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Pre-Sleep and Sleeping Platform Construction Behavior in Captive Orangutans (*Pongo* spp.): Implications for Ape Health and Welfare

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Key Words
Orangutan · Sleep · Sleeping platform · Nest · Animal welfare · Ethology

Abstract
The nightly construction of a 'nest' or sleeping platform is a behavior that has been observed in every wild great ape population studied, yet in captivity, few analyses have been performed on sleep related behavior. Here, we report on such behavior in three female and two male captive orangutans (*Pongo* spp.), in a natural light setting, at the Indianapolis Zoo. Behavioral samples were generated, using infrared cameras for a total of 47 nights (136.25 h), in summer (n = 25) and winter (n = 22) periods. To characterize sleep behaviors, we used all-occurrence sampling to generate platform construction episodes (n = 217). Orangutans used a total of 2.4 (SD = 1.2) techniques and 7.5 (SD = 6.3) actions to construct a sleeping platform; they spent 10.1 min (SD – 9.9 min) making the platform and showed a 77% preference for ground (vs. elevated) sleep sites. Comparisons between summer and winter platform construction showed winter start times (17:12 h) to be significantly earlier and longer in duration than summer start times (17:56 h). Orangutans should be provisioned with seasonally appropriate, high quality materials suitable for construction of sleeping platforms to increase sleep quality and improve animal health and welfare.

Introduction

Great apes, including humans, spend one-third of their lives asleep in bed-like structures. Sleeping platforms have been shown to enhance sleep quality in captive orangutans (*Pongo* spp.) (Samson and Shumaker, 2013) and improve post-sleep cog-

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nition (Martin-Ordas and Call, 2011; Shumaker et al., 2014). Research on primate sleep has shown that it has an important association with behavior, ecology and health (Anderson 1998; Zepelin et al. 2005; Capellini et al., 2009; Lesku et al., 2009), which inform our understanding of the general evolution of sleep patterns and sleep disorders (Nunn et al., 2010). Furthermore, for humans, sleep quality has been linked to a host of health and cognitive related measures. Great apes, including humans, are unique in that we are the only primates that universally build complex and secure substrates on which to sleep. Therefore, the study of orangutan sleep behaviors may be essential to unravel the function and benefits of high quality sleep environments to primate health.

Wild orangutan sleeping platforms, when compared to those of African apes, have been described as sturdier, more elaborate and more complex (Sabater Pi et al., 1997; Ancrenaz et al., 2004; van Casteren et al., 2012). Orangutans build sleeping platforms in tall trees with trunks of a large diameter at breast height (DBH), as they build them at greater heights than African apes do; this has been suggested to be related to abiotic (i.e., wind) and biotic (i.e., elephants pushing over trees) forces rendering smaller trees riskier substrates for a nightly sleep period (Ancrenaz et al., 2004). Relative to gorillas and chimpanzees, Sabah orangutans more often build night sleeping platforms in fruit-cropping trees (Ancrenaz et al., 2004). Day sleeping platforms are similar in function for chimpanzees, bonobos and orangutans and serve as quickly constructed rest points throughout the day (Brownlow et al. 2001; Ancrenaz et al., 2004). Mature orangutans (unflanged and flanged males and females) have been observed making larger sleeping platforms than immatures (Rayadin and Saitoh, 2009). Both flanged and immature males frequently make open, exposed sleeping platforms, whereas parous adult females prefer sheltered, closed sleep sites (Rayadin and Saitoh 2009).

An important difference between orangutan sleeping platforms and those of the African ape species is in inferred complexity, evinced by longer decay rates [Bernstein, 1967; Tutin et al., 1995; Blom et al., 2001; Ancrenaz et al., 2004]. Orangutan sleeping platforms share with the African apes the characteristic of being constructed on a lateral branch, where the orangutan will bend frame-supporting branches inward into a central point, where further twisting will result in a weaved and locked mattress [Goodall, 1962; Russon, 2007; Stewart et al., 2007; Stewart, 2011; van Casteren et al., 2012]. Yet, orangutans often exhibit unique sleep site manufacture behaviors [Van Schaik et al., 2003], such as roof construction above the sleep site or preplucked leaves brought to the site from as far as 50 m away [Russon, 2007].

Despite the importance of nest manufacture and sleep-related behaviors in the wild, in captivity, few systematic analyses have been performed on sleeping platform construction or pre-sleep behavior in the great apes. Bernstein [1962, 1967, 1969] was the first to observe and describe sleeping platform construction in a captive environment. He observed the reaction of wild-born chimpanzees to the introduction of sleeping materials. The wild-born chimpanzees (which had been captured in adolescence) were observed to make beds, while the captive-born chimpanzees did not. This research suggested that sleeping platform construction was a cultural or learned behavior.

Videan [2005, 2006] built upon earlier attempts by empirically showing that sleeping platform construction is a socially learned behavior in chimpanzees. By recording sleeping platform constructions, she found that mother-reared individuals

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built sleeping platforms significantly more often than nursery-reared ones, and wild-born individuals built sleeping platforms significantly more often than captive-born individuals. She also observed that the most advanced technique ‘bend and weave’ (interweaving foliage to create sturdy, interconnected sections of the sleeping platform) was most common among wild-born and mother-reared chimpanzees.

Lukas et al. [2003] provided a systematic characterization of sleeping platform construction among captive gorillas. The study revealed that gorillas preferred elevated rather than ground platforms; there were no significant sex, age class or rearing history differences in sleeping platform construction technique, nor in time spent on a sleeping platform, or platform location preference. However, the gorillas did spend significantly more time constructing sleeping platforms (on elevated sleep sites) in the winter compared to the summer. This behavior was interpreted as a thermoregulatory response to colder, winter temperatures. A study analyzing orangutan substrates [Renner, 2012] observed a similar frequency of time spent on an arboreal platform (77.2% of observed scans), which was similar to results found by Lukas et al. [2003] (72% of observed scans).

