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Effects of Human Presence on Chimpanzee Nest Location in the Lebialem-Mone Forest Landscape, Southwest Region, Cameroon

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Chimpanzee · Nest · Cameroon · Predation · Human-wildlife conflict · Africa

Abstract

In several areas of Africa, great apes experience increasing predation pressure as a result of human activities. In this study, terrestrial and arboreal nest construction among chimpanzee *(Pan troglodytes ellioti)* populations was investigated in the Lebialem-Mone Forest Landscape (LMFL), Southwest Region, Cameroon, to examine the anthropogenic effects on nest location. Data on the height, distribution and approximate age of chimpanzee night nests were collected during two 4-week primate field surveys (July to August 2010; July 2011) at two field sites (Bechati and Andu) within the LMFL. Data were collected using the line transect method. Chimpanzee night nests were categorized by their location: arboreal versus terrestrial. During the two field surveys, arboreal night nests were the most frequently constructed nest type at both sites, and the only type of night nest constructed at Bechati. Terrestrial night nests were also constructed at Andu. The main difference between these two sites is the level of human predation and agricultural development. At Bechati chimpanzees inhabit forest regions around dense, expanding villages and are regularly hunted by humans. However, at Andu the chimpanzee populations are not under the same threat. Therefore, terrestrial night nest construction in the LMFL appears to be a behavior exhibited where there is less human presence.

Introduction

The topic of chimpanzee *(Pan troglodytes)* nest construction has always been an important aspect of primate field research [Goodall, 1962; Reynolds, 1965; Baldwin et al., 1981; Anderson et al., 1983; Sept et al., 1992; Fruth and Hohmann, 1994; Reyn-

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olds and Reynolds, 1997; Pruetz et al., 2008; McGrew, 2010]. Chimpanzee nests have been used to understand better our last common ancestor's behavior and its role in primate evolution [Hernandez-Agullar, 2009]. Primatologists have also used chimpanzee nests as a metric to estimate population size and density [Blom et al., 2001; Plumptre and Cox, 2006; Yao Kouakou and Boesch, 2009].

Explaining and understanding the cross-site variability in chimpanzee nest construction has been difficult. There is considerable variation in the style of chimpanzee nest construction and in nest location across sites [Koops et al., 2007]. Although all studies to date have observed that chimpanzees overwhelmingly prefer arboreal nests, especially overnight, terrestrial nests have been constructed for both day and night use by chimpanzee populations throughout Africa in ecologically diverse landscapes (e.g. caves, lowland and submontane rain forests) [Boesch, 1995; Matsuzawa and Yamakoshi, 1996; McGrew, 2010]. Terrestrial nests usually make up between 5 and 10% of nests constructed in a given population and rarely exceed the 20–30% range [Matsuzawa and Yamakoshi, 1996; Koops et al., 2007]. The majority of these nests are simple day nests for napping, resting, eating and playing [Brownlow et al., 2001; McGrew, 2010]. Various factors potentially influencing terrestrial nest building exist [McGrew, 2010; Stewart, 2011; Koops et al., 2012a, b]. Seasonality, altitude, nonhuman predation, temperature, day/night use, relation to old age/injury, mate-guarding behavior, availability of arboreal nesting opportunity, wind speeds, agricultural development and human hunting have all been considered [Boesch, 1995; Hirata et al., 1998; McGrew, 2010; Stewart, 2011; Koops et al., 2012a, 2012b].

Fruth and Hohmann [1994] hypothesized that chimpanzees prefer to nest higher off of the ground during the rainy seasons, and Koops et al. [2012a] have validated this hypothesis. Boesch [1995] suggested that terrestrial nests were constructed for daytime use only to avoid strong winds and protect the body from the cold ground. A similar hypothesis was proposed by Hirata et al. [1998], who claimed that terrestrial nests were built by chimpanzees as 'cushioning' for the wet ground. Altitude has also been linked with terrestrial nest construction. In the Ivory Coast and Guinea, Matsuzawa and Yamakoshi [1996] noted that terrestrial chimpanzee nests were frequently found at high altitudes on steep mountainsides surrounded by small trees, bushes and grassland. They hypothesized that terrestrial nests were preferred at high altitudes because of the higher wind speeds, which deterred chimpanzees from arboreal nesting [Matsuzawa and Yamakoshi, 1996]. However, this was tested and refuted [Koops et al., 2007]. Koops et al. [2007] also forwarded a social hypothesis for terrestrial nest building, claiming that it is a sex-linked behavior used by males for overnight mate-guarding when females are in estrus. However, a recent paper refuted this hypothesis with data indicating that ground nests were constructed by maternally related males and this was a widespread group-level behavioral pattern [Koops et al., 2012b]. Physical injuries and old age may also cause a chimpanzee to nest terrestrially because they are physically unable to construct nests arboreally [Reynolds and Reynolds, 1997]. An absence of mammal predation by lions *(Panthera leo)*, leopards *(Panthera pardus)*, wild dogs *(Lycaon pictus)* and hyenas *(Crocuta crocuta)* has also been used to explain the phenomenon, as arboreal nests may provide more adequate protection [Pruetz et al., 2008].

