

## RESEARCH ARTICLE

A Thermodynamic Comparison of Arboreal and Terrestrial Sleeping Sites for Dry-Habitat Chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda

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The nightly construction of an arboreal sleeping platform (SP) has been observed among every chimpanzee's population studied to date. Here, we report on bioclimatic aspects of SP site choice among dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. We placed a portable weather monitor within 1 m of chimpanzee SPs and compared the microenvironment of this site with terrestrial monitors placed 10 cm above the ground directly underneath the simultaneously studied SP. We calculated physical "comfort levels" of monitored sites using the *RayMan* thermophysiological model that we modified to take ape body proportions into account. The *RayMan* tool gauges energy balance using wind speed, temperature, relative humidity, and heat index in conjunction with the study subject's mass and stature to determine whether the individual is in energy balance or homeostasis. We found that (1) terrestrial microclimates have greater homeostatic potential than arboreal microclimates, and (2) there is a significant positive linear relationship between wind speed and height of SP in the forest canopy. Advantages of terrestrial sites are that they require lesser energetic expenditure to stabilize the body when the SP is under construction and perhaps during use as well. We found that terrestrial sites also had better homeostatic potentials. This combination of advantages explains why SPs are so often sited terrestrially in habitats where predation risk is low. Early hominins must have had technological or social measures to avoid or deter predators that were significantly advanced over those found among chimpanzees before they began sleeping on the ground. *Am. J. Primatol.* 74:811–818, 2012. ©2012 Wiley Periodicals, Inc.

**Key words:** Chimpanzee; thermodynamics; nest; terrestrial; sleep; evolution

## INTRODUCTION

Great apes spend half of their lives in a "night nest" or sleeping platform (SP), a complex construction [Shumaker et al., 2011] manufactured each evening by manipulating and modifying foliage so as to serve as a stable and comfortable mattress [Goodall, 1962, 1968]. SPs have been observed in every chimpanzee (*Pan troglodytes*), bonobo (*Pan paniscus*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo pygmaeus*) population yet studied. The construction of a new SP each day requires an investment of time and effort: individuals alter their ranging behavior to reach advantageous SP sites; they must determine which of the possible sites are most desirable; they must climb to the site and maneuver into position to construct the SP; and finally they must manipulate a large volume of foliage to manufacture the SP.

Nissen [1931] was the first to describe the wild chimpanzee SP in a field study. He used the term "nest," which had been popularized during 19th century African expeditions [Du Chaillu, 1861]. The pop-

ularity of the term "nest" has been lamented by several authors [Baldwin et al., 1981; Groves & Sabater Pi, 1985; Hansell, 1984, 2005; Hediger, 1977; McGrew, 1992; Thorén et al., 2010] because while great ape nests appear similar to large bird nests, the resemblance is superficial. A bird (and even strepsirrhine [Kappeler, 1998]) nest is a fixed point that serves as cache for resources and as a central base during foraging. It is a persistent structure that is often used for months and even years for breeding and

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rearing young, SPs are widely regarded the product of an evolved behavior to be unique to apes, and their form is argued to be functionally more closely related to human beds than nests [Fruth & Hohmann, 1996; Kappeler, 1998; Videan, 2006]. The term SP was first used by Goodall [1962, p 455]. McGrew [1992, 2004] argued that SP is a more accurate descriptive term when referring to sleeping devices extant great apes construct.

As late as 2004 McGrew noted that most hypotheses purporting to explain the function(s) of SPs had not yet been tested. He listed among the proposed function of SPs predation avoidance [Kortlandt, 1992; Pruett et al., 2008], thermoregulation [McGrew, 2004], pathogen or parasite avoidance [Anderson, 1998; Fruth & Hohmann, 1996; Nunn & Heymann, 2005], and/or promotion of mental health, that is, permitting better quality sleep [Anderson, 1998; Fruth & Hohmann, 1996; Sabater Pi et al., 1997]. Since McGrew's implicit challenge, a number of attempts to test hypothesized functions for SPs have appeared [Ancorenaz, 2004; Hernandez-Aguilar, 2009; Koops et al., 2007; Ogawa et al., 2007; Stewart et al., 2007; Stewart, 2011]. Stewart and colleagues [Stewart et al., 2011] suggested that not only do SPs confer important benefits to great apes, SP sites are a result of "niche construction" through the repeated use of high-quality trees, chosen on the basis of re-growth stages and healing of previously used support structures.

