Fruth, B, Tagg, N and Stewart, FA

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http://researchonline.ljmu.ac.uk/id/eprint/9357/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Fruth, B, Tagg, N and Stewart, FA (2018) Sleep and nesting behavior in primates: A review. Amercian Journal of Physical Anthropology, 166 (3). pp. 499-509. ISSN 0002-9483

American Journal of
Physical Anthropology

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Journal:	*American Journal of Physical Anthropology*
Manuscript ID	AJPA-2017-00276.R2
Wiley - Manuscript type:	Review Article
Date Submitted by the Author:	30-Nov-2017
Complete List of Authors:	Fruth, Barbara; Liverpool John Moores University, Natural Sciences & Psychology; Centre for Research and Conservaton, Royal Zoological Society of Antwerp; Ludwig Maximilians Universität München, Department of Biology; Max-Planck-Institut fur evolutionare Anthropologie, Developmental and Comparative Psychology Tagg, Nikki; Centre for Research and Conservation, Royal Zoological Society of Antwerp Stewart, Fiona; Liverpool John Moores University, Natural Sciences & Psychology; University of Cambridge, Archaeology and Anthropology
Key Words:	evolution, great apes, nest building, sleep
Subfield: Please select 2 subfields. Select the main subject first.:	Human biology [living humans; behavior, ecology, physiology, anatomy], Primate biology [behavior, ecology, physiology, anatomy]

Sleep and nesting behavior in primates: a review

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Number of text pages: 19, plus bibliography: 31, number of figures: 0, tables: 1, graphs: 0, and charts: 0

Abbreviated title (running headline): Sleep in primates

Key words: evolution; great apes; nest building; sleep

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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” paper 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 non-human primates, namely its role in energy allocation, health, and cognition.

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 et al. 2006; Rattenborg and 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 non-exclusive, 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 and Kavuru 2010), immunological enhancement (Besedovsky et al. 2012), and memory formation (Rasch and 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 et al. 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 et al. 2007; Rasch and 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 and Wynn 2006; Lima et al. 2005; Samson and 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 symposium “Burning the midnight oil: Great ape nocturnal activity and the implications for the understanding of human evolution”, 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.

Historical aspects of sleep research

The origin of Chronobiology dates back to the 17th century (Barrera-Mera and Barrera-Calva 1998). Since then, the discipline has influenced sleep research in both animal and human studies (Aschoff and Wever 1981; Dunlap et al. 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 (EEG) 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 and 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 and 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 and Kappeler 2014), whilst certain African lorisiformes show variable sleep patterns even within species (Svensson et al. (in review). 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 in review; Tagg et al. in review). 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 and Richard 1991; Eppley et al. 2015; Kümpel et al. 2008).

Temperature is another environmental factor that has been shown to influence pattern and quality of sleep in lemurs (Samson in review-b), and chimpanzees (Pruetz in review). While the external drivers mentioned above may trigger nocturnal activity in diurnal great apes, internal factors, such as the need to defecate (Koichiro 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.

Primate sleeping sites

With a total of around 410 primate species predominantly inhabiting the tropical belt of our planet (Mittermeier et al. 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 utilizing tree holes (Kappeler 1998), while many larger primates sleep on bare branches, even when predominantly terrestrial at times of activity (Anderson 2000; Fruth and 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 and Hohmann 1996; Tagg et al. 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 and Hohmann 1996), somewhere between 18–14 mya (Duda and 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 and 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 et al. (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).

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 inter-species 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, non-woody vegetation is often used. Average arboreal nest heights range from 10–20 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. 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 and Hohmann 1994a).

Nests are built by each weaned individual great ape independent of sex and age, and take between one and seven minutes 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 and 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 the current 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 about here>

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

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 et al. 1981; Nissen 1931). This hypothesis found support by Stewart et al. (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 et al. (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.

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 and 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 and Pruetz 2013). Data from Koops et al. (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 and Pruetz 2013).

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 and 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 (in review), 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 in review).

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 et al. 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 et al. 2009).

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 and 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 and Yamagiwa 2002; Fruth and 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 (in review) 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.

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 and 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 and Tobias 1996); *Homo habilis* (Richmond et al. 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 arborealadapted, 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 and colleagues (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 and 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 and Wynn 2009; Reed 1997; Ruff 2009; Wrangham and 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 and Wynn 2006). Furthermore, longer bouts of wakefulness as societies became more social would have afforded more time for social interactions (Samson and 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: (1) threat simulation, social rehearsal and priming; (2) creativity and innovation; and (3) 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 and Schäfer 1999; Eibl-Eibesfeldt et al. 1985; Owens 1988).

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; an aspect that finds elaboration in this volume by Anderson et al. (in review).

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 fulfilment 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 (in review-a) 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 and Nunn 2015). This gives support to the new and intriguing “sleep intensity hypothesis” (discussed earlier). Nunn and Samson (in review) 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 and colleagues (in review) 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 (non-industrial) populations suggests that „flexibility" in sleep timing and duration are important characteristics in human sleep (Samson et al. 2017).

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: (1) the role of sleep in an organism's energy budget, (2) its role in health, and (3) 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.

Acknowledgements

The authors would like to thank all the symposium set contributors; the editors of AJP, and staff of CRC/KMDA, LMU, CU, MPI and LJMU. Special thanks go to James Anderson and David Samson for providing excellent reviews on an earlier draft of this manuscript.

