

Orangutans (*Pongo Spp.*) Have Deeper, More Efficient Sleep than Baboons (*Papio papio*) in Captivity

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ABSTRACT The nightly construction of arboreal sleeping platforms or “nests” has been observed among every great ape population studied to date. However, this behavior has never been reported in any other non-human primate and comparisons between ape and monkey sleep illuminate the link between sleeping substrates, positional behavior, and sleep efficiency. Here, we compare sleep depth and efficiency and nighttime positional behavior between a large-bodied cercopithecoid (*Papio papio*) and a large-bodied hominoid (*Pongo spp.*) at the Indianapolis Zoo. We used infrared videography to assess nightly sleep and awake behavioral states, gross body movements, and postures in baboons ($N=45$ nights) and orangutans ($N=128$ nights). We calculated the *total waking time*, *total sleep time*, *sleep fragmentation* (the number of brief awaken-

ings ≥ 2 min/h), *sleep motor activity* (number of motor activity bouts per hour), *sleep efficiency* (sleep duration/time in bed), and percentage of time spent in each posture. By every measure, orangutans experienced overall deeper, more efficient sleep. Baboons were more likely to sleep in guarded, upright positions (weight bearing on their ischial callosities) and never opted to use additional materials to augment sleep environments, whereas orangutans slept in insouciant, relaxed positions on constructed sleeping materials. Our results suggest that relaxed sleeping postures may have been enabled by sleeping platforms as a *behavioral facilitator* to sleep, which could have allowed for greater sleep depth and next-day cognitive capacities in both great apes and hominins. Am J Phys Anthropol 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

Humans and great apes are unique in that they share the behavior of sleeping platform building. Other primates characterized by large body and brain mass (e.g., *Papio* and *Mandrillus*) and/or high levels of intelligence (e.g., *Cebus*) do not construct sleeping platforms, nor do gibbons, the other extant ape. Body mass is a significant predictor of life history (Fleagle, 1999), and therefore a direct comparison between a large-bodied hominoid such as *Pongo* and among the largest-bodied *Cercopithecidae* may yield insight into the important differences and derived traits that can categorize great ape sleep and sleep architecture as unique among primates.

Sleep can be viewed as a brain state, a process, and a behavior (Webb, 1988; Vyazovskiy and Delogu, 2014); it is an emergent network property that serves multiple purposes, including energy restoration, immunocompetence, niche-specific predation avoidance, reproductive timing, brain metabolic homeostasis, neural ontogenesis, and cognitive and emotional processing (Everson, 1995; Marks, 1995; Walker, 2009; McNamara et al., 2010; Xie et al., 2013). Sleep is regulated by preceding activity history (Achermann et al., 1993) and circadian time (Fisher et al., 2013).

When an animal is asleep, its brain shifts between qualitatively and quantitatively different states—non-rapid eye movement (NREM) and rapid eye movement (REM) sleep (Aserinsky and Kleitman, 1953; Saper et al., 2010), which are differentiated by state-specific brain wave patterning (Aserinsky and Kleitman, 1953; Zamboni et al., 1999; Buzsaki et al., 2013). Furthermore, these brain states can be measured by electroen-

cephalography (EEG) and reveal NREM sleep (also known as slow-wave sleep) to be subdivided into two important stages: a) deep sleep slow-wave activity (SWA: 0.5–4.0 Hz, NREM Stage 3–4), characterized by *delta* rhythms, *K-complexes*, and global slow cortical oscillations; b) the lighter N2 (NREM Stage 2: 11–15 Hz), often associated with sleep spindles (which involve localized corticothalamic interactions) and transitioning phases to REM (Destexhe et al., 1999; Massimini et al., 2004; Vyazovskiy and Harris, 2014; Ackermann and Rasch, 2014). In contrast, brainwave activity during REM sleep is similar to waking-state activity. SWA occurs mostly during the first half of the sleep period, whereas N2 is evenly distributed throughout; REM sleep occurs mostly during the second half of the sleep period (Ackermann and Rasch, 2014).