Fundamental to understanding the function of SPs is the observation that aspects of the local environment and socioecology affect ape SP site selection and placement. Early cross-site comparisons [Baldwin et al., 1981] showed SPs to be higher and more open during the wet season. In addition, habitat analysis revealed that SPs were higher in gallery forests, grouped more densely in woodlands, and clustered around seasonal watercourses in many habitats. In Ugalla, SP sites were selected preferentially on slopes and are consistently reused throughout the woodland vegetation habitat [Hernandez-Aguilar, 2009]. At Budongo [Brownlow et al., 2001] and Ishasha [Sept, 1992], analysis of SP selection showed a preference for *Cynometra alexandri*. When chimpanzees are sympatric with gorillas, they adjust their SP siting strategy by sleeping in tree species bearing ripe fruits rarely eaten by gorillas [Basabose & Yamagiwa, 2002]. Bonobos choose SP tree species with smaller leaves and may select SP sites as an intragroup conflict avoidance strategy [Fruth & Hohmann, 1993]. In addition, among bonobos, nests are clustered in larger numbers when fruits are abundant [Mulavwa et al., 2010]. Gorillas construct arboreal SPs significantly more often during the wet season [Sunderland-Groves et al., 2009; Tutin et al., 1995]. Sabah Orangutans have a highly fragmented environment, characterized by low tree density and small tree size; in logged forests, they build less SPs

and preferentially select the tallest and largest trees for use [Ancorenaz, 2004].

Most chimpanzee nighttime sleep sites are arboreal—approximately 95% in East Africa [Furuichi & Hashimoto, 2000; Maughan & Stanford, 2001] but less in West Africa. Despite this strong preference, terrestrial sleeping sites are selected occasionally, more often during the day [Boesch, 1995; Goodall, 1968; Humle, 2003; Reynolds & Reynolds, 1965]. In the Nimba Mountains of Guinea and Côte d'Ivoire terrestrial sleeping site, frequencies are particularly high [Humle & Matsuzawa, 2001]—reportedly as great as 35.4% [Matsuzawa & Yamakoshi, 1996]. Furuichi and Hashimoto [2000] and Maughan and Stanford [2001] suggested that the absence of predators is the principal reason SPs are sited terrestrially; arboreal site selection is an antipredator strategy. Yamagiwa [2001] argued that the large body mass of gorillas and lack of natural predators account for higher frequencies of terrestrial SPs. While this reasoning explains why gorillas might be free to sleep at a terrestrial site, it does not explain why such sites might be preferred [Koops et al., 2007]. If apes choose terrestrial sites whenever predators are not a threat, terrestrial sites must be superior in some way. Among the factors that make terrestrial sites superior might be: they have superior homeostatic potentials (i.e., offer better "comfort"); they require lesser energetic expenditure to stabilize the body when the SP is under construction and during use; and that terrestrial sites preclude costs to ascend and descend to the SP site.

As a means of determining whether temperature, humidity, and wind speed are factors in site choice, we compared thermodynamic qualities of microenvironments in arboreal versus terrestrial sleeping sites. We used bioclimatic indices to assess thermal stress to better determine whether SPs improve maintenance of thermal homeostasis. We compared the microenvironments among open arboreal sites, arboreal SPs, and terrestrial sites directly below arboreal sites. We test the following predictions:

- (1) There is a difference in thermal stress and purported comfort or ability to sustain homeostasis among microenvironments with an arboreal SP, in open arboreal sites (i.e., sites with more exposure to open airways within the canopy), and terrestrial sites.
- (2) Arboreal microenvironments are characterized by greater wind speeds than terrestrial microenvironments.
- (3) Microhabitats within arboreal SP microenvironments allow homeostasis (i.e., greater comfort) compared to open arboreal sites and terrestrial sites.