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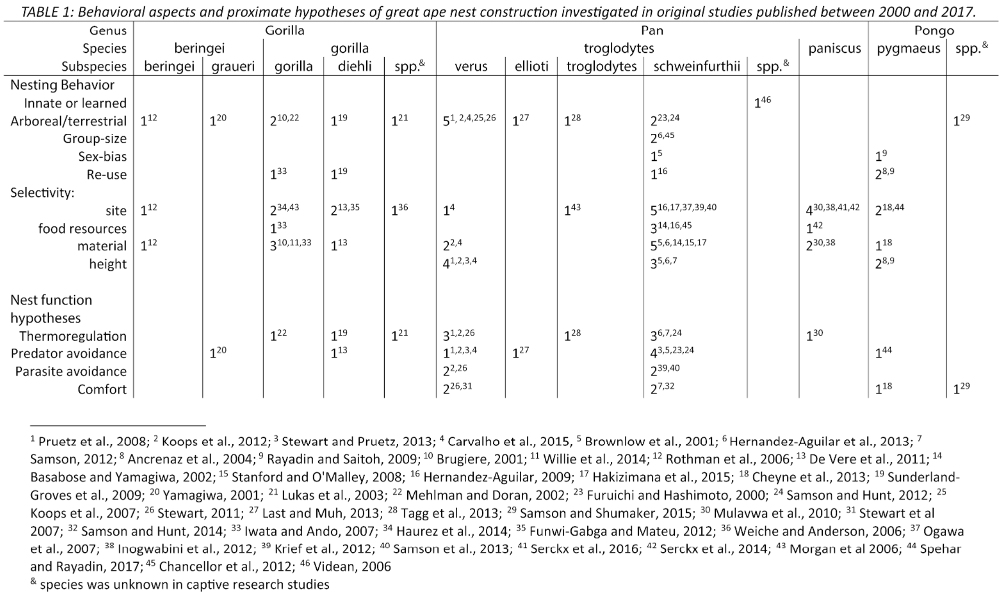

TABLE 1: Behavioral aspects and proximate hypotheses of great ape nest construction investigated in original studies published between 2000 and 2017.

Genus	Gorilla					Pan						Pongo	
Species	beringei		gorilla			troglodytes					paniscus	pygmaeus	spp.[&]
Subspecies	beringei	graueri	gorilla	diehli	spp.[&]	verus	ellioti	troglodytes	schweinfurthii	spp.[&]			
Nesting Behavior													
Innate or learned										1[46]			
Arboreal/terrestrial	1[12]	1[20]	2[10,22]	1[19]	1[21]	5[1, 2,4,25,26]	1[27]	1[28]	2[23,24]				1[29]
Group-size									2[6,45]				
Sex-bias									1[5]			1[9]	
Re-use			1[33]	1[19]					1[16]			2[8,9]	
Selectivity:													
site	1[12]		2[34,43]	2[13,35]	1[36]	1[4]		1[43]	5[16,17,37,39,40]		4[30,38,41,42]	2[18,44]	
food resources			1[33]						3[14,16,45]		1[42]		
material	1[12]		3[10,11,33]	1[13]		2[2,4]			5[5,6,14,15,17]		2[30,38]	1[18]	
height						4[1,2,3,4]			3[5,6,7]			2[8,9]	
Nest function hypotheses													
Thermoregulation			1[22]	1[19]	1[21]	3[1,2,26]		1[28]	3[6,7,24]		1[30]		
Predator avoidance		1[20]		1[13]		1[1,2,3,4]	1[27]		4[3,5,23,24]			1[44]	
Parasite avoidance						2[2,26]			2[39,40]				
Comfort						2[26,31]			2[7,32]			1[18]	1[29]

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[1] Pruetz et al., 2008; [2] Koops et al., 2012; [3] Stewart and Pruetz, 2013; [4] Carvalho et al., 2015, [5] Brownlow et al., 2001; [6] Hernandez-Aguilar et al., 2013; [7] Samson, 2012; [8] Ancrenaz et al., 2004; [9] Rayadin and Saitoh, 2009; [10] Brugiere, 2001; [11] Willie et al., 2014; [12] Rothman et al., 2006; [13] De Vere et al., 2011; [14] Basabose and Yamagiwa, 2002; [15] Stanford and O'Malley, 2008; [16] Hernandez-Aguilar, 2009; [17] Hakizimana et al., 2015; [18] Cheyne et al., 2013; [19] Sunderland-Groves et al., 2009; [20] Yamagiwa, 2001; [21] Lukas et al., 2003; [22] Mehlman and Doran, 2002; [23] Furuichi and Hashimoto, 2000; [24] Samson and Hunt, 2012; [25] Koops et al., 2007; [26] Stewart, 2011; [27] Last and Muh, 2013; [28] Tagg et al., 2013; [29] Samson and Shumaker, 2015; [30] Mulavwa et al., 2010; [31] Stewart et al 2007; [32] Samson and Hunt, 2014; [33] Iwata and Ando, 2007; [34] Haurez et al., 2014; [35] Funwi-Gabga and Mateu, 2012; [36] Weiche and Anderson, 2006; [37] Ogawa et al., 2007; [38] Inogwabini et al., 2012; [39] Krief et al., 2012; [40] Samson et al., 2013; [41] Serckx et al., 2016; [42] Serckx et al., 2014; [43] Morgan et al 2006; [44] Spehar and Rayadin, 2017; [45] Chancellor et al., 2012; [46] Videan, 2006

[&] species was unknown in captive research studies

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