Systematic behavioral and mechanical studies on wild orangutan sleeping platform construction have increased our understanding of wild great ape sleep ecology [Russon, 2007; Rayadin and Saitoh, 2009; van Casteren et al., 2012, 2013], yet no such counterpart for captive studies has been published to date. The goal of this study was to provide a more systematic characterization of captive ape sleep-related behavior by documenting pre-sleep (i.e. activity preceding sleep onset) and sleeping platform construction behavior in orangutans. Specifically, the purpose of this study was to describe nighttime sleep behavior, quantify the motor patterns of sleeping platform construction and compare seasonal differences in bed building. An ultimate goal of this work is to improve animal welfare by disseminating critical management practices to institutions that house captive large-bodied primates, such as zoos or research facilities.

We test the hypothesis that there will be seasonal differences in sleep-related behavior. Given exposure to natural lighting, we predict that individuals will construct sleeping platforms at earlier times in winter. Additionally, we predict that individuals will allocate more time to sleeping platform construction in the winter season. Although the sample size of individuals is small, it is broadly distributed across sex and developmental status and at a minimum these data reveal the capability of the species [Healey, 2009]. Therefore this research serves as foundational work for future research, which is needed to confirm the interpretations of this study.

Materials and Methods

Animals

Focal subjects (total n = 5) were 3 females, Katy (aged 24), Knobi (33) and Lucy (28), and 2 males, Azy (35) and Rocky (8; see table 1 for the history of the individuals in this study). These were the only orangutan subjects available for study; given the cost of housing large-bodied hominoids and the endangered status of orangutans, sample sizes such as the one in this work are common; age was not included as an independent variable given Rocky’s near adult status. None of the subjects was geriatric, as the life span in the wild for orangutans is approximately 60 years [Shumaker et al., 2008]. All subjects were hybrids of Bornean and Sumatran *Pongo* species; there are few substantive differences in behavioral ecology between these two species. Rocky, Katy and

Table 1. Demography of orangutan subjects, ranked by age class, sex and rearing history

Subject	Year born	Age class	Sex	Rearing history
Azy	1977	adult	male	AZA-born; extremely well socialized
Rocky	2004	adolescent	male	Privately owned; part of entertainment industry
Katy	1988	adult	female	Privately owned; part of entertainment industry
Knobi	1979	adult	female	AZA-born; well socialized
Lucy	1984	adult	female	Privately owned; part of entertainment industry

AZA = Association of Zoos and Aquariums.

Lucy were privately owned and part of the entertainment industry prior to moving into the Association of Zoos and Aquariums (AZA) community, specific information about their personal histories is therefore limited [Shumaker, pers. commun.]. The individuals from the entertainment industry were hand-reared by humans, none having any exposure to its mother during early growth and development. Specifically, Katy lived in a static environment with 2 other adults, in a nonenriched enclosure. She had few objects to manipulate and little to no exposure to sleeping platform materials (sometimes small quantities of newspaper). Rocky was removed from his mother less than 24 h after birth and hand-reared by humans. For the first 3 years of his life he was enculturated with exposure to human objects and materials. After the age of 3, he was held in a small outdoor enclosure without access to other orangutans or enrichment materials until being introduced into the AZA community. Lucy was hand-reared by humans and had limited socialization for most of her adult life; she was one of Katy's cohorts. She also had limited exposure to enrichment and no access to sleeping platform materials. Knobi was hand-reared by humans (and had inconsistent access to sleeping platform materials during this time) until her introduction into the AZA community where she began socialization with Azy at an early age. Azy has always lived within the AZA community, and has a well-documented biography and rich social experience (which includes exposure to conspecifics and human handlers). The primary differences between 'entertainment' and 'AZA' subjects are (1) exposure to enrichment and sleeping platform materials and (2) opportunity for social learning. The subjects remained in good health throughout the study with the exception of Knobi who had a history of reproductive health problems (she was diagnosed with adenomyosis). In January 2012 she underwent a hysterectomy as part of a corrective surgical procedure. During the procedure and during a period of convalescence (lasting 1 week) she was not targeted for data generation.

Subjects and Housing

The Indianapolis Zoo is accredited by the AZA and has a committed basic and applied scientific research program. Orangutan subjects were housed in interconnected indoor and outdoor enclosures, and had regular access to all areas throughout the spring, summer and fall seasons. The outdoor enclosure was inaccessible during the period of the winter months when external temperatures fell below 10°C (above this temperature they had access to the outdoor enclosure). The indoor enclosure contained laminate raised platforms located 1 m off the floor; these are the elevated sleeping substrates used in tests between ground versus raised platforms. Subjects had access to naturally (brush, lianas, straw, etc.) and artificially (play toys, rope, hammock, cardboard, etc.) enriched environments. The indoor enclosure was set at a constant temperature of

Table 2. Ethogram for sleep-related behaviors associated with sleep preparation and sleeping platform material and construction

'Appropriate' behavior	'Inappropriate' behavior	Sleeping platform construction technique
Construct: construction and manipulation of sleeping area	Display: takes hold of material, shakes it with jerky movements	Arrange: positions material circularly or semicircularly around self
Inspect: eyes, head or whole body is oriented toward the material	Eat: consumes the material	Flatten: crushes or compresses material using hands and/or feet
Lie on: torso is pronograde and in contact with the sleeping material	Play: nonaggressive action involving the material and includes a play face	Alter form: includes crumple, wad, rip, break, etc.
Sit on: torso is orthograde, and ischia are in contact with sleeping material	None: no action toward material	Outside-in: takes material from outside edge of bed and places it on inside edge
Stand on: torso is orthograde, and feet and/or hands are in contact with material	Other: any other action directed towards material	Bend-weave: bending portions of material and interlacing them together Tuck: pushes or slips material underneath self Use feet: uses feet as a brace or to hold item(s) in place Cover: places material over self

Amended from Videan [2005].

23.3°C. Natural lighting was the primary source of light for the group and was accessible by way of windows and access to the outdoor enclosure; in addition, low lux lights were manually turned on by the keepers at 7:30 h and turned off at 16:30 h. During the summer baseline, Indianapolis' monthly average temperature high and low were 24.5 and 13.3°C and during the winter baseline 7.6 and –1.9°C, respectively. The average precipitation in summer was 104.8 mm and in winter 79.4 mm per month.

