

RESEARCH ARTICLE

Do Chimpanzee Nests Serve an Anti-Predatory Function?

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Sleep is a vulnerable state for animals as it compromises the ability to detect predators. The evolution of shelter construction in the great apes may have been a solution to the trade-off between restorative sleep and predation-risk, which allowed a large bodied ape to sleep recumbent in a safe, comfortable spot. In this article we review the evidence of predator pressure on great apes and specifically investigate the potential influence of predation-risk on chimpanzee nesting behavior by comparing nests between chimpanzees living in a habitat of several potential predators (Issa, Ugalla, Tanzania) and a habitat relatively devoid of predators (Fongoli, Senegal). Chimpanzees in Issa did not nest more frequently in forest vegetation than chimpanzees in Fongoli although forest vegetation is expected to provide greater opportunity for escape from terrestrial predators. Nor do chimpanzees in Issa nest in larger groups or aggregate together more than Fongoli chimpanzees, as would be expected if larger groups provide protection from or greater detection of predators. Nests in Issa also did not appear to provide greater opportunities for escape than nests in Fongoli. Chimpanzees in Issa nested more frequently within the same tree as other community members, which may indicate that these chimpanzees nest in greater proximity than chimpanzees in Fongoli. Finally, Issa chimpanzees built their nests proportionately higher and more peripherally within trees. The selection of high and peripheral nesting locations within trees may make Issa chimpanzees inaccessible to potential predators. Many factors influence nest site selection in chimpanzees, of which danger from terrestrial predators is likely to be one. *Am. J. Primatol.* 9999:1–12, 2013. © 2013 Wiley Periodicals, Inc.

Key words: nest; bed; predation; savanna chimpanzee; shelter

INTRODUCTION

All vertebrates spend proportions of their lives in a vulnerable state of sleep or sleep-like behavior [reviewed in Lima et al., 2005]. Although the functions of sleep are still debated, researchers agree that the primary function of sleep involves neural maintenance [Siegel, 2005]. However, sleep compromises the ability to detect predators [Anderson, 1998, 2000; Lima and Rattenborg, 2007; Lima et al., 2005; Rattenborg et al., 1999], and early research into sleep function highlighted the role predation pressure may have played in the evolution of sleep [Meddis, 1975]. Some species sleep only one-half of the brain at a time, which enables them to detect predators [e.g., *Anas platyrhynchos*; Rattenborg et al., 1999]. In an effort to address why more species do not engage in such unihemispheric sleep, Lima and Rattenborg [2007] developed a theoretical model that suggests unconsciousness may be the safest way for animals to achieve necessary neural maintenance functions of sleep. As with trade-offs in predation risk versus energy intake in animal foraging strategies, there are likely trade-offs in predation risk versus sleeping site selection, sleep architecture, and sleep duration

[Lima et al., 2005]. The evolution of shelter construction in the great apes thus may be a solution to the trade-off between sleep and predation-risk, allowing a large-bodied ape to sleep recumbent in a safe, comfortable spot. REM (rapid eye movement) sleep in large mammals is accompanied by loss of muscle tone and so may require a horizontal platform and recumbent posture. Increased REM sleep has been

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proposed to have enabled cognitive evolution in great apes and *Homo*, through increased memory consolidation and enhancement [Coolidge and Wynn, 2009; Fruth and Hohmann, 1996].

This article aims to investigate the potential influence of predation-risk on chimpanzee nesting behavior. We begin with a review of the evidence of the selective pressure of predation on sleep in apes and other primates and then compare variation in nests and nest position between a site where predators are present and another where they are absent. Comparison of two such sites is pertinent to the question of whether or not chimpanzee nests function to reduce risk of predation.

Predator Avoidance in Other Primates

Most primates live arboreally; however even more terrestrial species such as baboons (*Papio* spp.), macaques (*Macaca* spp.), and chimpanzees (*Pan* spp.) return to the refuge of elevated sleeping sites at night. Safety from predators is the primary factor underlying sleep-related behaviors and sleeping site selection in primates [Anderson, 1984, 1998, 2000]. Sleep-related behavioral adaptations include huddling [Li et al., 2010], adjustment of sleeping site locations [Matsuda et al., 2010] and differential selection of sleeping sites by younger or female versus male individuals [Fan and Jiang, 2008]. Many primates select locations for sleeping that are difficult to access, for example by height, distance from the trunk of the tree, or presence of an alternative escape route [Anderson, 1984, 1998, 2000]. There are many examples of the influence of predator avoidance on sleeping site selection across a range of primates [see Anderson, 1984, 1998, 2000 for comprehensive reviews]. Hamilton [1982] found that baboons' sleeping site preference ranged from cliff edges, through emergent trees, to open woodland and proposed that these descending preferences reflected the increasing danger of attack by predators. Gibbons select trees that are difficult for predators to access, for example, larger, taller trees with few low branches or attached lianas or vines [e.g., *Nomascus concolor*, Fan and Jiang, 2008; *Hylobates lar*, Reichard, 1998]. Many primates sleep towards the terminal ends of branches, which may allow early detection of an arboreal predator and permit escape [Anderson, 2000]. Alternatively, early detection may give the primates time to raise alarm and mob predators as a counter-strategy [Busse, 1980].

Are Chimpanzees and Other Large Apes at Risk of Predation?

Predation is a major cause of mortality in non-human primates [e.g., Cheney et al., 2004], but its selective influence is often difficult to study, given

that direct observations of predation are rare and few studies approach the question through direct study of sympatric predators [e.g., Hawkins and Racey, 2008; Jenny and Zuberbühler, 2005; Mitani et al., 2001]. The extent to which great apes are at risk from predation is debated, given that predation rate decreases with increasing primate body size across taxa [Cheney and Wrangham, 1987].

Predator-prey interactions of potential chimpanzee predators have been studied at only one site where chimpanzees live sympatrically with predatory species, the Tai forest [Jenny and Zuberbühler, 2005; Shultz et al., 2004; Zuberbühler and Jenny, 2002]. Through radio-tracking data of two leopards and subsequent fecal analysis, Zuberbühler and Jenny [2002] determined that leopards preferred large and abundant prey. Despite this general trend, the authors found chimpanzees to be an exception, as they were rarely preyed upon, and so they suggested that apes may be large enough to be beyond the prey range of leopards [Zuberbühler and Jenny, 2002]. Shultz et al. [2004] re-analyzed these same data to control for prey abundance by calculating predation rates for all predators as a proportion of available prey. They extrapolate a leopard predation rate of 10% of available chimpanzees [Shultz et al., 2004]. Hayward et al. [2006a] analyzed leopard prey preferences across their range and found that leopards preferentially prey on species of 10–40 kg, and the most preferred prey weight is 23 kg. Chimpanzees fall very close to this preferred weight because body weights were adjusted for leopard bias to hunting juveniles and females; adjusted weight for chimpanzees is 22.5 kg [Hayward et al., 2006a]. In their analysis chimpanzee and gorilla are estimated to be taken by leopards in accordance to their abundance.

