



Documenting orang-utan sleep architecture: sleeping platform complexity increases sleep quality in captive *Pongo*

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Abstract

Of the extant primates, only 20 non-human species have been studied by sleep scientists. Notable sampling gaps exist, including large-bodied hominoids such as gorillas (*Gorilla gorilla*), orang-utans (*Pongo* spp.) and bonobos (*Pan paniscus*), for which data have been characterized as high priority. Here, we report the sleep architecture of three female and two male orang-utans housed at the Indianapolis Zoo. Sleep states were identified by scoring correlated behavioural signatures (e.g., respiration, gross body movement, muscle atonia, random eye movement, etc.). The captive orang-utans were focal subjects for a total of 70 nights (1013 h) recorded. We found that orang-utans slept an average of 9.11 h (range 5.85–11.2 h) nightly and were characterized by an average NREM of 8.03 h (range 5.47–10.2 h) and REM of 1.11 (range: 0.38–2.2 h) per night. In addition, using a sleeping platform complexity index (SPCI) we found that individuals that manufactured and slept in more complex beds were characterized by higher quality sleep. Sleep fragmentation (the number of brief awakenings greater than 2 min per hour), arousability (number of motor activity bouts per hour), and total time awake per night were reduced by greater quality sleep environments. Therefore, comfortable sleeping environments reduced arousability and improve sleep quality in captive orang-utans. These results support Fruth & Hohmann's (1996) hypothesis, which purported that the tree-limb-to-sleeping platform transition in Miocene apes improved sleep quality.

Keywords

sleep, orang-utan, nest, REM, NREM, comfort, ape, evolution.

1. Introduction

Sleep plays a central role in shaping primate behaviour, ecology and health (Anderson, 1998; Zepelin et al., 2005; Capellini et al., 2009; Lesku et al., 2009). Therefore, the study of primate sleep is particularly valuable to our understanding of human sleep disorders, the ecology of sleep in nonhuman primates and the general evolution of sleep patterns (Nunn et al., 2010). Modern sleep studies focus on three basic parameters of sleep architecture in primates, which are known as ‘sleep quotas’ (McNamara et al., 2010). Sleep quotas include (1) the total time spent asleep per day, (2) the time spent within the two major forms of mammalian sleep, rapid eye movement (REM) and non-rapid eye movement (NREM) and (3) sleep cycles (the duration measured from the onset of NREM to the end of REM). Of the 350 extant primates (Groves, 2001), only 20 non-human species have been studied by sleep scientists (Campbell & Tobler, 1984; Zepelin, 1989; Nunn et al., 2010). Within the subset of primates that has been studied, notable sampling gaps exist. We have sleep measures on only two species of hominoids: chimpanzees and humans. Nunn and colleagues (2010: 138) have put forth an explicit challenge: “A high priority for future research should be to collect sleep data in the other great apes, specifically gorillas (*Gorilla gorilla*), orang-utans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*), along with one or more species of gibbons (*Hylobates* spp.)”.

Given the danger to workers performing nighttime observation in wild primates, sleep studies have thus far been primarily conducted in captivity (Sri Kantha & Suzuki, 2006). Polysomnography (i.e., the recording of biophysiological changes that occur during sleep with electrodes) has been the standard method for studying sleep among captive mammals. The first systematic studies of great ape sleep were conducted with polysomnography on chimpanzees in the 1960s and early 1970s (Kripke & Bert, 1968; Freemon et al., 1969; McNew et al., 1971; Balzamo et al., 1972; McNew, 1972). Yet, it has been determined to be unreliable due to disturbance to subjects and oftentimes requires restraints which can be stressful to the animal (Sri Kantha & Suzuki, 2006). In addition, primate species’ typical sleep architecture is particularly difficult to document because they are unusually susceptible to sleep disruption when exposed to artificial light within the visible spectrum (Sri Kantha & Suzuki, 2006). The challenges of studying sleep among primates likely account for the paucity of sleep studies among great apes. With

the advent of new technology, the increasing affordability of such technology, and new non-invasive methods of observing nocturnal behaviour among chimpanzees (Mizuno et al., 2006; Videan, 2006; Morimura et al., 2012) and other primate species (Zhdanova et al., 2002; Ancoli-Israel et al., 2003) the study of nocturnal behaviour of diurnal primates has become more practical. Recently, two alternative methods to polysymnography have been successfully used: actigraphy and high sensitivity video recordings (Munozdelgado, 1995; Balzamo et al., 1998). Actigraphy is difficult to apply to apes given that the application of sensors to the body conflict with their autogrooming instinct; in addition, many zoos have strict policies about anesthetizing animals for non-medical reasons. Applying chemical or physical restraint to subjects is inconsistent with this study's methodology.

Given these serious concerns, a non-invasive approach is needed. Videography is an appealing method in this context for several reasons. Previous work has illustrated a linear correlation between EEG and video recordings of sleep behaviour in rhesus monkeys (Balzamo et al., 1998). Subject behaviour was analyzed manually and scored into three distinct states in a minute by minute analysis: wakefulness, NREM and REM. Specifically, the correlation coefficient for REM sleep ($r = 0.987$), for NREM sleep ($r = 0.996$) and wakefulness ($r = 0.999$) were significant (Balzamo et al., 1998), illustrating the validity of the behavioural recording method in scoring sleep stages. A notable difference between this study and ours is in that our subjects were not physically restrained. A weakness is that this method cannot differentiate between the different stages of NREM.

