Montane Grassland Resources Drive Gorilla (Gorilla Gorilla) Nesting Behaviours in the Ebo Forest, Littoral Region, Cameroon

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Abstract

Great apes show strong attachment to their nesting sites which provides them with substantial survival elements. Their nesting behaviors are influenced by geographical and ecological variables including habitat type, slope, elevation gradients, and sometimes anthropogenic pressures. This study aimed to assess environmental variables that influenced the Ebo gorilla (Gorilla gorilla) nesting behavior in relation to nesting site selection, nest types, and nesting materials. We collected data from January 2013 to November 2017 along reconnaissance tracks (recce, hereafter) using the marked nest counting method. We recorded 0.16 nesting sites per km as an encounter rate, with an average number of four nests per gorilla group. The mean nest diameter was 90.33 ± 23.92 cm (n = 640, range 25–199 cm). Ebo gorillas preferred nesting sites at high altitude located in the grassland areas with open canopy, ligneous undergrowth composition and very closed visibility. Ebo gorillas used more than 281 plant species as materials for nesting with Marantaceae and Zingiberaceae species being the most common material used. Terrestrial herbaceous nests were the most common nest type (55%). During the dry season, gorillas visited more often the mature forest habitat and mostly constructed arboreal nests. Finally, reuse of nesting sites by Ebo gorillas was minimal (16%), and visitation period occurred from 3 days to 33 months. Our study provides the first systematic investigation of gorilla nesting behavior within the Ebo forest constituting therefore an essential starting point for the long-term conservation planning of this little-known population.

1. Introduction

Great apes including chimpanzee (*Pan troglodytes*), bonobo (*Pan paniscus*), gorilla (Gorilla sp.), and orangutan (Pongo sp.) have demonstrated an aptitude for building daily nests (Caldecott and Miles 2005), which provide them more comfortable sleeping postures, thermoregulation, protection against pathogens and predators (Fruth and Hohmann 1996; Yamagiwa 2001). Intra and inter-species differences in nesting site selection among great apes have been linked to environmental variation including fruit availability, habitat type, altitude or elevation, seasonality and the potential disturbance by sympatric large mammals (Basabose et al. 2002; Tutin et al. 1995). For instance, chimpanzees (*Pan troglodytes schweinfurthii*) in Kahuzi Biega National Park mostly nest on fruiting trees after foraging (Basabose et al. 2002). While frugivorous western gorillas (Gorilla gorilla) demonstrated a preference for nesting sites with easy proximity to preferred fruit sources (Tutin et al. 1995), folivores eastern gorillas (*Gorilla beringei*) avoid previously trampled areas where it may be difficult to have dense herbaceous materials for feeding or building their nests (Watts 1998). The western lowland gorillas (*Gorilla gorilla gorilla*) in the Dja reserve-Cameroon target the sites that have herbaceous underground as good nest materials and dietary sources (Willie et al. 2013). Similar to western lowland gorillas, Cross River gorillas (*Gorilla gorilla diehli*) nest predominantly at difficult terrains to avoid disturbance by sympatric animals or humans (Neba 2011).

Among great apes, gorillas exhibit much greater variability in the types and heights of nest construction. Variation in nest construction can provide insight into adaptations related to regional variations in climate and ecology as well as social behavior (Mehlman and Doran 2002). In general, gorilla night nests are either vegetative or non-vegetative (i.e. bare earth sleeping nests) (Mehlman and Doran 2002; Sanz et al. 2007; Willie et al. 2014). Gorillas construct more nests on the ground (e.g. 96.2% of ground nests at the Dja reserve in Cameroon, and 90% at Bai Hokou, Central African Republic) and mostly select sites with dense herbaceous undergrowth (Remis 1993; Willie et al. 2013). However, the proportion of arboreal nests was relatively high (35%) for gorilla populations in the tropical forests of Petit Loango, Gabon, where terrestrial herbaceous vegetation is very rare (Tutin et al. 1995). In addition, great apes including gorillas increase nest height and arboreal nesting with greater predation risk (Anderson et al. 2019). The vulnerability of female and immature gorillas following the death of the silverback male in Kahuzi-Biega National Park (DRC), encouraged arboreal nesting attitudes in the group to avoid predation (Yamagiwa 2001).

Great apes nesting investigation can provide a physical signature useful to estimate group sizes, population composition, densities and distribution of the species in a particular area (Ismaila and Maloueki 2021; Mehlam and Doran 2002). Additionally, many studies reported that gorillas demonstrated plant selectivity for nesting. Such information has been used to describe gorilla resource distribution and to identify their most suitable habitats (Fruth and Hohmann 1996; Sanz et al. 2007; Willie et al. 2014). For example, gorillas in the Dja Reserve in Cameroon use a particular set of terrestrial herbaceous vegetation dominated by plant species from Marantaceae and Zingiberaceae to construct their nests (Willie et al. 2014). The availability of this terrestrial herbaceous vegetation in the forest appears to be a good predictor of ground-nesting site selection for gorillas in this habitat. Gorillas nesting in higher elevations tend to use more materials to increase the thickness of the nest in order to cope with cooler temperatures over the night (Nkwatoh et al. 2017). This nesting habit in elevated zones was also observed in the chimpanzee population in the Nimba forest (Koops et al. 2011).

Seasonality also influences gorilla nest site selection and nest type (Mehlman and Doran 2002; Sunderland-Groves et al. 2009; De Vere et al. 2010). For example, the selection of arboreal nests during the wet season may help gorillas with effective thermoregulation (Fruth and Hohmann 1996; Neba 2011).

As other great apes, the reuse of nests or nesting sites is observed with gorillas and it is mostly linked to habitat preference and the availability of suitable nesting material (Fruth and Hohmann 1996). The frugivorous diet of western gorillas may cause them to stay for some days in areas with fruiting trees and, consequently, reuse their nesting sites (Iwata and Ando 2007). Iwata and Ando (2007) suggested that gorillas return to an area during the same season or after where preferred fruit is readily available.

The Ebo forest in the Littoral Region of Cameroon is one of the most important tracts of intact forest in the Gulf of Guinea biodiversity hotspot, harboring the two species of Cameroon great apes, chimpanzee and gorilla (Dunn et al. 2014). In the Ebo forest, the taxonomic affinity of gorillas remains unknown (Dunn et al. 2014; Groves 2005). While the western gorillas are classified as Critically Endangered by the IUCN Red List of Threatened Species (Maisels et al. 2018), the status of the Ebo population remains data deficient compared to its sympatric chimpanzees (*Pan troglodytes ellioti*: Endangered) population (Abwe 2018; Dunn et al. 2014). There is no recorded information on the Ebo gorilla nesting ecology to date.

Furthermore, local populations from the villages surrounding the Ebo forest encroach into the gorilla habitat for hunting, collection of non-timber forest products, and farming (Mfossa et al. 2022; Whytock and Morgan 2010). The limited knowledge about this relic and geographically isolated gorilla population may hamper long-term conservation action for the population

The objective of this exploratory study was to provide preliminary estimations of the gorilla population abundance in the Ebo forest and its nesting behavior. More specifically, we investigated nesting site selection, individual nest characteristics following seasons (i.e. dry and rainy season) in relation to plant availability in order to identify the key plant species used by this population to build their nests. We first aimed to assess gorilla nest abundance (based on nest encounter rate), number of groups, and average group size in nesting sites using the nest counting method while taking into consideration nest reuse. Second, we studied seasonal habitat use for nesting, nesting site selection linked to environmental variables (i.e. canopy openness, horizontal visibility, undergrowth composition, slope, altitude), and seasonal nest characteristics such as nest types (ground versus arboreal), nest material, and plant species composition. As anthropogenic evidence was spread all over the gorilla habitat (Mfossa et al. 2022), we hypothesized that nesting site selection was mainly driven by nest materials availability to build a comfortable nest and by avoidance of disturbance by sympatric species including human (Fruth and Hohmann 1996; Yamagiwa 2001). Therefore, we predicted that nest type and composition would follow seasonal plant availability, for instance with an increase of arboreal nest selection and/or ligneous nest construction during the rainy season.