Prey preferences of other potential ape predators have not been studied where they live sympatrically with great apes. Prey preferences of lions differ dramatically from that of leopards, with preferred prey body size falling within the range 190–550 kg [Hayward and Kerley, 2005]. Spotted hyena predatory behavior studies are similarly biased towards open grassland savanna habitats where they preferentially prey upon few species; most prey are taken according to their abundance [Hayward, 2006]. African wild dog (*Lycaon pictus*) prefer prey of either 16–32 kg or 120–140 kg depending on their group size [Hayward et al., 2006b]. Indiscriminate predation on available mammals by spotted hyena, and the preferred prey size of African wild dog, suggests that a large and often terrestrial primate like the chimpanzee would be at risk from predation by these species. However, studies of lion, spotted hyena, and African wild dog living in ecosystems other than open grassland savanna are lacking, such as the wooded savannas where all live sympatrically with chimpanzees. Predation risk is intuitively greater when chimpanzees

are terrestrial, and although this may put pressure on arboreal nesting and pre- and post-sleep behaviors, it is unlikely to select for further inaccessibility of nests within trees. However, leopards, and potentially lions, may put pressure on location of ape nests within trees because they are able to climb adeptly [Makacha and Schaller, 1969] and leopards are reported to take primates from their sleeping trees during the night [Busse, 1980; Cowlshaw, 1994].

Direct observation of predation on apes is rare and most evidence is indirect. Leopard predation on chimpanzees (over five years) is reported in the Tai forest and includes nine likely attacked individuals, but none directly observed and only one leopard scat with chimpanzee bones and hair [Boesch, 1991; Zuberbühler and Jenny, 2002]. Leopards in Tai were once reported to scavenge a chimpanzee carcass [Jenny and Zuberbühler, 2005]. Evidence of leopard predation on chimpanzees (6/196 leopard scats) has also been recorded in Lope, Gabon [Henschel et al., 2005]. Evidence of leopard predation on other great apes is rare, although Fay et al. [1995] described a probable leopard attack on lowland gorilla including a digit in leopard scat and recent systematic studies of leopard scats in sympatric areas have revealed evidence of predation on gorillas [9/196 scats: Henschel et al., 2005] and bonobos [1/5 scats: D'Amour et al., 2006]. Rates of leopard predation on apes therefore range up to 5% of scat samples.

Lion predation has been described once in Mahale Mountains National Park during 45 years of research, where the deaths of four individuals were attributed to lion over a four-month period, due to repeated observations of chimpanzee hair and bone found in lion feces during that period [Tsukahara, 1993]. Lions were observed in the area over two years and are not commonly observed close to the habituated Mahale M-group of chimpanzees, although lions do commonly inhabit the National Park and the wider ecosystem.

Great apes are thought to be at low risk of predation by large carnivores due to their low densities [Hayward et al., 2006a], large body size [Zuberbühler and Jenny, 2002], or predominant distribution within closed forest habitats [Lehmann and Dunbar, 2009]. However, even relatively low rates of predation could have a significant impact on great apes, especially considering their long life histories, including slow maturation to reproductive age and long inter-birth intervals resulting from extended maternal care. Finally, great apes may also have evolved behavioral counter-strategies to predation, resulting in low currently observed rates of predation, which does not preclude a significant selective pressure now and during hominoid evolution. Chimpanzees have been reported to vocalize ("bark" or "alarm call") in response to leopards [Boesch, 1991]. There are several reports of chimpanzees' aggression towards leopards and lions,

including aimed throwing of sticks and rocks, which may be a response to a recognized threat [Boesch, 1991; Goodall, 1968; Hiraiwa-Hasegawa, 1989; Izawa and Itani, 1966; Kano, 1972; Nishida, 1989; Pruett et al., in prep]. Nest building could be another such behavior that limits risk of predation.

Shelter Construction and Predator Defense

One of the primary functions of animal construction behavior is defense against predators. Anti-predatory function of shelters takes two forms; concealment and repulsion of attack following detection [Hansell, 2005]. Crypsis could be a possible function of nest building in great apes, as a leafy mass may be less detectable than the silhouette of a large-bodied primate on a branch; this hypothesis deserves testing. Two other large mammals build convergent structures to great apes: Brown nosed coatis, *Nasua nasua* [Olifiers et al., 2009], and Andean (spectacled) bears, *Tremarctos ornatus* [Goldstein, 2002]. Coatis' nests are also hypothesized to function for predator defense against four large felid species; *Panthera onca*, *Puma concolor*, *Leopardus pardalis*, and *Puma yagouaroundi* [Olifiers et al., 2009]. Andean bear nests are often built next to areas of conflict with humans (the only predators of bears) where bears have killed and eaten domestic cattle [Goldstein, 2002].

Great ape nesting is hypothesized to serve an anti-predator function by making the builders inaccessible. Many studies have examined great ape nesting in detail and reveal preferences for particular species of trees, areas of the landscape, and morphological characteristics of trees [Ancrenaz et al., 2004; Brownlow et al., 2001; Fruth, 1995; Hernandez-Aguilar, 2006; Tutin et al., 1995; Wrogemann, 1992]. Some of the physical characteristics of trees selected for nesting are in accordance with anti-predatory function of arboreal nesting; for example chimpanzees in Issa select trees that are taller, larger, and have higher lowest branch height than other suitable trees in the vicinity [Hernandez-Aguilar, 2006]. Koops et al. [2012a] found no evidence of selection of trees or nest sites that would be expected to have an anti-predatory function. However, their study was conducted at a site where predators are absent, and few studies have directly compared nesting behavior across sites that differ in characteristics hypothesized to influence nest function, such as predator presence [Pruetz et al., 2008].

Baldwin et al. [1981] found that chimpanzees in a predator-rich, dry savanna site in Senegal (Mt Assirik) nested higher, in larger groups, and more often within the same trees as conspecifics than chimpanzees in a likely predator-poor, tropical forest in Equatorial Guinea. However, without controlling for differences in tree height, community size, and available nesting trees it is not possible to determine

whether variation in nesting was due to predator pressure or other cross-site differences. Pruetz et al. [2008] addressed this issue in cross-site comparisons by contrasting nesting behavior in Mt Assirik and predator-poor Fongoli in Senegal, which are separated by only 45 km and have similar vegetation. Chimpanzees in Mt Assirik nested at greater heights and closer together than chimpanzees in Fongoli, supporting the hypothesis that nesting in great apes protects against predation [Pruetz et al., 2008].