The great apes alone construct sleeping platforms (for further detail on 'nest' nomenclature, and its reference as the more functionally descriptive term 'sleeping platform' see Samson, 2012) by modifying foliage so that it functions as a stable and comfortable mattress (Goodall, 1962; Goodall, 1968); this has been observed in every chimpanzee, bonobo, gorilla, and orang-utan population yet studied — yet it is found among no other primate, even though most primates sleep in trees, some are large-bodied (e.g., mandrills, baboons), and/or intelligent (e.g., atelids, *Cebus* spp.), suggesting that perhaps sleep architecture and nest-making are related. Fruth & Hohmann (1996) hypothesized that sleeping platforms increased comfort in extinct Miocene apes, which augmented memory consolidation by way of an increase in duration and quality of both REM and NREM. They propose that the ability for ancestral apes to have greater quality sleep architecture could

not have happened without building safe and/or comfortable substrates upon which to rest. This suggests that humans and great apes share stable sleeping substrates and, thus, may well share sleep architecture.

The goals of this research were twofold: (1) document the sleep architecture of captive *Pongo* spp. using infrared videography and (2) to test Fruth and Hohmann's hypothesis regarding ape sleeping platform construction as a method of augmenting sleep quality. We test the following predictions derived from the aforementioned hypothesis:

- (1) If subjects sleep on more complex platforms, sleep architecture (i.e., time spent in the behavioural states of awake, NREM and REM) will be affected.
- (2) If subjects sleep on more complex platforms, depth of sleep will increase and intensity measures (i.e., arousability, sleep fragmentation and sleep quality) will decrease.

2. Material and methods

The orang-utans in this study were housed at the Indianapolis Zoo (IZ). The focal subjects (total $N = 5$) consist of three females, Katy (24), Knobi (33) and Lucy (28), and two males, Azy (35) and Rocky (8); all subjects were classified as adults, except the single adolescent Rocky. None of the subjects are geriatric, as life span in the wild for orang-utans is approximately 60 years old (Shumaker et al., 2008). All subjects were hybrids of Bornean and Sumatran *Pongo* species. Rocky, Katy and Lucy were privately owned and part of the entertainment industry prior to moving into the Association of Zoos & Aquariums (AZA) community, specific information about their personal histories is, therefore, limited. Azy and Knobi have always lived within the AZA community and have well documented biographies, and rich social experience. Subjects were housed in interconnected indoor and outdoor enclosures, and had regular access to all areas throughout the duration of the study. The indoor enclosure contained laminate sleeping platforms located approximately 1 m off the floor. Bedding materials (e.g., straw, cardboard, paper, sheets and blankets) were provided for the animals to build sleeping platforms. In accordance with the noninvasive policies enforced by the IZ, the experimental conditions of the subjects were unrestrained to ensure normative sleep. In addition, the subjects' free range of movement allowed



Figure 1. Infrared videography was used to monitor and score sleep states (left: Azy sleeping in the prone position; right: Lucy sleeping on her right side).

them to choose to sleep on the ground or on raised platforms. The indoor space included five possible rooms where the subjects could sleep. Subjects had access to natural and artificially enriched environments. The indoor enclosure was set at a constant temperature of 23.3°C. Lights were manually turned on by the keepers at 07:30 and turned off at 17:30, in addition to the natural lighting which was present in the enclosure with windows and access to the outdoor enclosure.

This study was conducted over twelve months during October 2011–October 2012. The nocturnal behaviour of the subjects was continuously recorded using infrared videography (Figure 1). Two instruments (AXIS P3344 and AXIS Q6032-E Network Cameras) were used to generate nightly sleep quota data on subjects within line of sight. One stationary camera (P3344) was manually placed in front of the subject at the time of sleeping platform construction; another rotatable camera (Q6032-E) was remotely controlled throughout the night to ensure focal subjects were continuously within line of sight from start to finish of the recording session. Nightly sessions in which subjects moved outside the line of sight were not used for analysis. A total of 70 nights (1013 h) were recorded. Data recording methods followed protocols set in previous studies (Balzamo et al., 1998; Mizuno et al., 2006). Sleep states were identified by categorizing behavioural signatures previously shown to be correlated with these states (Weitzman, 1965; Kripke et al., 1968). Behaviours such as closed eyes without movement, gross motor movement, and regular respiration were scored as NREM sleep, whereas closed eyes, reduced head muscular tone, eye movement, face/limb twitching, and irregular respiration frequency were associated with REM

Table 1.

Classification of behavioural states and their criteria (amended from Mizuno et al., 2006).