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Vyazovskiy and Delogu (2014) theorize that NREM and REM sleep have complementary roles in recovery after activity periods. Specifically, they posit that slow oscillations during NREM sleep enable information processing, synaptic plasticity, and cellular maintenance in a general “recovery” phase, whereas selection on brain networks follows this general recovery period during REM sleep; such a two-stage sleep process would ensure its functions are fulfilled in accordance to the current need, within the shortest possible time. Several measures of sleep intensity, such as sleep motor activity (number of motor activity bouts per hour) and fragmentation (the number of brief awakenings >2 min/h), are correlated with deep, SWA (Borbely and Achermann, 1999), and have been demonstrated in many mammals including human and nonhuman primates (Tobler, 2005).

In accordance with Vyazovskiy and Delogu’s model, we can use these measures as proxies for sleep depth in primates. In fact, the ideal comparative measure for research on sleep is the distribution of sleep architecture (NREM and REM); however, the gold standard to directly measure sleep architecture is with polysomnography which is invasive—making it impractical to apply to primate sleep research. Finally, the measures of *sleep intensity* (i.e., behavioral correlates associated with the intensification of sleep and enhanced EEG power in the *delta* range) are underreported in the literature and are high priority data to generate for primates (Nunn et al., 2010).

Work on the sleeping habits of east African monkeys (*Colobus*, *Cercopithecus*, and *Papio*) has focused on predation as the driving force behind sleeping site selection (Buxton, 1951; DeVore and Hall, 1965; Altmann and Altmann, 1970; Busse, 1980; Hamilton, 1982; Anderson and McGrew, 1984). Furthermore, the few field studies that have observed baboon nocturnal sleeping behavior have noted night-time huddling as a common behavior (Bert et al., 1975); it remains unknown whether these huddles augment sleep by improving thermoregulation or disrupt it because of the resulting social interactions. Whether these sites are in tree canopies, on cliff faces, or in caves, the animals do not intentionally modify them.

In contrast, in great apes all individuals other than unweaned infants construct nightly sleeping platforms or “nests” (Goodall, 1962, 1968). Sleeping group sizes are smaller than baboon huddles; typically, all members of a gorilla group sleep in one site, whereas chimpanzee and bonobo sleep in groups smaller than community size and sleep group size is generally small for orangutans (Fruth and Hohmann, 1996). Sleeping platform builders must select an appropriate site, climb to the site, and manipulate a large volume of foliage while maintaining balance. They bend and break stems (Goodall, 1962) as they incorporate foliage into the bed architecture, bending material inward, and interweaving it into a “mattress,” often breaking frame supporting branches in two. Great ape sleeping platform mattresses are characterized by edges that are elevated over the mattress surface and are less compliant than the center (Stewart et al., 2007), causing the platform to assume a concave surface under pressure that also minimizes sway and maximizes comfort (van Casteren et al., 2012, 2013; Samson and Hunt, 2014).

The “sleep quality hypothesis” holds that the construction of sleeping platforms leads to higher quality sleep because it allows uninterrupted sleep and hence

promotes longer individual sleep stages (Fruth and Hohmann, 1996; McGrew, 2004; Videan, 2005, 2006; Stewart, 2011; Samson, 2012). The compliant, but constraining, structure allows an individual to sleep in a relaxed lateral, supine, or prone position instead of while sitting upright or while lying prostrate on a branch in a position that may not allow the degree of muscle relaxation achievable in a sleeping platform. Furthermore, compared to only sleeping on bare substrates, captive orangutans exhibit deeper sleep with less gross-motor movements and greater overall sleep times when using complex sleeping platforms (Samson and Shumaker, 2013). In the wild, such platforms should reduce physical stress and obviate the need to adjust posture to prevent falls.

The goal of this study was to describe and document baboon and orangutan sleep within a comparative framework to elucidate the differences in sleep between branch sleeping large-bodied monkeys and sleeping platform using apes. In addition, hypotheses related to 1) overall sleep efficiency and 2) sleep-associated positional behaviors were tested. First, we hypothesize that orangutans will be characterized by longer, deeper, and more efficient sleep than baboons. Second, we hypothesize that baboon sleep will be characterized by more social disruption and less relaxed sleeping posture. Specifically, we tested the following predictions:

1. Orangutans will have greater total sleep time, sleep efficiency, and less waking times, and deeper sleep compared to baboons.
2. Baboons will exhibit a greater frequency of guarded, less prone positions, and will have a greater number of observed group-associated huddles with lighter sleep and lower sleep efficiency.