We aim to further test hypotheses of how nests and nesting behavior may serve an anti-predator function by comparing nesting behavior of two communities of savanna-dwelling chimpanzees that differ in the presence of predators and by controlling for other sources of variation wherever possible. Specifically, we hypothesize:

- (a) Chimpanzees in Issa, a predator-rich site, prefer to nest in forest patches more often than do chimpanzees in Fongoli, a site relatively devoid of predators, as forest may provide greater opportunity for arboreal escape.
- (b) A greater proportion of the community nests together in Issa than in Fongoli, as greater group size may provide more protection from and detection of predators in a predator rich site.
- (c) Nesting sites in Issa more often have an arboreal, alternative escape route (rather than descent from the nest site to the ground), than in Fongoli. If arboreal predation is a risk, apes in a predator rich site are predicted to select locations for ease of escape.
- (d) Chimpanzees nest more frequently within the same tree as conspecifics in Issa, than in Fongoli, as sleeping in close proximity to conspecifics may provide greater protection from and opportunity for detection of predators.
- (e) Chimpanzees at Issa nest comparatively higher within trees and further out from the tree trunk than in Fongoli, controlling for tree size, as nesting higher and/or peripherally within the tree crown at a predator rich site may make a nester more inaccessible to potential predators.

METHODS

Study Sites

Fongoli

The Fongoli study site (12°13.90N, 12°11.30W) is at the north-western edge of the chimpanzee species' distribution and is in south-eastern Senegal, about 35 km north of the border with Guinea and 85 km west of the border with Mali [Pruetz, 2006]. Fongoli is 10 km northwest of the town of Kedougou and 45 km southeast of the Assirik study site in the Parc National du Niokolo-Koba [Pruetz, 2006]. The vegetation of south-eastern Senegal is a mosaic

woodland-savanna habitat dominated by open deciduous woodland and wooded grassland, interspersed with areas of bamboo, plateau, and thicket, plus small patches of closed canopy gallery forest (including "ecotone" forest) that make up 2% of the landscape [Pruetz, 2006; Pruetz et al., 2002]. Vegetation types were classed similarly for the purpose of this study and are described in Table I. Pruetz and Bertolani [2009] reported vegetation composition at Fongoli to be 46% woodland, 36% grassland, 12% bamboo, 4% field, and 2% forest. Previous work has shown that Fongoli chimpanzees nest most frequently in woodland (65% of nests), followed by grassland (23%), and gallery forest (8%). However, gallery forest is the preferred nesting habitat when vegetation availability is considered [Pruetz et al., 2008].

The Fongoli chimpanzees range over 86 km² [Skinner and Pruetz, 2012]. During the study period, the community numbered 33–34 individuals, following the birth of an infant female, and the disappearance of an old male. Fauna has been heavily affected by hunting and those species that remain occur only at very low densities [Pruetz et al., 2002]. Fongoli has few large mammals, and no evidence of large predatory species (lion, *Panthera leo*; wild dog, *L. pictus*; leopard, *P. pardus*; spotted hyena, *Crocuta crocuta*) was found in systematic surveys [Pruetz et al., 2008], although leopard, spotted hyena, and side-striped jackal (*Canis adustus*) have since been seen occasionally [Pruetz et al., in prep.]. Pruetz et al. [2008] reported that predators in Fongoli were common within the last century and so may have been more common during the lifetimes of some of the older members of the Fongoli community.

Issa

The Issa study area (05°23.34S, 30°35.04E) lies in the west of the Ugalla region, 81 km inland and east of Lake Tanganyika in western Tanzania. Ugalla is likely the eastern most distribution of chimpanzees in Africa [Massawe, 1992]. Ugalla is a 3,352 km² region of broad valleys broken up by steep mountains and flat hilltop plateaus of 900–1,800 m in elevation. Most streams are seasonal. Two permanent rivers, the Malagarasi to the north and the Ugalla to the west, form the boundaries of the region. The vegetation of the Ugalla region is miombo woodland, named for the dominant tree genera of *Brachystegia* and *Julbernardia* (Fabaceae). Hernandez-Aguilar [2006, 2009] described the vegetation mosaic of the Issa study area as: swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest (Table I). The first four vegetation types are open-canopy, grass-understorey vegetation, which covers 98.5% of the study area, whilst the other three are broadly classified as closed-canopy forest and comprise only 1.5% [Hernandez-Aguilar, 2009]. In this study and in previous research, the apes used only forest and

TABLE I. Closed Vegetation Types of Forest and Open Vegetation Types of Woodland, Wooded Grassland, Bamboo, Grassland and Swamp in Issa and Fongoli

This study	Issa vegetation types [from Hernandez-Aguilar, 2009]	Fongoli vegetation types [from Pruetz et al., 2002]
Forest	<i>Hill forest</i> : Evergreen and semi-deciduous species growing on escarpment edges or at points of seasonal runoff on hillsides <i>Thicket “msitu” forest</i> : Evergreen and semi-deciduous vegetation, dominated by lianas and climbers <i>Gallery “kabamba” forest</i> : Evergreen forest with open understory, usually along seasonal water courses	<i>Ecotone forest</i> : Evergreen woody vegetation at sites of water runoff from plateau edges <i>Gallery forest</i> : Tropical semi-deciduous lowland forest, usually along seasonal water courses. Multi-layered continuous canopy cover, and trees >10 cm in DBH average 12.5 m in height
Woodland	<i>Woodland</i> : Deciduous trees and shrubs with grass understory and discontinuous canopy	<i>Woodland</i> : Drought-deciduous lowland woodland with mostly grass understory. Canopy cover discontinuous and trees over 10 cm DBH average 7.6 m in height
Wooded grassland	<i>Wooded grassland</i> : Dominated by grasses with isolated shrubs and trees.	<i>Wooded grassland</i> : Narrow-leafed savanna with isolated palms and deciduous trees
Bamboo	Not present	<i>Bamboo</i> : Flat-leafed savanna with isolated deciduous trees
Grassland	<i>Dry grassland</i> : Short grasses with isolated shrubs in broad valley lowlands or high plateaus, which are seasonally inundated	<i>Plateau (short grass) grassland</i> : Narrow-leafed savanna with isolated deciduous shrubs
Swamp	<i>Swamp “mbuga” grassland</i> : Tall grasses <3 m. Permanently inundated with few scattered trees or shrubs	Not present

woodland vegetation types for nesting. Hernandez-Aguilar [2009] measured >5,000 nests within the Issa study area, 93% of which were built in woodland and 7% in forest. In both vegetation-types, nests were associated with steep slopes, although some also were built in flat valley bottoms or plateaus [Hernandez-Aguilar, 2009].

Research in Issa focuses within an 85 km² study area, within which genetic analyses have identified at least 67 individuals who form the Issa community [Rudicell et al., 2011]. The Ugalla ecosystem remains intact, but in recent years, the area has been under greater pressure from human disturbance such as agricultural expansion, cattle herding, fire, logging, and poaching. Unlike Fongoli, and despite some human hunting pressure, Issa has a full complement of potential chimpanzee predators, including lion, leopard, hyena, and wild dog (Table II). These same

predator species were present historically, but whether their numbers are stable or declining is unknown without longitudinal data on densities [Hernandez-Aguilar, 2006; Kano, 1972].