2. Methods

Study area

We conducted our study in the estimated gorilla habitat (ca. 39 km²) located in the eastern north of the Ebo forest which is extended geographically between the longitudes 010 ° 02'59.2"E and 010 ° 38'30.9"E and the latitudes 04 ° 05'09.5"N and 04 ° 31'01.6"N (Morgan 2010; Mfossa et al. 2022). The area is characterized by a warm and humid tropical equatorial climate with dry and rainy seasons (Abwe 2018). The rainy season extends from March to November. The main annual rainfalls exceed 2,500 mm and the average elevation in the area is 850 m (Abwe 2018). The dominant vegetation in the study area is composed of mature forest, secondary forest, inundated forest or swampy zone, and grassland (Fig. 1, Mfossa et al. 2022). The Ebo forest harbors a rich biodiversity including plant species narrowly endemic to Ebo (Gosline et al. 2022), endangered threatened mammal species (Whytock et al. 2021), and a rich assemblage of diurnal primates including gorilla (Gorilla sp.), Nigeria-Cameroon chimpanzee (*P. t. ellioti*), drill (*Mandrillus leucophaeus*), Preuss's red colobus (*Piliocolobus preussi*), and Preuss's monkeys (*Allochrocebus preussi*) (Dunn et al. 2014; Abwe 2018). Common African wild predators of great apes such as cats (lion, leopard, etc.) no longer exist in Ebo. The gorilla's habitat is surrounded by four villages depending on the forest resources for survival (Dunn et al 2014; Mfossa et al. 2022; Whytock and Morgan 2010).

Data collection

The gorilla population occurred only in the northern part of the Ebo forest with a distribution range restricted to about 22 km² (Mfossa et al. 2022). Due to the high anthropogenic pressure in the study area (Mfossa et al. 2022), we were not permitted to use a line transect method which can destroy vegetation and increase in return facility of poaching and hunting (Fedigan 2010; Zhou et al. 2013) and opted for alternative method with minimal environmental impact. To obtain a preliminary gorilla abundance index and data on nesting site characteristics, we used the recce survey method which was relatively low cost, caused minimal environmental disturbance, and allowed us to cover the entire study area while balancing the survey effort across the habitat types (Fig. 1) (Ismaila and Maloueki 2021; Kühl et al. 2008; White and Edwards 2000). Data collection was organized during trips of five to ten days every month from January 2013 to November 2017. The survey typically started at 7 am and ended at 4 pm. The surveyors, consisting in a team of three to four experimented biological data collectors, conducted random nest searches in the study area using GPS (Garmin GPSmap 60CSx) to navigate along recces (Kühl et al. 2008; Ross and Reeve 2011; White and Edwards 2000). Recces were not permanent, and the team randomly chose the survey direction. To reduce the risk of imperfect detection of gorilla nests in different habitat types, the team moved carefully and slowly (1–2 km/h), maintaining their direction regardless of the habitat type. When a gorilla nest was spotted, team members scanned the area within a 50 m radius to search for more nests (Morgan et al. 2006). We aimed to patrol the entire study area (~ 39km²) to describe environmental variables of sites where nests where present or absent. However, because recce surveys can provide biased samples as the encounter rates likely result from variation in vegetation density or topography (Kühl et al. 2008; Tagg and Willie 2013), we equalized survey efforts between habitat types proportionally to their coverage in the study area by calculating the total distance walked over each of them (Table 1). We recorded the entire track of the daily survey line using GPS tracklog option with record interval set at 1 minute and surveyed a total of 1077.5 km random tracks in 338 days (see Fig. 1 for the distribution of recce tracks). Thereafter, we extracted recce tracks in each habitat type in QGIS software (version 3.14), and controlled the survey effort per habitat type (Table 1).

Table 1
Effort survey in various habitat types within the Ebo forest

Habitat types	Coverage proportion (%)	Track distance (km)	Track Proportion (%)
Grassland	2.63	49.60	4.60
Mature forest	87.04	921.97	86.99
Secondary forest	7.90	58.58	5.53
Swampy area	2.43	29.74	2.81

Gorilla nest abundance index

Since gorillas are sympatric to chimpanzees in this habitat (Dunn et al. 2014), we used the presence of feces, shed hair, signs of passage and other signs in nesting sites to attribute nests to either great ape species (Sanz et al. 2007). When these evidences were absent, we referred to Tutin and Fernandez's criteria (1984) to distinguish between nests of the species by attributing (i) all sites with only ground nests to gorillas; (ii) all tree nests closely associated as nearby ground nests of the same age to gorillas; (iii) all sites with only tree nests not associated with ground nests to chimpanzees. We considered a nesting site as all nests of the same age within 50 m of one another (Morgan et al. 2006). We recorded the location of the nesting site with a GPS at the location of the identified central nest, and collected environmental variables for each nest and site. To avoid duplication of nest counts in subsequent surveys, we marked encountered nests with brightly colored flagging tapes (Abwe 2018) with date, age and other information including the group size (i.e. the number of similar-age nests within a nesting site). Finally, we calculated the Encounter Rate of nesting sites (ER) to estimate their abundance index in this habitat as follows: **ER = N/Lt;** where N = number of nesting sites, Lt = Total distance surveyed in km.

Nesting site characteristics: used versus available sites

To investigate the preference in nesting site selection by gorillas (i.e. if gorillas select specific nesting sites among those available in the Ebo forest), we collected environmental data from 178 nesting sites (nest present) and 703 available sites (nest absent) along recces. For both available sites and nesting sites, characteristics variables associated with environmental data included habitat types, canopy openness, horizontal visibility at the ground level, undergrowth composition, slope, and altitude.

To assess the habitat-use for nesting, we considered the four habitat types categories (i.e., mature forest, secondary forest, grassland and swampy area or inundated forest) identified by Mfossa et al. (2022). The altitude of the available sites and nesting sites was recorded at the estimated central location while taking the GPS coordinates of the site. Since the altitude records of the nest sites felt between 800 and 1300 m, we classified nests into five 100 m-altitude classes according to their value (Alt): Alt $\leq$ 900 m, 900 m $<$ Alt $\leq$ 1000 m, 1000 m $<$ Alt $\leq$ 1100 m, 1100 m $<$ Alt $\leq$ 1200 m, and Alt $>$ 1200 m. The description of other variables and their attributes is given in Table 2.

Table 2
Description of environmental variables used to investigate the preference in nesting site selection by Ebo gorillas

Environmental variables	Attributes	Description
Canopy: the percentage of light available above the site	Very open (Voc)	No or little few tree branches or foliage above the site (76–100%)
	Open (Oc)	Site partially covered with few foliage or branches (51–75%)
	Closed (Cc)	Foliage and branches relatively covered the site (26–50%)
	Very closed (VCc)	Site totally covered with very few lights reaching the soil (0–25%)
Undergrowth: the vegetative composition under trees	Ligneous (Li)	Exclusively with sapling and/or liana
	Herbaceous (He)	Exclusively with herbs
	Herbaceous/Ligneous (He/Li)	Combination dominated by herbs
	Ligneous/Herbaceous (Li/He)	Combination dominated by ligneous
Visibility: the distance at eye level (1.7 m) beyond which objects can no longer be seen[a]	Very open (VOv)	Visibility more than 15 m
	Open (Ov)	Visibility between 11 and 15 m
	Closed (Cv)	Visibility between 5 and 10 m
	Very closed (VCv)	Visibility less than 5 m
Slope: the inclination of the terrain (angle) from team members eyes appreciation	Flat (Fl)	Angle $\leq$ 5%
	Gentle (Ge)	5%< angle $\leq$ 15%
	Moderate (Mo)	15%< angle $\leq$ 25%
	Steep (St)	Angle > 25%
Source: [a]Dupain et al. 2004		

Characteristics of individual nests

To investigate the nesting behavior of gorillas, we recorded for each individual nest the size (diameter), age, height from the ground, nest type and nest materials.

We measured nest diameters at the lateral size of the nest considered as the size of the gorilla back at the seating position. We used the nest group size (i.e., the number of nests of similar-age age within a nesting site) as a proxy for the gorilla's group size (excluding infants) in this population.