Objects

Bedding materials (e.g. straw, cardboard, shredded and full sheets of newspaper, sheets and blankets) were provided for the orangutans to build sleeping platforms (before the keepers left at 16:30 h); the materials provided were the same in all seasons. Each night, straw was distributed throughout the enclosure in sufficient quantity for use by all individuals. Several cardboard sheets (of approx. 1 m^2) were distributed. Full sheets of newspaper and construction paper were distributed. Some paper was shredded to complement the straw. Several twin size mattress bed sheets, blankets and comforters were included for use; all materials were evenly distributed. Prior to this study, the predominant material provided to the subjects was straw, with the occasional addition of sheets.

Data Collection

This study was conducted over 15 months during October 2011 to January 2013. To characterize species-specific sleep behavior and evaluate the effect of season on pre-sleep behavior,

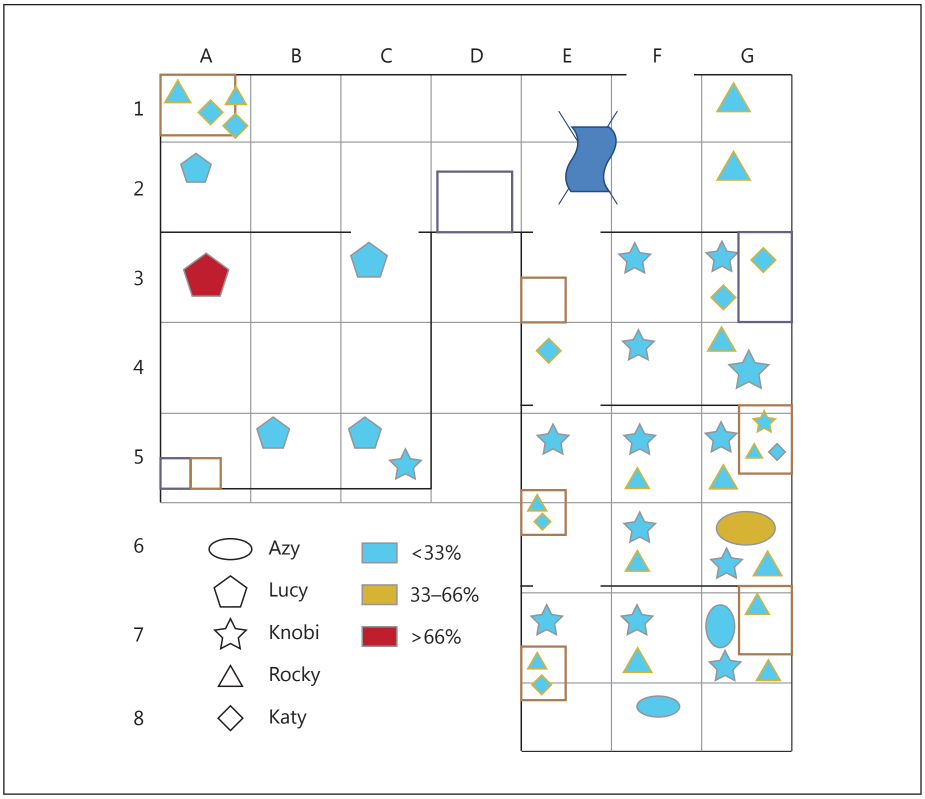

Fig. 1. The orangutan indoor enclosure (each square in the grid is approx. 1.5 m^2); symbols and colors illustrate subject sleeping site preference distributed throughout the enclosure. Purple rectangle/square symbols represent 2-meter raised platforms; brown rectangle/square symbols represent 1-meter raised platforms. The symbol in quadrant E2 is a hammock.

Table 3. Sleeping platform complexity index

	Score
Cardboard	0.5
Paper	0.5
Straw	1
Sheet	1
Pillow	1
Blanket	1.5
Camp foam	1.5
Comforter	2
Memory foam mattress	2.5

Materials used in sleeping platform construction were summed each night per individual to assign an overall complexity score (for more detail, see Samson and Shumaker [2013]).

daily behavioral samples were generated in summer (n = 25) and in winter (n = 22) for a total of 47 complete nights (136.25 h) where the entire group was observed [Altmann, 1974]. Because behavioral samples were generated via a remote-control, rotatable camera (AXIS Q6032-E Network Camera), there was no limit to the duration of time we were able to observe subjects. The only limitation was in rare instances when individuals were outside the line of sight (in which case data were omitted for that specific scan sample). Sampling methods included 3 elements: (1) *group scan sampling* of substrate, posture and behavior at 5-min intervals for individuals within the focal group from starting time (16:00 h) to the time the last individual adopted a final resting position for the night; (2) *all-occurrence sampling* of platform construction behaviors generated for individuals building within the line of sight (total n = 217) which included 'appropriate' behavior, 'inappropriate' behavior and sleeping platform construction techniques (table 2); (3) *one-time scans* of location and substrate for all subjects at the end of each data collection session (total instances n = 422). Each subject's location was plotted on a map of the holding facility (fig. 1), and the substrate was recorded.

A sleeping platform was defined as a structure of straw or other manipulatable materials (table 3) constructed by orangutans for sleeping on. For a structure to be labeled a sleeping platform, an orangutan exhibiting one or more defined platform construction behaviors must have been observed. Categories for substrate, posture and behavior during the sleeping platform construction contained exhaustive and mutually exclusive behaviors (table 4) recorded in previous studies [Lukas et al., 2003; Videan, 2005].

The seasonal study occurred in two phases: summer and winter. Since the enclosure had several large, skylight windows (providing sufficient natural lighting for photic entrainment), the two phases differed in the hours of sunlight. The solstices were used as threshold dates to define summer and winter phases (summer: March 20 to September 22; winter: September 23 to March 19). Dates between March 20 and September 22 were classified as 'summer', whereas dates between September 23 and March 19 were classified as 'winter' dates. The summer solstice had a day length of 14 h 59 min (range: from 6:16 to 21:16 h) versus the winter solstice of 9 h 21 min (range: from 8:02 to 17:24 h).