In Issa, the only previous long-term study, in 2001–2003, reported frequent observations of potential predators. Hernandez-Aguilar [2006] found on average evidence of leopard every two weeks, spotted hyena every month, African wild dogs every three months, and lion every six months over the course of a 22-month study. When FS visited the area of her camp in 2005 she saw a lion nearby. Hernandez-Aguilar [2006] also reported chimpanzees to vocalize in response to leopard or lion vocalizations. Kano [1972] found the highest density of all four carnivore species in Ugalla, compared to other areas he surveyed in western Tanzania.

TABLE II. Evidence of Carnivore Species in Fongoli and Issa During the Study Periods

Species	Fongoli	Frequency (6 months)	Issa	Frequency (12 months)
<i>Crocuta crocuta</i>	Vocalizations	2	Scat and foot prints	7
<i>Lycan pictus</i>	No evidence	0	Seen	1
<i>Panthera leo</i>	No evidence	0	Vocalizations, scat, and possible roan antelope kill	5
<i>Panthera pardus</i>	No evidence	0	Seen, vocalizations, scat, and footprints	12

Data Collection

This research was approved by the Division of Biological Anthropology, University of Cambridge, and adhered to the legal requirements of Senegal and Tanzania and the American Society of Primatologists Principles for the Ethical treatment of Non Human Primates. Data were collected in two periods: At Fongoli data were collected only during the dry season from October 2007 to March 2008, while at Issa data were collected for a whole annual cycle from October 2008 to 2009. Only nests measured in Issa in the dry season (May–October) were included in these analyses, in order to be comparable to Fongoli. In addition, only tree nests are compared. No nests were built on the ground in Issa, however, 12% of confirmed night nests were built on the ground in Fongoli in this study [Stewart, 2011], and Pruettz et al. [2008] have suggested that a high prevalence of ground nests may be due to absence of predators in the area.

Predator presence

At both study sites opportunistic data were collected on presence of large mammals. Fongoli had little evidence of predators; while in Issa signs of several predatory species were observed (Table II). No predators, except for spotted hyenas, were recorded at Fongoli during the study period; spotted hyena vocalizations twice were heard at night during the study period.

Nest data

In both sites, only fresh night nest groups (from the night before) were selected for measurements. Nest groups were defined as all nests built on the same night within a 100-m search radius. Previous studies of forest-dwelling apes have defined post hoc a nest group to span a 30 m radius [e.g., Fruth, 1995]; we expanded this due to the more open habitat which allows greater visibility. In Fongoli, focal individuals were followed to the nesting site, and nests were often seen or heard being built before researchers returned to measure the following morning. In Issa, fresh nests groups were found opportunistically or after hearing vocalizations either during reconnaissance walks, or via the aid of solar powered acoustic transmission units, which allowed us to monitor distant vocalizations from a central computer at camp [Piel and Moore, 2010]. Nests were judged to be fresh if the nest was seen built the previous night or if moist feces or urine were found beneath the nest.

The following variables were compared: (1) Vegetation type. We recorded the vegetation type in which each nest was built and compared the frequency of use of open (open canopy, deciduous vegetation of woodland, wooded grassland, and

grassland) versus closed (closed canopy, evergreen forest) vegetation types for nesting. The number of groups built in open versus closed vegetation type was compared (where a nest group spanned open and closed vegetation, both were counted). Fongoli and Issa had similar availability of closed versus open vegetation types [Issa: 1.5% forest, Hernandez-Aguilar, 2006; Fongoli: 2% forest, Pruettz, 2006]. (2) Group size. Nesting group size was measured as the number of fresh nests found on the same day within 100 m of the nearest fresh nest. The size of Issa's community is estimated to be twice that of Fongoli, so we compared the size of nesting groups recorded in each site as a proportion of total community size. (3) Escape route. We noted the presence or absence of an alternative escape route out of the nesting tree, that is, connectivity by one or more branches to a neighboring tree canopy, other than descending to the ground. (4) Nest tree sharing. A proxy measure of proximity, number of nests per tree, was used to assess whether chimpanzees in Issa nest closer together than in Fongoli. (5) Position of nest within the tree crown. All height measures were taken with a clinometer (Suunto PM-5/360PC, range $0 \pm 90^\circ$ and $0 \pm 150^\circ$, precision 1° and 1%) to the nearest meter. All horizontal distances were measured to the nearest meter using a tape measure. In order to control for differences in tree size between Issa and Fongoli the following variables of nest position within trees were calculated post hoc (see Fig. 1):

- (i) Nest position as a proportion of tree crown height (a): The height of the nest above the tree crown base (b) was calculated by subtracting the crown base height (c) from the nest height above trunk base (d). We then divided the height of the nest above the tree crown base (b) by the height of the tree crown (a) to give the nest position as a proportion of the tree crown height. Nest position ranges from 0 (bottom of the tree crown) to 1 (top of the tree crown).
- (ii) Nest position as a proportion of tree crown radius: The sum of the distance of the nest to the trunk (e) and the nest to the tree crown edge (f) is taken as the radius of the tree crown (g) (specifically along the horizontal axis of the nest position relative to the tree trunk). We divided the horizontal distance of the nest to the trunk (e) by this tree crown radius (g) to calculate the position of the nest as a proportion of the tree crown radius. Nest position ranges from 0 (exactly above the trunk base) and 1 (at the periphery of the tree crown).

Analyses

All data were analyzed in Predictive Analytics Software PASW Statistics 18, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, www.spss.com).

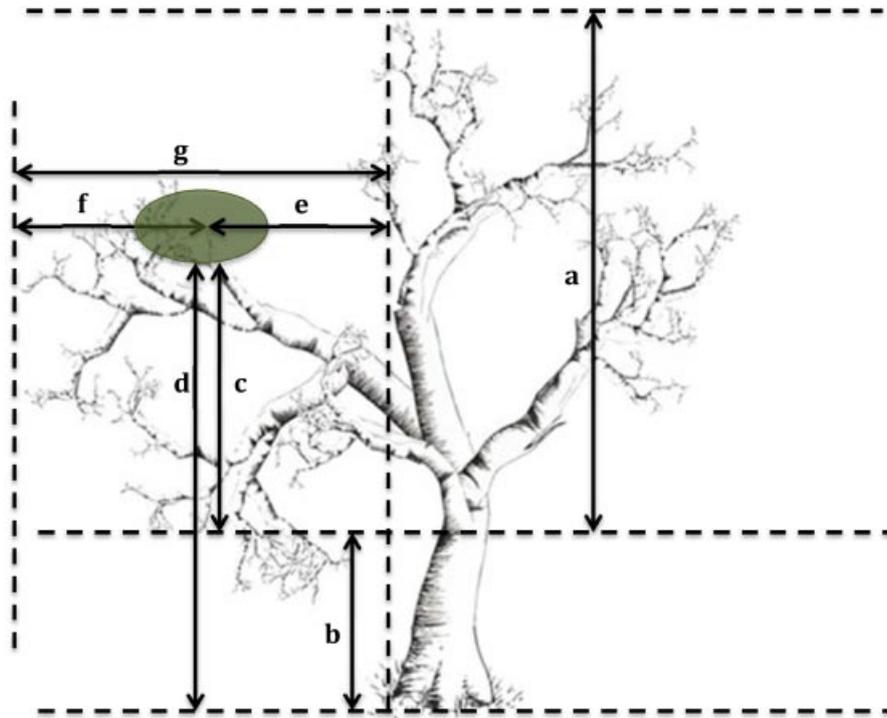


Fig. 1. Nest position as a proportion of tree crown height and nest position as a proportion of tree crown radius were calculated using the depicted measurements. (1) Nest position = ca ($c = d - b$). (2) Nest position = eg ($g = e + f$).