In this study, the rare behavior of chimpanzee terrestrial night nest construction was studied with the aim of understanding the factors affecting chimpanzee nest lo-

Fig. 1. Map of Cameroon, LMFL highlighted by arrow.

cation. Data were collected during two 4-week primate field surveys of wild chimpanzee *(Pan troglodytes ellioti)* populations (Bechati and Andu) in Cameroon, only one of which suffers from severe anthropogenic disturbance. We tested the hypothesis that nest location at night (terrestrial vs. arboreal) varied in relation to the frequency and intensity of human hunting and the existence of in-forest agricultural development. We predicted that terrestrial night nests would be constructed where intense human hunting and farming pressure was absent because this may allow chimpanzees to relax their sleeping site requirements.

Methods

Study Site and Study Animals

This study was conducted over two 1-month surveys (July to August 2010 and July 2011) in 2 of the 6 forest blocks of the Lebialem-Mone Forest Landscape (LMFL) in the Southwest Region of Cameroon (fig. 1). The LMFL is home to 617 km^2 of forest and possesses lowland forests at altitudes of 200 m above sea level to submontane forest altitudes as high as 2,500 m above sea level [Harvey and Tchlengue, 2010; Wright and Priston, 2010]. The LMFL is located at latitudes 5°38 N and 5°43 N and between longitudes 9°58 E and 10°27 E [Foncho et al., 2009]. This region experiences two dramatically different climatic seasons: the rainy season, which lasts from April to September, and the dry season, which lasts from October to March [ERUDEF, 2011a]. The months of July and August experience the greatest amount of precipitation, and annual rainfall is estimated to be between 3,000 and 10,000 mm [ERUDEF, 2011a]. The two forest blocks surveyed are very similar geographically, Bechati is located in the Tofala Forest Area (TFA), and Andu is located in the Mak-Betchou (M-B) [B. Muh, pers. commun.]. Bechati and Andu are both characterized by dense forests and mountainous terrain with altitudes that produce lowland and submontane forest environments [Oates et al., 2007; Berggorilla- und Regenwald-Direkthilfe, 2008]. Bechati has an altitude range of 200–1,700 m and Andu has an altitude range of 300–1,300 m [L. Nkembi, pers. commun.].

Chimpanzees *(P. troglodytes ellioti)* inhabit both forest blocks, whereas gorillas *(Gorilla gorilla diehli)* inhabit only the Bechati forest block [Oates et al., 2007; ERUDEF, 2011b]. The only nonhuman mammal predators of chimpanzees within these forest blocks are leopards.

The *P. t. ellioti* chimpanzee subspecies is primarily located in the Gulf of Guinea region around the Nigeria-Cameroon border. There are estimated to be approximately 6,000–10,000 individuals remaining in the wild [Ghobrial et al., 2010]. Within Bechati there are approximately 285 chimpanzees, and at Andu there are approximately 200 chimpanzees. Population estimates within the Bechati and Andu forest blocks were made using the marked-nest count method via line transect surveys conducted by biomonitoring teams working for the Environment and Rural Development Foundation [L. Nkembi, pers. commun.]. Recent genetic evidence suggests that the subspecies *P. t. ellioti* is significantly different genetically from the other subspecies of chimpanzee in western Africa [Gonder et al., 2011].