Data Analysis

Descriptive statistics were generated to characterize an average sleeping platform construction period in captive orangutans. In addition, χ^2 analysis was used to test preference between elevated and ground platform location. To explore the effect of season on sleep behavior, we used a multivariate analysis of variance (MANOVA) on the following variables, taking into account sex and rearing history: total observation time from start (14:00 h) to sleep, total proportion of observation time spent constructing a sleeping platform, starting time for sleeping platform construction, total time spent constructing the sleeping platform, sleeping platform complexity, platform location preference (scored as 1 for raised platform and 0 for ground platform), total number of techniques used in construction and total frequency of actions used in construction. All reported errors are standard deviations. Statistical tests were conducted using IBM SPSS 22, and all tests were 2-tailed with significance set at the 0.05 level. The data collection protocol was reviewed and approved by the Indiana University Institutional Animal Care and Use Committees.

Results

On average, captive orangutans used a total of 2.4 (SD = 1.2) techniques and 7.5 (SD = 6.3) actions to construct a sleeping platform (table 4). The most frequent technique, 'arrange', was used 65.7% of the time while constructing a platform; the most frequent posture, used 65.8% of the time, was 'sit on', while play, observed for 10.6% of the time, was the most frequent (non-posture) behavior. The average number of sleeping construction episodes (bouts separated by greater than 10 min, from the moment of last action, were considered separate periods) it took to complete a plat-

Table 4. Averaged orangutan platform construction techniques and associated behaviors (n = 5 subjects)

Platform construction behavior	N	Range (proportion)	Mean	SD
Average number of techniques used in construction		8	2.4	1.2
Total frequency of actions used in construction		36	7.5	6.3
Construction technique, %				
Arrange	217	0–1.0	65.7	24.6
Flatten	213	0–0.67	16.4	16.3
Alter form	217	0–0.67	7.8	13.1
Outside-in weave	217	0–0.15	0.07	1.0
Bend-weave	217	0	0	0
Tuck	217	0–0.33	0.87	3.8
Use feet	217	0–0.50	4.1	8.9
Cover	217	0–1.0	3.5	11.9
Use mouth	217	0–0.33	0.46	2.9
Behavior during construction, %				
Inspect platform	232	0–1.0	31.3	33.6
Lie on	232	0–1.0	27.3	31.3
Sit on	232	0–1.0	65.8	36.5
Stand on	232	0–1.0	12.4	30.4
Display	232	0–0.80	2.6	9.0
Eat	232	0–1.0	1.7	11.8
Play	232	0–1.0	10.6	4.6
None	232	0–0.71	0.3	4.6
Other	232	0–0.05	0.02	0.32

Techniques and behaviors are described as the percentage of time spent exhibiting a technique or behavior of the total time in which the individual was constructing a sleeping platform. N is the number of sleeping platform construction sessions observed.

form's construction was 1.5 (range = 1–3; SD = 0.67). The average start time for platform construction was 17:47 h (range = 16:16 h to 20:54 h; SD = 61 min). The average total time spent constructing sleeping platforms was 10.1 min (range = 1–52 min; SD = 9.9 min). The average sleeping platform complexity index measure was 1.93 (range = 0–6.0; SD = 1.10). Ground sleeping platform frequency for all individuals was 77.3% compared to elevated 22.7% (n = 419; see fig. 2 for individual preference). Finally, individuals were characterized by sleeping site preference (see fig. 1 for individual distribution throughout the enclosure). Individuals idiosyncratically constructed a sleeping platform and slept in their preferred quadrant as follows: Azy, G6 = 45.5%; Lucy, A3 = 83%; Knobi, G4 = 24.7%; Rocky, E6P = 17%, and Katy, G5P = 29.6%.

Regarding elevated versus ground platform preference, χ^2 tests show that for each individual, the observed frequency of chosen sleep site differed significantly from that which was expected (i.e. number of total available sites = 41, number of elevated sites = 8; expected 20% site selection on elevated platforms). Azy selected the

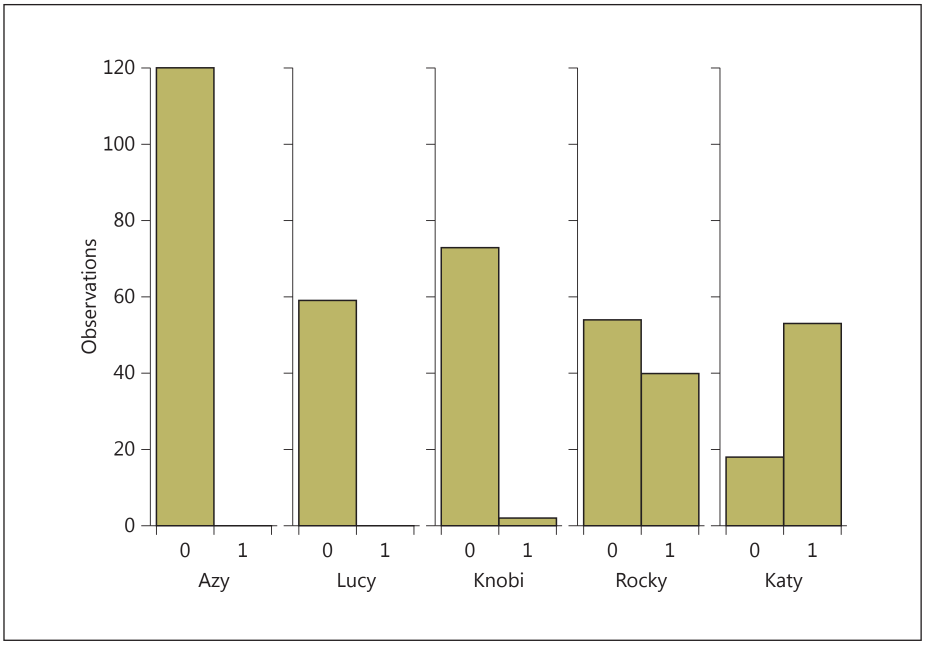

Fig. 2. Individual preference for ground (0) or raised (1) sleeping platform location.