## METHODS

### Study Area

Chimpanzees have been studied in the Toro-Semliki Wildlife Reserve (TSWR) in western Uganda since 1996, when one of us (KDH) established the Semliki Chimpanzee Project. TSWR is northwest of Fort Portal, close to the eastern edge of the Great Rift Valley (0°50' to 1°05'N, 30°20' to 30°35'E) and encompasses 548 km<sup>2</sup>. Semliki is predominantly dry *Combretum ghasalense* savanna and *Borassus aethiopicum* palm savanna. But within the open habitat are gallery forests (50–250 m wide) with emergent trees reaching heights of 50 m [Allan et al., 1996; Hunt & McGrew, 2002]. The chimpanzee study community range is mostly limited to the Mugiri River and its tributaries, as well as open woodland and bushland on the escarpment near the northeastern reserve boundary. The range of the Mugiri chimpanzees is limited to the northeast by tea estates and peasant holdings at the top of the escarpment. The Mugiri chimpanzee community is heavily dependent on the fruiting species such as *Beilschmiedia ugandensis*, *C. alexandri*, *Cola gigantea*, *Phoenix reclinata*, and *Tamarindus indica* [Hunt & McGrew, 2002]. Their community home range is the largest known at 72.1 km<sup>2</sup> (measured with the minimum convex polygon of any area where identified individuals have been observed), with the second and third largest home ranges being the dry-habitat sites of Fongoli at 64 km<sup>2</sup> [Pruetz, 2006] and Assirik at 50 km<sup>2</sup> [McGrew et al., 1996; Tutin et al., 1983]. There are estimated to be 30 males, which suggests a community size of approximately 104 (estimated using the average sex ratio across *Pan troglodytes schweinfurthii* sites) [Stumpf, 2007]. Toro-Semliki has an average rainfall of 1,389 mm (KDH records), though rainfall is at historic highs in the rift valley and earlier annual rainfall records were reported to vary between 700 and 1,300 mm [Plumptre, 2011; Pratt et al., 1977]. Semliki has two rainy seasons: the long rains from August to December and secondary short rains from March to April. Of chimpanzee study sites, only Assirik is hotter [Hunt & McGrew, 2002]. Relative humidity (RH) daily maxima averaged 95% and 92%, respectively [Hunt et al., 1999], while the daily mean temperature high was 34°C and the daily mean low was 20°C [Hunt & McGrew, 2002].

### Study Design

We generated microenvironmental data with use of the Kestrel (Nielsen-Kellerman, Boothwyn, PA) 4200 pocket air flow tracker, a portable weather monitor that captures wind speed, temperature, windchill, relative humidity, and heat stress index (HSI). Two monitors were installed and reinstalled on an approximately weekly basis at chimpanzee sleeping sites. The monitors were placed in varying macroenvironments ( $N = 11$ ) ranging from gallery

forest, gallery forest–savanna ecotone, grassland savanna, and swamp wetland (see Table I). Monitors measured data for a mean of seven consecutive nights (total  $N = 79$ ) and were placed at 11 sites. We placed a monitor <1 m from each arboreal SP. Either a throw line with a 340 g weight was cast over a branch and a monitor pulled within a meter of the target SP, or one of us (DRS) climbed the tree and manually installed the monitor. A second monitor was installed directly below the target SP, 10 cm from the ground. We time synced both monitors. Data were collected at 5 min intervals from 19:05 to 07:00 (sunrise);  $N = 290$  data points generated per night,  $N = 145$  per monitor,  $N = 22,910$  total. Data were collected during both dry and rainy seasons, from August 2010 to January 2011.