Proportions of nests and nest groups were compared using chi-square tests. Normally distributed data were analyzed using one-way analysis of variance (ANOVA), whilst non-normally distributed data were analyzed using Kruskal–Wallis and Mann–Whitney tests. Where multiple comparisons were used, all P -values were Bonferroni corrected.

RESULTS

In Fongoli, 58 nest groups were measured, compared to 40 in Issa. The proportion of nest groups built in open versus closed vegetation did not differ between Fongoli and Issa ($\chi^2 = 1.65$, $df = 1$, $P > 0.05$). At Issa, 47% of nest groups were built in forest and 53% in woodland, while in Fongoli 32% were built in forest and 68% in open vegetation types. If low availability of forest vegetation types is taken into account, nests were more frequently found in forest than expected by chance in both sites (Fongoli: $\chi^2 = 322.4$, $df = 1$, $P < 0.001$; Issa: $\chi^2 = 279.1$, $df = 1$, $P < 0.001$), but open habitat (woodland, wooded grassland, and grassland) was used randomly in Fongoli ($\chi^2 = 2.7$, $df = 1$, $P > 0.05$) and avoided in Issa ($\chi^2 = 6.0$, $df = 1$, $P < 0.05$).

The median number of nests per group in Fongoli (median = 6, range = 1–18) did not differ from Issa (median 4.5, range = 1–26; Mann–Whitney, $N_1 = 58$, $N_2 = 40$, $Z = 1.07$, $P = 0.29$). However, the proportion of the community that nested together

was greater in Fongoli (median = 21%, range = 3–53%) than in Issa (median = 12%, range = 1–39%; Mann–Whitney, $N_1 = 58$, $N_2 = 40$, $Z = 3.64$, $P < 0.001$).

In both Fongoli and Issa, most nests (>80%) had an alternative escape route. There was no significant difference in the proportion of nests built in closed forest that have alternative escape routes in Issa versus Fongoli ($\chi^2 = 0.23$, $df = 1$, $P = 0.63$). However, in open vegetation types a greater proportion of nests in Fongoli had an alternative escape route than in Issa ($\chi^2 = 21.26$, $df = 1$, $P < 0.001$).

More nests were built in the same trees as other nests in Issa ($\chi^2 = 3.87$, $df = 1$, $P = 0.049$); in Fongoli 36% ($N = 411$) of nests and in Issa 43% ($N = 307$) of nests shared a tree with one or more nests. The number of nests per tree tended to be greater in Issa (median = 1, mean = 1.4, range = 1–7, $N = 226$) than in Fongoli (median = 1, mean = 1.2, range = 1–6, $N = 317$; Mann–Whitney, $Z = 1.93$, $P = 0.054$).

There was no difference in proportional nest height within the tree crown among tree nests built in forest, woodland, or grassland vegetation types in Fongoli ($F = 1.82_{(2, 331)}$, $P = 0.17$). In Issa, there was a tendency for nests to be built higher within the tree crown in forest than in woodland ($t = 1.93$, $N_1 = 186$, $N_2 = 99$, $P = 0.055$). A one-way ANOVA shows differences between sites and vegetation types ($F = 10.49_{(3, 568)}$, $P < 0.001$). Post hoc comparisons

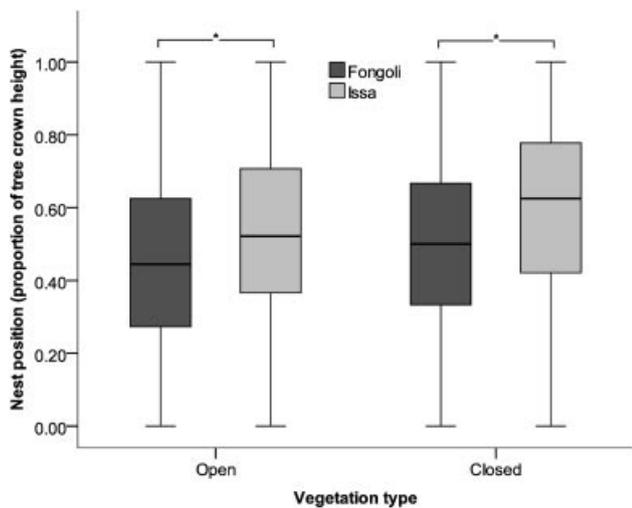


Fig. 2. Nest position in tree crown as a proportion of tree crown height in open and closed vegetation types in Fongoli versus Issa (indicates significant difference). Bars outside boxes indicate range.

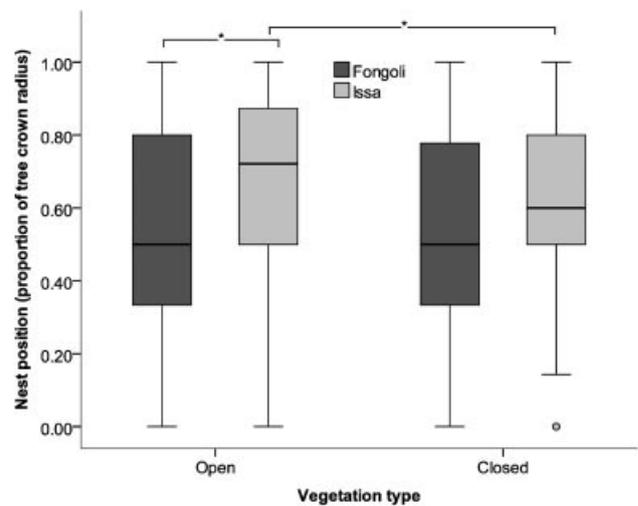


Fig. 3. Nest position in the tree crown as a proportion of tree crown radius in different vegetation types in Fongoli and Issa (indicates significant difference). Bars outside boxes indicate range, excluding outliers, which are indicated by circles.

confirm that no difference existed between nests built in woodland versus forest vegetation in Fongoli ($P = 0.73$) or Issa ($P = 0.30$). Nests in Issa were built proportionately higher within the tree crown than nests in Fongoli (forest, $P = 0.002$; woodland, $P = 0.046$; Fig. 2).