Data Collection

Data on chimpanzee nesting sites were gathered during a total of 8 weeks (5 weeks of July and August 2010, as well as 3 weeks of July and August 2011), using the line transect method [Yapp, 1956]. Line transect locations and directions were determined with respect to topography and all cardinal directions were covered. Observers walked five 3-km-long line transects per day (6 days per week on average) and recorded the number of nests seen. Nests were also located by following and directly observing chimpanzee groups, as well as incidental discovery. Data on height, distribution and approximate age were collected at each nest site located. A nest site was defined as any location that included one nest or more of the same approximate age.

To estimate the age of the nests, we followed the classification system used by Tutin et al. [1983]. Nests were categorized as either 'fresh', 'recent', or 'old'. 'Fresh' nests had green, unwilted leaves and feces and urine around or on them. 'Recent' nests contained wilted green leaves. 'Old' nests had brown leaves or leaves that were turning brown. Nest decay rates are highly variable (approx. 100–150 days) depending on site and season [Tutin et al., 1983; Tutin and Fernandez, 1984; Plumptre and Reynolds, 1996; Matthews and Matthews, 2004; Plumptre and Cox, 2006]. In a recent study conducted in southwestern Cameroon, researchers discovered that chimpanzee nests remained recognizable for a mean of 130 days [Matthews and Matthews, 2004]. However, fresh nests are normally considered to be less than 2 days old, recent nests less than 1 week old, and old nests to be in between 1 week and 1 month old [Koops et al., 2012a]. Therefore, it is likely that all nests were constructed during the rainy season (April to August), although based on Matthews and Matthews [2004], it is still possible that old nests were constructed during the dry season (February to March). Nests were classified as either arboreal or terrestrial, and mean heights were estimated with the aid of a measuring tape. Mean arboreal nest heights ranged from 6 to 40 m above ground, and all are treated here as functionally arboreal. The Sanz et al. [2007] stepwise variable selection method was employed to distinguish between chimpanzee and gorilla nests at Bechati.

Whether each nest was a day or night nest was recorded based on the level of complexity of the structure and the material composition. Night nests had a well-defined circular shape and a high amount of interweaving, whereas day nests had a complete absence of interweaving and an irregular shape. These structural differences between day and night nests have been well established in the literature [Brownlow et al., 2001; Stewart et al., 2007]. Stewart et al. [2007] acknowledged the variability in the structure, complexity and material composition of chimpanzee nests. Chimpanzee day nests are structurally simpler than night nests, and usually built around feeding or play areas [Brownlow et al., 2001]. They are constructed weakly because they are commonly used as rest stops between feeding episodes [Brownlow et al., 2001]. In contrast, night nests are more complex and constructed strongly with robust material in order to provide adequate support throughout the night [Brownlow et al., 2001]. Complex, strong nests have a well-defined circular shape and a high amount of interweaving to increase security of the structure [Stewart et al., 2007]. It is important to note that the day/night nest categorization in this study may have a margin of error due to the fact that it is based on indirect evidence.

Data were also collected on anthropogenic disturbance. At both sites, data on the number of snare traps and shell casings were collected. Data on the location, structure and utility of in-

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Fig. 2. Arboreal night nest, Tofala Forest Area (Bechati), LMFL (photograph by C.L.).

forest farms were also collected, including any direct and indirectly observed sightings of chimpanzee crop raiding.

Data were analyzed using nonparametric statistics, including the Mann-Whitney U test (two-tailed). Where means are given, they are reported with the standard deviation. The level of significance was set at $p < 0.05$.

Results

Data on 30 chimpanzee night nest sites (113 individual nests) were collected, 28 arboreal night nest sites (102 individual nests), and 2 terrestrial night nest sites (11 individual nests). This is a relatively representative sample of nests considering the estimated chimpanzee population sizes at Bechati (285) and Andu (200). At Bechati, 100% of night nest sites observed (n = 20) were arboreal. In contrast, at Andu there was variability among night nest sites, with 80% (n = 8) being arboreal night nest sites and 20% (n = 2) being terrestrial night nest sites. The 2 terrestrial night nest sites were not located near each other. Also, 19 shell casings, 7 snare traps and 12 in-forest farms were observed at Bechati. There was a complete absence of shell casings, snare traps and in-forest farms at Andu.