Table 5. Individuals varied in the time invested, technique used and the frequency of object manipulation for sleeping platforms

Dependent variable	Individual	N	Mean	SD
Time spent constructing platform, min	Azy	92	17.3	10.4
	Lucy	21	10.1	9.7
	Knobi	42	3.2	2.2
	Rocky	48	7.3	5.7
	Katy	29	1.7	0.9
Total number of techniques used in platform construction	Azy	92	3.1	1.1
	Lucy	19	2.1	0.9
	Knobi	37	1.8	1.0
	Rocky	47	2.3	1.1
	Katy	28	1.5	0.9
Total number of actions used in platform construction	Azy	90	12.5	5.6
	Lucy	21	6.0	5.4
	Knobi	40	3.9	3.2
	Rocky	51	5.9	5.1
	Katy	31	1.6	1.2

N = Number of sleeping platform construction bouts in which the dependent variable could be measured.

Color version available online

Fig. 3. Example of Azy lying on a newly constructed sleeping platform using a layer of straw, a secondary layer of a sheet and a tertiary layer of paper tucked under the head.

Fig. 4. Example of Knobi lying on a newly constructed sleeping platform (straw only).

ground in 99% of observations ($\chi^2 = 22.6$, d.f. = 1, $p < 0.001$), Lucy selected the ground in 100% ($\chi^2 = 25.0$, d.f. = 1, $p < 0.001$), Knobi selected the ground in 97% ($\chi^2 = 18.06$, d.f. = 1, $p < 0.001$), Rocky selected the ground in 57% ($\chi^2 = 33.06$, d.f. = 1, $p < 0.001$), and Katy showed a preference for elevated sleep sites as she selected the ground in 25% of observations ($\chi^2 = 189.06$, d.f. = 1, $p < 0.001$) (fig. 2). Azy spent the greatest amount of time on platform constructions, performed the widest variety of techniques and manipulated objects with the greatest frequency while constructing a sleeping platform (for examples of individual sleeping platforms constructed, see table 5, fig. 3, 4 and online suppl. videos; see www.karger.com/doi/10.1159/000381056 for all online suppl. material).

Season affected sleeping platform construction behavior. A statistically significant MANOVA effect was obtained (Wilk's $\lambda = 0.578$, $F_{8, 111} = 10.1$, $p < 0.001$). The multivariate effect size was estimated at 0.42, which implies that 42% of the variance in the canonically derived dependent variable was accounted for by season. A series of 1-way ANOVAs on each of the dependent variables was conducted as a follow-up test to the MANOVA, with effect sizes (partial η^2) ranging from a low of 0.002 (total number of techniques) to a high of 0.13 (construction starting time). Seasonal differences were found in sleeping platform construction starting times and total proportion of observed time constructing platforms. The winter was characterized by significantly earlier starting construction times than summer (n = 52, winter mean =

17:12 h, SD = 37 min vs. n = 68, summer mean = 17:56 h, SD = 69 min; $F = 17.8$, $p < 0.001$); in addition, winter was characterized by a greater proportion of observed time constructing sleeping platforms (n = 52, winter mean = 0.11, SD = 0.08 vs. n = 68, summer mean = 0.07, SD = 0.08; $F = 9.6$, $p = 0.002$).

Discussion

Orangutans built sleeping platforms with multiple layers and materials. They also took multiple construction episodes to complete their sleeping platform. In general, irrespective of raised or ground sleep sites, individuals would first arrange a base substrate composed of straw (a behavior observed in every subject). Then a layer of cardboard/paper would often be arranged on top of the straw. For more elaborate sleeping platforms, a single or multiple sheet(s) would be placed on top of the preceding straw and cardboard/paper. Furthermore, comforters or sheets could then be arranged to cover the body. Individuals could tuck other materials, such as paper/cardboard or additional straw under their head to serve as a pillow (online suppl. video). Average sleeping platform construction start time was 17:17 h, and the average duration from start to finish was 10.1 min. Most of the orangutans were observed placing their sleeping platforms more often on the ground. Yet, there were significant individual differences in platform complexity, construction duration, platform site selection, construction technique and action frequency; subjects showed preferences for particular sleeping sites, although some individuals were characterized by greater sleep site variability than others. We acknowledge that the sample is of only 5 individuals, which may not be statistically representative of *Pongo;* notwithstanding, these data reveal the capability of the species [Healey, 2009], and future research is needed to confirm the interpretations of this study.

Azy, the male subject with the highest level of socialization, greatest experience and largest body mass (fully flanged), spent the greatest amount of time constructing a platform, performed the widest variety of techniques and manipulated objects with the greatest frequency (table 5); he also constructed the most complex sleeping platforms. Videan [2005] showed that development and exposure to platform construction in chimpanzees (i.e. learning) predicted the adult capacity to construct more complex sleeping platforms; therefore, it may be that Rocky's propensity to inspect older individuals while they were constructing platforms (particularly Azy who was habitually observed during platform construction) is related to his ability to build complex platforms (with multiple layers), whereas his naivety in building experience explains why he spent less time and fewer actions oriented towards constructing platforms. These observations are consistent with Videan's [2005] interpretation of rearing (i.e. social learning) having an effect on sleeping platform complexity. Moreover, Azy's favorite sleeping location was an open ground site, which had no surrounding raised platforms; this observation is consistent with observations that wild, fully flanged males prefer open sleep sites.

Researchers have observed that male bonobos [Fruth and Hohmann, 1993, 1994] and common chimpanzees [Brownlow et al., 2001] build sleeping platforms in significantly lower sites than do females. Reynolds [1967] originally postulated that this was due to sexual dimorphism in body mass. It has been shown that chimpanzee sleeping platform complexity increases with the height of a sleep site [Samson, 2012].

