

Ground night nesting in chimpanzees: new insights from central chimpanzees (*Pan troglodytes troglodytes*) in southeast Cameroon

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Running head: Chimpanzee ground night nesting in Cameroon

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Abstract

Some chimpanzee populations exhibit ground night nesting, which occurs in different habitat types, is driven by a variety of interconnected factors, and may reflect cultural or social differences. This has important implications for ape conservation management, given that accurate nest builder identification is required to estimate density, crucial in monitoring and allows inferences about environmental and social factors that may have contributed to the transition from tree to ground sleeping in early hominins. We conducted a 24-month marked nest count survey in La Belgique, Cameroon, and recorded the occurrence of chimpanzee tree and ground night nests, temperature and rainfall, predator and large mammal abundance, human activities, nesting tree species, and *Uapaca* spp. consumption. Ground night nesting occurred at a rate of 3.47% (N = 1008), with more in swamps, in the dry season and with increasing human activities. We found no influence of leopard/elephant presence, but a possible influence of lack of nesting trees. We suggest chimpanzees visit swamps in the dry season (low water levels) for relief from hunting pressure and to consume *Uapaca* spp. fruits. Ground nesting may be enabled due to high abundance of terrestrial herbaceous vegetation, and favoured for inconspicuousness and safety from gun hunters.

Introduction

All weaned great apes build structures to sleep in, by bending, breaking, and interweaving branches and manipulating foliage into a platform, which are commonly known as ‘nests’. The basic features of nest building exist in all populations of orangutans (*Pongo spp.*), bonobos (*Pan paniscus*), gorillas (*Gorilla spp.*) and chimpanzees (*Pan troglodytes*; Fruth and Hohmann 1996), however there is interspecies variation in terms of nesting site location. The general consensus among primatologists has been that orangutans, bonobos and chimpanzees build their night nests almost exclusively in trees (e.g., Tutin and Fernandez 1984; Hall et al. 1998; Poulsen and Clark 2004). Gorillas, on the other hand, appear to exhibit a more flexible nesting pattern, sleeping in nests built on the ground (e.g., for western lowland gorillas, *Gorilla gorilla gorilla*, 7.3% in Petit Loango, Gabon, Furuichi et al. 1997; to 96.2% in La Belgique, Dja Biosphere Reserve, Cameroon, Willie et al. 2013). However, bonobos have been observed to ground nest (Kano 1983) and chimpanzee ground night nests have increasingly been found to occur in many chimpanzee study sites from east to west (Furuichi and Hashimoto 2000; Maughan and Stanford 2001; Koops et al. 2007; Abwe and Morgan 2008; Pruetz et al. 2008; Hicks 2010; Last and Muh 2013), providing evidence of more flexible nesting patterns than previously assumed.

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The importance of the study of nesting behaviour

There is an urgent need to improve population density estimates, as the lack of reliable estimates is detrimental to the management, monitoring and conservation of great apes (Sanz et al. 2007). Nest counts are used to estimate density and there is a widely recognised potential error of incorrectly assigning gorilla nests as chimpanzee nests, because gorillas sometimes nest in trees (Morgan et al. 2006; Iwata and Ando 2007). Similarly, chimpanzee ground nesting has important implications for all previous and subsequent great ape density estimations, as chimpanzees are often assumed to be exclusive arboreal night-nesters and their ground nests may be incorrectly assigned to gorillas.

From the study of nesting behaviour one can infer important information about ecological adaptation and hominin evolution (McGrew 2010). As species of *Pan* are our closest living relatives we can investigate factors that influence chimpanzee behaviour (Pruetz and LaDuke 2010; Koops et al. 2012b) and make inferences about corresponding behaviour patterns of early hominins, including the transition from tree to ground sleeping (Sabater-Pi et al. 1997; Stanford 2006). Tree nesting occurs in all extant great ape species, so it is likely to have evolved in a distant ancestor and the last common ancestor of *Pan* and *Homo* may have slept in trees (Sabater-Pi et al. 1997; McGrew 2010; Koops et al. 2012b). It is likely that early arboreal hominins (before *Homo erectus*; 1.8 million years ago, mya) were nest-builders (Sabater-Pi et al. 1997): as hominins made the transition from forest to a more open wooded savannah they would have been subjected to the higher trophic pressures seen in open areas (Sabater-Pi et al. 1997). In addition, they likely had poor nocturnal and crepuscular vision similar to extant diurnal primates, were not likely to have used fire to deter predators (but see Wrangham 2009), and probably had a physiological requirement for recumbent relaxed sleeping postures, as a result of muscular atony (Sabater-Pi et al. 1997). As modern humans lack nesting behaviour, it is assumed that nest building disappeared during the process of hominization in the Miocene (Fruth and Hohmann 1996; Yamagiwa 2001). Sleeping in comfortable and safe tree nests enabled a better quality of sleep, increasing the occurrence of REM sleep which is important for release of growth hormones, to establish memory, and for neural maintenance (Fruth and Hohmann 1996; Siegel 2005). The resulting increased cognitive, manipulative and technological abilities may have enabled early hominins to develop the necessary measures to allow them to give up their safe tree nests (Fruth and Hohmann 1996). *Homo erectus* may have exhibited less sexual dimorphism in terms of stature than seen in australopiths (5 mya) and modern-day gorillas (McHenry, 1985). This suggests that *Homo erectus* may not have exhibited

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male protection and probably, therefore, possessed safety measures that were presumably significantly advanced over those found among recent-day chimpanzees (Sabater-Pi et al. 1997; Yamagiwa 2001; Samson and Hunt 2012); for example they may have used fire to deter predators (Wrangham 2009; Samson and Hunt 2012). On the ground conditions may have been more favourable (e.g., warmer; Samson and Hunt 2012) and stable enough to allow the development of human sleep architecture and its procedural memory consolidation (Fruth and Hohmann 1996). Therefore, ground sleeping may have facilitated the development of certain advanced cognitive traits (e.g., visual motor skills, locomotor adaptations and threat simulation), which ultimately enabled humans to modify their environment as we see today (Fruth and Hohmann 1996; Samson and Hunt 2012).