Bechati: Arboreal Night Nests

At Bechati, arboreal night nests were highly complex structures built on large branches (fig. 2). They were generally composed of an intricate arrangement of twigs and branches for a base, which was then covered with a large amount of leaves, presumably for comfort and cushioning. The mean height of arboreal night nest sites was 21.9 ± 8.3 m (range: 6–40; table 1). This mean height was slightly higher than the mean height at Andu, but not significantly so (Mann-Whitney: $n_1 = 20$, $n_2 = 8$; $U = 56.0$, $p = 0.211$). Nest sites had an average number of 3.4 ± 2.9 nests. Also, no day nests were found near or around night nest sites at Bechati. Throughout the study period, 12 arboreal night nest sites at Bechati were likely constructed during the rainy sea-

Table 1. Bechati arboreal night nests

Nest site	Nests n	Mean height m	Age
1	4	20	recent
2	5	15	old
3	14	30	fresh
4	2	35	recent
5	2	16	old
6	3	25	recent
7	2	30	recent
8	6	20	recent
9	3	13	old
10	1	6	fresh
11	14	25	old
12	3	10	fresh
13	1	20	recent
14	3	30	old
15	4	20	old
16	4	20	old
17	1	40	fresh
18	2	20	old
19	1	20	fresh
20	3	20	fresh

Table 2. Andu arboreal night nests

Nest site	Nests n	Mean height m	Age
1	7	15	old
2	5	10	recent
3	4	21	fresh
4	5	27	fresh
5	6	12	recent
6	3	14	recent
7	1	20	old
8	3	20	recent

son, and 8 arboreal night nest sites at Bechati were likely constructed during the dry season.

Andu: Arboreal Night Nests

Arboreal night nests at Andu were similar in design and material composition to the arboreal night nests at Bechati. The mean height of the arboreal night nest sites was 17.4 ± 5.6 m (range: 10–27; table 2). Nest sites were organized in slightly larger sizes than the arboreal night nests at Bechati, with the mean site being composed of 4.3 ± 1.9 nests. However, this difference was not significant (Mann-Whitney: $n_1 = 20$, $n_2 = 8$; $U = 49.5$, $p = 0.123$). Similar to the Bechati site, there were no nest type varia-

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Fig. 3. Terrestrial night nest, Mak-Betchou (Andu), LMFL (photograph by C.L.).

tions at any nest site at Andu. Of all arboreal night nest sites at Andu, 6 were likely constructed during the rainy season and only 2 were likely constructed during the dry season.

Andu: Terrestrial Night Nests

Terrestrial night nests at Andu were constructed as complex sleeping platforms, but lacked a twig/branch framework that the arboreal night nests possessed (fig. 3). Terrestrial night nests were not constructed directly up against a trunk, and instead constructed in a flat, clear area. The average nest site was composed of 5.5 ± 4.9 nests, which is slightly larger than the average nest sites of arboreal night nests. However, this difference was not significant (Mann-Whitney: $n_1 = 28$, $n_2 = 2$; $U = 22.0$, $p = 0.662$). There was no nest type variation at either terrestrial night nest site and all nests were constructed during the rainy season.

Discussion

Nest site location (terrestrial vs. arboreal) within the LMFL varies in relation to the frequency and intensity of human hunting and the existence of in-forest agricultural development. At Bechati, arboreal night nest sites were the only night nest sites constructed in an area with intense human hunting and farming pressure, whereas night nest sites at Andu, where human hunting and farming pressure was absent, were located both arboreally and terrestrially. Two terrestrial night nest sites, composed of 11 individual nests, were discovered at Andu. This is an uncommon behavioral trait for any chimpanzee subspecies, even though it has been observed at Bili [Hicks, 2010] and Nimba [Koops et al., 2007, 2012a]. Andu arboreal night nest sites were found at lower heights than the arboreal night nest sites at Bechati. However,

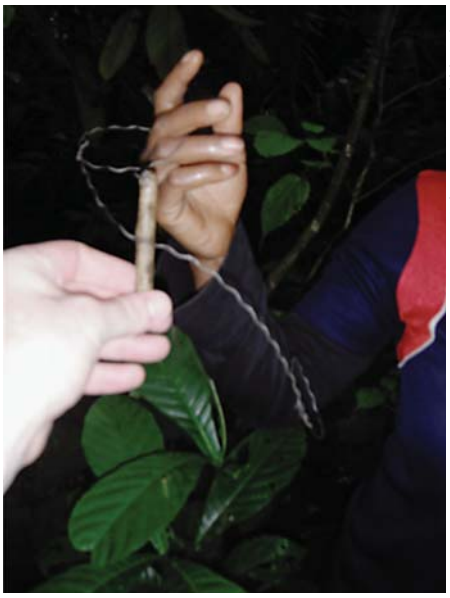
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Fig. 4. Disarmed snare trap (photograph by C.L.).
Fig. 5. Fired shell casing (photograph by C.L.).

they were not significantly lower, which could either indicate that nest height is unrelated to increased safety in the LMFL, or it is a product of small sample size. To explain the existence of terrestrial night nest sites at Andu, several factors are considered and discussed, including agricultural development, human hunting and trapping, nonhuman mammal predation, seasonality and group social and demographic factors.