The proportional distance of the nest from the tree trunk did not differ across vegetation types used for nesting in Fongoli (Kruskal–Wallis, $H = 0.64_{(2, 297)}$, $P = 0.72$), but in Issa, nests built in forest vegetation types were proportionately closer to the trunk than nests built in woodland (Mann–Whitney, $N_1 = 194$, $N_2 = 100$, $Z = 2.44$, $P = 0.015$). There was no difference in the proportional distance of the nest from the trunk in Issa versus Fongoli in forest vegetation (Mann–Whitney, $N_1 = 108$, $N_2 = 194$, $Z = 1.81$, $P = 0.140$), although nests were built proportionately farther away from the tree trunk in Issa than in Fongoli in woodland vegetation (Mann–Whitney, $N_1 = 147$, $N_2 = 100$, $Z = 2.83$, $P = 0.010$; Fig. 3).

DISCUSSION

The results of this cross-site comparison provide some clarification on how predation influences ape nesting behavior in a savanna habitat. Although relative to availability, forest vegetation types are preferred for nesting in both sites, Issa chimpanzees avoided nesting in open vegetation relative to its availability, whilst Fongoli chimpanzees nested randomly in open vegetation. Pruetz et al. [2008] found the same in comparing use of closed and open vegetation types relative to availability in Assirik (full complement of predators present) versus Fongoli. However, year-round data from Issa show that

avoidance of nesting in woodland is seasonal; in the wet season selection of vegetation types for nesting was reversed with a greater proportion of nest groups built in woodland [Stewart, 2011]. Pruetz et al. [2008] found that Fongoli chimpanzees nested in forest six times less often than chimpanzees in Assirik, for a total frequency of 8% of nests in forest. In Issa, Hernandez-Aguilar [2009] found that only 7% of nests were built in forest compared to a total proportion of 36% of nest groups (or 49% of nests) in this study. Higher proportions of forest nests recorded in this study could be influenced by several factors; sample size was lower, only fresh nests were included, and nests were located by tracking chimpanzees compared to systematic survey of nests of all stages of decay by Pruetz et al. [2008] and Hernandez-Aguilar [2009]. Their results may have been influenced by decay and re-use rates of nests, as nests in forest disintegrate and are re-used at faster rates than nests in woodland [Stewart et al., 2011]. Thus, the relationship between predator presence and increased use of forest vegetation types found in this study and by Pruetz et al. [2008] may be due to other factors.

The seasonal difference in use of forest patches for nesting may be more influenced by seasonal availability of food resources or to greater availability of leafy vegetation in forest in the dry season. Issa and Fongoli are both highly seasonal environments. In Issa, woodland feeding tree species fruit less in the wet than in the dry season, but yet fruit more than forest vegetation in both wet and dry seasons [Hernandez-Aguilar, 2006]. In Fongoli, open vegetation types also provide most of chimpanzee food species, and availability of fruits is greatest in the late dry season [Pruetz, 2006]. Most trees in Issa and Fongoli lose

their leaves from the beginning to the end of the dry season, with very few trees in leaf towards the end of the dry season [Issa, Hernandez-Aguilar, 2006; Fongoli, pers. obs.]. Thus, in both of these dry sites the chimpanzees are likely foraging and ranging in open vegetation in the dry seasons, but returning to leafy evergreen forest patches for night nesting.

No difference in nesting group size was found in this study. Baldwin et al. [1981] found that chimpanzees in Senegal (Mt Assirik) nested in larger groups than chimpanzees in Equatorial Guinea and hypothesized that this difference was influenced by greater predation threat in Mt Assirik. The median and range of group sizes found at Fongoli and Issa fall within the range of other chimpanzees [Fruth and Hohmann, 1996]. Tutin et al. [1983] suggested that the greater threat of predation at Mt Assirik, led savanna chimpanzees to be more cohesive, as a higher proportion of the community remained together compared to other populations. If chimpanzees at Issa were also aggregating at night due to predation pressure, we expect a greater proportion of the community to nest together than in Fongoli. However, the reverse was found. A large number of factors in addition to predation-risk influence subgroup sizes within chimpanzee communities, including food availability and estrous females [Anderson et al., 2002]. Our results could also have been influenced by methodological differences; data collection in Fongoli was biased towards nest groups containing males, as only males are targeted as focal subjects [Pruetz, 2006]. However, data collection in Issa may have been similarly biased to mixed and large parties, because most fresh nest groups were detected via the chimpanzees' vocalizations.

Baldwin et al. [1981] also found no difference in inter-nest distance between the two sites compared but did find that more nests were built in the same trees in Mt Assirik than Equatorial Guinea. A similar tendency was found in this study, and a greater proportion of nests were built in the same tree as other nests in Issa versus Fongoli, suggesting that the presence of predators may influence proximity of the nesters, providing protection in numbers and greater opportunity for predator detection. However, tree sharing may also reflect the size of the tree or availability of suitable trees, which was not controlled here. Larger groups might though have reduced crypsis and be more easily detected by predators.

Most nests in Assirik were found to have at least one alternative escape route [Baldwin, 1979], which was interpreted as a possible solution to predation pressure from leopards that may be able to climb nesting trees. However, this proportion has not previously been compared to other chimpanzee study sites regardless of predator guild. Contrary to the hypothesis that a greater proportion of nests would have an alternative escape route in a predator-rich

(Issa) habitat, results show a greater proportion of nests in open vegetation types in a predator-scarce (Fongoli) habitat had escape routes. As tree density is similar in open habitats in Fongoli (0.035 stems >5 cm DBH/m², FS unpublished data) and Issa (0.031 stems >5 cm DBH/m²; FS unpublished data) the difference in presence of an escape route does not appear to be influenced by tree density. Potential for escape from a site may be a less important characteristic of a good sleeping site than inaccessibility to predators. For example, two studies demonstrated reluctance of baboons to leave a sleeping tree: Bert et al. [1967 cited in Anderson, 1998] found that baboons refused to flee when the authors shone lamps and created disturbance at the base of the tree. Busse [1980] watched baboons harass a leopard in their sleeping tree from the refuge of the terminal branches. Similarly, chimpanzee nests may allow these large apes to take refuge in the terminal branches where leopards likely cannot get to them.

Only by comparing nest position within trees was it possible to control for cross-site difference in other variables that influence nest characteristics; for example, nest height correlates with tree height in Fongoli and Issa [Stewart, 2011]. Our results support the hypothesis that nests may function to allow chimpanzees refuge in locations more peripheral and inaccessible in trees to protect against predator attack. Assirik chimpanzees nest higher within trees than both those of Fongoli [Pruetz et al., 2008] and Equatorial Guinea [Baldwin et al., 1981]. Our results show that chimpanzees in Issa also nest more peripherally within trees than chimpanzees in Fongoli.

