RESEARCH ARTICLE

Environmental and anthropogenic effects on the nesting patterns of Nigeria–Cameroon chimpanzees in North-West Cameroon

Chefor Fotang[1] | Udo Bröring[1] | Christian Roos[2] |
Evidence C. Enoguanbhor[3] | Paul Dutton[4] | Luc R. D. Tédonzong[5] |
Jacob Willie[5,6] | Yisa G. Yuh[7,8,9] | Klaus Birkhofer[1]

[1]Department of Ecology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Brandenburg, Germany

[2]German Primate Centre Leibniz Institute for Primate Research, Gene Bank of Primates and Primate Genetics, Gottingen, Germany

[3]Department of Geography, Humboldt University of Berlin, Applied Geoinformation Science Laboratory Berlin, Brandenburg, Germany

[4]Independent Researcher, Waikato, New Zealand

[5]Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium

[6]Department of Biology, Terrestrial Ecology Unit (TEREC), Ghent University (UGent), Ghent, Belgium

[7]Hochschule fur nachhaltige Entwicklung Eberswalde, Forestry and Environment, Eberswalde, Germany

[8]Szkola Glowna Gospodarstwa Wiejskiego, Warszawa, Poland

[9]Concordia University Montreal, Montreal, Quebec, Canada

Correspondence
Chefor Fotang, Department of Ecology, Brandenburg University of Technology, Konrad-Wachsmann-Allee 6, 03046 Cottbus, Germany.
Email: fortangchefor@gmail.com and Chefor.Fotang@b-tu.de

Abstract

Environmental conditions and human activity influence the selection of nest sites by chimpanzees and may have serious conservation implications. We examined the characteristics of nesting trees preferred by chimpanzees, investigated the effect of vegetation composition and topography on nest site locations and seasonality on nesting heights of chimpanzees, and verified the effect of predator occurrence and human activity on the nesting behavior of the Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*) in Kom-Wum Forest Reserve (KWFR) and surrounding un-protected forest in Cameroon. We recorded 923 nests, 502 signs of human activity, and 646 nesting trees along line transects and recces (reconnaissance) for two seasons. We found that chimpanzees constructed more arboreal nests on tall primary trees with high lowest branch height and large diameter at breast height. Moreover, they oriented their nests within trees in the slope direction when the nesting trees were located on slopes. Additionally, the occurrence of chimpanzee nests was positively related to increasing elevation and slope and decreased with distance to primary forest. In contrast, the number of nests increased with distance to secondary forest, open land, and villages, and nesting height was not influenced

by seasons. While we recorded no signs of large nocturnal chimpanzee predators at nesting trees, we found signs of hunting activity at nesting locations. Nesting high in trees is likely a way of avoiding hunting, while nest orientation within trees in slope direction shortens escape routes from human hunters. Our findings suggest that chimpanzees select safe trees (tall trees with high lowest branch height) located in nesting areas (primary forest, high elevation, and steep slopes) that are not easily accessible by humans. Therefore, conservation efforts should focus on protecting primary forests at high elevation and steep slopes and reducing human impact.

KEYWORDS
ecological factors, human activity, nesting behavior, Nigeria–Cameroon chimpanzee, predation

1 | INTRODUCTION

All weaned non-human great apes construct sleeping or resting platforms (hereafter "nests") by modifying branches and leaves of trees (Goodall, 1962; Tutin & Fernandez, 1984). This behavior is common for chimpanzees, bonobos, orangutans (Fruth & Hohmann, 1996), and gorillas (Iwata & Ando, 2007). Like other great apes, chimpanzees build a new nest every night or may re-use old nests after adding new material to reinforce them (Hernandez-Aguilar, 2006, 2009). Generally, their nests can be arboreal (Poulsen & Clark, 2004) or can be built on the ground (Abwe & Morgan, 2008; Furuichi & Hashimoto, 2000; Tagg et al., 2013). They can further be categorized as night or day nests (Brownlow et al., 2001; Koops et al., 2012). Usually, night nests are arboreal and more elaborate constructions (Fruth & Hohmann, 1996; Reynolds, 2005), while day nests tend to be terrestrial and the structure is less sophisticated (Brownlow et al., 2001; Koops et al., 2012). Day nests on the ground are constructed with leaves or consist of ferns which are used for resting during the day, whereas night nests on the ground consist of bent and broken branches (Furuichi & Hashimoto, 2000). Unlike day nests on the ground are mostly found without trees in their neighborhood, night nests on the ground usually occur in groups and are linked with arboreal nests in their surroundings (Koops et al., 2007). Furthermore, day nests on the ground are used to protect chimpanzees from the cold soil surface (Boesch, 1995).

The selection of individual nesting trees by chimpanzees has been attributed to the morphological characteristics of trees, including the tree diameter, tree height, and lowest branch height (Hakizimana et al., 2015; Hernandez-Aguilar et al., 2013) as well as the species type (Brownlow et al., 2001; Sanz et al., 2007; Stanford & O'Malley, 2008). In addition to the selection of individual trees, chimpanzees also select nesting areas within forests, including a preference for primary forest cover (Bryson-Morrison et al., 2017; Koops et al., 2012), high elevation (Barca et al., 2018; Koops et al., 2012), steep slopes (Abwe, 2018; Dutton et al., 2016; Kamgang et al., 2018), and closed canopy (Abwe, 2018). Besides habitat and topographic factors, seasonality may affect nest construction in great apes. For example, Takemoto (2004) noted that chimpanzees tend to

show arboreal behavior in the wet season to minimize the effect of heat loss and spend more time on the ground during the dry season due to an increase in surrounding temperatures. Similarly, Koops et al. (2012) demonstrated that nesting at elevated heights in the wet season is a strategy to avoid constructing nests in humid conditions closer to the ground.

Non-human primates select nesting sites in trees to reduce access or detection by predators (Anderson, 1984). For instance, Stewart and Pruetz (2013) showed that chimpanzees nest at high and peripheral nesting positions within trees in areas with potential terrestrial predators such as leopard (*Panthera pardus*) and lion (*Panthera leo*). Furthermore, human activity may also affect the selection of nesting locations by chimpanzees (Heinicke et al., 2019; Tagg & Willie, 2013). Particularly, the construction of night nests on the ground by chimpanzees is more frequently observed in areas with limited human activity (Hicks et al., 2010; Last & Muh, 2013).

Agricultural activity, illegal timber exploitation, uncontrolled burning, and illegal hunting are major anthropogenic threats to the Nigeria–Cameroon chimpanzee (Morgan et al., 2011). This chimpanzee subspecies has about 3500 individuals remaining in the wild, is the most threatened subspecies, and relatively unstudied. Since the recognition of the Nigeria–Cameroon chimpanzee subspecies in 1997 (Gonder et al., 1997), several studies have been conducted to improve our understanding of their nesting behavior at several sites, including the selection of nest trees and areas in relation to ecological conditions and human activity in Ngel Nyaki Forest Reserve (Dutton et al., 2016) and Gashaka-Gumti National Park (Fowler, 2006) in Nigeria. In Cameroon, recent studies focused on the selection of nest locations in relation to the availability of fruits in Ebo Forest Reserve (Abwe, 2018), the effects of preference for a particular habitat type and topography in Mbam-Djerem National Park (Kamgang et al., 2018), and in Ebo Forest Reserve (Abwe, 2018), the effect of human activity on arboreal and ground nest location in Lebialem-Mone Forest (Last & Muh, 2013), Tolafa Hill Wildlife Sanctuary (Njukang et al., 2019), Mone-Oku Forest (Wade, 2020), and Babanki–Finge Forest (Doumbé, 2014). However, information on nesting behavior of the Nigeria–Cameroon chimpanzee is still missing from priority conservation areas as outlined in the IUCN-endorsed regional

conservation action plan (Morgan et al., 2011). The Kom–Wum Forest Reserve (KWFR) is considered a high priority conservation area for the Nigeria–Cameroon chimpanzee, and recommendations were made to conduct surveys on their abundance, behavior, and distribution (Morgan et al., 2011). Initial chimpanzee surveys in KWFR focused on confirming the presence of chimpanzees (Doumbé, 2015), estimating the population size (Chuo et al., 2017; Fotang et al., 2021), and indicating habitat preferences (Fotang et al., 2021). Doumbé (2015) and Chuo et al. (2017) further suggested that chimpanzee predators are absent from KWFR, potentially resulting in specific nesting behavior. However, previous studies provided very little information about potential drivers of nesting behavior in this high-priority conservation area.