Behavioural feature	NREM	REM	Awake
Eyes	Closed	Closed	Open
Gross movement	Present	Absent	Present
Respiration	Regular	Irregular	Regular
Eye movement	Absent	Present	n.a.
Vocalization	Absent	Either	Either
Muscle atonia/limb twitching	Absent	Present	Absent

The video illustrating differences in respiration and additional behavioural features associated with NREM and REM can be watched as supplementary material that is part of the online version of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>.

sleep (Table 1 and Figure 2); awake was defined as eyes being open and/or by continuous gross body movement (especially of the head) observed throughout the majority of the epoch.

Respiration frequency was visually documented by the scorer (DRS); reliability of observation was tested between DRS and an independent judge. Regular (NREM) respiration patterns were established for each individual

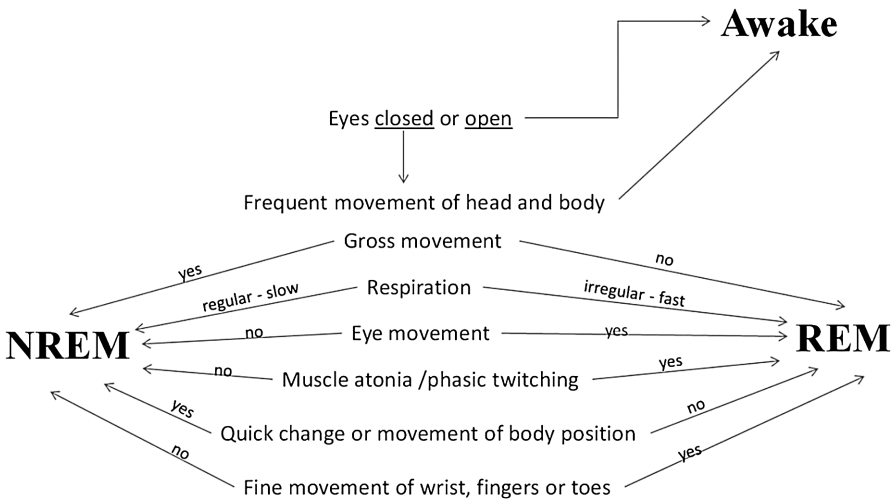


Figure 2. Flow chart illustrating the behavioural criteria used in assessment of sleep and awake states. In large-bodied great apes, respiration is of primary importance given its identifiability.

and sleep states assessed given the behavioural context queues associated with each epoch. The behavioural analysis differentiating sleep states were analysed 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). 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). Units of measurement were recorded in minutes.

Sleep behaviour was recorded from the moment the body reclined into a horizontal, immobile position until the moment the body raised and permanently left the sleeping platform/area (Videan, 2006). Using all-occurrence sampling on individual subjects (Altmann, 1974), the video recordings yielded sleep quota time allocation data for: total time spent awake, total NREM, total REM, total sleep time (sum of NREM and REM) and total time in bed (absolute difference between rising and retiring times). From these, NREM and REM sleep time as percentage of length were calculated. In addition, frequency data of gross body movement and motor activity were used to generate variables (Tobler, 2005) such as: sleep fragmentation (the number of brief awakenings greater than 2 min per hour), arousability (Krueger et al., 2008) (number of motor activity bouts per hour), sleep quality (sleep duration/time in bed), posture and sleeping partner (additional subjects less than 1 m from the focal subject).

To evaluate the effect of sleeping platform quality on sleep architecture and sleep quality, sleep materials were experimentally introduced to the enclosure for individual use; experimental nights were characterized by the inclusion of all the sleeping materials, whereas control nights only included hay. Each subject was free to select preferred sleeping materials among several items of each type (see below); each item was assigned an indexed value based upon a relative assessment of complexity termed the sleeping platform complexity index (SPCI). For example, a simple item such as paper was deemed less complex than an elaborate item such as a memory foam mattress. The materials used were as follows: no sleeping materials (bare floor) = 0; paper/cardboard sheet = 0.5; hay = 1; sheet = 1; pillow = 1; blanket = 1.5; memory foam = 1.5; camping pad = 1.5; comforter = 2; sleeping bag = 2. The final SPCI score given to a sleeping platform was additive (e.g., if an individual manufactured a sleeping platform consisting of hay, sheet and a comforter, it resulted in an SPCI score of 3.5). All reported

errors are standard deviations. Statistical tests were conducted using IBM SPSS 18 and all tests were two-tailed with significance set at the 0.05 level.

3. Results

Orang-utans slept an average of 9.11 h (SD 1.16 h) nightly and were characterized by an average NREM of 8.03 h (SD 1.06 h) and REM of 1.11 (SD 0.35 h) per night (see Table 2 for species average and Figure 3 for individual subject sleep architecture averages). Total retired time averaged 12.78 h (SD 0.92 h) per night (Table 2). Sleep quality averaged 0.71 (SD 0.08) per night (Table 2). The subjects did not sleep continuously throughout the night — they awakened, on average, 11.98 (SD 4.3) times per night.

Behavioural percentage of sleep architecture did not significantly vary between sex (independent samples *t*-test: awake; $t = -1.37$, $p = 0.31$; NREM; $t = -1.32$, $p = 0.41$; REM; $t = -0.54$, $p = 0.45$) nor age (ANOVA: NREM; $F_{4,75} = 0.46$, $p = 0.77$; REM; $F_{4,75} = 0.46$, $p = 0.77$) except for the percentage of time spent awake (ANOVA: $F_{4,88} = 4.95$, $p = 0.001$). Rocky, the youngest and only adolescent individual, was characterized by significantly more motor movement at night compared to the older individuals

Table 2.
Orang-utan sleep quota and sleep behaviour values.