Advantages of tree nest building

Predation is argued to have exerted and continue to exert a very strong pressure on primate evolution (Anderson 2000). As tree nest-building is suggested to increase the safety of sleeping apes (Baldwin et al. 1981), predation is likely to influence nesting patterns (e.g. Ogawa et al. 2007), for example with an increase in nesting height (Pruetz et al. 2008; Stewart and Pruetz, in press). Gorillas commonly build nests on the ground, and their sexual dimorphism and increased tendency for immature gorillas and adult females to nest in trees, suggests a protective role of ground sleeping males (Yamagiwa 2001). Leopard predation has been observed in mountain gorillas (*Gorilla gorilla beringei*; Schaller, 1963), western lowland gorillas (Goldsmith, 1999; Robbins et al. 2004), bonobos (D'Amour et al. 2006) and chimpanzees (Boesch 1991). However, there is no support for predation pressure having selected for large body size in primates, and it is suggested that chimpanzees are less affected by predation than expected (Zuberbuehler and Jenny 2002). Other studies have failed to support the anti-predation hypothesis (gorillas in Mondika, Central African Republic, and Lopé, Mehlman and Doran 2002; chimpanzees, Koops et al. 2012a; Stewart and Pruetz in press), although they do not exclude the possibility that arboreal nests functioned (partly) as an anti-predator strategy in the past. Furthermore, additional factors likely contribute to nest site location (Brownlow et al. 2001; Pruetz et al. 2008; Koops et al. 2012a; Stewart and Pruetz, in press), and to the need for construction of a nest (Pruetz et al. 2008; Stewart 2011a).

Environmental and climatic factors may influence nest building, as the structure of the nest may provide a thermoregulatory function to protect against low ambient temperatures (Fruth and Hohmann 1996). Western lowland and Cross river gorillas (*Gorilla gorilla diehli*) make more and

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fuller nests as rainfall increases (Mehlman and Doran 2002; Etiendem and Tagg in prep). Chimpanzees adapt to thermoregulatory stressors, for example, by using caves in Fongoli, Senegal (Pruetz 2007) and nesting at greater heights in periods of higher humidity in Seringbara, Guinea (Koops et al. 2012a).

The anti-vector hypothesis suggests that disease vectors, such as mosquitoes, can be avoided when sleeping in tree nests (McGrew 2004). Malaria parasite (*Plasmodium* spp.) infections have been detected in wild chimpanzees at the same levels as in untreated humans, although it is unsure whether these infections are pathogenic (Kaiser et al. 2010; Prugnolle et al. 2010). Stewart (2011a) experienced fewer insect bites when sleeping in a tree nest than on the ground, suggesting that the nest may physically shield or dislodge biting insects from the body. Orangutans nest in tree species with known anti-mosquito properties and carry these species' twigs as covers for other nests (Largo et al. 2009). Similarly, some chimpanzees preferentially nest in *Cynometra* sp. trees which have natural mosquito repellent qualities (Samson et al. 2013). However, Koops et al. (2012a) found no difference in mosquito density at different heights or altitudes in the Nimba Mountains, Guinea.

Nest building may play a role in social organisation and dynamics (e.g., increased group cohesion or information centres; Anderson 1998; Ogawa et al. 2007); avoiding contact with nocturnal frugivores such as bats (Anderson 2000); or providing comfort (Stewart et al. 2007) and good quality sleep (Anderson 1998). Nest building can also be influenced by seasonality and habitat differences (Baldwin et al. 1981), sex and age (Fruth and Hohmann 1994), learning and culture (when social traits are passed through a population by learning; Humle 2003; McGrew 2004), or a combination of factors (e.g., Brownlow et al. 2001; Koops et al. 2012a).

Chimpanzee ground nests

Chimpanzee ground nests are often used for resting during the day, and have been documented in many sites (Budongo, Uganda, Reynolds and Reynolds 1965; Gombe, Tanzania, Goodall 1968; Tai and Nimba Mountains, Ivory Coast, Matsuzawa and Yamakoshi 1994, Boesch 1995; Bossou, Guinea, Humle and Matsuzawa 2001; Seringbara, Humle 2003). Ground day nests are generally of a weak cushion-like construction (Brownlow et al. 2001; Koops et al. 2007), and may simply comprise the gathering of leaves or ferns, or the bending of a small sapling (Boesch 1995). Day nests fulfil a distinctly different function to night nests, i.e., minimising the discomfort of resting on

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cold or wet ground (Boesch 1995) and are used for short periods in the daylight, when alert individuals may be present and without the risks or pressures of sleeping at night.

By contrast, ground night nests are of a sophisticated and elaborate construction; made from bent and broken branches, ferns, saplings and other materials (Horn 1980; Matsusawa and Yamakoshi 1996; Furuichi and Hashimoto 2000; Hicks 2010). Early observations of chimpanzee ground night nesting were attributed to sickness of the individuals preventing them from ascending trees (e.g., Gombe, Goodall 1968). Other studies omitted to elaborate on nest function: at Río Muni, Equatorial Guinea, 4% of central chimpanzee (*Pan troglodytes troglodytes*) nests were built on the ground (Sabater-Pi 1984), but information on nest structure or use is not provided; similarly, in western chimpanzees (*Pan troglodytes verus*) in Bossou, observed ground nests were not identified as day or night nests (Humle and Matsuzawa 2001). However, a growing body of studies confirms the occurrence of a systematic construction of elaborate night nests on the ground in three of the four subspecies of chimpanzee (Table 1). In the western chimpanzee ground night nesting has been studied extensively in the Nimba Mountain population, and repeatedly observed in a number of different study sites in the region, being confirmed by DNA analysis in one (Seringbara, Koops et al. 2007; 2012b). Ground night nesting appears to be ubiquitous in eastern chimpanzees (*Pan troglodytes schweinfurthii*) of northern Democratic Republic of Congo and also occurs in Kalinzu, Bwindi Impenetrable National Park and Budongo, Uganda. The behaviour has also been documented in Nigeria-Cameroon chimpanzees (*Pan troglodytes ellioti*) in Ebo Forest and the Lebialum-Moné Forest Landscape, Cameroon.

In this paper we present evidence of ground night nesting in central chimpanzees in 'La Belgique' study site in southeast Cameroon (Dupain 2001; Dupain et al. 2003; Tagg et al. 2011) and investigate the potential influence of factors in the occurrence of this behaviour in the site. Simultaneously, we review the current understanding of the occurrence and explanations of ground night nesting in chimpanzees and discuss the potential factors influencing this behaviour.

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Table 1. Documented rates of chimpanzee (*Pan troglodytes*) ground night nesting across their range (na = data not available).