To improve our understanding of factors affecting nest building in chimpanzees in general, and to add to previous knowledge of nesting ecology of the Nigeria–Cameroon chimpanzee in particular, our study aims to analyze: (a) which traits of tree species are preferred for nesting (nesting tree selection); (b) the effects of environmental factors (vegetation, topography, seasonality) on nesting behavior (nesting area selection); and (c) if predator presence and human activity affect the selection of nest sites and nest distribution in trees (disturbance) in KWFR. We hypothesize that the selection of nesting trees by chimpanzees is driven by specific tree traits and that the selection of nesting areas further depends on the local vegetation composition, topography, and seasons (Koops et al., 2012). We predict that chimpanzees (i) construct more nests on tall primary trees (trees that provide the main support for nests), trees with larger diameter and high lowest branch height; (ii) orientate their nests in the direction of the decreasing slope, (iii) frequently nest in primary forests, at higher elevations, on steep slopes, and that (iv) nest higher in the wet season than the dry season. We further hypothesize that chimpanzees nest higher in trees if predators are present or when humans are active in the nesting location. We recommend conservation actions required to ensure the long-term survival of chimpanzees in the reserve.

2 | MATERIALS AND METHODS

2.1 | Study area

The KWFR is located in the Boyo and Menchum Divisions in the North-West region of Cameroon (Figure 1a; Latitude 6°16′12.53″N and Longitude 10°7′57.85″E). It is a lowland-montane tropical forest of approximately 80 km^2 and spreads on an undulating landscape with an elevation of 565–1640 m above sea level (Figure 1b). The temperature ranges from 15°C to 38°C with a mean yearly rainfall of about 2400 mm and a humidity of 82% (PNDP, 2011). The area has two distinct seasons, a wet season (mid-March to mid-October) and a dry season (mid-October to mid-March). Rivers Meteh, Tschuh Akooghe, and Mughom flow within the reserve and join rivers Menchum that flows at the boundaries of the reserve towards Nigeria (Kah, 2015). This reserve is home to seven diurnal and six nocturnal primate species (Chuo et al., 2017; Doumbé, 2015; Fotang, 2018). Among primates, chimpanzee population size estimates range from 10 (direct observation) to 83 individuals (distance sampling) based on the method used (Fotang et al., 2021). In addition to primates, there are important timber species in the reserve, including *Khaya ivorensis*, *Triplochiton scleroxylon*, *Milicia excelsa* (Morgan et al., 2011). The KWFR encompasses the village communities of Mughom and Bueni in the south and borders the village communities of Bu, Mbengkas, Baiso, and Mbongkissu in the North-West region of Cameroon (Figure 1b). Unsustainable exploitation of non-timber forest products and hunting are the major threats to forest resources in KWFR (Fotang et al., 2021; Kah, 2015).

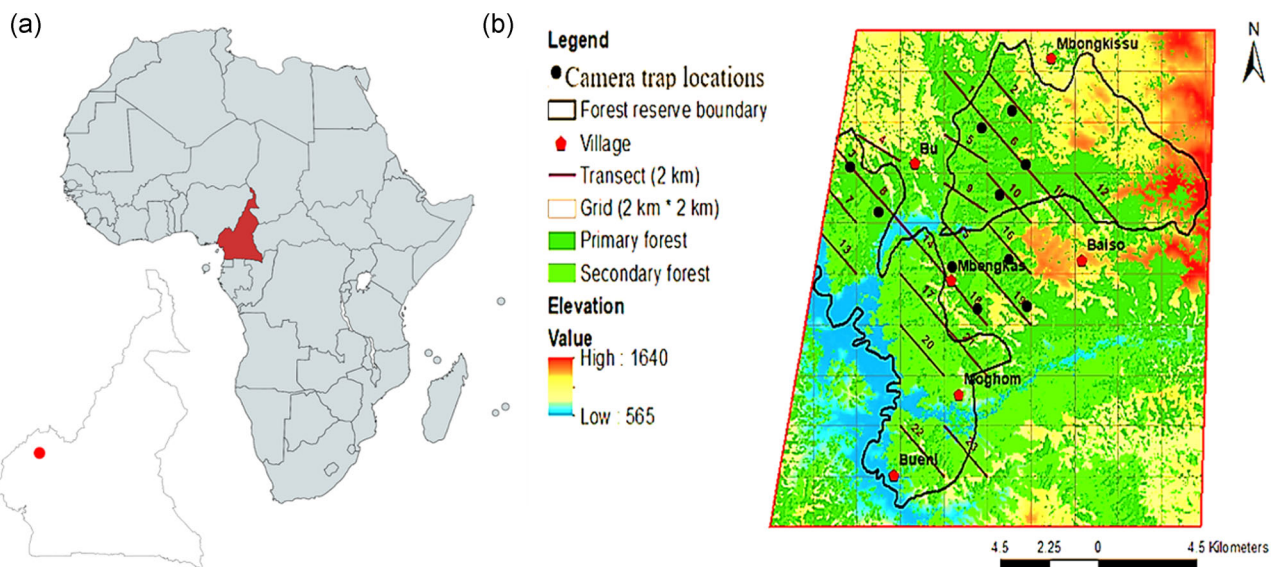**FIGURE 1** Maps of (a) Cameroon and the study location Kom-Wum Forest Reserve (KWFR) in North-West Cameroon (redpoint), (b) map of KWFR including major villages with transects for surveys (1–23) and location of camera traps (Fotang et al., 2021)

2.2 | Ethics statement

We conducted this study respecting the principles for research on non-human primates outlined in the American Society of Primatologists manual for primates' ethical handling. We obtained authorization from the Ministry of Scientific Research and Innovation in Cameroon and respected the protocols of the 1994 forestry and wildlife law governing research on chimpanzees.

2.3 | Chimpanzee nest surveys and description of nesting trees

We generated a 2 × 2 km grid across the study area (100 km²) to place line transects (each 2 km in length) equally spaced (1000 m) following a systematic design (Buckland et al., 2001). Additionally, we considered the reconnaissance (recce) method to identify hotspots of chimpanzee activity since they are unhabituated (Kühl et al., 2008). Based on the results from recce surveys, we monthly surveyed 13 line transects (46 km) and 42.09 km recce with at least one chimpanzee nest during two seasons: wet (May–September 2018) and dry (November 2019–March 2020). For every nesting site encountered, we recorded the characteristics of nesting trees following Baldwin et al. (1981). We also marked nesting tree locations using a GARMIN GPSMAP 64 s device and recorded the nest height, tree height, and lowest branch height using a hypsometer (Nikon Forestry Pro 6x216x21\11-55YD). Furthermore, we noted the number of nests per tree and the number of trees per nest (integrated nest), and measured the diameter at breast height (DBH) and the horizontal distance of the nest from the tree trunk using a 30-m tape. For each nest, we recorded the nest type following Furuichi and Hashimoto (2000). Additionally, we defined the nest age classes per tree as fresh—when all leaves in the nest were green; recent—drying leaves of distinct colors; old—nest structure is unbroken with most of the leaves being brown; and very old—nest with holes displaying little or no leaves, but still be distinguished by bent twigs following Tutin and Fernandez (1984). Simultaneously, we calculated the vertical position of a nest within the crown following Hernandez-Aguilar et al. (2013). We recorded the slope direction for nests and the nest orientation within a tree using a Gearmax® Professional military clinometer following Hernandez-Aguilar et al. (2013). For nesting trees located on slopes, we classified nests as oriented to the east (>22.5° and ≤167.5°), west (>202.5° and ≤337.5°), north (>337.5° and ≤22.5°), and south (between >167.5° and ≤202.5°). Nesting trees in the field were identified by a PhD botanist student (Nkemnkeng Francoline, Jong) from the University of Dscang, Cameroon. Samples and pictures of unidentified plants were taken to the Cameroon National Herbarium for identification by experts. We conducted a Bivariate Spearman's rank correlation analyses to test the relationship between tree height and nest height, DBH, and lowest branch height. The χ^2 tests were used to analyze whether chimpanzee nest orientation depended on slope direction and the Wilcoxon rank-sum tests to compare mean nest heights between wet and dry seasons.