METHODS

Study subjects and housing

The study animals were housed at the Indianapolis Zoo (IZ) in species-specific, interconnected indoor and outdoor enclosures. They had complete access to both enclosures throughout spring, summer, and fall, but had access only to the indoor enclosures during the winter. The IZ is accredited by the Association of Zoos and Aquariums (AZA). For both species, the indoor enclosures were set at a constant temperature of 23.3 °C. Natural lighting was the primary source of light for both groups and was accessible by the way of windows and access to the outdoor enclosure; in addition, low lux lights were manually turned on by the keepers at 07:30 h and turned off at 16:30 h.

The baboons could choose to sleep on the floor of the indoor enclosure or on a raised laminate platform that ran along the entirety of its walls and that provided ample surface area (Fig. 1); subjects’ free range of movement allowed them to choose to sleep on the ground or on a raised platform. Straw and browse were introduced to the baboon enclosure to test whether baboons would use sleeping materials to improve comfort. Within the baboon enclosure, the visual field of the camera was focused on a confined area (stall 3), limiting observations to individuals who were within line of sight for the total sleep period. The orangutan indoor enclosure contained laminate raised platforms located 1 m off the floor. Subjects had access to natural materials (brush, lianas, and straw) and artificial materials (rope, hammock,



Fig. 1. Baboon individual sleeping on raised platform in the guarded, upright position (top); orangutan individual sleeping in the insouciant, supine position on a constructed ground sleeping platform. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

cardboard, sheets, and blankets) from which to construct sleeping platforms.

Baboon focal subjects ($N = 12$) consisted of eight males: Bailik (age, 19 years), Kito (age, 8 years), Odai (age, 7 years), Daillo (age, 5 years), Obi (age, 4 years), Bunzi (age, 2 years), Rafiki (age, 2 years), and Romeo (age, 1 year) and four females: Addie (age, 30 years), Penjade (age, 11 years), Rachel (age, 9 years), and Nyani (age, 8 years). Orangutan focal subjects ($N = 5$) were three females, Katy (age, 24 years), Knobi (age, 33 years), Lucy (age, 28 years), and two males Azy (age, 35 years) and Rocky (age, 8 years) (Table 1; total subject $N = 17$). None of the subjects were geriatric; life span in the wild for orangutans is approximately 60 years (Shumaker et al., 2008) and 40 years for baboons (Altmann et al., 1981; Ross, 1991). All orangutan subjects were hybrids of Bornean and Sumatran *Pongo* species; there are no compelling reasons to assume that the differences in behavioral ecology between these two species (Bornean and Sumatran) would influence the results of this study. For further detail regarding background and night-time sleep related behaviors in captive orangutans, see Samson and Shumaker (2013).

Data collection

Data were generated between October 2011 and December 2013. The nocturnal behavior of the subjects was continuously recorded using infrared videography. For baboons, nocturnal behavior was continuously

recorded using a single infrared video camera (AXIS P3344; $N = 45$ nights [384 observation hours]). For orangutans, nocturnal behavior was continuously recorded using multiple infrared video cameras (AXIS P3344 and AXIS Q6032-E Network Cameras; $N = 128$ nights [1,561 observation hours]). Nightly sessions in which subjects moved outside the line of sight were not used for analysis. Videographic units of measurement were recorded in minutes. Sleep-related behavior was recorded from the moment the head reclined into an immobile position until the moment the body raised and permanently left the sleeping platform/area.

Data recording methods followed the protocols set in the previous studies (Balzamo et al., 1998; Muzino et al., 2006), where simultaneously collected EEG and videography showed a highly significant association between brainwave activity and observed sleep behavior. The behavioral analysis differentiating sleep states were analyzed and scored in 1 min epochs at $8\times$ real-time speeds (allowing a 12-h sleep period to be scored in approximately 2 h). Awake was defined as eyes being open and/or by continuous gross body movement (especially of the head) observed throughout the majority of the 1-min epoch. Sleep was defined as closed eyes without movement, reduced head muscular tone, face/limb twitching (for more detail regarding the use of these methods for large bodied primates, see Samson and Shumaker, 2013). If greater detail was needed to more accurately observe the state of vigilance, the speed of the display was slowed down to normal speed. The sleep stage that constituted the majority of a minute was assigned the 1-min epoch (Balzamo et al., 1998).