We applied bioclimatic indices modeled to estimate the energy balance of individuals in relation to different environments to estimate comfort levels. The *RayMan* thermophysiological model [Gulyas et al., 2006; Matzarakis et al., 2007, 2010] calculates thermal stress using meteorological parameters and body proportions. Variables included in the model are air temperature, RH, and wind speed. We calculated Physiological Equivalent Temperature (PET) as a measure of “comfort” assuming an age of 25 (metabolic rates vary little during adulthood, but differ during the growth period or after senescence). We assumed a stature of 0.816 m [Rowe, 1996], a body mass of 42.7 kg [Fleagle, 1999], body insulation at 80% (i.e., body hair covering a proportion of surface area—given adult pelage can be sparse along the head, hands, and feet [Montagna & Yun, 1963]), a metabolic rate 44 watts per hour (normal basal metabolic for chimpanzee-sized individual [Mifflin et al., 1990]), and horizontal positioning. We also made a separate calculation of HSI that we consider less reliable than *RayMan* PET since it assumes an average human male mass and height [Steadman, 1979].

We compared *RayMan* comfort indices to weather monitor data (paired samples *t*-test). We compared wind speed among open arboreal sites, arboreal SP sites, and terrestrial microenvironments (paired samples *t*-test). To detect the relationship between climatic variability and sleeping site/height choice, we compared SP environments and meteorological data (Pearson correlation and Spearman rho correlation for non-normal data). Finally, we cross-compared macroenvironments and meteorological data (independent samples *t*-test). All statistical tests were two-tailed, set at an  $\alpha = 0.05$  significance level.

Research complies with Indiana University Animal Care Committee, American Society of Primatologists Principles for Ethical Treatment of Nonhuman Primates, and Ugandan Wildlife Authority regulations.

**TABLE I. The Definitions of Macroenvironments Used to Contextualize the Microenvironments Used in This Study**

Macroenvironments	Definition
Gallery forest	Evergreen forest with tall emergent trees up to 50 m high. Except for saplings and seedlings, the understory is generally open with high cover from the canopy. Dominant species are <i>Cynometra alexandri</i> , <i>Cola gigantea</i> , and <i>Beilschmiedia ugandensis</i> .
Forest-savanna ecotone	The transition area between two adjacent gallery forest and the grassland savanna landscapes; less cover than the gallery forest.
Grassland savanna	Dry grassland dominated by grasses up to 3 m high. Few trees grow in this vegetation type, with the occasional <i>Acacia seberiana</i> , <i>Combretum molle</i> , and <i>Dombeya mukole</i> ; generally little cover.
Swamp wetland	Wet grassland and woodland dominated by grasses up to 3 m high, and crosscut by multiple reverine tributaries. The dominant tree species is <i>Phenoix reclinata</i> ; generally moderate cover.

**TABLE II. Descriptive Statistics of Averaged Nightly Measurements of Wind Speed, Temperature, Relative Humidity, Heat Stress Index, and Physiological Equivalent Temperature ( $N = 79$ )**

Variable	Mean and SD	Range	Mean Difference between high and low monitors	
WS high	0.047 ± SD 0.08	0.04–0.61	0.03 ± SE 0.010	$P = 0.001$
WS low	0.014 ± SD 0.04	0.00–0.19		
Temp high	20.95 ± SD 1.56	18.96–24.17	0.49 ± SE 0.132	$P < 0.001$
Temp low	20.46 ± SD 1.82	18.98–23.09		
RH high	90.12 ± SD 10.06	75.80–96.20	–4.44 ± SE 0.470	$P < 0.001$
RH low	94.57 ± SD 8.31	88.47–96.95		
HSI high	21.82 ± SD 1.57	19.70–25.38	0.25 ± SE 0.045	$P < 0.001$
HSI low	21.57 ± SD 1.44	19.78–24.62		
PET high	22.20 ± SD 1.42	19.00–25.29	0.17 ± SE 0.058	$P = 0.005$
PET low	22.03 ± SD 1.30	19.99–24.56		