Variable	<i>N</i>	Mean	SD	Range
Total awake (h)	70	3.66	1.25	1.20–6.40
Total NREM (h)	59	8.03	1.06	5.47–10.23
Total REM (h)	59	1.11	0.35	0.38–2.20
Total sleep time (h)	70	9.11	1.16	5.85–11.22
Total time in bed (h)	70	12.78	0.92	10.60–14.73
REM sleep time (%)	66	0.13	0.04	0.05–0.25
NREM sleep time (%)	66	0.87	0.40	0.75–0.95
Sleep fragmentation	61	1.34	0.57	0.49–3.25
Arousability	68	14.14	5.75	6.11–35.39
Sleep quality	68	0.71	0.08	0.51–0.90

N = number of nights analysed. Sleep fragmentation is defined as the number of awakenings greater than 2 min per hour. Arousability is defined as the number of motor activity bouts per hour. Sleep quality is defined as the total time in bed divided by the duration of sleep. Sample sizes differ across measures due to differences in camera resolution between nights.

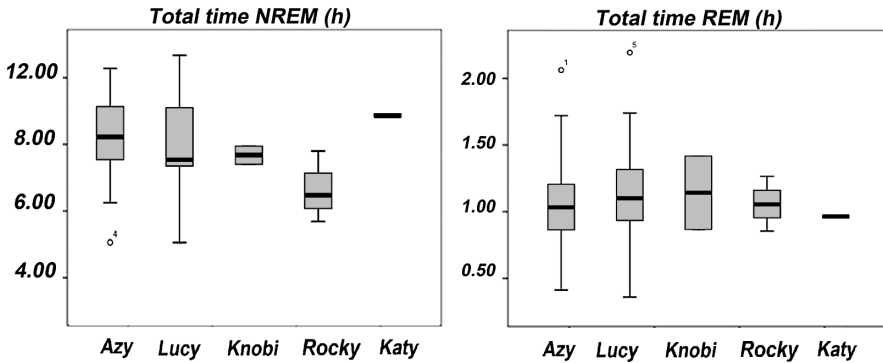


Figure 3. Sleep architecture categorized by individuals ($N = 5$).

(independent samples t -test: sleep continuity; $t = 3.02$, $p = 0.03$; arousability; $t = 10.84$, $p < 0.001$).

Nighttime activity included vocalizations, vigilance behaviours, changes in sleeping location, and rare occasions of social grooming and sexual activity. Sleep location was relatively consistent across nights. Sleep associated with a partner was also rare, occurring twice out of the 70 nights recorded. Sleeping postures varied between individuals and proved to be idiosyncratic (ANOVA: dorsal; $F_{5,74} = 9.2$, $p < 0.001$; ventral; $F_{5,74} = 5.3$, $p < 0.001$; right; $F_{5,74} = 23.1$, $p < 0.001$; left; $F_{5,74} = 4.8$, $p = 0.01$; vertical; $F_{5,60} = 55.8$, $p < 0.001$). Overall, orang-utan sleep posture was characterized by the average position of dorsal (20.5%), ventral (8.6%), right (31.5%), left (33.2%) and vertical position (6.2%) ($N = 21$). Interobserver reliability of infrared recording was established by an independent scorer. For each epoch and sleep category, an agreement of 81% was achieved for Azy, resulting in a significant reliability coefficient of $r = 0.56$ ($N = 241$, $p < 0.001$). For Lucy, an agreement of 89% was achieved, resulting in a significant reliability coefficient of $r = 0.75$ ($N = 241$, $p < 0.001$).

On average, orang-utans built sleeping platforms with multiple layers and materials (SPCI average = 2.15, SD = 1.15, $N = 68$). Of the sleep architecture measures, time spent in the behavioural state of awake was significantly affected by sleeping platform quality (measured by the SPCI): $r = -0.26$ ($N = 66$, $p = 0.03$), whereas NREM ($r = 0.06$, $N = 54$, $p = 0.64$) and REM ($r = -0.18$, $N = 54$, $p = 0.20$) were not. In addition, the SPCI proved significantly correlated with: sleep fragmentation ($r = -0.68$, $N = 59$, $p < 0.01$), arousability ($r = -0.59$, $N = 66$, $p < 0.01$), and approached signif-