We used videography to determine how individuals allocated sleep-related behavior among *total waking time*, *total sleep time*, and *total time in bed* (absolute difference between rising and retiring times). Also, we used all-occurrence sampling (Altmann, 1974) to count the instances of motor activity and to generate the following variables which are often underreported in primate sleep literature (Tobler, 2005; Nunn et al., 2010; see Table 2 for variable definitions): *sleep fragmentation* (the number of brief awakenings >2 min/h), *sleep motor activity* (Krueger et al., 2008) (number of motor activity bouts per hour), sleep efficiency (sleep duration/time in bed), percentage of time spent in a *posture* (calculated as the

TABLE 1. Demography of baboon and orangutan subjects, ranked by age, age class, and sex

Genus	Subject	Year born	Age class	Sex
<i>Papio</i>	Bialik	1993	Adult	Male
<i>Papio</i>	Kito	2004	Adult	Male
<i>Papio</i>	Odai	2005	Adult	Male
<i>Papio</i>	Diallo	2007	Subadult	Male
<i>Papio</i>	Obi	2008	Juvenile	Male
<i>Papio</i>	Bunzi	2010	Juvenile	Male
<i>Papio</i>	Rafiki	2010	Juvenile	Male
<i>Papio</i>	Romeo	2011	Juvenile	Male
<i>Papio</i>	Addie	1982	Adult	Female
<i>Papio</i>	Penjade	2001	Adult	Female
<i>Papio</i>	Rachel	2003	Adult	Female
<i>Papio</i>	Nyani	2004	Adult	Female
<i>Pongo</i>	Azy	1977	Adult	Male
<i>Pongo</i>	Rocky	2004	Adult	Male
<i>Pongo</i>	Katy	1988	Adult	Female
<i>Pongo</i>	Knobi	1979	Adult	Female
<i>Pongo</i>	Lucy	1984	Adult	Female

TABLE 2. Comparative definitions for primate sleep measures

Definition	Standard measurement	Operationalized with videography	Process being quantified	Previously used terminology	References
Sleep motor activity	Electromyography (EMG)	The number of observed motor activity movements per sleep period hour	Homeostatic regulation; intensification of sleep; correlated with enhanced EEG power in the Delta range	Sleep intensity, sleep arousability	Campbell and Tobler (1984); Krueger et al. (2008); Tobler (2005)
Sleep fragmentation	Electroencephalography (EEG)	The number of observed awakenings ≥ 2 min per sleep period hour	Homeostatic regulation; intensification of sleep; correlated with enhanced EEG power in the Delta range	Sleep intensity, brief awakenings, sleep continuity	Campbell and Tobler (1984); Tobler (2005)
Sleep efficiency	Actigraphy, questionnaires	Observed sleep duration divided by total time spent in sleep site	Insufficient or disrupted sleep	Sleep quality (human only), sleep efficiency	Pilcher et al. (1997); Videan (2005); Dewald et al. (2010)

total proportion of epochs in a posture, per subject sleep period), and the total number of sleeping partners during a sleep period (additional subjects <1 m from the focal subject). Huddles were recorded as present or absent. We also counted huddle cluster size (maximum number of individuals within a huddle per night).

Data analysis

We compared the sleep duration, sleep motor activity, sleep fragmentation, and sleep efficiency of *Pongo* and *Papio* with Mann–Whitney *U*-tests. Sleeping position categories were compared using the prone, relaxed positions (supine, left, and right) against the guarded position (upright, sitting). Pearson’s correlation analysis was performed on huddle frequency and maximum cluster size versus sleep efficiency and the number of sleep period awakenings. All reported errors are standard deviations. Statistical tests were conducted using SPSS 18 and R (Team, 2014); all tests were two-tailed with significance set at the 0.05 level.