2.4 | Environmental determinants of nesting sites

We described vegetation at nesting sites following White and Edwards (2000): primary forests—mixed forest with many large trees, unbroken canopy, and scanty vegetation cover on the ground, and mixed forest with dense vegetation cover on the ground dominated by lianas and Marantaceae; old secondary forest included—sections of forest with large trees, but showing indicators of previous disturbance by humans, with no grown crops, but occasionally with old palm or mango trees still present; and grassland—grazing land depicted by short-grass mixed with arable fields and cattle paths. Following Koops et al. (2012), we classified canopy cover as: no cover (0%)—nests with no branches with leaves over a nest; little cover—when 1%–25% of nests were covered by branches with leaves; light cover—when 26%–50% of nests were covered; moderate cover—when 51%–75% of nests were covered; and complete cover—when 76%–100% of nests were covered. The slope for each nest was classified as flat ground (0°), gentle (1°–5.7°), steep (5.7°–26.6°) or precipitous (>26.6°) following De Vere et al. (2011).

In addition to field surveys, we acquired land cover from remote sensing data (Landsat 8, 30 m pixel, on September 02, 2017). The imagery was classified into primary forest, secondary forest, bare lands, and water bodies using supervised image classification and the maximum likelihood algorithm (Ganasri & Dwarakish, 2015). We obtained the elevation from a Shuttle Radar Topography Mission 30 m resolution Digital Elevation Model (Jarvis, 2008).

To assess whether nests are distributed randomly regarding the environmental variables or not, we created 2000 random points for each variable; that is, 2000 points for elevation, slope, primary forest, secondary forest, bare land, villages, aspects, rivers, and signs of human activities (Figure 2). We used the whole KWFR Reserve and surrounding forest with chimpanzee nests to define the limits of the random points. We then created layers representing distances to the random points generated to each environmental variable by calculating Euclidean distances and extracted these distances to nest locations following Enoguanbhor et al. (2020).

We first checked collinearity among environmental variables by calculating the variance inflation factor (VIF) using the package usdm (Naimi et al., 2014). We excluded all environmental variables with a VIF >5 (Table 1). We then performed a Pearson correlation test to calculate the collinearity among pairs of environmental variables. For each pair of significantly correlated environmental variables (slope vs. aspect and elevation vs. rivers), we eliminated one of the environmental variables (i.e., aspect and rivers). Our final model considered seven environmental variables, including elevation, slope, distance to primary forest, distance to secondary forest, distance to bare land, distance to villages, and distance to signs of human activities (Table 1). We used the package car (John Fox; Sanford Weisberg, 2019) and a linear model function to perform a multiple regression analysis of the relationship between the dependent variable (chimpanzee nest locations) and independent variable, including ecological (distance to primary forest, distance to secondary forest, elevation, slope, aspect, distance to rivers) and human factors (distance to villages, distance to bare land, distance to signs of human activity). All spatial analyses were conducted in ArcGIS 10.6.1 (ESRI, 2018) and
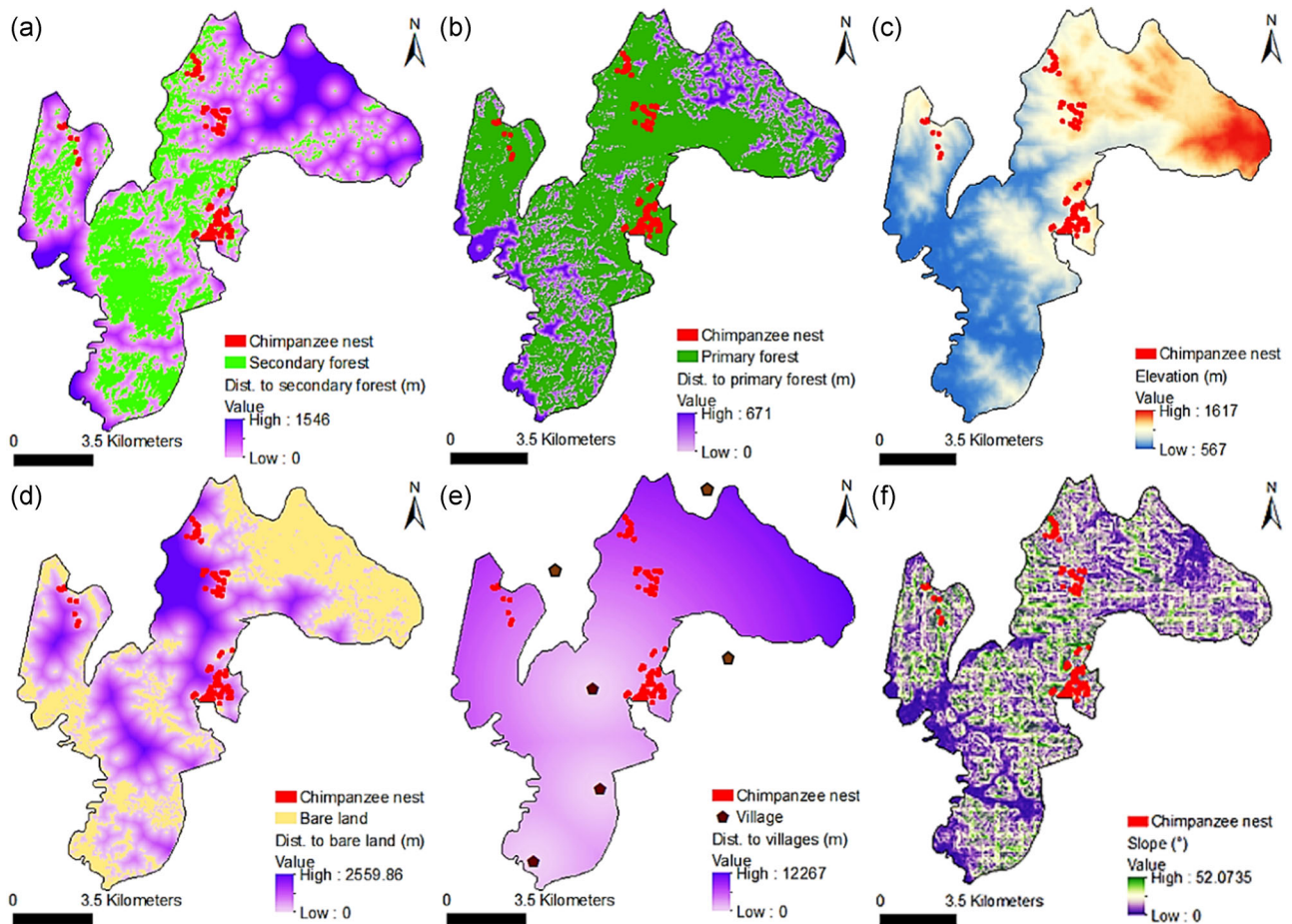
FIGURE 2 The distribution of chimpanzee nests with (a) distance to primary forest, (b) distance to secondary forest, (c) elevation, (d) distance to bare land, (e) distance to villages, and (f) slopes

TABLE 1 Multiple linear regression model showing environmental variables, of chimpanzee nest site selection and the variance inflation factor

Environmental variable	Parameter estimates	Standard errors	p	Variance inflation factor
Intercept	544.41	145.38	<0.001	
Elevation	0.49	0.14	<0.001	1.40
Slope	0.22	0.09	<0.05	1.01
Distance to primary forest	2.98	0.55	<0.001	1.54
Distance to secondary forest	−1.71	0.15	<0.001	1.72
Distance to bare land	−0.41	0.12	<0.001	1.51
Distance to villages	−0.22	0.03	<0.001	1.41
Distance to signs of human activity	1.09	0.02	<0.001	1.65

hypothesis testing in R (R core team, 2016) version 3.5.1 (Venables et al., 2009).