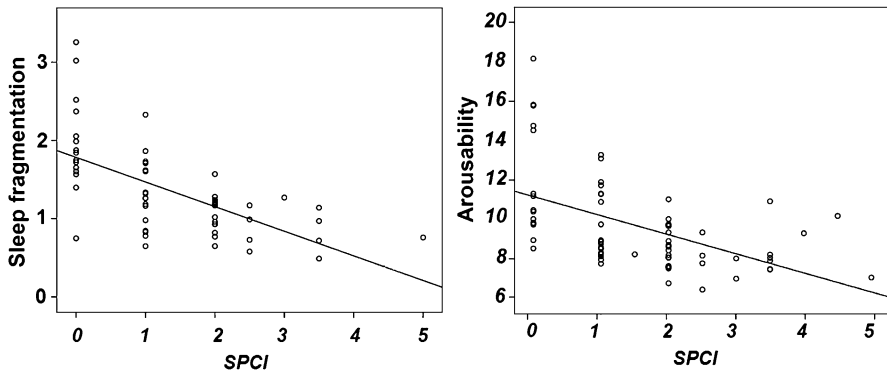


Figure 4. There is a significant negative linear correlation between the sleeping platform complexity index (SPCI) and sleep fragmentation (the number of awakenings per hour during a sleep session; individuals $N = 5$, nights $N = 61$). In addition, there is a significant negative linear correlation between SPCI and arousability (the number of subject movements exhibited per hour during a sleep session; $N = 5$, nights $N = 61$).

ificance for sleep quality ($r = 0.22$, $N = 66$, $p = 0.08$). SPCI significantly correlated with: sleep fragmentation ($r = -0.74$, $N = 33$, $p < 0.01$), arousability ($r = -0.68$, $N = 37$, $p < 0.01$; see Figure 4), while sleep quality was not significant ($r = 0.26$, $N = 37$, $p = 0.12$).

4. Discussion

With the addition of orang-utan sleep quotas, the sleep architectures of 21 non-human primates have been quantified (Table 3). Orang-utans in this study slept an average of 9.11 h per night which is within the chimpanzee range reported by unrestrained studies (Videan, 2006), but it is less than previous reports which used polysomnography to generate chimpanzee data (Kripke & Bert, 1968; Freemon et al., 1969; McNew et al., 1971; Balzamo et al., 1972; McNew, 1972). These early studies included infants and used restraints to perform polysomnography. The discrepancies in chimpanzee data illustrate the need to gather sleep quota data on chimpanzees using non-invasive methods such as the infrared videography used in this study. Although the sleep duration exhibited by orang-utans in this study was longer than western human volunteers studied in controlled environments, the value falls within the range of durations reported for aboriginal populations (7–10 h) of New Guinea and South America (Siegmund et al., 1998; Reimao et al., 2000).

Table 3.

All primate species which have had average sleep quotas recorded.

Species	Total sleep (h)	REM duration (h)	NREM duration (h)	REM (%)	NREM (%)
<i>Aotus trivigatus</i> ^a	17.0	1.82	15.15	0.11	0.89
<i>Callithrix jacchus</i> ^a	9.5	1.61	7.90	0.17	0.83
<i>Chlorocebus aethiops</i> ^a	10.1	0.65	9.44	0.06	0.93
<i>Erythrocebus patas</i> ^a	10.9	0.86	9.99	0.08	0.92
<i>Eulemur macaco</i>	9.4			0.00	0.00
<i>Eulemur mongoz</i> ^a	11.9	0.72	11.16	0.06	0.94
<i>Homo sapiens</i> ^a	8.5	2.10	6.37	0.25	0.75
<i>Macaca arctoides</i> ^a	9.0	1.38	7.65	0.15	0.85
<i>Macaca mulatta</i> ^a	10.2	2.05	8.19	0.20	0.80
<i>Macaca nemestrina</i> ^a	14	0.92	13.00	0.07	0.93
<i>Macaca radiata</i> ^a	9.1	1.05	8.06	1.15	0.89
<i>Macaca sylvanus</i> ^a	11.7	1.07	10.7	0.09	0.91
<i>Microcebus murinus</i> ^a	15.4	0.99	14.4	0.06	0.94
<i>Pan troglodytes</i> ^a	11.5	2.06	9.46	0.18	0.82
<i>Papio anubis</i> ^a	9.2	1.00	8.20	0.11	0.89
<i>Papio papio</i> ^a	10.1	1.06	9.00	0.10	0.89
<i>Perodicticus potto</i>	11.0			0.00	0.00
<i>Phaner furcifer</i>	11.5			0.00	0.00
<i>Pongo</i> spp.	9.11	1.11	8.00	0.13	0.87
<i>Saguinus oedipus</i>	13.2			0.00	0.00
<i>Saimiri sciureus</i> ^a	9.7	1.77	7.80	0.18	0.80
<i>Theropithecus gelada</i>	10.9			0.00	0.00

Blank cells indicate that no data are available. Table amended from McNamara et al. (2008) and Nunn et al. (2010).

^aBased on EEG data.

Around sunset, individuals locate a sleep location and gather bed materials (see methods for detail on materials) to manufacture a sleeping platform. Interestingly, subjects choose idiosyncratic sleep locations and rarely deviated from these areas throughout the study. Although the skill level of bed construction varies across individuals, all orang-utans in this study built at minimum a basic bed (one layer of hay or a single sheet of cardboard) while some (e.g., Azy invested energy and time, ranging from 5 to 45 min) manufactured a bed with multiple layers of materials in addition to using blankets to cover the body through the night.