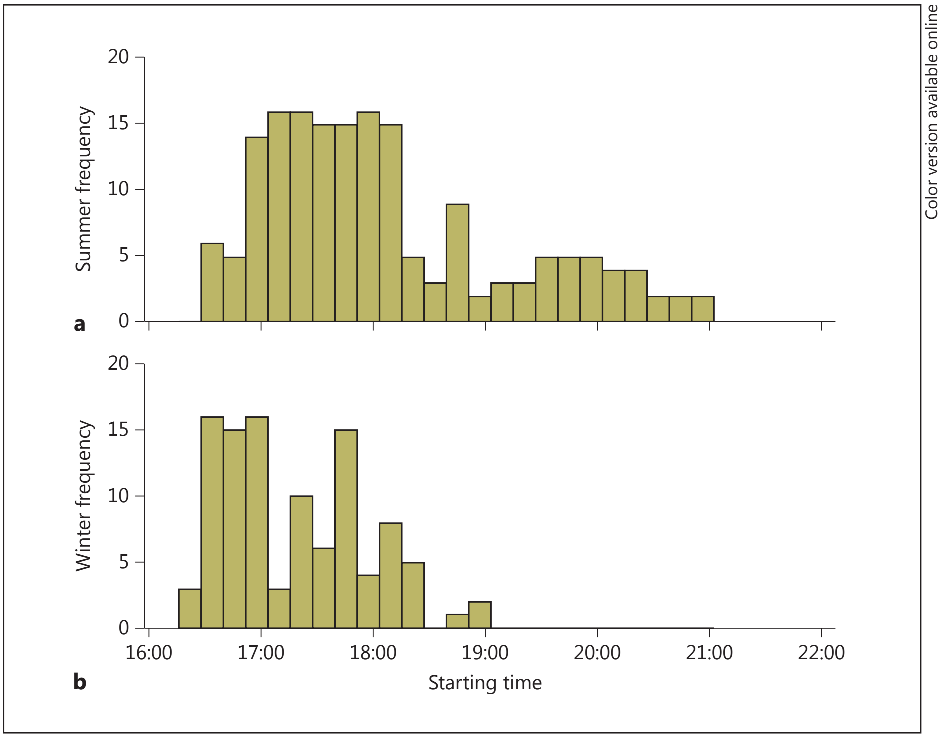

Fig. 5. Starting times for sleeping platform construction compared by season. **a** Summer. **b** Winter.

Ancrenaz et al. [2004] observed that terrestrial predators coupled with highly fragmented ecology resulted in a Sabah orangutan preference for tall trees and the highest of sleeping platform sites of all the apes; additionally, van Casteren et al. [2012, 2013] have reported that wild orangutans are characterized by a sophisticated understanding of the engineering properties of nest construction and biomechanical properties of compliance and sway of arboreally placed sleeping platforms. Since gorillas are the only other ape with comparable sexual dimorphism, and their more continuous habitat enables them to sleep habitually on the ground or low in the canopy if necessary [Tutin et al., 1995], it may be that male orangutans make highly complex sleeping platforms due to the adaptive necessity of a massive-bodied animal sleeping at great heights. Indeed, the averaged time of >10 min allocated to construct a sleeping platform is greater than the 4- to 5-min average time taken by wild chimpanzees [Goodall, 1968]. Finally, this is further evidence in support of the 'weight-bearing hypothesis' of Baldwin et al. [1981], which suggested that the main adaptive advantage (and, thereby, evolutionary origin) of building a sleeping platform in a tree, rather than merely using existing branches, is the greater stability required by large-bodied great apes [Samson, 2012].

Comparisons between summer and winter sleeping platform construction showed winter start times to be significantly earlier than summer times (fig. 5) and the

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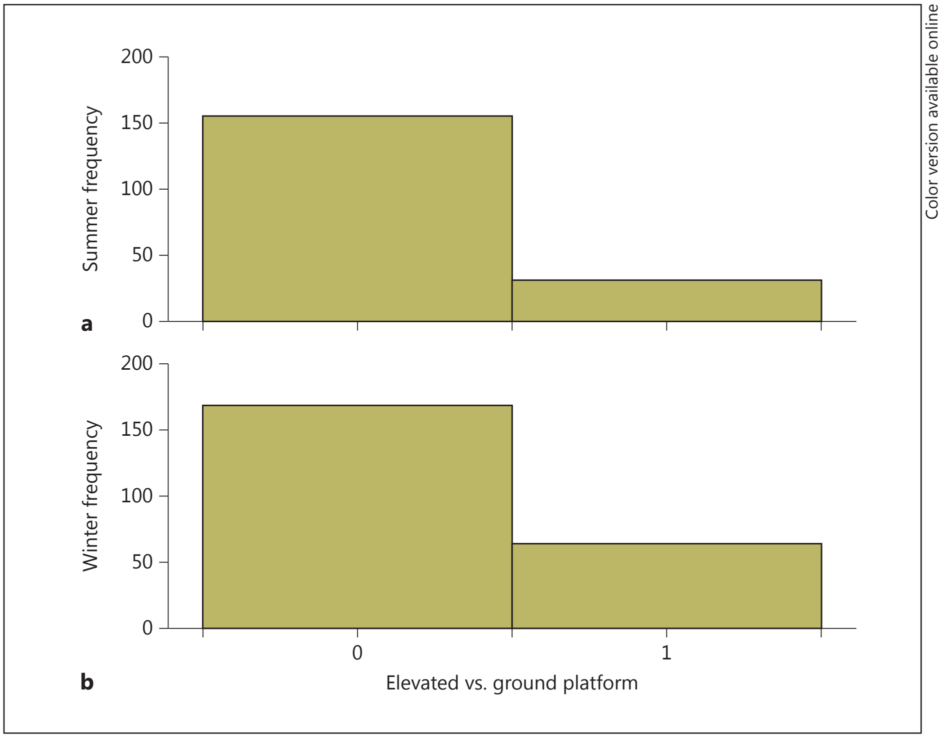