## RESULTS

Terrestrial microenvironments were significantly cooler than arboreal microenvironments (paired samples  $t$ -test:  $t[78] = 3.71$ ,  $P < 0.001$ ), less windy (Fig. 1; paired samples  $t$ -test:  $t[78] = 3.34$ ,  $P = 0.001$ ), imposed significantly less thermal stress on

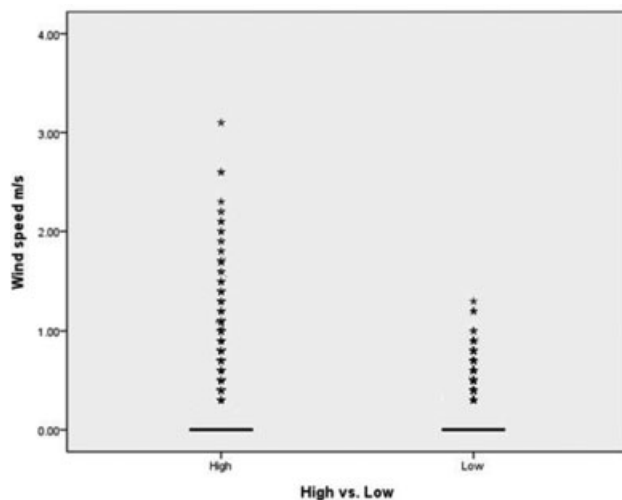


Fig. 1. A comparison between high and low microenvironments and wind speed. Note that the arboreal environments have a higher range in wind speed than do terrestrial. These data were taken from the overall, not nightly averaged, sample.

our RayMan hypothetical chimpanzee (paired samples  $t$ -test on HSI and PET, respectively:  $t[78] = 5.61$ ,  $P < 0.001$ ;  $t[78] = 2.86$ ,  $P = 0.005$ ), and were significantly more humid (paired samples  $t$ -test:  $t[78] = -9.46$ ,  $P < 0.001$ ). See Table II for the total number of comparable nights ( $N = 79$ ), with averaged nightly measurements ( $N = 143$ ).

We found significant correlations among climatic variability, sleeping site elevation, and wind speed. Wind speed increased as SP elevation increased (Fig. 2;  $N = 158$ , Spearman correlation  $\rho = 0.35$ ,  $P < 0.001$ ) and as the ratio of SP elevation to canopy height increased ( $N = 158$ , Spearman correlation  $\rho = 0.26$ ,  $P = 0.001$ ). In contrast, the relationship between percentage of canopy above the SP (i.e., foliage of surrounding trees blocking a fish eye view of open sky) ( $N = 148$ , Spearman correlation  $\rho = -0.22$ ,  $P = 0.792$ ) and wind speed was not significant. However, other variables share a relationship with canopy above SP%, such as PET ( $N = 148$ , Pearson correlation  $r^2 = -0.19$ ,  $P = 0.024$ ) and RH (Fig. 3;  $N = 148$ , Spearman correlation  $\rho = 0.22$ ,  $P = 0.007$ ).

Sites on steep slopes, sites open to the sky, and sites higher on the escarpment were hotter (independent samples  $t$ -test:  $t[156] = -2.94$ ,  $P = 0.004$ ), less humid (independent samples  $t$ -test:  $t[156] = 5.50$ ,  $P < 0.001$ ), and nearly twice as windy (escarpment mean  $0.045 \pm 0.060$  vs. flatland  $0.025 \pm 0.064$ ; in-