Captive orang-utans' nighttime behaviour is not characterized by a continuous sleeping bout. Awakenings occur on average 11 times per night and

activities during these times include vigilance behaviours, vocalizations, social grooming, and on rare occasions, changes in sleeping location. Sleeping postures varied by individual, with Azy preferring to sleep on his left side whereas Lucy preferred her right; individuals rarely slept on their ventral side. Individuals within the enclosure did not display synchrony during all nocturnal awakenings (focal subjects awakened at times when no other individuals were awake). Differences in arousability levels such as this are consistent with the dynamic nighttime behaviour observed in captive chimpanzees (Videan, 2006) and traditional human populations (Worthman & Melby, 2002; Worthman, 2008). Finally, no sex differences in sleep architecture were observed for either sex or age; although, a possible age effect may be evinced from the observation that the single adolescent proved to have more motor activity at night when compared to older individuals.

The use of infrared videography as a means of observing and recording sleep variables in non-human primates deserves scrutiny. A weakness of this method is that it cannot differentiate between NREM stages. Also, periods of quiet wakefulness may be classified as sleep (a weakness also shared by actigraphic methods to differentiate sleep states) which lead to an underestimation of sleep latency and an overestimation of total sleep time (McCall & McCall, 2012). We advocate a more flexible view that data such as those presented in this study are valuable additions to sleep research in primates. Sleep researchers currently lack viable, non-invasive options for performing EEG (electroencephalography) on large-bodied great apes, but as more workers generate data such as in this study, interspecies comparison will become more widespread. Since the present study appears to be the first report on the sleep architecture of orang-utans, the mean total sleep time, REM/NREM length values for this species awaits further confirmation. Additional studies should be conducted with more subjects across different captive environments to more rigorously examine orang-utan sleep architecture. Furthermore, as actigraphic technology advances and equipment becomes less intrusive, researchers that use entrainment methods to habituate and incentivize large-bodied great apes to voluntarily adorn actigraphic monitors or introduce sleeping platforms with fine scale sensors which could capture actigraphy would be able to validate and improve upon the videographic method. Finally, it should be noted that although the sample recorded in this study is only five individuals, which may not be statistically representative of *Pongo*, it reveals the capability of the species (Healey, 2009).

Overall, the predictions set forth in this study — that an increase in sleeping platform complexity would have a positive effect on sleep architecture and sleep quality — were supported. Greater sleeping platform complexity correlated with reduced time spent awake throughout a sleeping bout; although, there was no change in time spent in NREM or REM. Furthermore, measures of sleep depth and quality were positively affected by sleeping platform comfort. For example, arousability (the number of movements an individual experienced per hour) and sleep fragmentation (the number of times an individual woke up per hour) reduced with greater complexity associated with sleeping platforms.

Fruth & Hohmann (1996) speculated that with the advent of Miocene apes manufacturing complex sleeping platforms to create more comfortable sleeping environments, a ‘great leap forward’ in cognitive abilities also followed. Although they postulated longer behavioural states of REM and/or NREM, it has been established that these categories are highly variable in mammals (Siegel, 2008), as well as primates (Nunn et al., 2010). It is likely the interaction between NREM and REM sleep in memory consolidation is a complex two-step model (Karni & Sagi, 1991; Gais et al., 2000), of which we do not yet have a complete understanding (Walker, 2009). Great apes share with humans theory of mind, tool use and several aspects of language recognition and use; it may be that these shared cognitive competencies require a similar sleep architecture or basic threshold of sleep quality to achieve. There is substantial experimental evidence to support cognition and memory consolidation as central functions of sleep (Kavanau, 1994, 1997; Peigneux et al., 2001; Hobson & Pace-Schott, 2002; Walker & Stickgold, 2006; Walker, 2009). Sleep quality may be of great importance to brain function and cognition (Preston et al., 2009), yet for apes this claim cannot be assessed until sufficient data have been accumulated. Although humans exhibit REM heavy sleep architecture within the Hominidae, until further great ape data is generated on the relationship between cognition and sleep quality, we cannot conclude with certainty that the aforementioned cognitive benefits do not exist in other great apes. For example, it has been illustrated that the great apes show cognitive task improvement after a night’s sleep (Martin-Ordas & Call, 2011); presumably this is due to some form of memory consolidation (facilitated by sleep) of the cognitive task.

In conclusion, we have quantified the sleep architecture of orang-utans using infrared videography to score behavioural signatures associated with

sleep states. These data add to the growing list of primate sleep architectures. Furthermore, this study illustrated that greater levels of complexity associated with sleeping platforms, decreases sleep arousability in captive orang-utans and, therefore, we suggest augments comfort during sleep. Evolutionarily, it may be that great apes make sleeping platforms out of necessity, given the dangers of sleeping high in the canopy with their massive bodies (Baldwin et al., 1981; Samson, 2012); additionally, 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 all primates could benefit from equally, but not all primates can accomplish. Finally, we do not yet know why it is that great apes construct sleeping platforms. It will be essential to generate sleep quota data on the remaining apes (*Hylobates*, *Gorilla* and *Pan paniscus*), as well as sleep quality and behavioural data in large bodied monkeys (e.g., *Papio*), relative to next-day cognitive performance, to gain a fuller understanding of the evolution of hominoid sleep and cognition.