Following Tutin and Fernandez (1984) and Kühl et al. (2008), we categorized nest age into five classes : (1) fresh nest (a construction less than 5 days, all leaves green and fresh feces/urine under, in or close to nest); (2) recent nest (a construction between 5 and 15 days, leaves green mixed with few turning brown, no fresh feces/urine); (3) old nest (a construction between 15 days and 6 months remains intact, leaves mixed in color as brown/dried and green); (4) very old nest (a construction between 6 months and 1 year, leaves completely brown but nest still complete) and (5) rotten (a construction more than a year, leaves are gone and only the skeletal branch and twig structure remain).

We categorized nests into five construction types according to Tutin et al. (1995): (1) nests with no vegetative construction (zero material or bare ground nests), (2) nests exclusively built with herbs (herbaceous nests), (3) nests with both herbs and woody materials (mixed nests), (4) nests exclusively built with woody materials (woody nests), and (5) nests built in trees (tree nests or arboreal nests).

To assess key plant species used by Ebo gorillas to construct their nests, we enumerated and identified all the components used to build each nest. We identified plant materials used to construct the nests to the species or genus level whenever possible. When plants could not be identified in the field, we collected and coded specimens for later identification at the National Herbarium, Yaoundé.

Seasonal variation in nesting

To investigate nesting seasonality, we assessed habitat type used for nesting and nest types according to the seasons (March to November for the rainy season and December to February for the dry season). We used the nest age estimate to identify the month when the nest was constructed.

Nesting site reuse

Based on GPS coordinates, we considered all nesting sites close one to another inside 50 m radius as reused nesting site (*i.e.*, a geographical site reused for nesting at different time by a group of gorillas). The difference in age and the number of nests in the group allowed us to separate different group nests in the site especially when the nests were fresh or recent.

Data analysis

We used R version 4.1.1 (R Development Core Team, 2021) for statistical analyses ($\alpha = 0.05$).

Nesting site characteristics: used versus available sites

To test the influence of the site characteristics (set as explanatory variables) on the probability that a given site was selected by gorillas for nesting (set as the binary response variable), we ran binomial family generalized linear models (glm) with a logit link function. Logistic regression models were chosen due to their sensitivity to binary data in comparison to other model families (Lewis 2004). We ran two distinct models: 1) an ordinal model including ordinal categorical variables (i.e., canopy openness, horizontal visibility, slope, and altitude) with the reference intercept set as the lowest value category for each variable, and 2) a nominal model including non-ordinal categorical variables (i.e., habitat type and undergrowth composition) with the reference intercept set as the category with the highest sample size. We tested seasonal interactions between the variables in the ordinal and nominal models. However, models poorly predicted outcomes and variable significance were overly sensitive indicating Type I error. Therefore, interactive models were not taken into account within the analyses. To determine the best-fit model, we performed automated model selection with the dredge function from the R package MuMIn (Burnham and Anderson 2002) using the ΔAkaike Information Criterion (ΔAIC) < 2 values and the model weight (AICWt). To test for the effects of multicollinearity, we performed Variable Inflation Factor (VIF) checks on the global model using the R package car and *vif* function (Fox and Weisberg 2018), with VIF > 10 indicating that the multicollinear variables may be highly correlated and therefore significantly influencing the coefficients in model output (Hair et al. 2010; Fox 2016). Thereafter, we used the R package DHARMa (Hartig and Hartig 2017) to test for residual patterns of over- and under-dispersion and mis-specification problems in the best-fit models. Finally, for plotting the best-fit models, we ran the R package margins (Greene 2012) to calculate the Average Marginal Effects (AME). Marginal Effects use model predictions for interpretations and can be used as a way of presenting results as a difference in probabilities by centering the scale of all the covariates (Perraillon 2013).

Characteristics of individual nests

To identify the most used plant species for gorilla nesting, we calculated the frequency rate (i.e., number of nests carrying the species divided by the total number of nests) and the species occurrence value (i.e., number of nests with the species divided by the total number of species) of each plant species (Willie et al. 2014, Setiawan et al. 2021). We used the chi-square test to assess the nesting seasonality for gorillas in accordance with nest types and habitat use.

3. Results

Gorilla nest abundance index within the Ebo forest

We surveyed 1077.5 km of recces in the study area from January 2013 to November 2017. We recorded 178 gorilla nesting sites totaling 766 individual nests. The encounter rate of the nesting sites was 0.16 nesting sites per km. The mean number of nests per nesting site was 4.3 ± 2.5 (mode = 4, median = 4) range from 1 to 13 nests per site (Fig. 2).

Nesting site characteristics: used versus available sites

Nesting site distribution according to environmental variables

We found that gorillas made their nests in four habitat types, mature forest, secondary forest, grasslands, and swampy area (Fig. 3; Table 3). The majority of the nesting sites were located in the grassland (51.7%) and mature forest (45.5%) and consequently, most of the individual nests were also located in the grassland (55.6%) and the mature forest (40.3%). More than 90% of gorilla nesting sites were found above 1,000 m of elevation. Although gorillas could nest in any slope categories, we found the majority of nesting sites in the gentle slopes (41.6%). While most of the majority of nesting sites (56.7%) were found in the very open canopy, most of them (46.1%) had very limited or closed visibility at the understory ground level. Finally, the main undergrowth composition for the majority of gorilla nesting sites in Ebo was ligneous (37.6%) and herbaceous (33.7%) (Table 3).

Table 3
Nest and nesting sites distribution in the study site according to environmental variables

Variables and attributes		Nesting site frequency (n = 178)	Percentage of nesting sites (%)	Individual nest frequency (n = 766)
Habitats types	Grassland	92	51.7	426
	Mature forest	81	45.5	309
	Swampy area	4	2.2	28
	Secondary forest	1	0.6	3
Canopy	Very open (> 75%)	101	56.7	470
	Open (51–75%)	29	16.3	102
	Closed (26–50%)	25	14.0	93
	Very closed (0–25%)	23	12.9	101
Undergrowth	Ligneous	67	37.6	234
	Herbaceous	60	33.7	301
	Ligneous/Herbaceous	30	16.9	132
	Herbaceous/Ligneous	21	11.8	99
Visibility	Very open (> 15 m)	25	14.0	84
	Open (10–15 m)	45	25.3	153
	Closed (5–10 m)	26	14.6	114
	Very closed (< 5m)	82	46.1	415
Slope	Flat (angle < 5°)	21	11.8	95
	Gentle (5° < angle < 15°)	74	41.6	362
	Moderate (15° < angle < 25°)	44	24.7	181
	Steep (angle > 25°)	39	21.9	128
Altitude	Alt ≤ 900 m	3	2.0	3
	900 m < Alt ≤ 1000 m	7	4.0	31
	1000 m < Alt ≤ 1100 m	41	23.0	176

Variables and attributes		Nesting site frequency (n = 178)	Percentage of nesting sites (%)	Individual nest frequency (n = 766)
	1100 m < Alt ≤ 1200 m	87	49.0	376
	Alt > 1200 m	40	22.0	180

Nesting site selection

The best performing ordinal model for predicting nesting site selection included altitude, canopy, slope, and visibility, with AIC weight 1.4 time higher than the second-best model that had a Δ AIC < 2 (Table 4, Fig. 4a.). The probability of nesting site use was positively influenced by the elevation with highly significant results for 1000 m < Alt ≤ 1100 m (estimate = 2.60 ± SE 0.75), 1100 m < Alt ≤ 1200 m (estimate = 3.00 ± SE 0.74), and Alt > 1200 m (estimate = 3.72 ± SE 0.78). Moreover, gorillas selected nesting site with more open canopy with highly significant effects for the open canopy category (estimate = 1.98 ± SE 0.36) and very open canopy category (estimate = 1.71 ± SE 0.38). Gentle (estimate = 0.69 ± SE 0.31) and steep (estimate = 0.81 ± SE 0.35) slope categories were significant but showed very low marginal effect, suggesting that slope may not have a large influence of gorilla nesting site selection (Fig. 4a.). Finally, we found significant negative effects of close visibility (estimate = -0.86 ± SE 0.32) and very open visibility (estimate = -0.83 ± SE 0.39) categories. However, it should be noted that the intercept category very closed visibility had the highest ratio of presence versus absence (1.02) compared to other categories (ratio presence/absence = 0.33, 0.22, and 0.10 for close visibility, open visibility, and very open visibility, respectively), suggesting gorillas may tend to select for nesting sites with more closed visibility. The variable inflation factor was < 2.7, indicating there was no significant multicollinearity.