Agricultural Development and Human Hunting and Trapping

Human predation and agricultural development have been hypothesized to affect primate nest location [Anderson, 1998]. Anderson [2000] notes that safety from predators is the most important principle underlying sleep for all nonhuman primates. He suggested that the general tendency to sleep arboreally may have evolved for safety reasons [Anderson, 2000]. The daily construction of arboreal sleeping platforms among chimpanzees, bonobos *(Pan paniscus)* and orangutans *(Pongo pygmaeus* and *P. abelii)* today is regarded as a universal behavior [Hansell and Ruxton, 2008; McGrew, 2010]. Gorillas *(Gorilla gorilla* and *G. beringei),* the largest and least preyed upon great ape by nonhuman predators, frequently construct daily terrestrial nests, although they will also construct occasional arboreal sleeping platforms [Sanz et al., 2007].

Within the LMFL, human predation and agricultural development appear to have a substantial impact on the location (terrestrial vs. arboreal) of chimpanzee night nests (sleeping platforms). At Bechati, all observed chimpanzee night nests were arboreal constructions. At Andu there was variation in arboreal and terrestrial night nest sites. The level of human predation and the level of human agricultural development may be the causative factor explaining these differences. Although there are sites where chimpanzees continue to nest arboreally even in the absence of

Table 3. Andu terrestrial night nests

Nest site	Nests n	Mean height m	Age
1	9	0	recent
2	2	0	recent

predation [Sanz et al., 2007], some populations may relax their sleeping site requirements and nest terrestrially more often when there is less predation pressure [Pruetz et al., 2008].

At Bechati, shell casings, snare traps and in-forest farms were common (19 shell casings, 7 snare traps, 12 in-forest farms); none of these existed in Andu. Within Bechati, many people hunt great apes with shotguns and use their skulls, scapulas and other bones for traditional medicinal purposes [Kumpel et al., 2008; A.E. Lefu, pers. commun.]. Great apes are also perceived by many villagers to be a delicacy and/or integral to their income when sold to larger areas of economic activity in the bush meat trade [Wilcox and Nambu, 2007; Wright and Priston, 2010]. This has led to the chimpanzees at Bechati being killed for bush meat at 2–13 times higher than sustainable rates [Hughes et al., 2011]. Also, farmers are expanding rapidly by clearing forest areas in the forest to plant important staple crops like plantains, bananas and cocoa [A.E. Lefu, pers. commun.]. This both encroaches on traditional chimpanzee territory and creates a dangerous social dynamic between farmers and nonhuman primates [Oates et al., 2007; Mittermeier et al., 2009]. Chimpanzees frequently raid crops; in fact, two such observations were made during the field survey, and farmers retaliate by actively seeking out and hunting down chimpanzees, whom they view as pests [Berggorilla- und Regenwald-Direkthilfe, 2008; Mittermeier et al., 2009]. In contrast, at Andu hunting, trapping and in-forest farming occur very rarely [A.E. Lefu, pers. commun.]. The local villagers at Andu believe that killing another ape is equivalent to killing a human from the village, and the local chief participates in and agrees with the local conservation nongovernment organization philosophies and goals [Wright, 2010; A.E. Lefu, pers. commun.].

Seasonality

Major differences in Equatorial West African seasonal weather patterns have been hypothesized to play a role in a chimpanzee sleeping site selection. It has been suggested that seasonal variation, regardless of ecological landscape, can increase or decrease the likelihood of terrestrial nest construction [Fruth and Hohmann, 1994]. In Equatorial Guinea, Senegal and Gabon, chimpanzees have constructed terrestrial nests in the dry season, but not in the rainy season [Fruth and Hohmann, 1994]. This hypothesis posits that in warmer, drier months chimpanzees relax their sleeping site requirements. However, this hypothesis has been challenged by two studies [Koops et al., 2007, 2012a] in Guinea that report a lack of seasonal differences in terrestrial nesting. Furthermore, both terrestrial sleeping sites discovered at Andu were likely constructed during the rainy season, seemingly refuting this hypothesis. More data need to be recorded during the dry season before this hypothesis can properly be tested.