Chimpanzee subspecies	Site	Country	Ground nests/total nests	Ground nesting rate (%)	Date of study	Reference	Comments
Western chimpanzee (<i>Pan troglodytes verus</i>)	Nuon (Yealé), Nimba Mountains	Guinea and Ivory Coast	164/464	35.4	1996	Matsuzawa & Yamakoshi 1996	A proportion of these nests resembled tree nests (except for their location) and were likely used at night
	Yealé, Nimba Mountains		11/378	2.9	1999–2001	Humle 2003	Likely night nests, due to their elaborate structure and association with other nests in close proximity
	Seringbara, Nimba Mountains		17/281	6.0			
			32/965	3.3	2003–2004	Koops et al. 2007	Night nests
			65/1355	4.8	2003–2008	Koops et al. 2012a	Night nests
	Fongoli	Senegal	45/1665	2.7	19 month study; 2001–2002	Pruetz et al. 2008	Calculated thus: 3% ground nesting rate (Pruetz et al. 2008); 90% likely night nests (Hicks 2010); therefore 45/1665 ground night nests = 2.7%
	na		12.0	2007–2008	Stewart 2011b	Night nests	
Eastern chimpanzee (<i>Pan troglodytes schweinfurthii</i>)	Bili-Uele Landscape	Democratic Republic of Congo	273/2507	10.9 (1.1–28)	2004–2009	Hicks 2010	Suggests caution in distinguishing elaborate (likely night) from flimsy (likely day) ground nests
	Kalinzu	Uganda	4/3452	0.12	1997–1998	Furuichi & Hashimoto 2000	Night nests
	Bwindi Impenetrable National Park		na	0.05–15	First seen 1959; then ~2001	Maughan & Stanford 2001	Majority resembled night nests
	Budongo		2/259	0.8	~1965	Reynolds 1965	Night nests
Nigeria-Cameroon chimpanzee (<i>Pan troglodytes ellioti</i>)	Ebo Forest	Cameroon	6/222	2.7	2006–2007	Abwe & Morgan 2008	Night nests
	Andu, Lebialum-Moné Forest Landscape		11/33	32.4	4 week study, July 2011	Last & Muh 2013	Night nests

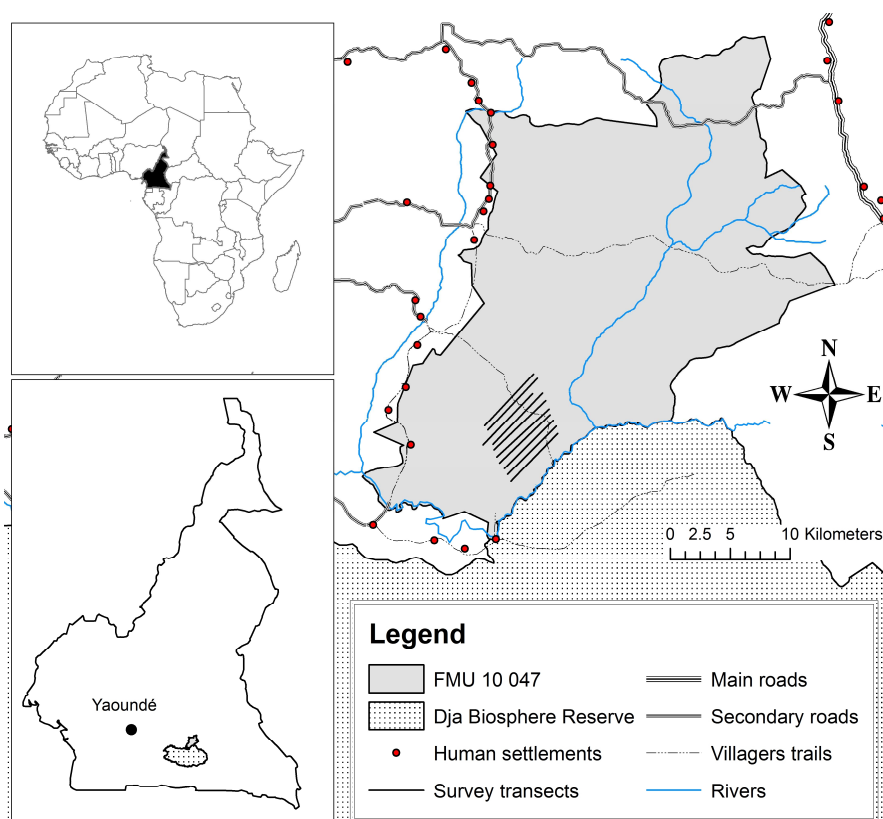
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Methods

Study site

The study was carried out in the research site ‘La Belgique’ (~40 km²), at the northern periphery of the Dja Biosphere Reserve, in southeast Cameroon (Dupain 2001; Fig. 1). The research site is located between 013°07’–013°11’ E and 03°23’–03°27’ N, within the forest management unit 10 047 and was partially and selectively logged >30 years ago. Annual mean rainfall was recently recorded as 1637.9 ± SD 105.1 mm; and mean minimum and maximum daily temperatures (°C) were 19.5 ± SD 1.3 and 26.3 ± SD 2.4 (Willie et al. 2013). Vegetation in the site falls into six habitat types: near primary forest (NPF), old secondary forest (OSF), young secondary forest (YSF), light gaps (LG), swamps (SW) and riparian forest (RF). NPF, OSF, YSF and LG are referred to collectively as *terra firma* forests. SW and RF are (periodically) flooded habitats (Willie et al. 2012). OSF, YSF, SW, RF, LG and NPF represented 35%, 31%, 20%, 6%, 5% and 3% of the total forest cover, respectively (Willie et al. 2012), with the majority of the site being secondary forest (66%; Willie et al. 2012). The site is traversed by human-made trails used for resource-provisioning of villagers and for research, and comprises a dense network of water courses and seasonal swamps.



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Figure 1. Location of study site, La Belgique, northern periphery of the Dja Biosphere Reserve, southeast Cameroon.

Data collection

During two walks in April 2009, we recorded and marked (red paint on the tree for tree nests or a stick for ground nests) chimpanzee nests of all ages on 20 6-km long transects, set 300 m apart and at a constant bearing of 45°. We subsequently conducted twice-monthly marked nest count (MNC) surveys from May 2009 to March 2011 on all transects (following the methods and assumptions of Hashimoto 1995; Kuehl et al. 2008), and recorded only newly-built night nests (and marked them to avoid subsequent re-counting). On encountering a nest, we searched an area of 30 m radius for additional nests, and considered neighbouring nests as belonging to the same group if they were of the same age category and located within 30 m (Dupain et al. 2004). We used these criteria as opposed to 50 m (White and Edwards 2000), as the data were also to be used for comparison with other surveys in the site (e.g., Dupain et al. 2004; Tagg and Willie 2013). We accurately measured the perpendicular distance from the transect line to each visible nest using a compass and a decametre and recorded nest height, nest diameter, nest type and habitat type. Given that sympatric populations of gorillas and chimpanzees live in the area and gorillas also build nests in trees (Willie et al. 2013), we also considered all ancillary evidence such as hairs, faeces, odour, footprints and associated feeding signs (Sanz et al. 2007), and required two pieces of ancillary evidence to confidently assign identity. In addition, we only recorded fresh nests given our short survey interval of two weeks, further reducing the chances of error. Assigning function of a ground nest can be difficult (Koops et al. 2007); again we required two pieces of ancillary evidence, such as presence of faeces and hairs, nest structure, or association with other nests, to confidently assign nest function. However, we must emphasise that we were not able to confirm beyond any doubt that the nests were slept in overnight. Day nests (tree and ground) were excluded from the study.