The best performing nominal model for predicting nesting site selection included habitat types and undergrowth composition (Table 4, Fig. 4b.). The probability of nesting site use was influenced by habitat types with highly positive significant effect of grassland (estimate = 3.13 ± SE 0.45), and highly negative significant effect of mature forest (estimate = -3.04 ± SE 0.24). Finally, Ebo gorillas highly selected nesting sites with ligneous undergrowth composition with positive significant effect of ligneous undergrowth (estimate = 2.78 ± SE 0.29). Similar to the ordinal model, we did not find an effect of multicollinearity with variable inflation factor < 5.1.

Table 4
Results of generalized logistic model for ordinal and nominal environmental variables predicting nesting site selection of gorilla (*Gorilla gorilla*) in the Ebo forest

Model	K	AIC	ΔAIC	AIC_{wt}
Ordinal model				
Altitude + Canopy + Slope + Visibility	14	664.20	0.00	0.57
Altitude + Canopy + Visibility	11	664.88	0.68	0.40
Altitude + Canopy	8	671.17	6.97	0.02
Altitude + Canopy + Slope	11	672.04	7.84	0.01
Altitude + Visibility	8	695.26	31.07	< 0.01
Altitude + Slope + Visibility	11	695.46	31.26	< 0.01
Canopy + Slope + Visibility	10	714.72	50.52	< 0.01
Canopy + Visibility	7	717.01	52.81	< 0.01
Canopy + Slope	7	723.88	59.68	< 0.01
Canopy	4	724.25	60.05	< 0.01
Altitude	5	741.13	76.93	< 0.01
Altitude + Slope	8	742.72	78.52	< 0.01
Slope + Visibility	7	749.85	85.65	< 0.01
Visibility	4	751.60	87.40	< 0.01
Slope	4	841.35	177.15	< 0.01
Null	1	842.97	178.77	< 0.01
Nominal model				
Habitat type + Undergrowth	7	644.0	0.00	1.00
Undergrowth	4	701.7	57.72	< 0.01
Habitat type	4	762.6	118.64	< 0.01
Null	1	843.5	199.47	< 0.01

Note: K is the number of parameters; AIC is the Akaike information criterion, ΔAIC represents the difference in AIC between current and top model, and AIC_{wt} the model weight indicating level of support.

Characteristics of individual nests

Nest types

Out of the 766 individual nests recorded for the entire study period, 95% of them were terrestrial and only 5% were found above the ground either on the shrubs or in the trees. The highest nest was located in a tree at about 10 m above the ground level.

The most common type of gorilla nest in the Ebo forest was herbaceous (55%), followed by mixed nests (26%) and woody nests (18%). Arboreal nests represented only 1% of all gorilla nests and they were mostly constructed in the shrubs or the small trees. We did not record nests with minimum construction or bare earth sleeping nests during this survey.

Nest diameter

The mean nest diameter was 90.33 ± 23.92 cm (n = 640, range 25–199 cm). The mean nest diameter in the rainy season was 98.78 ± 25.43 cm (n = 423, range 25–199 cm) and in the dry season 91.77 ± 19.36 cm (n = 217, range 30 – 190 cm).

Nesting materials

Ebo gorillas used only leaves and/or twigs from one or more plants to construct their nests. The number of plants used by gorillas to construct a nest ranged from 1 to 11 (Fig. 5), and the mean number of plant species in a nest was 2 ± 1.5 (Median = 2, Mode = 2).

In total, we identified 281 plant species used by Ebo gorillas to construct their nests. These plants included 24 lianas, 20 herbaceous, and 237 ligneous species. Sixteen species were the most commonly used plants for nest construction (Table 5). Four herbaceous plant species including Aframomum angustifolium, Hyselodelphis violaceae, Aframomum albiflorum and Costus afer (all from Zingiberaceae and Marantaceae families), represented the most important plant species for gorilla nesting (58.9%, 20.0%, 18.6%, and 11.7%, respectively). For woody species, Thomandersia sp 1, Alchonia floribunda and Garcinia conrouana were the most common tree species for nest construction (Table 5). Aframomum angustifolium had the highest occurrence value (1.07) and this was three-time higher than the occurrence value of succeeding species including Hyselodelphis violaceae (0.36), Aframomum albiflorum (0.34) and Costus afer (0.21) (Table 5).

Table 5
Frequency rate and occurrence value of the top 16 plant species identified in gorilla nests in the Ebo forest

Scientific name	Vegetal Type	Number of nests	Frequency rate (%)	Occurrence value
Aframomum angustifolium	Herbaceous	301	58.90	1.07
Hyselodelphis violaceae	Herbaceous	102	19.96	0.36
Aframomum albiflorum	Herbaceous	95	18.59	0.34
Costus afer	Herbaceous	60	11.74	0.21
Thomandersia sp 1	Ligneous	27	5.28	0.10
Alchornea floribunda	Ligneous	26	5.09	0.09
Garcinia conruana	Ligneous	21	4.11	0.07
Pteridium aquilinum	Herbaceous	18	3.52	0.06
Marantochlia sp 1	Herbaceous	16	3.13	0.06
Psychotria sp	Ligneous	13	2.54	0.05
Garcinia ovalifolia	Ligneous	13	2.54	0.05
Afromomum zambeziacum	Herbaceous	12	2.35	0.04
Liana 2	Liana	11	2.15	0.04
Afrostyrax lepidophyllus	Ligneous	10	1.96	0.04
Treculia sp	Ligneous	10	1.96	0.04
Brillantaisia sp 1	Herbaceous	9	1.76	0.03

Seasonal variation in habitat used for nesting and nest type

The selection of the habitat type for nesting was significantly related to seasons ($\chi2 = 23.9$, df = 3, p-value < 0.001). Gorillas constructed nests in the secondary forest only in the rainy season and further nested in the swampy area during the dry season (Fig. 6). Although gorillas in Ebo constructed all types of nests both in the rainy and dry seasons, the nest type was also influenced by seasonality ($\chi2 = 36.7$, df = 3, p-value = < 0.001). Gorillas constructed more ligneous and arboreal nests during the rainy season than during the dry season (Fig. 7).

Nesting site reuse

Thirty of 178 nesting sites were reused for nesting (Fig. 3). The gorillas reused one of the nesting sites on four occasions, three on five occasions, six on three occasions, and 20 on two occasions. The average group size of reused nesting sites ranged from 1 to 7.5 individual nests. The range of visit time period between reused nesting sites was from 3 days to 33 months, and the majority occurred at least a year later (49% of reused nesting sites). Only four sites were visited a few days after (3 to 10 days). Seasonally, gorillas exclusively reused eight sites during the dry season and six during the rainy season.

4. Discussion

From January 2013 to November 2017, we used the marked nest counting method along recces to assess the abundance and the nesting ecology of the little-known gorillas in the Ebo forest, Cameroon. During this study, we recorded 178 nesting sites (with 766 individual nests), providing an encounter rate of 0.16 nesting sites per km. The mean nest group size used as a proxy of the social group size for gorillas in the Ebo forest was four individuals per group. This group size is quite different to that of Cross River gorillas in Mone and Mbulu forest reserves and the Kagwene Gorilla Sanctuary as well as the group size of the Western lowland gorilla populations at Monika Research Center in Central Africa Republic (Table 6).