2.5 | Antipredator/human avoidance

To investigate the effect of predator or human activity on the nesting behavior, we searched for signs of chimpanzee predators or human activity along transects and recces. We further attached ten camera traps to trees at a height between 30 and 80 cm along frequently used chimpanzee routes leading to nesting sites to increase the probability of detecting chimpanzee predators (Fotang et al., 2021). We recorded human signs (farms, spent cartridges, snares, non-timber forest product collection, timber extraction, grazing activities) within a 50 m radius of each nesting site following White and Edwards (2000).

We calculated the Kilometric Count Index for human signs (encounter rates of human signs) as the total number of human signs encountered (N) during the survey divided by the total length of the transect (L) in km (Mathot & Doucet, 2005).

3 | RESULTS

3.1 | Physical characteristics of nesting trees

We found arboreal, ground, and liana nests in descending order during our survey (Table 2). Most nests were recorded in the wet season. Consequently, more trees were used for nesting in the wet season (Table 2). Most nests were built in a single tree, and the rest (integrated nests) were built by integrating the branches from other trees (non-single trees). The majority of trees provided the main support for nests (primary trees), and the rest provided minor support (secondary trees). The mean height and DBH of primary trees were greater than those of secondary trees (Table 3). The height of nesting trees and nest height ($r = 0.91$, $N = 625$), the tree DBH ($r = 0.59$, $N = 625$), and the lowest branch height ($r = 0.62$, $N = 221$) were positively correlated.

Of the 923 nests, 20 nests had no vegetation above the nest (0% cover), 223 had little vegetation above the nest (1%–25% of the nest was cover by branches with leaves), 250 (26%) had light vegetation above the nest (25%–50% of the nest was covered by branches with leaves), 271 moderately covered (51%–75% of a nest was covered by branches with leaves) and 159 of the nest was completely covered by vegetation (branches with leaves covered 100% of the nest). Of 307 arboreal nests recorded in the dry season, 213 were constructed on western slopes, 49 on eastern slopes, and 45 on north or south-facing slopes. Of the nest constructed on the eastern slopes, 25 were oriented east of the tree trunk, 19 were found exactly on the top of the base of the tree trunk (no orientation), three were oriented north of the tree trunk, one was oriented west of the tree trunk, and one was oriented south of the tree trunk. Of the 213 nests constructed on western slopes, 90 were oriented west from the tree trunk, 77 had no orientation within the tree since they were found exactly on the top of the trunk, 28 north, 17 east, and one south. Of 307 nests, 106 were oriented west within the tree (>202.5° and <337.5°), 107 directly on the trunk, 50 were oriented east within the tree (>22.5° and <167.5°), 22 north within the tree and 22 south within the tree.

There was a significant relationship between nest orientation within the tree and slope direction (χ^2 test = 40.675, $p < 0.010$). Most nests located on the west slope were oriented in western direction (χ^2 test = 79.752, $p < 0.001$). Of the 72 ground nests recorded, 57 were night nests and 15-day nests. All ground nests were located on precipitous slopes (>26.6°) and were found under high canopy cover (75%–100%). A majority of the ground nests were further supported either by a tree trunk, tree roots, fallen wood, a stone, or liana from different plants.

TABLE 2 Number of nests and trees recorded per season (wet and dry), in total and percentage of each nest category

Season	N wet	N dry	N total	Percentage
Nests				
All nests	552	371	923	100
Arboreal nests	541	307	848	92
Ground nests	11	61	72	8
Nests built in liana	0	3	3	<1
Nests built in single trees	531	300	831	–
Integrated nests	10	7	17	–
Nesting trees				
All trees	425	221	646	100
Primary trees	404	221	625	97
Secondary trees	10	11	21	–
Single trees	392	216	608	–
Non-single trees	24	14	38	3

TABLE 3 Physical characteristics of nesting trees and nests

	Mean	Median	SD	Range	N
Nesting trees					
DBH of primary trees (cm)	42.0	37.0	23.8	3.8–155.3	625
Height of primary trees (m)	17.0	17.0	5.8	1.0–37.9	625
Number of nests per tree (N)	1.4	1.0	5.3	1.0–6.0	625
Lowest branch height (m)	10.0	9.8	4.9	0.8–30.4	221
Crown height (m)	6.3	5.3	4.2	0.4–20.8	221
DBH of secondary trees (cm)	15.3	5.8	25	1.0–105.1	21
Height of secondary trees (m)	8.6	10.4	6.0	1.0–24.5	21
Nests					
Nest height (m)	15.5	15.6	5.4	1.0–33.4	851
Distance from tree trunk (m)	1.4	0.9	2.0	0.0–13.8	307
Number of trees per nest (N)	2.2	2.0	0.8	1.0–5.0	38

3.2 | The environmental determinants of the selection of nesting locations

The multiple linear regression model indicates that the locations of chimpanzee nests decreased with distance to primary forest and increases with slope and elevation (Table 1; $df = 1992$, $R^2 = 0.69$, $F = 628.8$, $p < 0.001$; Figure 2b,f,c). In contrast, the number of

chimpanzee nests increased with distance to secondary forests, bare land, and villages (Table 1; Figure 2a,d,e). Of 923 chimpanzee nests, we found 532 (58%) in primary forest and 391 (42%) in secondary forest. Chimpanzees built nests at elevations between 836 and 1279 m above sea level (Figure 2c) with increasing nest locations at higher elevation (Table 1). We found 290 nests below 1000 m and more 633 above 1000 m (N = 923). Of the 923 nests, we found 17 on flat ground, one on a gentle slope (0°–5.7°), 30 on a steep slope (5.7°–26.6°), and 875 on a very steep slope (>26.6°). The mean nest height of chimpanzees nest did not differ between the wet season (15.9 m SD ±3.3, N = 541) and the dry season (14.8 m ± SD 2.8; Wilcoxon rank-sum test: W = 41, p = 0.460, N = 307).

3.3 | Antipredator/human avoidance hypothesis

We found no signs of chimpanzee predators (vocalizations, feces, or footprints) during the line transect and recce surveys, and the cameras recorded no pictures of large nocturnal chimpanzee predators (leopards). In total, we recorded 502 signs of human activity over a survey effort of 700.9 km for the two survey periods. These included 325 signs of hunting (spent cartridges, active wire snares, hunter huts, carcass of a killed chimpanzee in a hunter's hut), 80 farms, 34 signs of grazing activity, 46 cases of illegal timber harvesting, and 17 signs of non-timber forest products collection. Of the 502 signs recorded, we found 34 (all hunting signs) within a 50 m radius of the nesting sites. The encounter rate of human activities within a 50 m radius of the nesting sites was 0.05 signs km^{-1}. The overall encounter rate of signs of human activity recorded for the two survey period was 0.72 signs km^{-1}.

3.4 | Nesting tree species

Chimpanzees used at least 17 plant species for constructing their nests. The four most frequently used tree species were strombosia (Strombosia sp.) (22%), pseudospondias (Pseudospondias macrocarpa) (20%), umbrella tree (Musanga cercropioides) (16%), and calabash nutmeg (Monodonra myristica) (10%, for a list of all species see Table SI).

4 | DISCUSSION

Our data support previous work that chimpanzees select safe trees for nesting and locate nests in areas with relatively low human disturbance. As predicted, chimpanzees prefer taller trees with high branches and large diameters for nesting. They preferentially located nests in primary forest vegetation at a higher elevation and on steep slopes where nests were oriented in the slope direction. On the contrary, nesting tree heights were not influenced by seasons. Furthermore, we found human signs within nesting at locations, but

chimpanzees avoided human activity by nesting high in trees, preferably located on steep slopes, and by constructing ground nests only on very steep slopes. While we recorded no signs of large nocturnal chimpanzee predators, we found remains of a killed chimpanzee in a hunter's hut, suggesting that humans still eat chimpanzee meat in the area.