To investigate the availability of suitable nesting trees in the site, trees used for each nest were identified and recorded based on a botanical survey of trees performed in April–July 2010 on 10 transects 600 m apart. All trees of diameter at 1.3 m above ground ($D_{1.30}$) \geq 10 cm were identified and counted in 130 plots of 25 × 40 m each, 250 m apart along transects, and totaling 13 ha (Willie et al. 2013).

Evidence of past or present (non-permanent) human activity was also recorded twice per month along all transects. Human activities include harvesting for honey, bark stripping, gathering

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(extraction of larvae, collection of palm wine), camps, fishing, gunshots, human footprints, hunting (spent cartridges, discarded batteries, remains of fire) and other signs (e.g., abandoned items of clothing or cigarette butts). We removed (e.g., spent cartridges) or marked (e.g., camps) traces to avoid subsequent double counts.

Signs of the presence of large mammals (African leopard, *Panthera pardus pardus*, and forest elephant, *Loxodonta africana cyclotis*—buffalo, *Syncerus caffer nanus*, are not present in the site), including faeces, footprints, vocalisations, and direct sightings, were recorded throughout the second year of the MNC surveys (April 2010–March 2011).

Temperature and rainfall data were collected daily. We defined dry-season periods as those with ≤ 100 mm of rain per month (Willie et al. 2013). We chose not to use 60 mm (e.g., Koops et al. 2012a) because in La Belgique July and August typically correspond to a short dry season, but rainfall often exceeds 60 mm in these months. In the equatorial zone, although the climate may remain fairly constant, there are often variations in meteorological conditions, therefore we use site-specific classifications (Willie et al. 2013).

Fruits of *Uapaca* spp. have a nutritional importance for chimpanzees (Tutin and Fernandez 1993; Poulsen et al. 2001), and are ubiquitous in La Belgique (Ottou 2009). We, therefore, investigated *Uapaca* spp. fruit consumption by chimpanzees by recording the number of seeds found in chimpanzee faeces collected in the research site during this period.

Data analysis

We performed a univariate generalized linear model (GLM) in SPSS to investigate the effects of Season and Human Activities on chimpanzee ground nest abundance. Replicates were months, and the total number of chimpanzee ground nests found each month along all transects was the dependent variable. We fitted a Poisson regression model using the Genlin procedure and the log link function. Predictors were prepared for model construction as follows: 1) Season (rainy or dry; categorical) and 2) Human Activities (quantitative). The overall model effect and the main effect of each individual predictor were investigated by calculating Likelihood Ratio and Wald Chi-square statistics. For the two levels of Season, estimated marginal means for the dependent variable were computed, and the statistical significance of the mean differences was tested using Wald Chi-square. The overdispersion parameter (calculated as Pearson Chi-square, divided by its degree of freedom) was not high (2.66), and original statistics were therefore maintained. Nonparametric tests were applied to other data as they did not meet the assumptions of normality. Following Dupain *et al.*

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(2004), a 'preference index' for ground nesting in a particular habitat type was calculated as the difference between the actual and expected numbers of chimpanzee ground nests found in that habitat type. For each habitat type, the expected number of ground nests was $X*Y/100$ where X is the proportion of the habitat type in the study site, and Y is the total number of ground nests found in the study site. The same approach was used to determine preference indexes for tree nesting and human activities.

Results

Chimpanzee ground nests

During the MNC surveys of 2009–2011, we found 1008 chimpanzee night nests (day nests were excluded from the study), with 35 (3.47%) being located on the ground (Table 2). In each case, ancillary evidence confirmed that chimpanzees had built and slept in these nests. There were no lone ground nests. Ground night nests were found more often than expected in swamps, roughly as often as expected in near primary forest, riparian forests and light gaps, and less than expected in old and young secondary forests (Table 3). No significant relationship was found between THV density and ground nesting (Spearman test: $r = 0.543$, $P = 0.266$, $N = 6$).

Effects of seasonality and human activities on chimpanzee ground nest abundance

There was a significant positive relationship between the monthly number of chimpanzee ground nests and monthly temperature (Spearman test: $r = 0.414$, $P = 0.049$, $N = 23$; Fig. 2). In terms of the GLM, the overall regression model was significant ($P < 0.01$), reflecting the effect of Season and Human Activities on chimpanzee ground nest abundance (Table 4). The estimated marginal mean numbers of chimpanzee ground nests during rainy and dry season months were 0.32 and 0.77, respectively. Differences between seasons were statistically significant (Wald Chi-square test: $\chi^2 = 2.766$, $df = 1$, $P = 0.028$), showing that chimpanzee ground night nests occurred more often in the dry season. When all predictors are fixed, human activities incurred a rate of change of 0.011–0.064 units in the number of chimpanzee ground nest abundance. Therefore, chimpanzee ground night nesting increased with increasing human activity.

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Table 2. Chimpanzee nest site size and proportion of ground and tree nests found during Marked Nest Count surveys (April 2009–March 2011) in La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon.

Ground nest site	Size	Number of ground nests	% ground nests	Number of tree nests	% tree nests
1	2	1	50.00	1	50.00
2	3	2	66.67	1	33.33
3	2	1	50.00	1	50.00
4	4	4	100.00	0	0.00
5	2	2	100.00	0	0.00
6	2	2	100.00	0	0.00
7	2	2	100.00	0	0.00
8	4	1	25.00	3	75.00
9	4	2	50.00	2	50.00
10	8	5	62.50	3	37.50
11	3	1	33.33	2	66.67
12	3	1	33.33	2	66.67
13	3	2	66.67	1	33.33
14	2	1	50.00	1	50.00
15	6	1	16.67	5	83.33
16	3	3	100.00	0	0.00
17	4	4	100.00	0	0.00

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Table 3. Density of terrestrial herbaceous vegetation, nesting trees and *Uapaca* spp. tree, and preference indexes for habitat type of chimpanzee tree and ground nesting and human activities in La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon (April 2009–March 2011).

Parameter	Near primary forest	Old secondary forest	Young secondary forest	Light gaps	Riparian forest	Swamps
% in the study site*	3	35	31	5	6	20
THV density (stems/m ²)*	2.38	2.99	3.29	4.66	3.18	3.41
Density of frequently-used nesting trees (stems/ha)**	42.35	44.12	28.50	0	26.67	26.67
Density of <i>Uapaca</i> spp.**(stems/ha)	22.65	21.37	9.50	0	86.67	30.00
Total number of chimpanzee tree nests	259	214	10	2	88	153
Preference index for tree nesting	+237.22	-40.10	-215.06	-34.30	+44.44	+7.80
Total number of chimpanzee ground nests	1	2	2	3	1	26
Preference index for ground nesting	-0.05	-10.25	-8.85	+1.25	-1.10	+19.00
Total number of human signs	33	116	34	5	6	41
Preference index for human activities	+25.95	+33.75	-38.85	-6.75	-8.10	-6.00