Other large-bodied primates like baboons have been suggested to sleep in peripheral locations within the tree crown as a protective measure against predation, resulting in males nesting closer to the trunk than females or juveniles [Anderson, 1984]. Yet other large primates, like gibbons, sleep leaning up against the trunk of smaller sleeping trees [Reichard, 1998]. Gibbons are vulnerable to predation by several sympatric species, including several felids, birds of prey, pythons and humans. They may have to rely on selecting inaccessible trees for protection from predators [Reichard, 1998]; especially as they lack nest-building technology that might allow larger-bodied apes to sleep more peripherally. Further investigation is needed to test whether limb locations selected for nesting are too thin to support the weight of the builder without the construction of a nest combining multiple supporting branches.

Pruetz et al. [2008] predicted that arboreal nesting in Fongoli will decrease as the chimpanzees continue to live in a predator-free environment. Mean nest height recorded at Fongoli in this study (2007–2008) was only 4.9 m [Stewart, 2011] compared to a mean of 7.1 m recorded during the dry seasons in

2000–2001 by Pruett et al. [2008]. The proportion of ground nests during the current study [12%; Stewart, 2011] was also a four times greater than that found by Pruett et al. [2008; 3%]. These results accord with their hypothesis. Chimpanzees in Fongoli may be able to nest on the ground because it is safe to do so in the absence of predators. However, this does not explain why they choose to do so [see Koops et al., 2012b]. It may be that ground nests are more efficient, requiring less effort to construct a comfortable platform; in Fongoli ground nests are less complex, built with fewer steps, and made more often with thin malleable materials [Stewart, 2011]. In Semliki, stability of thermal conditions of ground nest, compared to tree nest, sites suggests that nesting on the ground may impose less thermal stress and is likely not done in some habitats due to the risk of predation [Samson & Hunt, 2012]. Thus, as predators continue to be absent from Fongoli, we may expect frequency of ground nesting to increase in this community.

However, the difference in nest heights recorded in the current study compared to Pruett et al. [2008] could be due to several alternative factors. Habituation efforts began at the same time as Pruett et al. [2008] collected data on nests in Fongoli. Hicks [2010] found that a higher prevalence of ground nesting was associated with lower human density and evidence of poaching, but was not associated with density of signs of other non-human predators, across 160 km of transects through the northern Democratic Republic of Congo. The Fongoli chimpanzees have long lived in close habitation with local humans, but the sudden increased researcher interest in chimpanzees (for habituation) during Pruett et al.'s [2008] study might have increased nesting height and decreased ground nesting temporarily in this community. Also, as only fresh nests were included in the current study, differences in proportion of ground nests and nest heights may have been influenced by a differential decay or detection rate of nests built at various heights or on the ground [e.g., variation in orangutan nest decay rates, Mathewson et al., 2008].

A large number of factors influence nest site selection in chimpanzees, of which danger from terrestrial predators is likely to be one. We have tried to control for the influence of factors, other than predator presence, in comparing nesting position within trees in Fongoli and Issa; relatively more peripheral nests built within trees where there is high predator presence supported the anti-predator function of nests. Future comparative and experimental research into great ape nest building will help to address the influence of predation pressure, environment, or cultural differences on observed variation in nests. More research is also needed on the diet of leopards and other predators living sympatrically with chimpanzees and in a variety of

habitats. The most systematic data available to date are from a single research site (Tai) [Jenny and Zuberbühler, 2005], and rates of the presence of ape remains within leopard feces appear to be low. However, the impact of even low rates of predation on long-lived, slowly reproducing species like the great apes is likely to be high and have had a high selection pressure on ape behavior.

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REFERENCES

- Ancrenaz M, Calaque R, Lackman-Ancrenaz I. 2004. Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. *Int J Primatol* 25:983–1000.
- Anderson JR. 1984. Ethology and ecology of sleep in monkeys and apes. *Adv Study Behav* 14:165–229.
- Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am J Primatol* 46:63–75.
- Anderson JR. 2000. Sleep-related behavioral adaptations in free-ranging anthropoid primates. *Sleep Med Rev* 4:355–373.
- Anderson DP, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing fission–fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch C, Hohmann G, Marchant LF, editors. *Behavioral diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press. p 90–101.
- Baldwin PJ. 1979. The natural history of the chimpanzee (*Pan troglodytes verus*) at Mt. Assirik, Senegal [Ph.D. dissertation]. Stirling: University of Stirling.
- 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.

- Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117:220–242.
- 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. *Am J Primatol* 55:49–55.
- Busse C. 1980. Leopard and lion predation upon Chacma baboons living in the Moremi wildlife reserve. *Botswana Notes Rec* 12:15–21.
- Cheney DL, Seyfarth RM, Fischer J, et al. 2004. Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25:401–428.
- Cheney DL, Wrangham RW. 1987. Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 227–239.
- Coolidge FL, Wynn T. 2009. *The rise of Homo sapiens: the evolution of modern thinking*. Malden, MA: Wiley-Blackwell.
- Cowlishaw G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131:293–304.
- D'Amour DE, Hohmann G, Fruth B. 2006. Evidence of leopard predation on bonobos (*Pan paniscus*). *Folia Primatol* 77:212–217.
- Fan P-F, Jiang X-L. 2008. Sleeping sites, sleeping trees, and sleep-related behaviors of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *Am J Primatol* 70:153–160.
- Fay JM, Carroll R, Kerbis-Peterhans JC, Harris D. 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *J Hum Evol* 29:93–99.
- Fruth B. 1995. Nests and nest groups in wild bonobos (*Pan paniscus*): ecological and behavioral correlates [Ph.D. dissertation. Aachen, Shaker: Ludwig-Maximilians-Universität München].
- Fruth B, Hohmann G. 1996. Nest building behavior in the great apes: the great leap forward? In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press p 225–240.
- Goldstein IR. 2002. Andean bear-cattle interactions and tree nest use in Bolivia and Venezuela. *Ursus* 13:369–372.
- Goodall J. 1968. The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Anim Behav Monogr* 1:165–311.
- Hamilton WJ. 1982. Baboon sleeping site preferences and relationships to primate grouping patterns. *Am J Primatol* 3:41–53.
- Hansell M. 2005. *Animal architecture*. Oxford: Oxford University Press.
- Hayward MW. 2006. Prey preferences of the spotted hyena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *J Zool* 270:606–614.
- Hayward MW, Kerley GIH. 2005. Prey preferences of the lion (*Panthera leo*). *J Zool* 267:309–322.
- Hayward MW, Henschel P, O'Brien J, et al. 2006a. Prey preferences of the leopard (*Panthera pardus*). *J Zool* 270:298–313.
- Hayward MW, O'Brien J, Hofmeyr M, Kerley GIH. 2006b. Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): ecological requirements for conservation. *J Mammal* 87:1122–1131.
- Hawkins CE, Racey PA. 2008. Food habits of an endangered carnivore, *Cryptoprocta ferox*, in the dry deciduous forests of western Madagascar. *J Mammal* 89:64–74.
- Henschel P, Abernethy KA, White LJT. 2005. Leopard food habits in the Lopé National Park, Gabon, Central Africa. *Afr J Ecol* 43:21–28.
- Hernandez-Aguilar RA. 2006. Ecology and nesting patterns of chimpanzees (*Pan troglodytes*) in Issa, Ugalla, Western Tanzania [Ph.D. dissertation]. Los Angeles: University of Southern California.
- Hernandez-Aguilar RA. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *J Hum Evol* 57:350–364.
- Hicks TC. 2010. A chimpanzee mega-culture? Exploring behavioral continuity in *Pan troglodytes schweinfurthii* across northern DR Congo [Ph.D. dissertation]. Amsterdam: Universiteit van Amsterdam.
- Hiraiwa-Hasegawa M. 1989. Sex differences in the behavioral development of chimpanzees at Mahale. In: Heltne PG, Marquardt LA, editors. *Understanding chimpanzees*. Cambridge, MA: Harvard University Press. p 104–115.
- Izawa K, Itani J. 1966. Chimpanzee in Kasakati Basin, Tanganyika. I. Ecological study in the rainy season 1963–1964. *Kyoto Univ Afr Stud* 1:73–156.
- Jenny D, Zuberbühler K. 2005. Hunting behavior in West African forest leopards. *Afr J Ecol* 43:197–200.
- Kano T. 1972. Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto Univ Afr Stud* 7:37–129.
- Koops K, McGrew WC, de Vries H, Matsuzawa T. 2012a. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and anti-vector hypotheses. *Int J Primatol* 33:356–380.
- Koops K, McGrew WC, Matsuzawa T, Knapp LA. 2012b. Terrestrial nest-building by wild chimpanzees (*Pan troglodytes*): implications for the tree-to-ground sleep transition in early hominins. *Am J Phys Anthropol* 148:351–361.
- Lehmann J, Dunbar R. 2009. Implications of body mass and predation for ape social system and biogeographical distribution. *Oikos* 118:379–390.
- Li D, Ren B, Grueter CC, Li B, Li M. 2010. Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. *Am J Primatol* 72:1092–1099.
- Lima SL, Rattenborg NC. 2007. A behavioral shutdown can make sleeping safer: a strategic perspective on the function of sleep. *Anim Behav* 74:189–197.
- Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ. 2005. Sleeping under the risk of predation. *Anim Behav* 70:723–736.
- Makacha S, Schaller GB. 1969. Observations on lions in the Lake Manyara National Park, Tanzania. *Afr J Ecol* 7:99–103.
- Massawe ET. 1992. Assessment of the status of chimpanzee populations in western Tanzania. *Afr Stud Monogr* 13:35–55.
- Matsuda I, Tuuga A, Higashi S. 2010. Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: why do they sleep alone inland on flooded days? *Ecol Res* 25:475–482.
- Mathewson PD, Spehar SN, Meijaard E, et al. 2008. Evaluating orangutan census techniques using nest decay rates: implications for population estimates. *Ecol Appl* 18:208–221.
- Meddis R. 1975. On the function of sleep. *Anim Behav* 23:676–691.
- Mitani JC, Sanders WJ, Lwanga JS, Windfelder TL. 2001. Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav Ecol Sociobiol* 49:187–195.
- Nishida T. 1989. A note on the chimpanzee ecology of the Ugalla Area, Tanzania. *Primates* 30:129–138.
- Olfifiers N, Bianchi RC, Mouro GM, Gompper ME. 2009. Construction of arboreal nests by brown-nosed coatis, *Nasua nasua* (Carnivora: Procyonidae) in the Brazilian Pantanal. *Zoologia* 26:571–574.
- Piel AP, Moore J. 2010. Monitoring movements: tracking unhabituated chimpanzees in Ugalla, Western Tanzania using a novel method—real-time acoustic monitoring. *Int. Primatol. Soc. XXIII Congr. Abstr* 656.
- Pruetz JD. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding ecology in apes and*

- other primates: ecological, physical and behavioral aspects. Cambridge: Cambridge University Press. p 161–182.
- Pruetz JD, Bertolani P. 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: implications for hominin adaptations to open habitats. *Paleoanthropology* 2009:252–262.
- Pruetz JD, Boyer KM, Kante D, Sadiakho M. in prep. Weapon use against predators by savanna chimpanzees at Fongoli, Senegal.
- Pruetz JD, Fulton SJ, Marchant LF, et al. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401.
- Pruetz JD, Marchant LF, Arno J, McGrew WC. 2002. Survey of savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 58:35–43.
- Rattenborg NC, Lima SL, Amlaner CJ. 1999. Half-awake to the risk of predation. *Nature* 397:397–398.
- Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *Am J Primatol* 46:35–62.
- Rudicell RS, Piel AP, Stewart FA, et al. 2011. High prevalence of Simian Immunodeficiency Virus Infection in a community of savanna chimpanzees. *J Virol* 85:9918–9928.
- Samson DR, Hunt KD. 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *Am J Primatol* 74:811–818.
- Shultz S, Noë R, McGraw WS, Dunbar RIM. 2004. A community-level evaluation of the impact of prey behavioral and ecological characteristics on predator diet composition. *Proc R Soc Lond B Biol Sci* 271:725–732.
- Siegel JM. 2005. Clues to the functions of mammalian sleep. *Nature* 437:1264–1271.
- Skinner MF, Pruetz JD. 2012. Reconstruction of periodicity of repetitive linear enamel hypoplasia from perikymata counts on imbricational enamel among dry-adapted chimpanzees (*Pan troglodytes verus*) from Fongoli, Senegal. *Am J Phys Anthropol* 149:468–482.
- Stewart FA. 2011. The evolution of shelter: ecology and ethology of chimpanzee nest building [Ph.D. dissertation]. Cambridge: University of Cambridge.
- Stewart FA, Piel AP, McGrew WC. 2011. Living archaeology: artefacts of specific nest-site fidelity in wild chimpanzees. *J Hum Evol* 61:388–395.
- Tsukahara T. 1993. Lions eat chimpanzees: the first evidence of predation by lions on wild chimpanzees. *Am J Primatol* 29:1–11.
- Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates* 24:154–173.
- Tutin CEG, Parnell RJ, White LJT, Fernandez M. 1995. Nest building by lowland gorillas in Lope Reserve, Gabon: environmental influences and implications for censusing. *Int J Primatol* 16:53–76.
- Wrogemann D. 1992. Wild chimpanzees in Lope, Gabon: census method and habitat use [PhD dissertation]. Bremen: Bremen University.
- Zuberbühler K, Jenny D. 2002. Leopard predation and primate evolution. *J Hum Evol* 43:873–886.