RESULTS

Overall, orangutans experienced longer, deeper sleep, and significantly less fragmentation and motor activity than baboons (Table 3 and Fig. 2). Baboon positional behaviors were heavily weighted toward the upright, sitting posture, which they on average assumed 69% of their total sleep time. Other sleep period averaged positional behaviors were prone = 5%, supine = 4%, right side = 10%, left side = 13%. In contrast, orangutans rarely slept upright (a mean of 6.2% of sleep time) and mostly used insouciant sleeping postures (prone = 8.6%, supine = 20.5%, right = 31.5%, and left = 33.2%). Baboons slept in the *guarded* positions more often, whereas orangutans slept in the insouciant, relaxed positions more often (e.g., see Fig. 1). Baboons slept with a partner 94% of the time, whereas orangutans slept with a partner (within 1 m of each other) 2% of the time. Baboons exhibited huddling (embracing ventral surface of body toward sleep partner), whereas orangutans never huddled, even when sleeping within 1 m of their sleep partner. In none of the 45 trials did baboons use introduced materials to construct sleeping platforms, whereas orangutans always constructed platforms. Nightly awakenings were not significantly related to huddle frequency (number of times group composition changed; $r = 0.008$, $N = 17$, $P = 0.98$) or maximum cluster size ($r = -0.09$, $N = 17$, $P = 0.74$), and sleep efficiency was not significantly related to huddle size ($r = -0.43$, $N = 17$, $P = 0.086$).

DISCUSSION

To our knowledge, this study is the first to compare sleep efficiency and positional behavior directly in captive cercopithecoids and hominoids; in addition, this is the first report of *sleep intensity* variables (fragmentation and motor activity) for nonhuman primates. The first hypothesis, that captive orangutan sleep would be characterized by longer, less fragmented sleep and higher sleep efficiency than baboons, was supported. *Papio* nightly sleeping bouts had a significantly greater number of total awakenings, a greater frequency of motor activity, lower sleep efficiency, more fragmentation, greater total time spent awake, and less total time spent asleep (Table 3). Furthermore, the second

hypothesis, that baboons would be characterized by more guarded sleeping positional behavior, was supported. Comparing the two genera, orangutan sleep was characterized by more frequent insouciant sleeping postures when compared to the more guarded position characterized by baboon sleeping postures. One of the

predictions of the second hypothesis, that sleep fragmentation increases positively with maximum cluster-group size, was not supported. Furthermore, maximum huddle size was not significantly related to sleep efficiency. Mochida and Nishikawa (2014) found that the composition of sleeping clusters could influence the aspects of sleep as individuals showed greater synchronicity in sleep states when they were sleeping in clusters with close kin than when they were not with close kin. The possibility that cluster composition, thermoregulation, and social disruption influence baboon sleep patterns deserves further study.

By removing the extraneous abiotic and biotic environmental variables associated with research of wild subjects, carefully controlled captive studies can identify causality (Tomasello and Call, 1997). Interestingly, baboons did not use any sleeping materials throughout the study when these were presented; unlike the great apes, baboons seem undisposed to manipulate their sleeping environments.

The baboons in this study, like those in the wild, slept with their body weight resting on the ischial callosities; this behavior may allow for greater vigilance and readiness to respond to intrinsic needs (e.g., thermoregulation) and external factors (e.g., predation risk and social interactions), possibly at a cost in terms of benefits associated with deeper, more efficient sleep, resulting in more time spent in N2 sleep stages. In contrast, the greater use of relaxed sleeping positions that sleeping platforms afford to orangutans and other great apes facilitates longer sleep durations, with fewer awakenings, and may allow great apes to gain more of the potential benefits of deeper, more efficient sleep (Fruth and Hohmann, 1996).

Baboons differ from great apes in that they sleep in large groups and oftentimes huddle on cliff faces and emergent trees (Anderson and McGrew, 1984). The functions of these sleeping behaviors may be numerous: thermoregulatory, antipredation, increasing stability in precarious terminal branch sleep sites (Hamilton, 1982; Anderson, 1984), but for baboons, the costs of sleeping in socially dynamic groups in wild environments are apparent in the overall loss of sleep (Bert et al., 1975). These ecologically influenced behaviors also carry-over to a captive environment, where baboons remain more vigilant, more prone to waking and exhibit guarded positional behavior. Evolutionarily, great apes may make sleeping platforms out of necessity, given the dangers of sleeping high in the canopy with their massive bodies