Fig. 6. Elevated (1) versus ground (0) sleeping platform location preference compared between seasons. **a** Summer. **b** Winter.

frequency of siting raised platforms to be greater in the winter (fig. 6). The phenomenon of daily variations in organisms' physiological processes is known as circadian rhythmicity. Wake and sleep cycles are influenced by endogenous and exogenous forces which are related to selective advantages conferred on organisms that tune their activity patterns to phases exhibited by the environment [Refinetti, 2006]. One of the most powerful environmental influences on sleep onset is photic entrainment. The circadian rhythm is sensitive to light, as is illustrated in studies showing the circadian pacemaker to be linked to phase response time [Mistlberger and Rusak, 2005]. The data in this study suggest that, in captive orangutans, exposure to the seasonal shortening of the photic period influences sleep onset, as would be consistent with Webb's [1988] behavioral model of sleep. Despite the fact that the enclosure was temperature controlled, the temperature of the concrete floor might be expected to fluctuate seasonally; the floor is continuously connected to the outside enclosure and the storage and conductivity potential of thermal energy in concrete can be significant [Tatro, 2006]. Gorillas in captivity [Lukas et al., 2003] increase the time dedicated to building sleeping platforms and the frequency of using raised platforms, just as gorillas in the wild may build sleeping platforms to shelter from the cold. The fact that orangutans sleep more often in elevated sites, and invest more time in sleeping platform construction during the winter season, may indicate a thermoregulatory response.

Fruth and Hohmann [1996] speculated that Miocene apes experienced greater quality sleep as a result of using secure and comfortable sleeping platforms. Two important tests of this 'sleep quality hypothesis' have since been performed. First, sleeping platform complexity has been shown to be positively correlated with reduced arousability and fragmentation [Samson and Shumaker, 2013] (i.e. the more comfortable the bed, the higher quality the sleep). Second, sleep events have been shown to stabilize and protect memories against interference [Martin-Ordas and Call, 2011]. Sleep research has illustrated that the quality and depth of sleep experienced by humans provides a host of cognitive benefits, at the tradeoff of a sleep pattern more prone to malfunction [Vyazovskiy and Delogu, 2014]. Considering apes share a similar sleep architecture to humans, it may be that apes too suffer disproportionately when their sleep quality is compromised. Although guidelines exist outlining essential features for enrichment of captive primates [United States Department of Agriculture, 1999], no standard has yet been implemented to ensure captive apes are provided with a baseline of materials to build sleeping platforms. A quality sleep environment may be one of the most critical factors for ensuring the health and welfare of captive apes.

Conclusion

In summary, despite differences in sleeping platform complexity, all individuals in this study exhibited sleeping platform construction behavior. In addition, season influenced sleep related behavior in starting sleep times (winter average, 17:12 h; summer average, 17:56 h) and the amount of time dedicated to the construction of a sleeping platform. Managing institutions often contribute to high levels of variability in the materials presented for captive ape sleeping platform construction; these materials are largely dependent on decisions made by caretakers and the availability of resources and can result in substandard sleep environments (Maple and Hoff, 1982). Furthermore, health and welfare challenges may be exacerbated for equatorial apes sleeping in temperate environments. Therefore, studies such as this have important implications for captive great ape welfare. Some recommendations for captive animal management are evident from these data, as several aspects of this natural behavior can be readily accommodated in captive settings, with the aim of improving sleep quality (Samson and Shumaker, 2013).

To facilitate natural behavior, to permit individual responses to thermoregulatory homeostasis and to minimize competition among individuals for sleep materials and sleep sites, managers of captive ape environments should provide sufficient materials to build platforms and ensure a minimum number of elevated platforms relative to the number of individuals within an enclosure. These types of provisions have been encouraged for captive ape management (Shumaker, 1997), and these suggestions are supported by this research. Sleeping materials are a cost-effective and essential component of the welfare for captive large-bodied hominoids – which may be especially prone to sleep disruption, negatively impacting health.

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References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 493: 227–266.

Ancrenaz M, Calaquem R, Lackman-Ancrenaz I (2004). Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. *International Journal of Primatology* 5: 983–1000.

Anderson JR (1998). Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* 46: 63–75.

Baldwin PJ, Sabater Pi J, McGrew WC, Tutin CEG (1981). Comparisons of nests made by different populations of chimpanzees *(Pan troglodytes). Primates* 22: 474–486.

Bernstein IS (1962). Response to nesting materials of wild born and captive born chimpanzees. *Animal Behavior* 10: 1–6.

Bernstein IS (1967). Age and experience in chimpanzee nest building. *Psychological Reports* 20: 1106.

Bernstein IS (1969). A comparison of nesting patterns among the three great apes. In *The Chimpanzee* (Bourne GH, ed.), vol 1: Anatomy, Behavior, and Diseases of Chimpanzees, pp 393–402. Baltimore, University Park Press.

Blom A, Almasi A, Heitkonig IMA, Kpanou JB, Prins HHT (2001). A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: a comparison between the census and survey methods of estimating the gorilla *(Gorilla gorilla gorilla)* and chimpanzee *(Pan troglodytes)* nest group density. *African Journal of Ecology* 1: 98–105.

Brownlow AR, Plumptre AJ, Reynolds V, Ward R (2001). Sources of variation in the nesting behavior of chimpanzees *(Pan troglodytes schweinfurthii)* in the Budongo Forest, Uganda. *American Journal of Primatology* 55: 49–55.

Capellini I, McNamara P, Preston BT, Nunn CL, Barton RA (2009). Does sleep play a role in memory consolidation? A comparative test. *PLoS ONE* 4: e4609.

Fruth B, Hohmann G (1993). Ecological and behavioral aspects of nest-building in wild bonobos *(Pan paniscus). Ethology* 94: 113–126.

Fruth B, Hohmann G (1994). Comparative analyses of nest building behavior in bonobos and chimpanzees. In *Chimpanzee Cultures* (Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, eds.), pp 109–128. Cambridge, Harvard University Press.