Table 6
Review of nest types and nest reuse in Ebo gorillas, Cross River Gorillas (CRG) and Western Lowland Gorillas (WLG) at different study sites

Study site	**Total nesting site counted**	**Total nest counted**	**Average number of nest per site**	**Ground nest (%)**	**Arboreal nest (%)**	**Nest site reuse (%)**	**Number of plant used for nesting**	**Duration of data collection (months)**
Ebo forest, Cameroon[a]	178	766	7	95	5	17	281	47
Kagwene Gorilla Sanctuary, Cameroon (CRG) [b]	569	7032	7	55	45	35	/	32
Kagwene Gorilla Sanctuary, Cameroon (CRG) [c]	268	1813	8	40	60	/	/	12
Dja Reserve, Cameroon (WLG)[d]	/	834	/	96	4	/	174	34
Lobeké National Park (WLG) [e]	81	169		85	5	/	41	4
Lopé National Park, Gabon (WLG) [f]	373	2435	7	64	36	/	98	48
Bai Hokou, Central African Republic (WLG) [g]	163	1231	8	83	17	/	/	27
Belinga, Gabon (WLG) [h]	/	419	/	76	24	/	/	27

Note : / No data; **Source**: [a]this study; [b]Sunderland-Groves et al. 2009; [c]Nkwatoh et al. 2017; [d]Willie et al. 2014; [e]Tsakem 2017; [f]Tutin et al. 1995; [g]Remis 1993; [h]Tutin and Fernandez 1984 ; [i]Mehlman and Doran 2002; [k]Iwata and Ando 2007

Study site	Total nesting site counted	Total nest counted	Average number of nest per site	Ground nest (%)	Arboreal nest (%)	Nest site reuse (%)	Number of plant used for nesting	Duration of data collection (months)
Monika Research Center in Central Africa Republic (WLG) [i]	512	3725	7	89	21	/	/	42
Moukalaba-Doudou National Park, Gabon (WLG)[k]	44	506	/	19	81	39	/	8
Note : / No data; **Source**: [a]this study; [b]Sunderland-Groves et al. 2009; [c]Nkwatoh et al. 2017; [d]Willie et al. 2014; [e]Tsakem 2017; [f]Tutin et al. 1995; [g]Remis 1993; [h]Tutin and Fernandez 1984 ; [i]Mehlman and Doran 2002; [k]Iwata and Ando 2007								

Nest group sizes ranged from one to thirteen nests with regular groups of 5, 4, 3 and 2 individuals (Fig. 2). Nest group size variation over time and seasons have also been reported in other gorilla populations and explained by the influence of the spatial and temporal distribution of food resources in the environment (Remis 1994; Sunderland-Groves et al. 2009; Watts 1990). The variation in nest group size that we observed might suggest that, either all individuals from a group did not nest at the same particular nesting site, or the group composition varied over seasons with interactions between social groups, as suggested by others (Bradley et al., 2004). These preliminary results call for further investigations in this area on the gorilla population composition and dynamics.

The mean diameter of Ebo gorilla nests was 90.33 ± 23.92 cm (n = 640, range 25 cm − 199 cm), which seem to close to the mean diameter (107 ± 0.15 cm, n = 3862, range 40 cm − 200 cm) of the Cross River gorilla nest at the Kagwene Mountain forest (Sunderland-Groves et al. 2009). Since body size has found to be correlated with nest size (Groves and Sabater Pi 1985; Basubi et al. 2020, Rayadin and Takashi 2009; Yamagiwa 2001), this indicates that the body sizes between the Cross River gorilla and the Ebo gorillas may be similar. Nevertheless, considering the small number of nests recorded during the 5-year survey (n = 766 nests in the Ebo forest vs. n = 7032 nests recorded by Sunderland-Groves et al (2009) at the Kagwene during 24 months of study), we may hypothesize that the Ebo gorilla population could be relatively small. This converges with the Morgan's study (2010) which also presumed a small population size of less than 25 individuals in 2010. Yet, future studies using alternative methods to nest counting surveys are necessary to provide a systematic estimation of gorilla density in this area. Non-invasive methods that could effectively allow Ebo gorilla monitoring include camera traps (Kuhl et al. 2008), passive acoustic monitoring to detect gorilla's chest beating (Heinicke et al. 2015; Zwerts et al. 2021), or genetic census (Arandjelovic et al. 2010; Gray et al. 2013; Guschanski et al. 2009).

Our study showed that the selection of nesting sites by Ebo gorilla was influenced by environmental variables, i.e., habitat type, altitude, canopy, slope, visibility at the ground level and undergrowth composition. Strikingly, although the grassland habitat occupied a limited proportion (3% of cover) of the study area (Mfossa et al. 2022), Ebo gorillas significantly used this habitat for nesting (Fig. 4b). Concomitantly, we found that gorillas selected nesting sites at high altitude with more closed visibility and ligneous undergrowth composition (Fig. 4). While the Cross River gorilla population at the Kagwene Gorilla Sanctuary showed preference for forest habitats with high food availability (Nkwagoh et al. 2017), Ebo gorillas may prefer the open canopy grassland habitat which provides high potentiality of nest materials (Zingiberaceae, Maranthaceaes and fens plants) and also reduces exposure to some natural dangers such as tree branch falling. The trend of Ebo gorillas to use grassland for nesting is consistent with the high proportion of ground nests we recorded. Grassland habitat could also provide gorillas with abundant grass ground cover for nesting with minimum efforts of building. Our results also indicated that Ebo gorillas tended to use nesting sites that had more closed horizontal visibility, which is similar to the lowland gorillas' population in Lopé forest in Gabon (Tutin et al. 1995). A more closed visibility results from the closed undergrowth, which mostly appears in the grassland habitat. Therefore, gorillas can strategically choose such environments for nesting to reduce disturbances from other large mammals (including humans) during the night. For instance, as Ebo gorillas are sympatric with forest elephants, it will be interesting in future studies to assess how activity patterns and habitat use of elephants could affect arboreal nesting behavior in the gorilla population. Although our results showed that slope might not have a critical influence on gorillas nesting site selection, they suggest that Ebo gorillas tended to select gentle and steep slopes to construct nests. Tendency of selecting steep slopes for nesting was also observed with Cross River gorilla in Takamanda (Sunderland-Groves et al. 2003). For some great apes population, nesting on difficult terrain including steep slopes and flooding habitat is likely a predation avoidance strategy from large carnivores and poaching (Abwe 2018; Anderson et al. 2019; Sunderland-Groves et al. 2003; Tagg et al. 2013). Finally, we found that there was a significant positive influence of the altitude on nesting site selection in Ebo with most gorilla nests located above 1000 m. This is consistent with the altitudinal nesting site selection with Cross River gorillas where higher altitudes of montane forests provide more herbaceous vegetation for nesting and lower temperatures for thermoregulation (Neba 2011, Nkwatoh et al. 2017). Even though the Ebo forest is mostly montane forest where anthropogenic activities are logistically challenging and gorillas are no longer a target for hunting by local community (Mfossa et al. 2018), previous works showed a constant hunting activity targeting other animal species in the study site (Mfossa et al. 2022). Therefore, we cannot exclude that the altitudinal nesting behavior of gorillas in Ebo could be an avoidance strategy by selecting areas with few visits from humans (Nkwatoh et al. 2017, Tagg and Willie 2013).

Although ligneous plants were the predominant undergrowth composition in the nesting sites (Fig. 4b.), herbaceous nests were the most common nest type construction for Ebo gorillas. The fact that herbaceous plants are not as pervasive as ligneous, being sparse or absent in many habitat types especially the mature and secondary forest, indicates a marked preference to ground herbaceous nests in this area. This result is in line with findings from many other sites where gorillas frequently construct herbaceous nests (Mehlman and Doran 2002; Tutin et al. 1995; Willie et al. 2014). However, the Cross River gorilla population at Kagwane Gorilla Sanctuary that is relatively close to the Ebo gorilla population (200 km) predominantly construct mixed and woody ground nests (Sunderland-Groves et al. 2009). This may be linked to the fact that Kagwene gorillas preferred nesting in forested habitats (De Vere et al. 2010; Nkwatoh et al. 2017) contrary to their Ebo conspecifics that mostly nested in the grassland habitat. Nevertheless, we recorded more ligneous nest types in the mature forest during the rainy season; which confirm that in the absence of preferable habitat for nesting, gorillas adapt their nest building strategy.