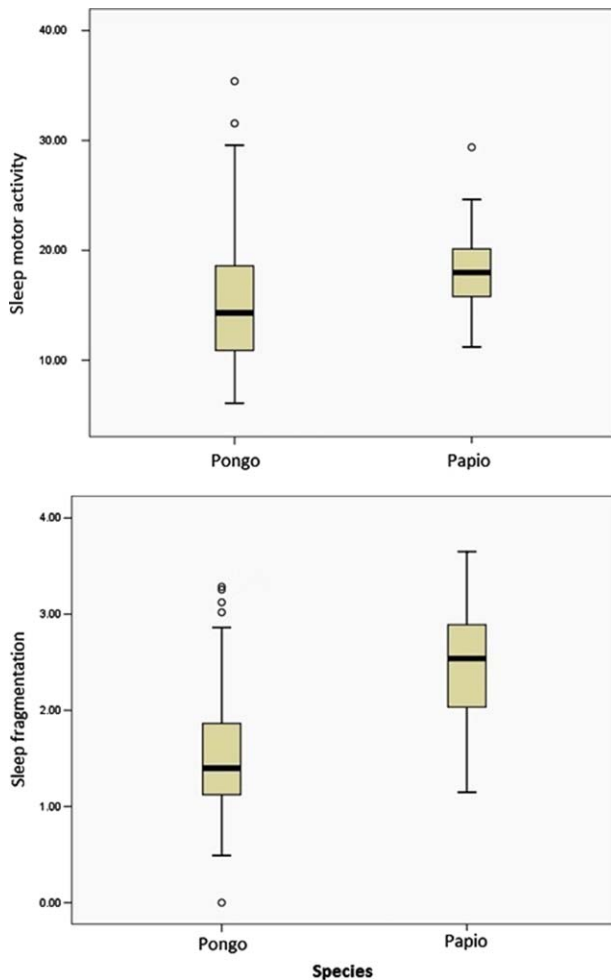


Fig. 2. Baboons were characterized by greater motor activity and awakenings throughout the night, when compared to orangutans. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE 3. Comparison between orangutan and baboon sleep efficiency (sleep duration/time asleep), sleep motor activity (number of motor activity bouts per hour), sleep fragmentation (the number of brief awakenings ≥ 2 min/h), and total awake and sleep time^a

Variable	N	Mean and SD	Range	Mean difference	P-value
<i>Papio</i> total awakenings	45	18.4 ± 4.5	19	-4.29 ± SE 0.85	<0.001
<i>Pongo</i> total awakenings	120	14.2 ± 5.00	23		
<i>Papio</i> sleep motor activity	45	20.2 ± 3.5	18.2	-2.60 ± SE 0.75	<0.001
<i>Pongo</i> sleep motor activity	128	15.5 ± 5.9	29.2		
<i>Papio</i> sleep efficiency	45	0.59 ± 0.05	0.31	0.10 ± SE 0.01	<0.001
<i>Pongo</i> sleep efficiency	128	0.73 ± 0.08	0.38		
<i>Papio</i> sleep fragmentation	45	3.0 ± 0.58	2.5	-1.00 ± SE 0.11	<0.001
<i>Pongo</i> sleep fragmentation	21	1.5 ± 0.63	3.28		
<i>Papio</i> total time awake	44	304.4 ± 31.8	283	-54.09 ± SE 11.99	<0.001
<i>Pongo</i> total time awake	128	210.7 ± 69.7	335		
<i>Papio</i> total sleep time	44	437 ± 66.3	279	115.60 ± SE 11.92	<0.001
<i>Pongo</i> total sleep time	128	559.8 ± 69.8	335		

^a Unit of measurement for sleep time is expressed in minutes.

(Baldwin et al., 1981; Samson, 2012), or it may be that great apes make sleeping platforms not because they must, but because they can—large brains provide them with the cognitive sophistication to manufacture a *complex construction* (Shumaker et al., 2011) that many primates could benefit from equally, but not all primates can accomplish. Either way, sleeping substrates could be a “behavioral facilitator” to sleep (Videan, 2005), which could have promoted deeper sleep and improved next-day cognitive capacities in both apes (Fruth and Hohmann, 1996) and australopithecines. Certain cognitive benefits, such as memory consolidation and social priming, could have been even more relevant when hominins such as *Homo erectus* began habitually sleeping terrestrially (Coolidge and Wynn, 2006, 2009).

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