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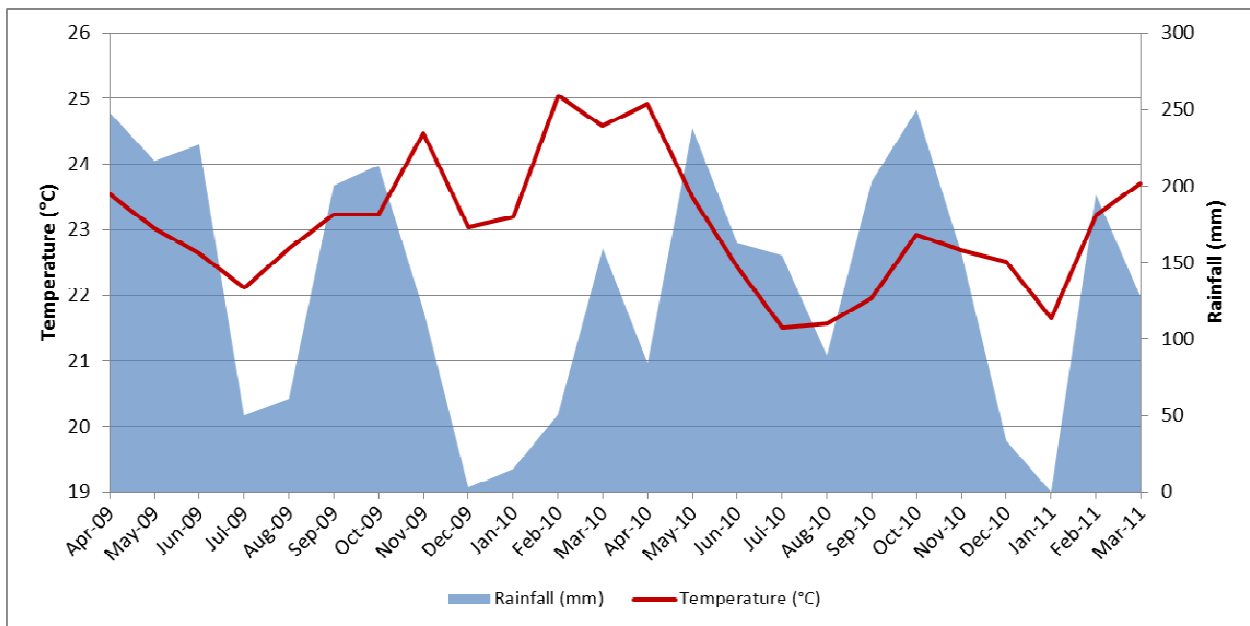


Figure 2. Climatic data at La Belgique, northern periphery of the Dja Biosphere Reserve, southeast Cameroon (April 2009–March 2011).

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Table 4. Results of generalized linear model (GLM) showing the influence of ecological and human variables on chimpanzee ground night nest abundance in La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon (April 2009–March 2011).

Model	Deviance		Likelihood Ratio		P-value		
	Value	df	Chi-square	df			
	56.076	21	12.490	2	0.002*		
Main effect			Wald Chi-Square	df	P-value		
Intercept			16.651	1	<0.001*		
Season			6.785	1	0.009*		
Human activities			7.627	1	0.006*		
Contribution of covariates	Regression coefficient	SE	95% Wald Confidence Interval		Wald Chi-square		P-value
			Lower	Upper	Value	df	
Intercept	-0.672	0.319	-1.297	-0.046	4.430	1	0.035
Human activities	0.038	0.014	0.011	0.064	7.627	1	0.006

The model includes intercept, season and human activities. The intercept term gives the expected mean of the dependent variable (number of ground nests) when the values of all predictors = 0. The main effect of individual predictors was assessed while controlling for the effects of other predictors. The regression coefficient and associated 95% Wald Confidence Interval measure the rate of change of the conditional mean of the dependent variable. In all cases, significance was assessed via a Wald Chi-square statistic and corresponding P-value. *Significant at $P < 0.05$.

Distribution of human activities and large mammals

In terms of the distribution of human activities, there appears to be a preference for old secondary forest and near primary forest. There is a tendency towards avoidance of riparian forest, light gaps and swamps; and marked avoidance of young secondary forest (Table 3). Large mammal surveys between April 2010 and March 2011 revealed no leopard signs in the site. No relationship existed between elephant encounter rate and chimpanzee ground nest abundance (Spearman test: $r = 0.264$, $P = 0.407$, $N = 12$).

Suitable nesting tree and Uapaca spp. availability

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A total of 87 tree species were identified in chimpanzee nests, but only four had a frequency of use of >5%: these were arbitrarily considered as ‘frequently-used’ species (Table 5). Five species of *Uapaca* spp. trees were found in the site (Table 5). A global comparison indicated significant differences in the density of frequently-used chimpanzee nesting trees across habitats (Kruskal-Wallis test: $\chi^2 = 11.52$, $df = 4$, $P = 0.018$; Table 4). The density of chimpanzee nesting trees in swamps significantly differed with that in old secondary forest (Table 6). Density of *Uapaca* spp. significantly differed across habitat types (Kruskal-Wallis test: $\chi^2 = 23.03$, $df = 4$, $P < 0.001$; Table 4). *Uapaca* spp. density in young secondary and riparian forest significantly differed with that of swamps (Table 6). The frequency of occurrence of *Uapaca* spp. seeds in chimpanzee faeces significantly differed across seasons (Chi-square test: $\chi^2 = 26.73$, $df = 1$, $P < 0.001$; Table 7).

Table 5. Plant species used by chimpanzees for nesting in La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon (April 2009–March 2011).

Species for nesting by chimpanzees	No. of nests in which species was found (N)	Proportion of nests in which species was found (%)
Frequently-used* species		
<i>Heisteria parvifolia</i>	428	38.28
<i>Strombosia grandifolia</i>	64	5.72
<i>Sorindeia grandifolia</i>	60	5.37
<i>Polyalthia suaveolens</i>	56	5.01
<i>Uapaca</i> species		
<i>U. paludosa</i>	36	3.22
<i>U. guineensis</i>	23	2.06
<i>Uapaca</i> sp. unk	22	1.97
<i>U. vanhoutei</i>	7	0.63
<i>U. acuminata</i>	6	0.54

*Species were considered ‘frequently-used’ when they occurred in more than 5% of nests.

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Table 6. Density of chimpanzee nesting trees and *Uapaca* spp. in swamps of La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon

	Near Primary forest	Old secondary forest	Young secondary forest	Riparian forest
Density of chimpanzee nesting trees in swamps				
Mann-Whitney U	226.0	241.5	171.5	20.0
P-value	0.116	0.002*	0.806	0.468
Density of <i>Uapaca</i> species in swamps				
Mann-Whitney U	248.5	350.5	78.5	4.0
P-value	0.260	0.134	0.002*	0.017*

*Significant difference at $P < 0.05$.