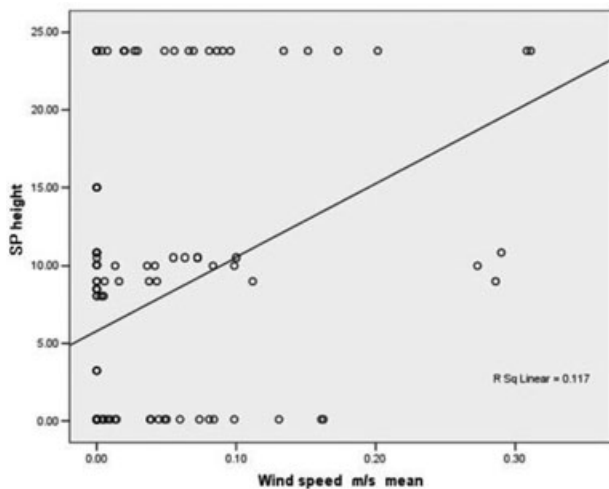


Fig. 2. A significant positive linear correlation between chimpanzee SP height and the averaged wind speed per night.

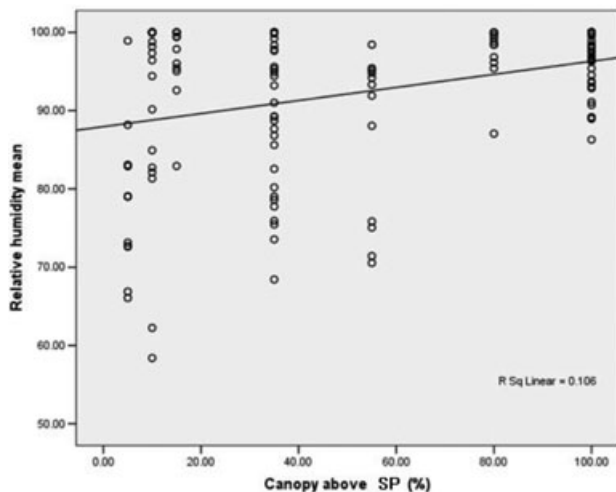


Fig. 3. A significant positive linear correlation between the percentage canopy above the SP and the averaged relative humidity per night.

dependent sample *t*-test:  $t[156] = -1.64$ ,  $P = 0.104$ ) compared to sites on shallow slopes, sites low on the escarpment, and sites in closed gallery forest. Measures of thermal stress were higher for sites on the escarpment slope compared to sites on the rift floor (independent samples *t*-test on HSI and PET, respectively:  $t[156] = -2.03$ ,  $P = 0.044$ ;  $t[156] = -2.27$ ,  $P = 0.025$ ).

## DISCUSSION

We found a clear difference among terrestrial, open-site arboreal, and SP microenvironments. Wind speeds were greater for arboreal sites than terrestrial sites. Not just average wind speed, but the

intensity of wind gusts was higher for arboreal sites (see Fig. 1), increasing thermal stress and presumably requiring muscular response to maintain stability (thus disturbing sleep). The positive relationship between SP height and wind speed (see Fig. 2) indicates high sleeping locations were more dangerous than lower. At Semliki, mean SP elevation was 11 m [Hunt & McGrew, 2002], and chimpanzees at Semliki manufacture their SPs at sites three-quarters the elevation of the entire tree canopy, leaving one-quarter of the canopy above the SP (KDH unpublished data;  $0.74 \pm 0.22$ ); this is comparable to Fongoli at 0.76 [Pruetz et al., 2008], and Assirik in the 1970s (0.80) but differs from more recent numbers recorded at Assirik (0.94). It is unclear whether intersite differences reflect differences in ambient wind speed or in SP construction materials. Physical attributes of tree branches likely differ among sites, and some raw materials may allow more stable and comfortable SPs at greater heights. More cross-site comparisons of environmental and tree species characteristics will be needed to test such hypotheses.

The third hypothesis, that microhabitats within arboreal SP microenvironments disturb homeostasis less than terrestrial sites, was rejected. Terrestrial microenvironments compared to arboreal microenvironments had temperature ranges that would impose less thermal stress on our hypothetical chimpanzee (i.e., are more comfortable; see Table II).