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References

- Altmann, J. (1974). Observational study of behaviour: sampling methods. — *Behaviour* 49: 227-266.
- Ancoli-Israel, S., Cole, R., Alessi, C., Chambers, M., Moorcroft, W. & Pollak, C.P. (2003). The role of actigraphy in the study of sleep and circadian rhythms. — *Sleep* 26: 342-392.
- Anderson, J.R. (1998). Sleep, sleeping sites, and sleep-related activities: awakening to their significance. — *Am. J. Primatol.* 46: 63-75.

- Baldwin, P.J., Sabater Pi, J., McGrew, W.C. & Tutin, C.E.G. (1981). Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). — *Primates* 22: 474-486.
- Balzamo, E., Bradley, R.J. & Rhodes, J.M. (1972). Sleep ontogeny in the chimpanzee: from two months to forty-one months. — *Electroencephalogr. Clin. Neurol.* 33: 47-60.
- Balzamo, E., Van Beers, P. & Lagarde, D. (1998). Scoring of sleep and wakefulness by behavioral analysis from video recordings in rhesus monkeys: comparison with conventional EEG analysis. — *Electroencephalogr. Clin. Neurol.* 106: 206-212.
- Campbell, S.S. & Tobler, I. (1984). Animal sleep: a review of sleep duration across phylogeny. — *Neurosci. Biobehav. Rev.* 8: 269-300.
- Capellini, I., McNamara, P., Preston, B.T., Nunn, C.L. & Barton, R.A. (2009). Does sleep play a role in memory consolidation? A comparative test. — *PLoS ONE* 4: e4609.
- Freemon, F.R., McNew, J.J. & Adey, W.R. (1969). Sleep of unrestrained chimpanzee — cortical and subcortical recordings. — *Exp. Neurol.* 25: 129-137.
- Fruth, B. & Hohmann, G. (1996). Nest building behaviour in the great apes: the great leap forward? — In: *Great ape societies* (Marchant, L.F. & Nishida, T., eds). Cambridge University Press, Cambridge, p. 225-240.
- Gais, S., Pilihal, W., Wagner, U. & Born, J. (2000). Early sleep triggers memory for early visual discrimination skills. — *Nature Neurosci.* 3: 1335-1339.
- Goodall, J.M. (1962). Nest building behavior in the free ranging chimpanzee. — *Ann. NY Acad. Sci.* 102: 455-467.
- Goodall, J.M. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. — *Anim. Behav. Monogr.* 1: 161-311.
- Groves, C.P. (2001). *Primate taxonomy*. — Smithsonian Institution Press, Washington, DC.
- Healey, J.F. (2009). *Statistics: a tool for social research*, 8th edn. — Thomson/Wadsworth, Belmont, CA.
- Hobson, J.A. & Pace-Schott, E.F. (2002). The cognitive neuroscience of sleep: neuronal systems, consciousness and learning. — *Nature Rev. Neurosci.* 3: 679-693.
- Karni, A. & Sagi, D. (1991). Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. — *Proc. Natl. Acad. Sci. USA* 88: 4966-4970.
- Kavanau, J.L. (1994). Sleep and dynamic stabilization of neural circuitry — a review and synthesis. — *Behav. Brain Res.* 63: 111-126.
- Kavanau, J.L. (1997). Origin and evolution of sleep: roles of vision and endothermy. — *Brain Res. Bull.* 42: 245-264.
- Kripke, D.F. & Bert, J. (1968). Techniques for telemetry of chimpanzee sleep electroencephalogram. — *J. Appl. Physiol.* 25: 461-462.
- Kripke, D.F., Reite, M.L., Pegram, G.V., Stephens, L.M. & Lewis, O.F. (1968). Nocturnal sleep in Rhesus monkeys. — *Electroencephalogr. Clin. Neurol.* 24: 581-586.
- Krueger, J.M., Rector, D.M., Roy, S., Van Dongen, H.P.A., Belenky, G. & Panksepp, J. (2008). Sleep as a fundamental property of neuronal assemblies. — *Nature Rev. Neurosci.* 9: 910-919.