The proportion of ground nests in the Ebo forest was higher than in other sites (Table 6). The gorillas' ground-nesting habit may be explained by the fact that the majority of nesting sites were located in the grassland, which had open canopy and very little trees. Such habitats are dominated by soft plant species like fens, Zingiberaceae and Maranthaceae which were mostly used to construct nests. More often, gorillas in other sites opt for arboreal nests when suitable ground-nesting material is not available (Tutin et al. 1995), as an anti-predator strategy (i.e. reduce access and detection by predators), or to reduce disturbance by other large sympatric animals (Yamagiwa 2001). As the Ebo forest is devoid of large predators, our results suggest that nesting selection is mainly driven by material availability and quality rather than an anti-predator strategy. However, arboreal nests in the Ebo forest were predominant during the rainy season. During this period, the ground is very wet and sometimes rainfall occurs all day long. Therefore, the main reason for arboreal nesting behavior for the Ebo population could be related to comfort and thermoregulation function of the nest. This hypothesis is supported by the high proportion of ground ligneous nests we also found during the rainy season (Fig. 7). Similar observations were reported with Cross River gorillas at Kagwene Sanctuary (Neba, 2011) and western lowland gorillas at Mondika Research Center in Democratic Republic of Congo (Mehlman and Doran 2002). Conversely, arboreal nesting behavior could be linked to foraging strategies since most of the arboreal nests appeared in the mature forest characterized by a high diversity of plants and a fruiting peak occurring during the rainy season in the Ebo forest (Abwe 2018). It is well known that the proximity of fruiting trees also influences nesting site selection, and feeding on seasonal fruit trees leads to arboreal nesting in gorillas (Fruth and Hohmann 1996; Remis 1993). Further investigation on the feeding ecology of Ebo gorillas and its relationships with nesting behavior is necessary to support this hypothesis.

Consistently, this study reveals a significant seasonality in habitat types selected for nesting by gorillas. The majority of nests in the swampy areas were constructed during the dry season and that could be linked to foraging effort. In this period, vegetation is drier in other habitat types especially the grassland providing probably less food resources compared to swampy areas.

Regarding nest type construction, Ebo gorillas exclusively used vegetative materials that included at least 281 herbaceous and ligneous species from 79 genera and 55 families. On the contrary, Willie et al. (2014) described vegetative and no vegetative nest construction for the gorilla population in the Dja Biosphere Reserve (Cameroon). Compared to their conspecifics in other sites (Table 6), gorillas in Ebo exhibit both a high diversity of plant species (n = 281) used for nesting with a predominance of ligneous plants and a selective preference for Zingiberaceae and Maranthaceae families that are largely found in the grassland habitat. The diversity in nesting material was also observed with the sympatric Nigeria-Cameroon chimpanzee population within the Ebo forest (Abwe 2018). The high number of plant species used by apes in Ebo to construct nests may be due to the fact that the Ebo forest is located in the key zone of the Gulf of Guinea biodiversity hotspot which has complete different ecoregions and rainfall seasonality to the sites of Congo basin (Letouzey 1985).

Finally, only 17% of the nesting sites were reused by gorillas during the study and there was no evidence of individual nest reuse, which is contrary to the frequent reuse of nest sites reported in other gorilla populations (i.e., < 30%, Table 6). Ebo gorillas tend to avoid sites recently used for nesting since the time period between reuses was usually more than six months. In fact, Ebo gorillas are depleting most of the herbaceous resources when building nests and foraging. In accordance with our hypothesis, our findings suggest that nesting site selection in Ebo is driven by nest material availability, as gorillas seem to adjust the visit interval to enable the regeneration of herbaceous resources.

Conclusion

This study provides the first exploratory investigation of the nesting behavior of the cryptic and presumably small gorilla population within the Ebo forest. We showed that Ebo gorilla nesting site selection was driven by some ecological attributes, mainly the habitat type with a strong preference for grassland resources, high altitude, ligneous undergrowth composition and an open canopy. With Western gorilla (*Gorilla gorilla*) classified as Critically Endangered in the IUCN Red List, the little-studied Ebo gorilla population needs well elaborated conservation measures to ensure its protection as well as the entire rich biodiversity of the Ebo forest, especially as anthropogenic threats including hunting wire snares and gunshut, wood extraction, and deforestation keep increasing in the area. Appropriate measures could include reducing human access to the gorilla habitat for hunting or collection of non-timber forest products. The preservation of the grassland habitat will provide a suitable environment for this small gorilla population. Further studies using more systematic survey methods need to focus on nest decay rates, feeding ecology, plant diversity and fruit phenology of the trees in order to model gorilla distribution in relation to nesting material availability and seasonality of fruiting plant resources.

Declarations

Conflict of Interest

The authors declare that they have no conflict of interest.

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Data Availability Statement

Data used in this research are available from the corresponding author upon reasonable request.

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Author contributions

D.M. Mfossa, E.A. Abwe, R.I. Tchouamo and R.C. Beudels-Jamar contributed to the study conception and conducted project administration. F. Brotcorne and R. I. Tchouamo supervised the work. E.A. Abwe secured the funds for the study. Field work and data collection were conducted by D.M. Mfossa and M.E. Ketchen. D.M. Mfossa, E. Gazagne and R.J. Gray carried out data processing, visualization and statistical analysis. D.M. Mfossa and E. Gazagne wrote the first draft of the manuscript. F. Brotcorne and R.J. Gray critically reviewed and edited the manuscript. All authors commented and approved the final version of the manuscript.