4.1 | Physical characteristics of nesting trees

Our results support previous work showing that tree height is the most preferred tree trait by chimpanzee for nesting than the lowest branch height and tree diameter (Hernandez-Aguilar & Reitan, 2020). Most tall trees had a high lowest branch height and large diameters confirming that nesting tree selection primarily depends on tree height. These results further support previous work that chimpanzees prefer tall trees with high lowest branch height for nesting (Hakizimana et al., 2015; Hernandez-Aguilar et al., 2013). At Mon-Oku Forest in Cameroon, tall and large trees were also selected trees to build multiple nests (Wade, 2020). Fowler (2006) reported that nesting trees' mean height and diameter were higher than those of surrounding non-nesting trees at Gashaka-Gumti-National Park in Nigeria. Our results also support previous work that chimpanzees prefer some tree species for nesting over others (Brownlow et al., 2001; Furuichi & Hashimoto, 2004; Hakizimana et al., 2015; Sanz et al., 2007; Stanford & O'Malley, 2008). Overall, four species (Strombosia sp., P. macrocarpa, M. cercropioides, and M. myristica) contributed 68% of all plant species used for nesting by chimpanzees in KWFR. Similarly, 84% of all chimpanzee nests were built in five plant species at Njuma in Cameroon (Abwe, 2018), and 52.7% of all chimpanzee nests were built in Dialium guineense at Lagoas de Cufada Natural Park, in Guinea (Carvalho et al., 2015). Furthermore, Strombosia sp. was among the most used tree species by chimpanzees for nest building in Ebo forest and Mbam and Djerem (Abwe, 2018), Babanki-Finge (Doumbé, 2014), Mone-Oku Forest Reserve (Wade, 2020), and Ngel Nyaki Forest Reserve (Dutton et al., 2016). At Albert Lake escarpment, in the Democratic Republic of the Congo, M. myristica, followed by Strombosia sp. were the most used tree species for nesting by chimpanzees (Laudisoit et al., 2021). Although two of the most important nesting trees P. macrocarpa and M. myristica, are also important fruit species in the chimpanzees' diet in KWFR (Fotang, 2018), further studies on tree phenology are required to fully understand if the observed preferences for nesting by chimpanzees is based on fruit availability. Our results suggest that preferences for some tree species are related to physical tree characteristics.

The average nest height of chimpanzees at most previous study sites was between 10 and 20 m, and the average nest height of chimpanzees in KWFR was at the upper end of this range (Table 4). The higher arboreal nesting height of the Nigeria–Cameroon chimpanzees in KWFR and some sites across its distribution range (e.g., Mone-Oku [Cameroon], Lebialem–Mone [Cameroon], and Ngel Nyaki [Nigeria]) can be explained by the more common human disturbance

TABLE 4 Physical characteristics of nesting trees of different chimpanzee subspecies across Africa

Subspecies and species	Country	Study site	Nest height(m)			DBH (cm)			
			N	Mean	SD	N	Mean	SD	
P.t. ellioti	Cameroon	Kom–Wum	851	15.53	5.44	625	42.08	23.8	This study
P.t. ellioti	Cameroon	Mone–Oku		18	8.7		36	20.3	Wade (2020)
P.t. ellioti	Cameroon	Bekob	397	10.8	5.2	383	23.46	15.52	Abwe (2018)
P.t. ellioti	Cameroon	Ganga	2014	13.27	5.9	1910	23.11	16.4	Abwe (2018)
P.t. ellioti	Cameroon	Njuma	639	13.18	5.85	623	22.71	17.89	Abwe (2018)
P.t. ellioti	Cameroon	Tofala Sanctuary	87	15.81	7.07				Njukang et al. (2019)
P.t. ellioti	Cameroon	Babanki–Finge	40	9.12	3.08				Doumbé (2014)
P.t. ellioti	Nigeria	Ngel Nyaki,	311	20.5	7.18		37.6	23	Dutton et al. (2016)
P.t. ellioti	Nigeria	Gashaka Gumti		8			61.8	41.5	Fowler (2006)
P.t. ellioti	Cameroon	Lebialem–Mone		21.9	8.3				Last and Muh (2013)
P. t. troglodytes	Congo R	Goualougo	247	17.3	7.4				Sanz et al. (2007)
P. t. verus	Cote d'Ivoire	Nimba Mts	764	8.02	4.57	764	27.9	24.01	Granier et al. (2014)
P. t. verus	Guinea	Seringbara	1376	11.3	6.3		24.5	19.5	Koops et al. (2007)
P. t. verus	Senegal	Fongoli	1665	8.3	4.1				Pruetz et al. (2008)
P. t. verus	Senegal	Assirik,	694	13.55	4.2				Pruetz et al. (2008)
P. t. verus	Senegal	Bagnomba	550	7.9	3.62				Badji et al. (2018)
P. t. verus	Sierra Leone	Gola National Park	96	21.3	5.6		32.6	10.2	Barca et al. (2018)
P. t. verus	Senegal	Diaguiri	871	10.9	1.7				Ndiaye et al. (2018)
P. t. verus	Guinea-Bissau	Lagoas de Cafada	459	14.6	2.14				Carvalho et al. (2015)
P. t. schweinfurthii	DR Congo	Kahuzi–Biega	104	9.4	4.8				Basabose and Yamagiwa (2002)
P. t. schweinfurthii	Burundi	Kibira Natioan Park		12.1	5.8		36.3	16.2	Hakizimana et al. (2015)
P. t. schweinfurthii	Tanzania	Ugalla		13.4	5.1		39.6	19.3	Ogawa et al. (2007)
P. t. schweinfurthii	Tanzania	Issa		12.2	4.19		35.6	15.8	Hernandez-Aguilar et al. (2013)
P. t. schweinfurthii	Uganda	Bwindi	3414	16.06	6.2				Stanford and O'Malley (2008)
P. t. schweinfurthii	Uganda	Semliki	324	11	5.81	405			Hunt and McGrew (2002)

compared to other sites (Gashaka Gumti National Park [Nigeria]) (Table 4). However, other factors like the availability of tall nesting trees and altitudinal differences may further affect nesting tree heights of the Nigeria–Cameroon chimpanzees. For example, the relatively low nesting heights of this chimpanzee species at the highly fragmented Babanki-Finge Forest (1500–2300 m) compared to KWFR (565–1640 m) in Cameroon have been previously explained by the absence of tall trees and altitudinal difference (Doumbé, 2014). The observed orientation of nests towards the slope direction could reduce the escape route through neighboring trees or increase the functional nest height and thereby minimize contact with predators (Goodall, 1968; Koops et al., 2012). Hernandez-Aguilar et al. (2013) reported that chimpanzees orientate nests in the slope direction to maximize exposure to sunlight during sunrise for nests orientated eastwards and during sunset for nests oriented westwards.

4.2 | Environmental determinants of the selection of nesting locations

Our results suggest that distance to primary forest, distance to secondary forest, and human activities are the most important determinants for selecting nesting sites by the chimpanzees. Additional local nest site conditions like elevation and slope are important too (Table 1). Most primary forest patches remaining in the study area are found at a higher elevation and on steep slopes that are rarely used by humans and harbor tall and mature trees that are important for nesting. Our results support previous findings that primary forest vegetation and high elevation areas are preferred for nesting over secondary forest and lowland areas (Carvalho et al., 2021; Granier et al., 2014; Koops et al., 2012; Njukang et al., 2019). The positive association between primary forest and nest locations reported in this and previous studies may also be due to the presence of a high density of large

fleshy fruits trees (Balcomb et al., 2000; Chitayat et al., 2021; Potts et al., 2011), and low impact of human activities (Strindberg et al., 2018). Although secondary forests may provide important food resources for chimpanzees (Basabose, 2005), our results strongly suggest that chimpanzees rarely nest in this vegetation type because of poaching and harvesting of timber and non-timber plant products (Fotang et al., 2021). Chimpanzees avoided low elevations areas in this study because these habitats are made up of rich soils suitable for farming, especially along the banks of three rivers that flow through the reserve (Chuo et al., 2017; Fotang et al., 2021; Kah, 2015). While riparian forest provides suitable nesting habitat for chimpanzee in the Greater Mahale Ecosystem in Tanzania (Chitayat et al., 2021; Dickson et al., 2020), this forest type is not suitable for chimpanzees nesting in KWFR because they are frequently cultivated. The avoidance of bare land by chimpanzees is due to the absence of nesting trees and the exposure to extensive cattle and subsistence agriculture by small-scale farmers. Similarly, chimpanzee nest sites were located far away (4 km) from the nearest settlement in Mone-Oku Forest in Cameroon (Wade, 2020). The positive statistical relationship between hunting signs and nesting locations suggests that hunters and chimpanzees frequently utilize transects and recces. However, the construction of nests on very steep slopes in this study could be a way of escaping human activities, as for example reported from Ebo Forest Reserve in Cameroon (Abwe & Morgan, 2008), in Mahale Mountains National Park in Tanzania (Chitayat et al., 2021), and Kibira National Park in Burundi (Hakizimana et al., 2015).