Hunt and McGrew [2002] reported that sixty-two percent of Semliki's SPs were under foliage cover—an observation similar to that reported for several other sites (Baldwin et al. 1981). At Semliki, SPs were significantly more likely to be covered in the dry season than the wet season [Hunt & McGrew, 2002], perhaps functioning to create favorable humidity levels (see Fig. 3). There is a clear difference in thermal comfort among macroenvironments within the Semliki chimpanzee range; the escarpment was hotter, windier, and (despite being less humid) imposed greater thermal stress than the flatter topographies. Captive chimpanzees selected cooler sleeping sites when humidity and temperature were higher [Videan, 2006]; western gorillas manufacture SPs when the ground is wet and cold ground, whereas during the dry season, they slept on bare earth [Mehlman & Doran, 2002]; lowland gorillas construct more substantial SPs during the wet season [Tutin et al., 1995]. Our data suggest that wild chimpanzees are similar in choosing SP sites in specific locations within habitats by taking into account thermoregulatory demands. Future research on ape sleep-site choice should test the threshold of wind speed necessary to dislodge a large-bodied ape from an SP.

Fruth and Hohmann [1996] suggested there may be multiple benefits to sleeping in SPs versus in the

open on branches. They suggested that apes began to construct SPs in the Miocene because increased memory consolidation demands required uninterrupted sleep and higher quality rapid eye movement (REM) and non-rapid eye movement (NREM) sleep. Our data and previous work are consistent with this interpretation. Of the neural functions of sleep, memory consolidation and emotional regulation are suggested to be among the most important benefits of sleep [Hobson, 1990; Hobson and Pace-Schott, 2002; Kavanau, 1994, 1997; Marks, 1995; Peigneux et al., 2001; Walker, 2009; Walker & Stickgold, 2006].

In part because terrestrial SPs have only been observed at sites where predation risk is low or absent [Matsuzawa & Yamakoshi, 1996], arboreal sleep site choice is widely regarded as a predation avoidance behavior [Kortlandt, 1992; Pruett et al., 2008]. Our data are consistent with this interpretation. Lions and leopards are both found at Semliki, and terrestrial night SPs have never been observed (unpublished Semliki Chimpanzee Project data).

Because dry-habitat chimpanzees occupy habitats with a mosaic of riverine forest, bushland, open woodland, and grassland and with species composition, predation risks, dietary demands, and thermoregulatory stresses similar to those of early hominins, they may be particularly informative about early hominin evolution [Hunt & McGrew, 2002; McGrew et al., 1996]. Our data show that in dry habitats, terrestrial sites offer thermoregulatory advantages, and suggest that without the threat of predation, early Plio-Pleistocene hominins also would have found advantages in terrestrial sleep sites. Modern hunter-gatherers display a variety of antipredation defenses, in addition to fire, including kralls, permanent structures, earthworks, and other constructions [Wobber et al., 2008; Worthman, 2008; Worthman & Melby, 2002; Wrangham et al., 1999]. We might expect these defenses must have appeared around the time of the first evidence of fully realized terrestrial locomotor adaptations.

Higher wind speeds and wind gusts suggest that SPs are subject to sway; it is not clear whether arboreal SPs are stable enough to permit human sleep architecture (i.e., distribution of REM and NREM sleep) [Coolidge & Wynn, 2006, 2009]. Coolidge and Wynn hypothesize that only terrestrial sleep sites are stable enough to allow human sleep architecture and its procedural memory consolidation, and therefore that human-like visual motor skills, social rehearsal, and threat simulation evolved only after hominins adopted terrestrial sleeping sites. Whereas our data do not address this speculation, they do suggest that in addition to greater stability, terrestrial sites were also less thermally stressful. We view the issue of whether arboreal SPs preclude human sleep architecture to be an important future research question.

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