long after becoming terrestrial, perhaps until the controlled use of fire. Archaeological and ecological evidence support *H. erectus* as the earliest hominin to use fire, although the timing and emergence of when this happened remains controversial (Clark & Harris, 1985; Goren-Inbar et al., 2004; Karkanas et al., 2007). Fire may have aided thermoregulation, vector, and predator deterrence, in addition to increasing energy intake *sensu* Wrangham and Carmody (2010), and may therefore have favored survival of terrestrial-adapted hominins. This hypothesis finds support in studies investigating post-cranial remains, limb strength, and locomotion of early hominins, allowing consideration of *Homo habilis* and *H. rudolfensis* as facultative arboreal species that were therefore very likely to have slept in nests. Whereas *H. erectus* has been identified, on the basis of anatomical features, as the first hominin to have fully engaged in terrestrial bipedalism and thus to have regularly slept on the ground (Coolidge & Wynn 2009; Reed, 1997; Ruff, 2009; Wrangham & Carmody, 2010). Provided there is relative security, perhaps from increased group size or fire, the transition from sleeping in trees to the ground may have favored the use of new (often treeless) habitats (Coolidge & Wynn, 2006). Furthermore, longer bouts of wakefulness as societies became more social would have afforded more time for social interactions (Samson & Nunn, 2015), resulting in increased opportunities for learning. Coolidge and Wynn (2006) emphasized the implications of the tree-to-ground sleep transition by framing three major benefits: (a) threat simulation, social rehearsal, and priming; (b) creativity and innovation; and (c) procedural memory consolidation and enhancement.

Interestingly, contemporary proof of a long-lasting preference for tree-based sleeping sites at night is reflected in people, such as the Korowai from Indonesia, who exhibit above average arboreality without specialized morphological traits (Stasch, 2011). Furthermore, modern humans show deeply-rooted architectural preferences that likely evolved in our distant past through natural selection; for example, preference for a good view is likely related to height and an avoidance of being discovered (Atzwanger & Schäfer, 1999; Eibl-Eibesfeldt, Hass, Freisitzer, Gehmacher, & Glück, 1985; Owens, 1988).

7 | PARTICULARITIES OF HUMAN SLEEP

While the above scenarios remain hypothetical, a few recent studies have begun to experimentally investigate how nests and sleep enhance cognitive performance in great apes. First, Samson and Shumaker (2015) documented orangutan sleep architecture, showing

how sleeping platform complexity increases sleep quality. They showed nest complexity to vary positively with reduced night-time motor activity, less fragmentation, and greater efficiency of sleep. Their data also have relevant implications for animal welfare.

However, to what extent sleep architecture has continued to change as a direct result of the tree-to-ground sleep transition, remains unresolved. Likewise, whether increased risks of ground sleep led to modified sleep duration and architecture or whether modified sleep architecture allowed fulfillment of sleep needs even when sleep durations were necessarily reduced, remains unknown. Ground sleeping may have allowed a deeper and less disturbed sleep in the absence of predators or enemies, however the question remains whether or not there has been safety from predators or enemies across human evolution. In this volume, Samson, Bray, and Nunn (2018) investigate to what extent security of sleeping sites favors increased sleep intensity (with reduced motor activity serving as a proxy) and demonstrate that humans exhibit a lower degree of motor activity at night than other primates.

Interestingly, when sleep was measured in terms of sleep duration and the ratio of REM to NREM, it became evident that human sleep was shorter and more efficient than would be expected in comparison with other primates (Samson & Nunn, 2015). This gives support to the new and intriguing “sleep intensity hypothesis” (discussed earlier). Nunn and Samson (2018) argue that the driver of shorter sleep may have been opportunity costs rather than the vulnerability to predation when ground sleeping. Most importantly, the increased awake time could then be spent learning and developing material culture, and therefore driving technological advances.

The growing body of research investigating human and non-human primate sleep patterns (e.g., sleep architecture [REM/NREM], intensity, duration, and continuity [rate of waking]) reveals greater differences within than between individuals. This is shown nicely by Yetish, Kaplan, and Gurven (2018) in an experimental approach to sleep among Tsimane hunter-horticulturalists in Amazonian Bolivia.

If we extrapolate these principles to modern humans, we see that the multitude of stressors such as light and noise pollution, extensive media use, professional requests (working shifts), or other unpredictable stressors during flight, political unrest or war, result in a remarkable variation of sleep architecture across and within populations. Sleep research focused on traditional (nonindustrial) populations suggests that “flexibility” in sleep timing and duration are important characteristics in human sleep (Samson, Crittenden, Mabulla, Mabulla, & Nunn, 2017).

8 | FUTURE DIRECTIONS

It will never be possible to determine extinct hominin sleep patterns, as such behavior is inaccessible via the fossil record. However, continued study of human and non-human primates, and application of the comparative method, allows insight into likely sleep patterns in hominins. Further investigation into human sleep in traditional and industrialized societies with electricity, and in a range of latitudes, is required. Study

of sleep patterns, and potentially architecture, in wild-living primates may become feasible through application of non-invasive approaches such as actigraphy, infra-red observations, acoustic sensors, camera trapping, and thermal imaging. Comparative research is necessary to help frame human sleep patterns within the scale and patterns of primate sleep. Complementary studies on primates in captivity could reveal further insight into sleeping patterns. For example, by testing animals in various learning tasks with respect to the different sleep stages. However, ethical constraints have to be considered in such laboratory studies, and limit, for example, the search for neural mechanisms. As necessary data continue to be compiled, the considerable variation in sleep architecture will eventually require a multivariate approach whereby major variables, such as ecological drivers or individuals, are kept constant. A phylogenetic approach to investigate sleep characteristics across mammalian taxa could further address what traits may have been evolved in other primate species as a result of relaxed sleep. Overall, three pillars of research are of major interest for current and future investigations of sleep: (a) the role of sleep in an organism's energy budget, (b) its role in health, and (c) its role in memory consolidation. Multifold and thorough investigations are required to determine how much of an individual's sleeping time is allocated to each of these three “pillars” and whether or not individual time allocations result in sleeping patterns that translate to successful strategies in the struggle of life.

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