4.3 | Antipredator/human avoidance hypothesis

Although the selection of tall trees for nesting by chimpanzees is related to the presence of chimpanzee predators such as leopard at some study sites (Hernandez-Aguilar et al., 2013; Pruetz et al., 2008; Stewart & Pruetz, 2013), the preference for tall trees for nesting in KWFR may be also related to human activities such as poaching and harvesting of timber and non-timber forest products (Fotang et al., 2021). In fact, chimpanzee predators such as leopard were not found in KWFR in the current and past surveys (Chuo et al., 2017; Doumbé, 2015). A low encounter rate of human activity signs within 50 m around nesting sites in this study further suggests that chimpanzees selected nesting areas that were difficult for humans to access. In Bili-Uéré, northern DR Congo, chimpanzees constructed nests higher up in the trees when faced with high levels of human hunting activity and presence (Hicks et al., 2010). Dutton et al. (2016) reported that the high nesting of chimpanzees in trees at Ngel Nyaki could be explained by the increasing presence of research in the forest since 2006. The construction of arboreal nests by chimpanzees in the Tofala Hill Wildlife Sanctuary in southwest Cameroon was also attributed to a strategy that focuses on avoiding predation by humans (Njukang et al., 2019). Overall, our findings support the human avoidance hypothesis that arboreal nesting increases with increasing human disturbance (Carvalho et al., 2015; Hakizimana et al., 2015; Last & Muh, 2013; Stewart et al., 2011).

4.4 | Conclusion and conservation implications

We show that chimpanzees prefer locating nests in primary forest vegetation, at higher elevations with slopes and away from villages and bare land exposed to cattle grazing and farming activities. They further selected tall trees with a high lowest branch height and large DBH for nest construction and orientated their nests in the slope direction for security reasons. We recorded no large nocturnal predators, but observed signs of human activity within nesting locations and evidence of chimpanzee hunting. Chimpanzees may escape human activities by nesting high in trees and constructing ground nests exclusively on steeper slopes. Our results suggest that primary forests at higher elevations and steep slopes are crucial for the conservation of chimpanzees as they are preferred habitats for nesting. We recommend protecting such habitats because they contain preferred nesting trees and a topography that is anyway not ideal for human use (e.g., as agricultural production areas). We also recommend regular law enforcement patrols to curb poaching and the implementation of sustainable land-use practices to prevent forest conversion into agricultural fields in the reserve. We propose that chimpanzee nesting locations in the surrounding forests should be included in the reserve's management plan.

CONFLICT OF INTERESTS
The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS
Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (equal); resources (equal); software (equal); validation

(lead); visualization (lead); writing original draft (lead); writing review & editing (lead): Chefor Fotang. *Conceptualization (equal); funding acquisition (equal); resources (equal); supervision (equal); validation (supporting); visualization (supporting)*: Udo Bröring. *Funding acquisition (equal); validation (equal); visualization (equal); writing original draft (equal); writing review & editing (equal)*: Christian Roos. *Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal); software (equal); validation (equal); visualization (supporting); writing original draft (supporting)*: Evidence Chinedu Enoguanbhor. *Conceptualization (supporting); validation (equal); visualization (equal); writing original draft (equal); writing review & editing (equal)*: Paul Dutton. *Formal analysis (equal); methodology (equal); software (supporting); visualization (supporting)*: Luc Roscelin Dongmo Tédonzong. *Methodology (equal); validation (supporting); visualization (supporting); writing original draft (supporting); writing review & editing (supporting)*: Jacob Willie. *Software (equal); validation (supporting); visualization (supporting); writing original draft (supporting); writing review & editing (supporting)*: Yisa Ginath Yuh. *Conceptualization (equal); formal analysis (supporting); funding acquisition (supporting); supervision (lead); validation (equal); visualization (equal); writing original draft (equal); writing review & editing (equal)*: Klaus Birkhofer.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are not publicly available to protect the species in the study area. However, these can be made available on reasonable request from the corresponding author.

ORCID

Chefor Fotang http://orcid.org/0000-0002-1146-6805
Christian Roos http://orcid.org/0000-0003-0190-4266
Luc R. D. Tédonzong http://orcid.org/0000-0002-9347-8630

REFERENCES

Abwe, E. E. (2018). Linking behavioral diversity with genetic and ecological variation in the Nigeria–Cameroon chimpanzee (Pan troglodytes ellioti) (PhD dissertation). Drexel University.

Abwe, E. E., & Morgan, B. J. (2008). The Ebo forest: Four years of preliminary research and conservation of the Nigeria–Cameroon chimpanzee (Pan troglodytes vellerosus). Pan Africa News, 15(2), 26–29.

Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), Advances in the study of behavior (Vol. 14, pp. 165–229). Academic Press.

Badji, L., Ndiaye, P. I., Lindshield, S. M., Ba, C. T., Pruetz, J. D. (2018). Savanna chimpanzee (Pan troglodytes verus) nesting ecology at Bagnomba (Kedougou, Senegal). Primates, 59(3), 235–241. https://doi.org/10.1007/s10329-017-0647-2

Balcomb, S. R., Chapman, C. A., & Wrangham, R. W. (2000). Relationship between chimpanzee (Pan troglodytes) density and large, fleshy-fruit tree density: Conservation implications. American Journal of Primatology, 51(3), 197–203. https://doi.org/10.1002/1098-2345(200007)51:3%3C197::AID-AJP4%3E3.0.CO;2-C

Baldwin, P. J., Pi, J. S., McGrew, W. C., & Tutin, C. E. G. (1981). Comparisons of nests made by different populations of chimpanzees (Pan troglodytes). Primates, 22(4), 474–486. https://doi.org/10.1007/s10764-020-00142-x

Barca, B., Turay, B. S., Kanneh, B. A., & Tayleur, C. (2018). Nest ecology and conservation of Western chimpanzees (Pan troglodytes verus) in Gola Rainforest National Park. Sierra Leone. Primate Conservation, 32, 133–139.

Basabose, A. K. (2005). Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. International Journal of Primatology, 26(1), 33–54. https://doi.org/10.1007/s10764-005-0722-1

Basabose, A. K., & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: Influence of sympatric gorillas. International Journal of Primatology, 23(2), 263–282. https://doi.org/10.1023/A:1013879427335

Boesch, C. (1995). Innovation in wild chimpanzees (Pan troglodytes). International Journal of Primatology, 16(1), 1–16. https://doi.org/10.1007/BF02700150

Brownlow, A. R., Plumptre, A. J., Reynolds, V., & Ward, R. (2001). Sources of variation in the nesting behavior of chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda. American Journal of Primatology, 55(1), 49–55. https://doi.org/10.1007/s10764-016-9916-y

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and habitat use of chimpanzees (Pan troglodytes verus) in the anthropogenic landscape of Bossou, Guinea, West Africa. International Journal of Primatology, 38(2), 282–302. https://doi.org/10.1007/s10764-016-9947-4

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). Introduction to distance sampling estimating abundance of biological populations: Oxford University Press.