Fruth B, Hohmann G (1996). Nest building behavior in the great apes: the great leap forward? In *Great Ape Societies* (Marchant LF, Nishida T, eds), pp 225–240. Cambridge, Cambridge University Press.

Goodall JM (1962). Nest building behavior in the free ranging chimpanzee. *Annals of the New York Academy of Sciences* 102: 455–467.

Goodall J (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve, pp 161–311. *Animal Behaviour Monographs.*

Healey JF (2009). *Statistics: A Tool for Social Research.* Belmont, Thomson/Wadsworth.

Lesku JA, Roth TC, Rattenborg NC, Amlaner CJ, Lima SL (2009). History and future of comparative analyses in sleep research. *Neuroscience and Biobehavioral Reviews* 33: 1024–1036.

Lukas KE, Stoinski TS, Burks K, Snyder R, Bexell S, Maple TL (2003). Nest building in captive *Gorilla gorilla gorilla*. *International Journal of Primatology* 24: 103–124.

Maple TL, Hoff MP (1982). *Gorilla Behavior*. New York, Van Nostrand Reinhold.

Martin-Ordas G, Call J (2011). Memory processing in great apes: the effect of time and sleep. *Biology Letters* 7: 829–832.

Mistlberger RE, Rusak B (2005). Circadian rhythms in mammals: formal properties and environmental influences. In *Principles and Practice of Sleep Medicine* (Kryger MH, Ruth T, Dement WC, eds.), 4th ed., pp 321–334. Philadelphia, Elsevier Saunders.

Nunn CL, McNamara P, Capellini I, Preston BT, Barton RA (2010). Primate sleep in phylogenetic perspective. In *Evolution and Sleep: Phylogenetic and Functional Perspectives* (McNamara P, Barton RA, Nunn CL, eds.), pp 123–145. New York, Cambridge University Press.

Rayadin Y, Saitoh T (2009). Individual variation in nest size and nest site features of the Bornean orangutans *(Pongo pygmaeus)*. *American Journal of Primatology* 71: 393–399.
Refinetti R (2006). *Circadian Physiology*. Boca Raton, CRC Press/Taylor & Francis Group.
Renner E (2012). Use of space prior to night-time nesting in zoo orangutans and gorillas. *American Journal of Primatology* 74: 38.
Reynolds V (1967). *The Apes: The Gorilla, Chimpanzee, Orangutan, and Gibbon – Their History and Their World*. New York, Dutton.
Russon AE (2007). Orangutan leaf-carrying for nest-building: toward unraveling cultural processes. *Animal Cognition* 10: 189–202.
Sabater Pi J, Vea JJ, Serrallonga J (1997). Did the first hominids build nests? *Current Anthropology* 38: 914–916.
Samson DR (2012). The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. *Primates* 53: 357–364.
Samson DR, Shumaker RS (2013). Documenting orang-utan sleep architecture: sleeping platform complexity increases sleep quality in captive *Pongo. Behaviour* 150: 845–861.
Shumaker R (1997). Gorilla enrichment. In *Management of Gorillas in Captivity* (Ogden J, Wharton D, eds.), pp 102–110. Atlanta, Gorilla Species Survival Plan and the Atlanta/Fulton County Zoo.
Shumaker R, Wich S, Perkins L (2008). Reproductive life history traits of female orangutans (*Pongo* spp.). In *Primate Reproductive Aging* (Atsalis S, Margulis SW, Hof PR, eds.), Interdisciplinary Topics in Gerontology, pp 147–161. Basel, Karger.
Shumaker RW, Samson DR, Schoenemann TP (2014). The effects of sleeping platforms on next day cognition in captive orangutans (*Pongo* spp.). *American Journal of Physical Anthropology* 153: 238–238.
Stewart FA (2011). *The Evolution of Shelter: Ecology and Ethology of Chimpanzee Nest Building.* PhD Thesis, University of Cambridge, Cambridge.
Stewart FA, Pruetz JD, Hansell MH (2007). Do chimpanzees build comfortable nests? *American Journal of Primatology* 69: 930–939.
Tatro S (2006). Thermal properties. In *Significance of Tests of Properties of Concrete and Concrete-Making Materials* (Lamond JF, Pielert JH, eds.), pp 226–236. West Conshohocken, International Standards Worldwide.
Tutin CEG, Parnell RJ, White LJT, Fernandez M (1995). Nest building by lowland gorillas in Lope Reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatology* 16: 53–76.
United States Department of Agriculture (1999). *Final Report on Environment Enhancement to Promote the Psychological Well-Being of Nonhuman Primates*. Washington, Animal and Plant Health Inspection Service, United States Department of Agriculture.
Van Casteren A, Sellers WI, Thorpe SKS, Coward S, Crompton RH, Ennos AR (2013). Factors affecting the compliance and sway properties of tree branches used by the Sumatran orangutan *(Pongo abelii)*. *PloS One* 8: e67877.
Van Casteren A, Sellers WI, Thorpe SKS, Coward S, Crompton RH, Myatt JP, Ennos AR (2012). Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proceedings of the National Academy of Science* 109: 6873–6877.
Van Schaik C, Ancrenaz M, Borgen G, Galdikas BMF, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M (2003). Orangutan cultures and the evolution of material culture. *Science* 299: 102–105.
Videan EN (2005). *Sleep and Sleep-Related Behaviors in Chimpanzee* (Pan troglodytes). PhD Thesis, Miami University, Oxford.
Videan EN (2006). Bed-building in captive chimpanzees *(Pan troglodytes):* the importance of early rearing. *American Journal of Primatology* 68: 745–751.
Vyazovskiy VV, Delogu A (2014). NREM and REM sleep: complementary roles in recovery after wakefulness. *Neuroscientist* 20: 203–219.
Webb WB (1988). Theoretical presentation: an objective behavioral-model of sleep. *Sleep* 11: 488–496.
Zepelin H, Siegel J, Tobler I (2005). Mammalian sleep. In *Principles and Practice of Sleep Medicine* (Kryger MH, Roth T, Dement WC, eds.), pp 91–100. Philadelphia, Elsevier Saunders.