Table 7. Results of chimpanzee faecal analysis to show seasonal consumption of fruits *Uapaca* spp. in La Belgique research site, northern periphery of the Dja Biosphere Reserve, southeast Cameroon (April 2009–March 2011)

	Rainy season	Dry season
Faeces containing <i>Uapaca</i> spp. seeds	56	68
Faeces not containing <i>Uapaca</i> spp. seeds	123	41

Discussion

This paper provides evidence that chimpanzee ground night nesting occurs among a population of central chimpanzees at the northern periphery of the Dja Biosphere Reserve, Cameroon, preliminarily observed at a rate of 3.47%. Chimpanzee ground night nesting was first observed here between 2003–2005 (at a rate of 9.1%; Guislain and Dupain 2005). Ground night nesting has now been documented to occur in all chimpanzee subspecies, and in all species of extant great apes. We will subsequently review the current understanding of the drivers of ground night nesting in chimpanzees, in the light of our observations at La Belgique.

Factors that enable ground nesting

Predator release

It is commonly accepted that chimpanzee ground nesting becomes possible with predator rarity or absence (Furuichi and Hashimoto 2000; Maughan and Stanford 2001; Koops et al. 2007; Pruett et

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al. 2008; Last and Muh 2013); supporting the assumption that arboreal site selection is an anti-predator strategy (Samson and Hunt 2012). At Assirik, Senegal, the abundance of leopards appeared to cause chimpanzees to nest higher in trees (Baldwin et al. 1981). Ground nests have been more commonly found in areas of reduced predator pressure, for example at high altitude areas in Nimba (>800 m; Matsuzawa and Yamakoshi 1996) and in the predator-free northern sector of Bwindi Impenetrable National Park (Maughan and Stanford 2001). Chimpanzees in Fongoli increasingly nest closer to and on the ground, possibly as a result of the extermination of predators from the area (mean nest height 4.9 m and proportion of ground nests 12% in 2007–2008, Stewart 2011b; compared to 7.1 m and 2.7%, respectively, in 2000–2001, Pruett et al. 2008). However, other contributing factors may be at play: for example habituation efforts began at the same time as the earlier study (Stewart 2011b). There is no support for the anti-predation hypothesis from Seringbara, despite current high rates of tree nesting possibly due to previous high densities of ground predators (Koops et al. 2012a), nor from Bili-Uele, Democratic Republic of the Congo (Hicks 2010). During the second year of the MNC survey no leopard signs were detected in La Belgique. However, leopards are present in the site (pers. obs.), and even at low densities they may influence chimpanzee nesting behaviour. Therefore, we cannot rule out the possibility that chimpanzee nesting patterns are or were partly determined by predator pressure.

Large, non-predatory terrestrial mammals, such as elephant and buffalo, may influence nesting; Lopé gorillas for example may build tree nests, in part, to avoid such disturbance (Tutin et al. 1995). In La Belgique, forest elephants are present (buffalo are absent), but we found no relationship between elephant encounter rate and chimpanzee ground nest abundance. Similarly, in Bili-Uele, elephant tracks and dung were often encountered in stream beds where chimpanzees were sleeping in ground nests (Hicks 2010). In Bwindi Impenetrable National Park chimpanzees nest on the ground in areas where gorillas do not occur, suggesting potential competition for ground nesting sites under some circumstances (Stanford 2006). However, chimpanzees also ground nest in sites where gorillas live sympatrically (Abwe and Morgan 2008). Gorillas are present in La Belgique and nest (in order of preference) in light gaps, young secondary forest and swamps (Willie et al. 2012). Our study showed chimpanzees to preferentially nest in near primary and riparian forest. Therefore, there appears to be some segregation between chimpanzees and gorillas in terms of general preference for habitat types, but chimpanzee ground night nesting occurs where gorillas also frequently nest (in swamps). Thus it appears as though large mammal presence does not discourage chimpanzee ground nesting in our site.

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Seasonal and environmental factors

Nest building (nest height, canopy openness, nest group size, number of nests per tree, minimum distance between nests, and tree diameter) can vary in response to environmental conditions (Baldwin et al. 1981). Though day and night nests were not distinguished, no seasonal difference in occurrence or structure of ground nests was observed at Nimba in two studies (except for more ground nests at higher altitudes in dry season; Koops et al. 2007; 2012a); indicating that ground nests do not function in insulating nest-builders from low ambient temperatures during dry season nights, or from wet ground in the rainy season (Koops et al. 2012a). No seasonal influence on nesting was observed in orangutans (Ancrenaz et al. 2004) or for gorillas in Kahuzi-Biega National Park (Yamagiwa 2001). In contrast, we observed more ground nesting in the dry season, with Season being a significant predictor in the GLM. Ground nesting occurred more in the dry season in all study sites at Bili-Uele; however, when considering only the study sites which were subjected to year-long studies, no seasonal effects were found (Hicks 2010). Chimpanzees nested higher in trees and at higher altitudes in the wet season in Seringbara (Koops et al. 2012a). Lowland gorillas also construct more tree nests during the rainy season (Tutin et al. 1995). As rainfall is intricately linked to season (season is a categorical measure of rainfall), this may be the factor that leads to the seasonal influence on nesting seen in gorillas in Lopé (Tutin et al. 1995), who built more tree nests as rainfall increased. However, others have refuted this theory, by observing chimpanzee ground nests in the wet season (Reynolds and Reynolds 1965; Last and Muh 2013).

Chimpanzee nesting patterns appear to reflect a thermoregulation strategy of humidity avoidance—also linked to rainfall and season—as they nested higher in trees (warmer and less humid) in the rainy season (Koops et al. 2012a). This is further supported in chimpanzees (Baldwin et al. 1981; Pruett et al. 2008; Last and Muh 2013) and in bonobos (Fruth and Hohmann 1994). We did not investigate humidity in our study, therefore we cannot rule out the possibility that the seasonal effect observed is related to humidity.

Similarly, temperature may influence nesting, as observed in Fongoli chimpanzees (Pruett and Bertolani 2009). Chimpanzees choose nesting sites in specific locations within habitats by taking into account thermoregulatory demands (Samson and Hunt 2012). An empirical study using a human subject demonstrated that greater differential temperatures correlated with decreased overnight temperatures during tree but not ground sleeping in Fongoli (Stewart 2011a). In Budongo, temperature has been shown to be a determinant factor influencing terrestriality in chimpanzees during daylight, with more time spent on the ground at high temperatures (Kosheleff and Anderson,

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2009). Western lowland gorillas nest more often on bare ground when temperatures increase (Mehlman and Doran 2002). The present study found more ground nesting at higher temperatures; likely because of the inherent link between temperature and season.

Finally, dangerous high wind speeds at elevated nesting sites may be one of the reasons for ground nesting to be abundant on slopes at high altitude in the Nimba Mountains (Matsuzawa and Yamakoshi 1996). Safety likely outweighs comfort when nest building in dangerous storms, as gorillas were observed to abandon tree nests for the bare ground (Tutin et al. 1995). Factors influencing nesting may be season-related, but may be complex and interconnected and either directly or indirectly related to season, for example, regarding fruiting patterns.