Carvalho, J. S., Graham, B., Bocksberger, G., Maisels, F., Williamson, E. A., Wich, S., Sop, T., Amarasekaran, B., Barca, B., Barrie, A., Bergl, R. A., Boesch, C., Boesch, H., Brncic, T. M., Buys, B., Chancellor, R., Danquah, E., Doumbé, O. A., Le-Duc, S. Y., ... Kühl, H. S. (2021). Predicting range shifts of African apes under global change scenarios. Diversity and Distributions, 1–17. https://doi.org/10.1111/ddi.13358

Carvalho, J. S., Meyer, C. F., Vicente, L., & Marques, T. A. (2015). Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. American Journal of Primatology, 77(2), 186–199. https://doi.org/10.1002/ajp.22321

Chitayat, A. B., Wich, S. A., Lewis, M., Stewart, F. A., & Piel, A. K. (2021). Ecological correlates of chimpanzee (Pan troglodytes schweinfurthii) density in Mahale Mountains National Park, Tanzania. PLOS One, 16(2), e0246628. https://doi.org/10.1371/journal.pone.0246628.s001

Chuo, M. D., Angwafo, T. E., Chefor, F., & Fru, B. S. (2017). Estimation of Chimpanzee's (Pan troglodytes ellioti) Abundance in the Kimbi-Fungum National Park and Kom–Wum Forest Reserve, Nw, Cameroon. Journal of Biodiversity Management & Forestry, 6(3), 20–30. https://doi.org/10.4172/2327-4417.1000185

Dickson, R., Baker, M., Bonnin, N., Shoch, D., Rifkin, B., Stewart, F. A., & Piel, A. K. (2020). Combining deforestation and species distribution models to improve measures of chimpanzee conservation impacts of REDD: A case study from Ntakata Mountains, Western Tanzania. Forests, 11(11), 1195. https://doi.org/10.3390/f11111195

Doumbé, O. A. (2014). Habitat Mapping of the Babanki-Finge Forest, and Survey on the Rarest Chimpanzee (Pan troglodytes ellioti) in the Bamenda Highlands, North-West Cameroon (Master dissertation). University of Roehampton, London.

Doumbé, O. A. (2015). Conservation of the Nigeria–Cameroon chimpanzee (Pan troglodytes ellioti) in the Northwest Region of Cameroon. Accessed October 18, 2019. https://www.rufford.org/projects/osiris_doumbe

Dutton, P., Moltchanova, E., & Chapman, H. (2016). Nesting ecology of a small montane population of the Nigerian-Cameroon chimpanzee (Pan troglodytes ellioti) in Nigeria. Folia Primatologica, 87(6), 361–374. https://doi.org/10.1159/000454921

Enoguanbhor, E. C., Gollnow, F., Walker, B. B., Nielsen, J. O., & Lakes, T. (2020). Simulating urban land expansion in the context of land use

planning in the Abuja city-region, Nigeria. GeoJournal, 1–19. https://doi.org/10.1007/s10708-020-10317-x

ESRI, R. (2018). ArcGIS desktop: release 10.6.1. Environmental Systems Research Institute, Redlands, CA.

Fotang, C., Bröring, U., Roos, C., Enoguanbhor, E. C., Abwe, E. E., Dutton, P., Schierack, P., Angwafo, T. E., & Birkhofer, K. (2021). Human activity and forest degradation threaten populations of the Nigeria–Cameroon chimpanzee (Pan troglodytes ellioti) in Western Cameroon. International Journal of Primatology, 42(1), 105–129. https://doi.org/10.1371/journal.pone.0246628.s001

Fotang, C. (2018). Ecology and behavior of the Nigeria–Cameroon chimpanzee in Kom-Wum Forest Reserve and Mbi Crater Kefem Landscape in the North-West Region of Cameroon. Accessed October 29, 2019. https://www.rufford.org/projects/chefor_fotang

Fowler, A. (2006). Behavioral ecology of chimpanzees (Pan troglodytes vellerosus) at Gashaka, Nigeria. University of London, University College London (United Kingdom).

Fruth, B., & Hohmann, G. (1996). Nest building behavior in the great apes: the great leap forward? In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), Great ape societies (pp. 225–240). Cambridge University Press.

Furuichi, T., & Hashimoto, C. (2000). Ground beds of chimpanzees in the Kalinzu Forest. Uganda Pan Africa News, 7(2), 26–28.

Furuichi, T., & Hashimoto, C. (2004). Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kalinzu Forest, Uganda. International Journal of Primatology, 25(4), 755–765. https://doi.org/10.1023/B:IJOP.0000029121.25284.7f

Ganasri, B. P., & Dwarakish, G. S. (2015). Study of land use/land cover dynamics through classification algorithms for Harangi catchment area, Karnataka State, INDIA. Aquatic Procedia, 4, 1413–1420. https://doi.org/10.1016/j.aqpro.2015.02.183

Gonder, M. K., Oates, J. F., Disotell, T. R., Forstner, M. R. J., Morales, J. C., & Melnick, D. J. (1997). A new west African chimpanzee subspecies? Nature, 388(6640), 337. https://doi.org/10.1007/s10764-006-9063-y

Goodall, J. (1968). The behavior of free-living chimpanzees in the Gombe Stream Reserve. Animal Behavior Monographs, 1, 161–IN12. https://doi.org/10.1016/S0066-1856(68)80003-2

Goodall, J. M. (1962). Nest building behavior in the free ranging chimpanzee. Annals of the New York Academy of Sciences, 102(2), 455–467. https://doi.org/10.1111/j.1749-6632.1962.tb13652.x

Granier, N., Hambuckers, A., Matsuzawa, T., & Huynen, M. C. (2014). Density estimates and nesting-site selection in chimpanzees of the Nimba Mountains, Côte d'Ivoire, and Guinea. American Journal of Primatology, 76(11), 999–1010. https://doi.org/10.1002/ajp.22278

Hakizimana, D., Hambuckers, A., Brotcorne, F., & Huynen, M. C. (2015). Characterization of nest sites of chimpanzees (Pan troglodytes schweinfurthii) in Kibira National Park, Burundi. African. Primates, 10, 1–12.

Heinicke, S., Mundry, R., Boesch, C., Amarasekaran, B., Barrie, A., Brncic, T., Brugière, D., Campbell, G., Carvalho, J., Danquah, E., Dowd, D., Eshuis, H., Fleury-Brugière, M. C., Gamys, J., Ganas, J., Gatti, S., Ginn, L., Goedmakers, A., Granier, N., ... Kühl, H. S. (2019). Characteristics of positive deviants in western chimpanzee populations. Frontiers in Ecology and Evolution, 7, 16. https://doi.org/10.3389/fevo.2019.00016

Hernandez-Aguilar, R. A. (2006). Ecology and nesting patterns of chimpanzees (Pan troglodytes) in Issa, Ugalla, Western Tanzania (PhD dissertation). University of Southern California, Los Angeles.

Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site re-use in a dry habitat: implications for early hominin ranging. Journal of Human Evolution, 57(4), 350–364. https://doi.org/10.1016/j.jhevol.2009.03.007

Hernandez-Aguilar, R. A., Moore, J. I., & Stanford, C. B. (2013). Chimpanzee nesting patterns in savanna habitat: Environmental influences and preferences. American Journal of Primatology, 75(10), 979–994. https://doi.org/10.1002/ajp.22163

Hernandez-Aguilar, R. A., & Reitan, T. (2020). Deciding where to sleep: Spatial levels of nesting selection in chimpanzees (Pan troglodytes) living in Savanna at Issa, Tanzania. International Journal of Primatology, 41(6), 870–900. https://doi.org/10.1007/s10764-020-00186-z

Hicks, T. C., Tranquilli, S., Swinkels, J., Faustin, L., & Roessingh, P. (2010). Morphology, distribution, nesting, and diet of the Bili apes. In T. C. Hicks (Ed.), A Chimpanzee Mega-Culture? Exploring Behavioral Continuity in Pan troglodytes schweinfurthii across Northern DR Congo (pp. 93–139). University of Amsterdam.

Hunt, K. D., & McGrew, W. C. (2002). Chimpanzees in the dry habitats of Assirik, Senegal and Semliki wildlife reserve, Uganda. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), Behavioral diversity in chimpanzees and Bonobos (pp. 35–51). Cambridge University Press. https://doi.org/10.1017/CBO9780511606397.005

Iwata, Y., & Ando, C. (2007). Bed and bed-site reuse by western lowland gorillas (Gorilla g. gorilla) in Moukalaba-Doudou National Park, Gabon. Primates, 48(1), 77–78. https://doi.org/10.1007/s10329-006-0003-4

Jarvis, A. (2008). Hole-field seamless SRTM data, International Centre for Tropical Agriculture (CIAT). Retrieved from https://srtm.Csi.Cgiar.Org

John Fox; Sanford Weisberg. (2019). An R Companion to Applied Regression (3rd ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Kah, H. K. (2015). History and livelihood challenges in a Cameroon's Montane Forest Reserve. Economic and Ecohistory, 11, 93–104.