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Figures

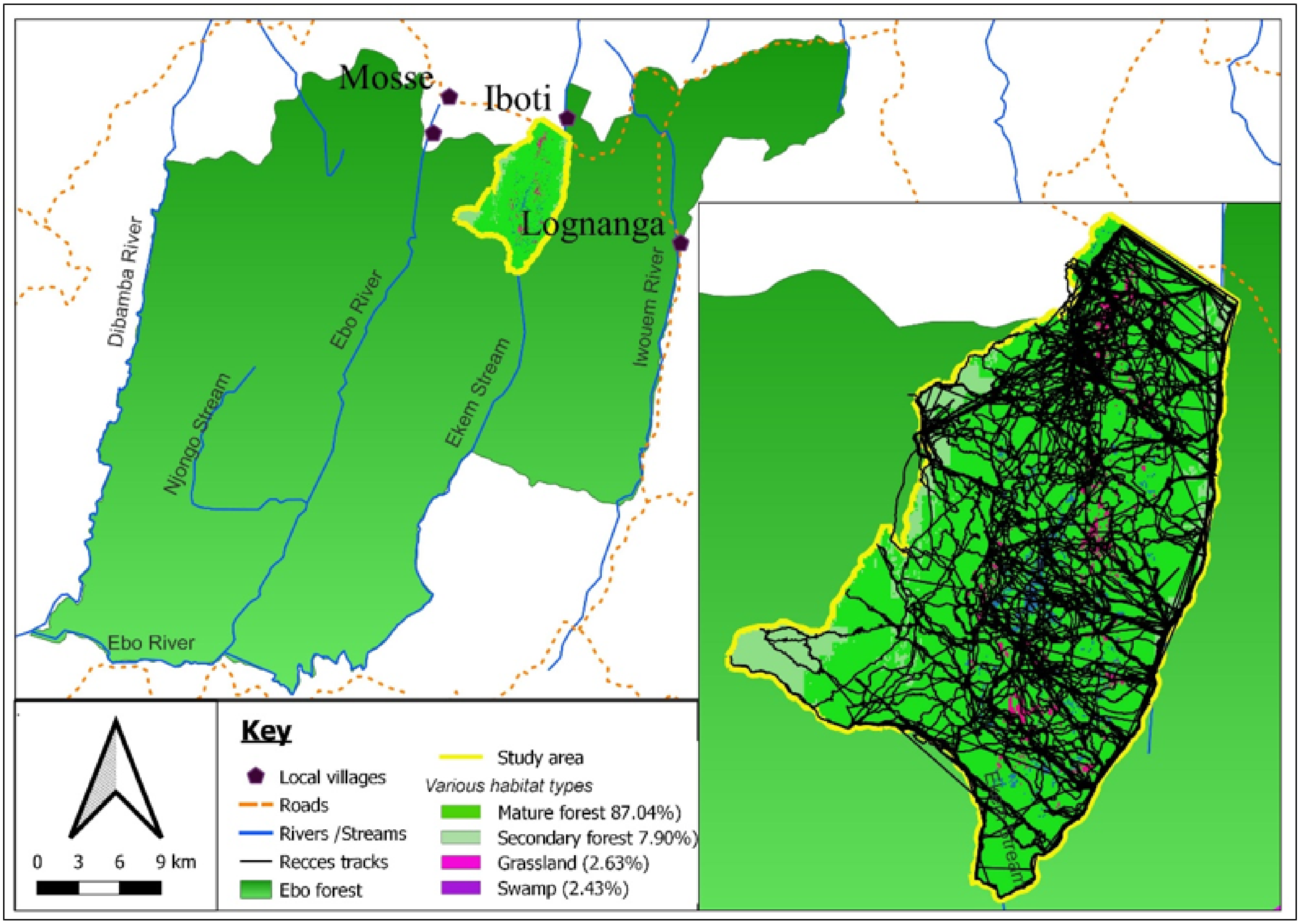

Figure 1

Study area within the Ebo Forest showing various habitat types and recce tracks distribution from January 2013 to November 2017

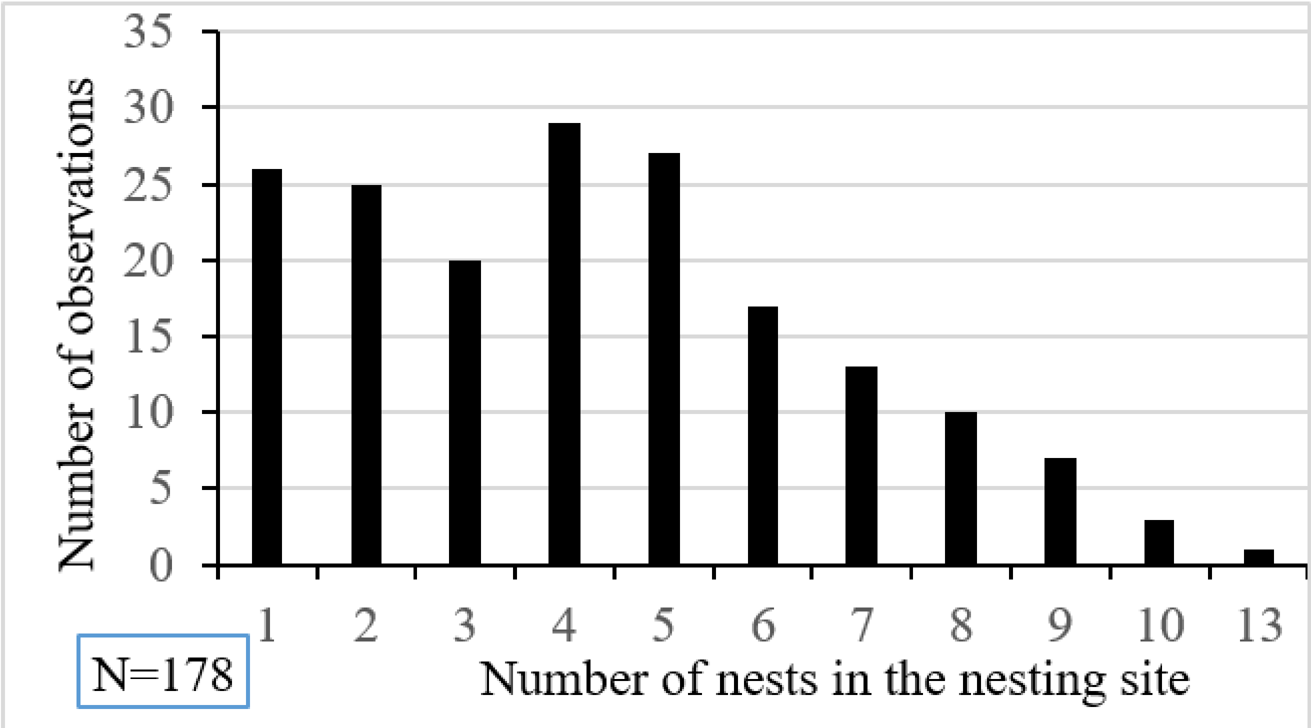

Figure 2

Frequency distribution of the number of gorilla nests per nesting site across the study site

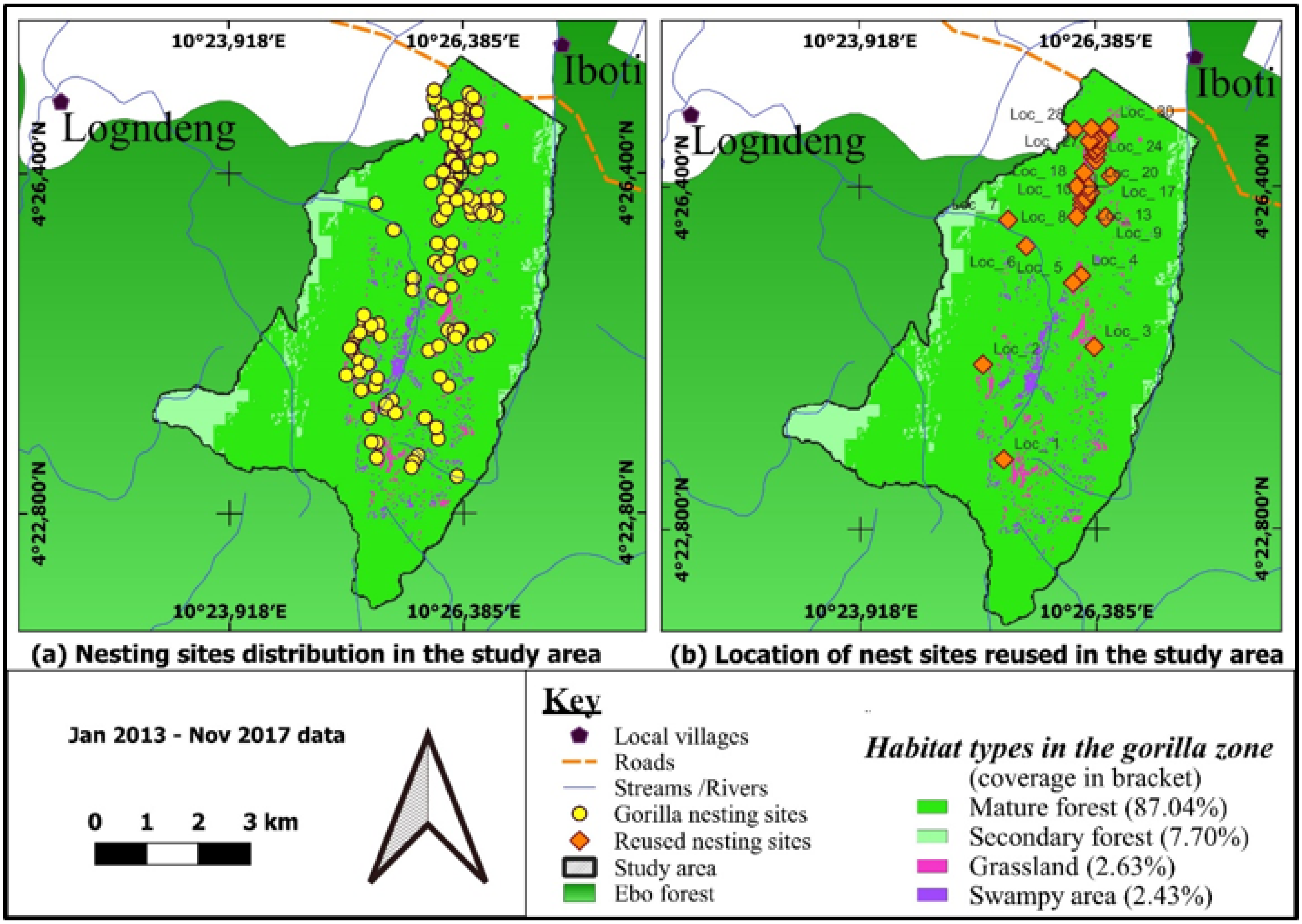

Figure 3

Distribution of all gorilla nesting sites (**a**-left) and reused nesting sites (**b**-right) in the study site