The opposite seasonal hypothesis to the idea that chimpanzees are more likely to construct terrestrial nests in the dry season is that terrestrial nests are more likely to be constructed in the rainy season for 'cushioning' or 'comfort' from the wet ground [Hirata et al., 1998]. Although this idea does not explain the absence of terrestrial sleeping sites at Bechati, the fact that both terrestrial sleeping sites at Andu were constructed in the rainy season could indicate that protection from the wet ground is a functional attribute of terrestrial sleeping sites.

Potential Alternate Explanations

Primatologists have also hypothesized that terrestrial sleep site selection may have important social and/or demographic variables to consider. Reynolds and Reynolds [1997] hypothesized that older and injured members of a chimpanzee group may nest terrestrially for either personal safety reasons or because they are physically unable to construct a nest. Koops et al. [2007] proposed that adult males may nest terrestrially to mate-guard females in estrus. Although ground nesting may still be a male-biased behavior, this hypothesis does not explain the patterns of terrestrial nesting at Andu. Both social hypotheses (i.e. injury/old age and mate-guarding) indicate that there should be variation at a nest site (i.e. one site would be composed of both arboreal and terrestrial nests). At Andu, both terrestrial night nest sites found were homogenous (i.e. composed of all terrestrial nests). This is further evidence in support of a recent paper by Koops et al. [2012b] that ground-nesting seems to be widespread at the group level in some chimpanzee populations.

Nonhuman mammal predation is often hypothesized to explain where chimpanzees and other primates choose to construct their nests or sleeping sites (i.e. arboreally or terrestrially) [Matsuzawa and Yamakoshi, 1996; Anderson, 1998, 2000; Pruetz et al., 2008]. The only nonhuman mammal predator that chimpanzees must confront in the LMFL is the leopard *(P. pardus)* [L. Nkembi, pers. commun.]. Within the context of this study, the relationship between leopards and chimpanzees is unclear. It is known that leopards exist within Cameroon and the LMFL, but there are no reliable estimates on their population size, or their numerical variation between forest blocks [Breuer, 2005; L. Nkembi, pers. commun.]. During our field survey there were no traces found or vocalizations heard at either study site indicating leopard presence. Therefore, with the current available evidence, it is difficult to draw any definitive conclusions regarding the role of nonhuman mammal predation in chimpanzee nest construction in the LMFL.

Chimpanzee nesting patterns could also be affected by other ecological factors like tree availability and climatic factors [Koops et al., 2007, 2012a]. Future studies on chimpanzee nesting patterns in the LMFL should consider these variables. However, tree availability was not likely to have played any role in the existence of terrestrial night nests at Andu because all terrestrial nests were located around suitable nesting trees. Also, climate and temperature were not likely to vary tremendously between Bechati and Andu due to proximity as well as similarity in forest structure (lowland and submontane) as well as similar variation in altitude.

This article reports the first detailed quantitative data on the construction of chimpanzee *(P. t. ellioti)* terrestrial nests in the LMFL. Terrestrial night nesting appears to function as an adaptation to predation-free, or relatively predation-free environments. This behavior is likely exhibited at Andu because in the absence or near-absence of predation, chimpanzees relax their sleeping site requirements. In contrast,

chimpanzees that strictly construct their night nests arboreally are exhibiting what appears to be an adaptive behavior in response to predation. The two factors that were found to most markedly affect this trend in the LMFL were active hunting and trapping by humans, and increased agricultural activity in chimpanzee areas, in the form of in-forest farms. Within Bechati all chimpanzee night nests found were arboreal. Throughout the survey at Bechati the human presence was ubiquitous in the form of shell casings, snare traps and in-forest farms. People in this area were also more hostile to conservation activity and are dependent on bush meat economically. At Andu no shell casings, snare traps, in-forest farms, or any other indicator of a hostile presence were found; indeed, chimpanzees within Andu displayed considerable variability in nesting habits. Both arboreal and terrestrial night nests were found, indicating that these populations of chimpanzees may be less affected than their counterparts in Bechati by human activities.

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