Kamgang, S. A., Bobo, K. S., Maisels, F., Ambahe, R., Ambassa Ongono, D. E., Gonder, M. K., Johnson, P., Marino, J., & Sinsin, B. (2018). The relationship between the abundance of the Nigeria–Cameroon chimpanzee (Pan troglodytes ellioti) and its habitat: A conservation concern in Mbam-Djerem National Park, Cameroon. BMC Ecology, 18(1), 40. https://doi.org/10.1186/s12898-018-0199-3

Koops, K., Humle, T., Sterck, E. H. M., & Matsuzawa, T. (2007). Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: Environmentally or socially determined? American Journal of Primatology, 69(4), 407–419. https://doi.org/10.1002/ajp.20358

Koops, K., McGrew, W. C., de Vries, H, & Matsuzawa, T. (2012). Nest-building by chimpanzees (Pan troglodytes verus) at Seringbara, Nimba Mountains: Antipredation, thermoregulation, and antivector hypotheses. International Journal of Primatology, 33(2), 356–380. https://doi.org/10.1007/s10764-012-9585-4

Kühl, H., Maisels, F., Ancrenaz, M., & Williamson, E. A. (2008). Best practice guidelines for the surveys and monitoring of great ape populations. IUCN/SSC Primate Specialist Group.

Last, C., & Muh, B. (2013). Effects of human presence on chimpanzee nest location in the Lebialem-Moné Forest landscape, southwest region, Cameroon. Folia Primatologica, 84(1), 51–63. https://doi.org/10.1159/000346305

Laudisoit, A., Huyghe, P., Willie, J., Ndjoku, B., Scholier, T., Dz'na, J., & Verheyen, E. (2021). Chimpanzees surviving in a fragmented high-altitude forest landscape of the Congolese Albertine Rift. Conservation Science and Practice, e403. https://doi.org/10.1111/csp2.403

Mathot, L., & Doucet, J. L. (2005). Wildlife surveys in rainforest concessions in order to identify protected areas. In M. De Dapper (Ed.), Tropical forest in a changing global context (pp. 241–254). Royal Academy of Overseas Sciences.

Morgan, B. J., Adeleke, A., Bassey, T., Bergl, R., Dunn, A., & Fotso, R. (2011). Regional action plan for the conservation of the Nigeria-Cameroon chimpanzee (Pan troglodytes ellioti). IUCN/SSC Primate Specialist Group and Zoological Society of San Diego.

Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37(2), 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Ndiaye, P. I., Lindshield, S. M., Badji, L., Pacheco, L., Wessling, E. G., Boyer, K. M., & Pruetz, J. D. (2018). Survey of chimpanzees (*Pan troglodytes verus*) outside protected areas in south-eastern Senegal. *African Journal of Wildlife Research*, 48(1), 013007. https://doi.org/10.3957/056.048.013007

Njukang, A. P., Angwafor, T. E., Akwanjoh, S. R., Lebga, A. K., & Chuo, M. D. (2019). Effects of anthropogenic activities on chimpanzee nest location in the Tofala hill wildlife sanctuary (THWS), South West Region, Cameroon. *International Journal of Forest, Animal and Fisheries Research*, 3(1), 1–9. https://doi.org/10.22161/ijfaf.3.6.1

Ogawa, H., Idani, G., Moore, J., Pintea, L., & Hernandez-Aguilar, A. (2007). Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *International Journal of Primatology*, 28(6), 1397–1412. https://doi.org/10.1007/s10764-007-9210-0

PNDP. (2011). National community driven development program, Wum council development plan. Retrieved from https://www.pndp.org/documents/23_CDP_Wum.pdf

Potts, K. B., Watts, D. P., & Wrangham, R. W. (2011). Comparative feeding ecology of two communities of chimpanzees (Pan troglodytes) in Kibale National Park, Uganda. *International Journal of Primatology*, 32(3), 669–690. https://doi.org/10.1007/s10764-011-9494-y

Poulsen, J. R., & Clark, C. J. (2004). Densities, distributions, and seasonal movements of gorillas and chimpanzees in swamp forest in northern Congo. *International Journal of Primatology*, 25(2), 285–306. https://doi.org/10.1023/B:IJOP.0000019153.50161.58

Pruetz, J. D., Fulton, S. J., Marchant, L. F., McGrew, W. C., Schiel, M., & Waller, M. (2008). Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in south-eastern Senegal. *American Journal of Primatology*, 70(4), 393–401. https://doi.org/10.1002/ajp.20508

R Core Team, (2016). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behavior and conservation*. Oxford University Press.

Sanz, C., Morgan, D., Strindberg, S., & Onononga, J. R. (2007). Distinguishing between the nests of sympatric chimpanzees and gorillas. *Journal of Applied Ecology*, 44(2), 263–272. https://doi.org/10.1111/j.1365-2664.2007.01278.x

Stanford, C. B., & O'Malley, R. C. (2008). Sleeping tree choice by Bwindi chimpanzees. *American Journal of Primatology*, 70(7), 642–649. https://doi.org/10.1002/ajp.20539

Stewart, F. A., Piel, A. K., & McGrew, W. C. (2011). Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, 61(4), 388–395. https://doi.org/10.1016/j.jhevol.2011.05.005

Stewart, F. A., & Pruetz, J. D. (2013). Do chimpanzee nests serve an anti-predatory function? *American Journal of Primatology*, 75(6), 593–604. https://doi.org/10.1002/ajp.22138

Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba'a, R., Abitsi, G., Agbor, A., Ambahe, R. D., Bakabana, P. C., Bechem, M., Berlemont, A., Bokoto de Semboli, B., Boundja, P. R., Bout, N., Breuer, T., Campbell, G., De Wachter, P., Ella Akou, M., … Wilkie, D. S. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, 4(4), eaar2964. https://doi.org/10.1126/sciadv.aar2964

Tagg, N., & Willie, J. (2013). The influence of transect use by local people and re-use of transects for repeated surveys on nesting in Western Lowland Gorillas (Gorilla gorilla gorilla) and Central Chimpanzees (*Pan troglodytes troglodytes*) in Southeast Cameroon. *International Journal of Primatology*, 34(3), 554–570. https://doi.org/10.1007/s10764-013-9681-0

Tagg, N., Willie, J., Petre, C. A., & Haggis, O. (2013). Ground night nesting in chimpanzees: new insights from central chimpanzees (*Pan troglodytes troglodytes*) in South-East Cameroon. *Folia Primatologica*, 84(6), 362–383. https://doi.org/10.1159/000353172

Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology*, 124(1), 81–92. https://doi.org/10.1002/ajpa.10342

Tutin, C. E., & Fernandez, M. (1984). Nationwide census of gorilla (Gorilla g. gorilla) and chimpanzee (*Pan troglodytes troglodytes*) populations in Gabon. *American Journal of Primatology*, 6(4), 313–336. https://doi.org/10.1002/ajp.1350060403

Venables, W. N., & Smith, D. M.R Development Core Team, & others (2009). An introduction to R. Accessed October 12, 2020. Retrieved from http://cran.r-project.org/doc/manuals/R-intro.pdf

De Vere, R. A., Warren, Y., Nicholas, A., Mackenzie, M. E., & Higham, J. P. (2011). Nest site ecology of the Cross River gorilla at the Kagwene Gorilla Sanctuary, Cameroon, with special reference to anthropogenic influence. *American Journal of Primatology*, 73(3), 253–261. https://doi.org/10.1002/ajp.20886

Wade, A. H. (2020). *Shared Landscapes: The human-ape interface within the Mone-Oku Forest, Cameroon* (PhD dissertation). University of Auckland.

White, L., & Edwards, A. (2000). *Conservation research in the African*. The Wildlife Conservation Society.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.