Habitat and diet

Differences in nest-building between populations are likely to be partly determined by habitat differences (Baldwin et al. 1981). When considering all reports of chimpanzee ground nesting, it appears as though the behaviour is fairly widespread, occurring in many different habitat types. However, in La Belgique, ground nesting occurred more frequently than expected in swamps in this study (Table 3) and exclusively in swamps in a previous study (9 months between February 2003 and January 2005; Guislain and Dupain 2005). Chimpanzee densities were 30% higher in swamp forest than in *terra firma* forest in the Lac-Tele Community Reserve, northern Congo, and Habitat was the best predictor of ape nest abundance (Poulsen and Clark 2004). Previous studies in La Belgique have shown chimpanzees to generally preferentially nest in swamps (24.7% of the time; Guislain and Dupain 2005); however, our study displayed a preference for near primary and riparian forests. Although there was a slight tendency to nest in swamps (Table 3), they are relatively highly represented in La Belgique and account for 20% of the habitat (Willie et al. 2012), and were not particularly favoured as the preference index is relatively very close to zero. The occurrence of ground nesting in swamps in La Belgique may explain the significance of Season in the GLM, as ground nesting is only possible when the water level of a seasonal swamp is at its lowest, and another factor may be driving swamp use.

Many aspects of primate ecology (e.g. ranging and social behaviour) are related to food availability and diet; similarly, nesting probably arose in relation to adaptations associated with diet (Fruth and Hohmann 1996). Dietary preferences may influence nesting habitat choice, which in turn will influence materials available for nest construction and hence nesting patterns (e.g. height, diameter of tree; Remis 1993; Tutin et al. 1995; Furuichi et al. 2001; Basabose and Yamagiwa

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2002). At Bai Hokou, Central African Republic, when gorillas feed on fruits from large trees in primary forest, more commonly in the rainy season, they have a greater tendency to nest arboreally (Remis 1993), presumably influenced by both habitat and feeding habits. In La Belgique, food availability may influence the use of swamps by chimpanzees. Swamp forests are known to contain abundant food for gorillas and likely chimpanzees too (Poulsen and Clark 2004), with the Dja being no exception (Williamson and Usongo 1996). Five species of the genus *Uapaca* are found at more than double the density in swamps than *terra firma* forest in La Belgique (Table 3), three of which figure in the list of the 10 most abundant trees in swamps in the site: *Uapaca vanhouttei* in third place, *U. paludosa* in fifth and *U. guineensis* in eighth (Ottou 2009). Chimpanzees regularly eat *Uapaca* spp. fruits (Tutin and Fernandez 1993; Poulsen et al. 2001) and La Belgique is no exception. Chimpanzee faecal dietary analysis revealed that frequency of occurrence of *Uapaca* seeds (not identified to species level) in chimpanzee faeces significantly differed across seasons (Table 7), and indicated that chimpanzees consumed more *Uapaca* spp. fruits in dry season periods. Therefore, we hypothesise that chimpanzees might visit swamps, when conditions allow, and feed on *Uapaca* spp. fruits, but what encourages ground nesting behaviour remains to be determined.

Factors that promote ground nesting

Nesting tree availability may influence ground nesting. Chimpanzees may be forced to ground nest on steep slopes as they are not good terrain for nesting trees (Matsuzawa and Yamakoshi 1996), however, Koops et al. (2007) found no overall correlation with slope or altitude and occurrence of ground nests. Additionally, other studies have failed to find support that ground nesting results from a lack of suitable nesting trees (Furuichi and Hashimoto 2000; Koops et al. 2007; Pruetz et al. 2008; Last and Muh 2013). In La Belgique swamps, the five abundant *Uapaca* spp. trees that chimpanzees consume are also used for nesting: *U. paludosa*, *U. guineensis*, *Uapaca* sp., *U. vanhouttei* and *U. acuminata* are the sixth, 10th, 22nd, 25th and 27th most common, respectively (N = 87). However, they are not classed as frequently-used species and chimpanzees may avoid nesting in fruit trees containing ripe fruits (Koops et al. 2012a). When considering only frequently-used species there was a significant global difference in availability of nesting trees by habitat type. In particular, there was a lower density in swamps than in old secondary forest, but not compared to any other habitat type. Therefore, we cannot rule out the possibility of a limited availability of nesting trees in swamps leading to more chimpanzee ground nesting by necessity.

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Ground nesting may be favoured if a high abundance of terrestrial herbaceous vegetation (THV) results in comfortable nests, which appears to be the case for gorillas (Tutin et al. 1995). THV abundance may explain differences in nesting behaviour between gorilla subspecies and between populations (e.g. abundant in Virungas where mountain gorillas commonly ground nest, and rare in Petit Loango where tree nesting is more common; Yamagiwa 2001). In La Belgique, THV density is greater in flooded compared to *terra firma* habitats and is second highest in swamps (Willie et al. 2012), suggesting that ground nests have the potential to be comfortable in the swamps; however we found no significant relationship between THV density and ground nesting. It was previously suggested that the lack of THV in Fongoli prevented higher rates of ground nesting (Pruetz et al. 2008); however, this was later refuted, with the understanding that ground nests may be comfortable in the absence of THV (Pruetz pers. comm.). Indeed, chimpanzee ground nests in Seringbara contained a high proportion of woody plants (Koops et al. 2012a). We did not investigate the plant species used in ground night nesting; this is recommended for future research.

Ground nests may be easier and quicker to construct, which may explain a general preference by gorillas of herbaceous ground nests (Tutin et al. 1995). Indeed, in Fongoli, ground nests are less complex, built with fewer steps, and often made with thin malleable materials (Stewart 2011b), possibly because ground sleeping does not require as supportive a structure. Ground nests are more efficient, requiring lower energetic expenditure to stabilize the body when the nest is under construction and during use; and do not demand the energetic costs of ascending and descending trees (Samson and Hunt 2012). Although chimpanzees have not been seen to ground nest in Toro-Semliki, Uganda, more stable temperature ranges on the ground compared to in the trees, suggests that nesting on the ground may impose less thermal stress and therefore offer more comfort (Samson and Hunt 2012), and so would allow more undisturbed sleep. Ground nesting may reduce the risk of injury from falls (Brownlow et al. 2001); though others refute this (Koops et al. 2007).