- Lesku, J.A., Roth, T.C., Rattenborg, N.C., Amlaner, C.J. & Lima, S.L. (2009). History and future of comparative analyses in sleep research. — *Neurosci. Biobehav. Rev.* 33: 1024-1036.
- Martin-Ordas, G. & Call, J. (2011). Memory processing in great apes: the effect of time and sleep. — *Biol. Lett.* 7: 829-832.
- McCall, C. & McCall, W.V. (2012). Comparison of actigraphy with polysomnography and sleep logs in depressed insomniacs. — *J. Sleep Res.* 21: 122-127.
- McNamara, P., Capellini, I., Harris, E., Nunn, C.L., Barton, R.A. & Preston, B.T. (2008). The phylogeny of sleep database: a new resource for sleep scientists. — *Open Sleep J.* 1: 11-14.
- McNamara, P., Barton, R.A. & Nunn, C.L. (2010). Evolution of sleep: phylogenetic and functional perspectives. — Cambridge University Press, Cambridge.
- McNew, J.J. (1972). Sleep-wake cycle of an unrestrained isolated chimpanzee under entrained and free running conditions. — *Aerospace Med.* 43: 155.
- McNew, J.J., Howe, R.C. & Ross, A.W. (1971). The sleep cycle and subcortical-cortical EEG relations in the unrestrained chimpanzee. — *Electroencephalogr. Clin. Neurol.* 30: 489-503.
- Mizuno, Y., Takeshita, H. & Matsuzawa, T. (2006). Behavior of infant chimpanzees during the night in the first 4 months of life: smiling and suckling in relation to behavioral state. — *Infancy* 9: 215-324.
- Morimura, N., Fujisawa, M., Mori, Y. & Teramoto, M. (2012). Environmental influences on sleep behavior in captive male chimpanzees (*Pan troglodytes*). — *Int. J. Primatol.* 33: 822-829.
- Munozdelgado, J. (1995). Behavioral characterization of sleep in stump-tail Macaques (*Macaca artoidea*) in exterior captivity by means of high-sensitivity videorecording. — *Am. J. Primatol.* 36: 245-249.
- Nunn, C.L., McNamara, P., Capellini, I., Preston, B.T. & Barton, R.A. (2010). Primate sleep in phylogenetic perspective. — In: Evolution and sleep: phylogenetic and functional perspectives (McNamara, P., Barton, R.A. & Nunn, C.L., eds). Cambridge University Press, New York, NY, p. 123-144.
- Peigneux, P., Laureys, S., Delbeuck, X. & Maquet, P. (2001). Sleeping brain, learning brain: the role of sleep for memory systems. — *NeuroReport* 12: A111-A124.
- Preston, B., Capellini, I., McNamara, P., Barton, R.A. & Nunn, C. (2009). Parasite resistance and the adaptive significance of sleep. — *BMC Evol. Biol.* 9: 7.
- Reimao, R., Souza, J.C., Gaudioso, C.E.V., Guerra, H.D., Alves, A.D., Oliveira, J.C.F. & Silverio, D.C.G. (2000). Nocturnal sleep pattern in native Brazilian Terena adults. — *Arq. Neuro-Psiquiatr.* 58: 233-238.
- Samson, D.R. (2012). The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. — *Primates* 53: 357-364.
- Shumaker, R.W., Wich, S.A. & Perkins, L. (2008). Reproductive life history traits of female orangutans (*Pongo* spp.). — In: Primate reproductive aging: cross-taxon perspectives (Atsalis, S. & Margulis, S., eds). Karger, Basel, p.147-161.

- Shumaker, R.W., Walkup, K.R. & Beck, B.B. (2011). Animal tool behavior: the use and manufacture of tools by animals. — Johns Hopkins University Press, Baltimore, MD.
- Siegel, J.M. (2008). Do all animals sleep? — Trends Neurosci. 31: 208-213.
- Siegmund, R., Tittel, M. & Schiefenhovel, W. (1998). Activity monitoring of the inhabitants in Tauwema, a traditional melanesian village: rest/activity behaviour of Trobriand islanders (Papua New Guinea). — Biol. Rhythm Res. 29: 49-59.
- Sri Kantha, S. & Suzuki, J. (2006). Sleep quantitation in common marmoset, cotton top tamarin and squirrel monkey by non-invasive actigraphy. — Comp. Biochem. Physiol. 144: 203-210.
- Tobler, I. (2005). Phylogeny of sleep regulation. — In: Principles and practice of sleep medicine (Kryger, M.H., Roth, T. & Dement, W.C., eds). Elsevier/Saunders, Philadelphia, PA, p. 77-91.
- Videan, E.N. (2006). Sleep in captive chimpanzee (*Pan troglodytes*): the effects of individual and environmental factors on sleep duration and quality. — Behav. Brain Res. 169: 187-192.
- Walker, M.P. (2009). The role of sleep in cognition and emotion. — Ann. NY Acad. Sci. 1156: 168-197.
- Walker, M.P. & Stickgold, R. (2006). Sleep, memory, and plasticity. — Annu. Rev. Psychol. 57: 139-166.
- Weitzman, E.D. (1965). Cyclic activity in Sleep of *Macaca mulatta*. — Arch. Neurol. 12: 463.
- Worthman, C.M. (ed.) (2008). After dark: the evolutionary ecology of human sleep. — Oxford University Press, Oxford.
- Worthman, C.M. & Melby, M.K. (eds) (2002). Toward a comparative developmental ecology of human sleep. — Cambridge University Press, Cambridge, p. 69-117.
- Zepelin, H. (ed.) (1989). Mammalian sleep. — W.B. Saunders, Philadelphia, PA.
- Zepelin, H., Siegel, J.M. & Tobler, I. (2005). Mammalian sleep. — In: Principles and practice of sleep medicine (Kryger, M.H., Roth, T. & Dement, W.C., eds). Elsevier/Saunders, Philadelphia, PA, p. 91-100.
- Zhdanova, I.V., Geiger, D.A., Schwagerl, A.L., Leclair, O.U., Killiany, R., Taylor, J.A. & Madras, B.K. (2002). Melatonin promotes sleep in three species of diurnal nonhuman primates. — Physiol. Behav. 75: 523-529.