Human influences

Human disturbance may influence primate nesting location (Anderson 2000). A higher prevalence of ground nesting was associated with lower human density and evidence of poaching and positively affected by distance to roads, across 160 km of transects through northern Democratic Republic of Congo (Hicks 2010). Similarly, ground nesting occurred in areas of reduced human hunting and agriculture in Lebialum-Moné (Last and Muh 2013). Ebo Forest chimpanzees

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constructed their beds mostly on steep slopes and rugged terrain, possibly to avoid human night hunting in the forest (Abwe and Morgan 2008); however, this may also be influenced by available vegetation in these extreme habitats. We found Human Activity to be a significant predictor of chimpanzee ground nesting, but with more ground nesting occurring as human activities increased. Unlike many study sites, La Belgique is located in a non-protected forest where human activity is intense and poses a real threat to the survival of the great apes in the area, and influences nesting behaviour (Tagg and Willie 2013). Guns are increasingly used for hunting arboreal monkeys, mostly in *terra firma* forests, and chimpanzees frequently nest in near primary and old secondary forest. They would, therefore, be exposed to strong human pressures and may avoid these habitat types in favour of swamps which are less frequented by hunters. In dry seasons, water levels are low and conditions enable swamp use. When nesting in swamps, chimpanzees may build more ground nests because the abundant ground vegetation may help prevent detection by humans. In addition, the increasing use of guns in the site poses less of a threat to ground sleeping apes, but more so for those in the trees; this threat to arboreal animals may drive chimpanzees to the ground. It is possible that avoiding this human threat is sufficiently important that it counterbalances the risks of predation or of accidental encounters with ungulates on the ground (Tutin et al. 1995; Hicks 2010).

Social and cultural factors

Ground nesting may have a social element, e.g., being sex-specific. Males were responsible for building all of the elaborate ground nests found in Seringbara (Koops et al. 2007); however, it is difficult to confirm nest-builder sex without the use of genetics so these suggestions should be taken as preliminary (Koops et al. 2007). Other studies have shown males to nest lower than females (Plumptre and Reynolds 1997; Brownlow et al. 2001; Koops et al. 2007; Pruett et al. 2008); this could be due to the larger body mass of males (Reynolds 1967; Brownlow et al. 2001) or as a mate guarding strategy when females are in oestrus (Koops et al. 2012a), as seen in bonobos (Fruth and Hohmann 1993). Given the relatively high proportion of males at Fongoli, this is also considered as a possible explanation for the occurrence of ground nesting at this site (Pruett et al. 2008), but requires further investigation. However, ground nesting is a widespread behaviour performed by large groups at Seringbara (Koops et al. 2012b), Lebialum-Moné (Last and Muh 2013) and Bili-Uele (Hicks 2010), unlikely to be only males. At La Belgique, chimpanzees are not habituated and genetic analyses not performed, so we cannot confirm nest-builder sex. Ground nests were found to

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occur in pairs or groups (Table 2) and more commonly associated with tree nests (18/35 = 51.4%); this variability does not clearly indicate a social element such as a male mating strategy.

Ground nesting behaviour might have a cultural element (Baldwin et al. 1981; Matsuzawa and Yamagoshi 1996; Whiten et al. 1999; Humle 2003; Koops et al. 2007; Hicks 2010). Although exhibited in some captive apes, nesting is generally assumed to be a learned behaviour (McGrew 2004). Ground nesting may be a habitual traditional behaviour pattern that is being exhibited less (Pruetz et al. 2008), leading to a loss in cultural diversity of chimpanzees (Hicks 2010), which may be temporary, with the behaviour gradually re-emerging when conditions alter. Alternatively, ground nesting may be a new cultural adaptation to certain conditions (Boesch 1995; Pruetz et al. 2008; Stewart 2011b). However, there was no evidence of cultural variation in nesting behaviour within and between gorilla populations at Lopé (Tutin et al. 1995). The low observed rates of chimpanzee ground night nesting highlight a preference for tree nesting across their range. Given the differences in diet, body size, social organisation and arboreality between gorillas and chimpanzees, it is to be expected that chimpanzees might nest more in trees than on the ground. However, a fairly broad range of ground nesting rates, including considerable variation over time within the same sites, highlights the flexibility of chimpanzee nesting behaviour.

Summary

In summary, we suggest that central chimpanzees in La Belgique visit swamps, when enabled to do so in the low water levels of the dry season, to seek relief from intense levels of human hunting in the non-protected site, which pose a real threat to apes. Swamp use may also indicate a strategy of dietary opportunism: chimpanzees can benefit from abundant *Uapaca* spp. fruits when most other fruit species are rare. There is a lower availability of suitable nesting trees in swamps which may encourage ground nesting, and an abundant supply of THV which may make ground nesting comfortable, but also, crucially, likely decreases detection by hunters. Ground nesting may be further encouraged by thermoregulatory demands during hot months and potential contributing influences of other factors not investigated in the present study.

Across the range of the chimpanzee, ground night nesting occurs in different habitat types, appears to be driven and influenced by different factors, and may reflect cultural or social differences between populations. As ground nesting occurs in all extant great apes, we suggest it to be an integral part of a flexible behaviour pattern influenced by a variety of contributing and interconnected factors. Furthermore, this growing realisation that chimpanzee nesting behaviour

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exhibits flexibility across the species' range reinforces the ideas of Stanford (2006), who noted that despite divergent behaviour and ecology in some respects, differences between gorillas and chimpanzees appear not to be as stark as previously thought and that our view of the varying ecology (diet, ranging, nesting, mating systems) of sympatric populations should be reconsidered. For example, gorillas have been observed using tools (Breuer et al. 2005), a phenomenon previously believed to occur in other great ape species, but not gorillas.

We stress the implications of the occurrence of chimpanzee ground nesting on great ape conservation management. Chimpanzee ground nests will invariably decay quicker than arboreal nests, due to the use of non-timber material and because of their direct contact with the ground. In addition, due to their rarity they may not be sought or recognised by researchers, therefore potentially leading to bias in density estimates. Investigation of the comparative properties and functions of night and day nests would be required to quantify this bias. In the meantime, the adoption of a multi-evidential method of assigning nest-builder identity, as already adopted by many studies (e.g. Furuichi et al. 1997; Matthews and Matthews 2004; Sanz et al. 2007), is suggested to avoid inaccurate density estimations.

Finally, as we share a common ancestor with the genus *Pan*, knowledge of what motivates chimpanzees to sleep in nests on the ground—a behavioural change that also occurred in early hominins—can inform on environmental or social factors that may have been influential in hominin evolution, including sympatric living, social organisation, foraging and diet, ranging, nesting and tool use (Stanford 2006; Pruettz and LaDuke 2010; Koops et al. 2012b). It has been suggested that pre-*Homo erectus* hominins already exhibited the tendency to sleep on the ground, even before taming fire or terrestrial living, and that the transition from tree to ground was gradual and not forced when moving out of the woods (Stanford 2006; Koops et al. 2012b). This contention is supported by our observations that ground night nesting occurs in all subspecies of chimpanzee and all species of extant great ape. As a clear understanding of the influences of chimpanzee ground nesting remains evasive, we recommend comparative studies across the range of the chimpanzee to assess influences of environmental, habitat, external, social and cultural factors with a view to furthering our understanding of hominin evolution.

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