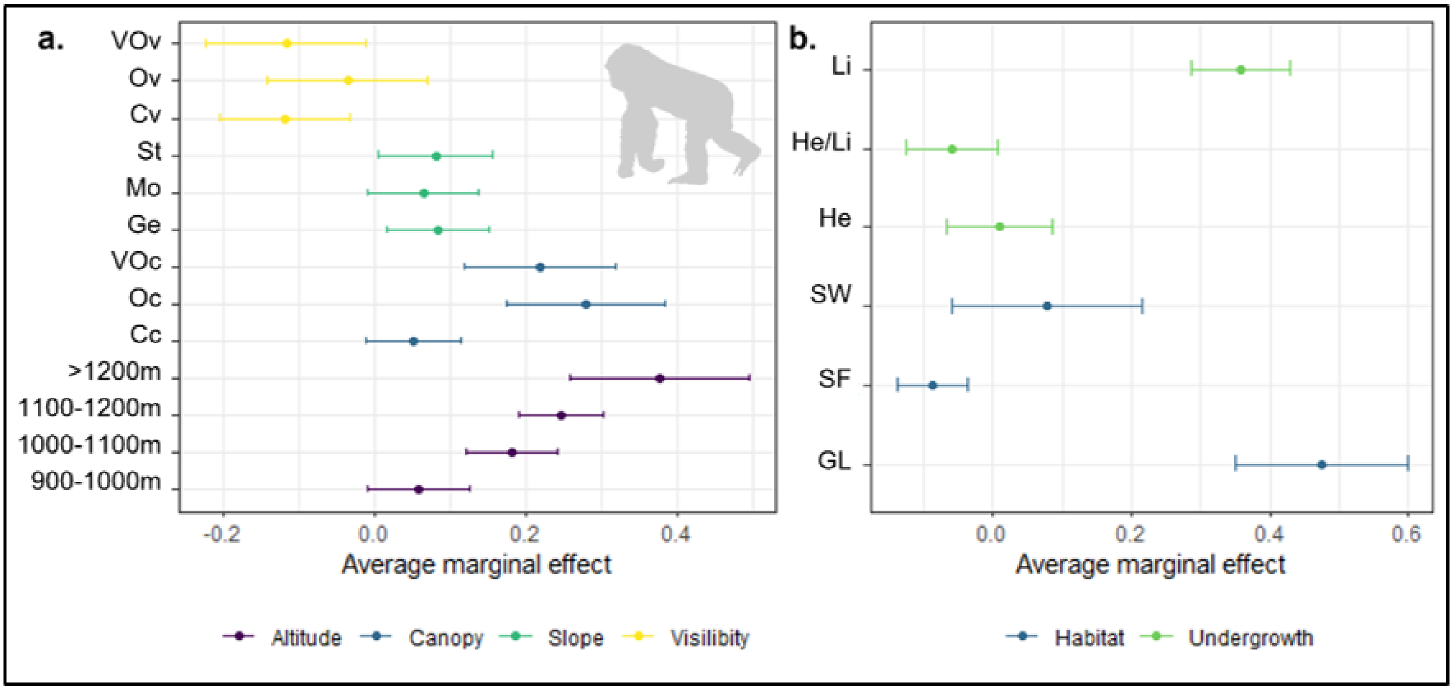

Figure 4

Probability of nesting site selection as a function of ordinal environmental variables (**a**) and nominal environmental variables (**b**) for the best-fit models for the Ebo gorillas. Visibility: very open (VOv), open (Ov), close (Cv) and very close (VCv). Slope: steep (St), moderate (Mo), gentle (Ge) and flat (Fl). Canopy: very open (Voc), open (Oc) closed (Cc) and very closed (VCc). Undergrowth: ligneous (Li), herbaceous/ligneous (He/Li), herbaceous (He) and ligneous/herbaceous (Li/He). Habitat type: swampy area (SW), secondary forest (SF), grassland (GL), and mature forest (MF)

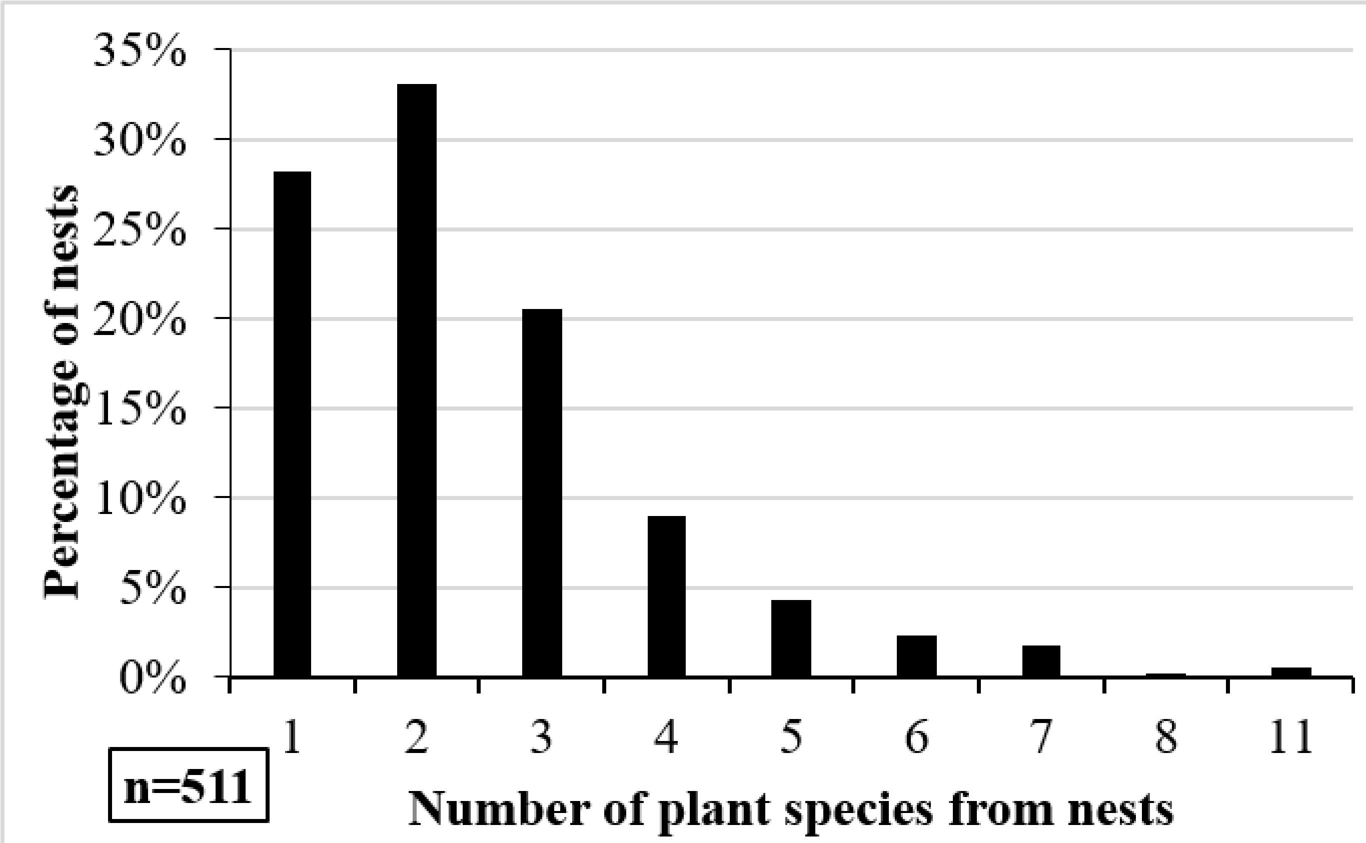

Figure 5

Number of plant species recorded in Ebo gorilla nests

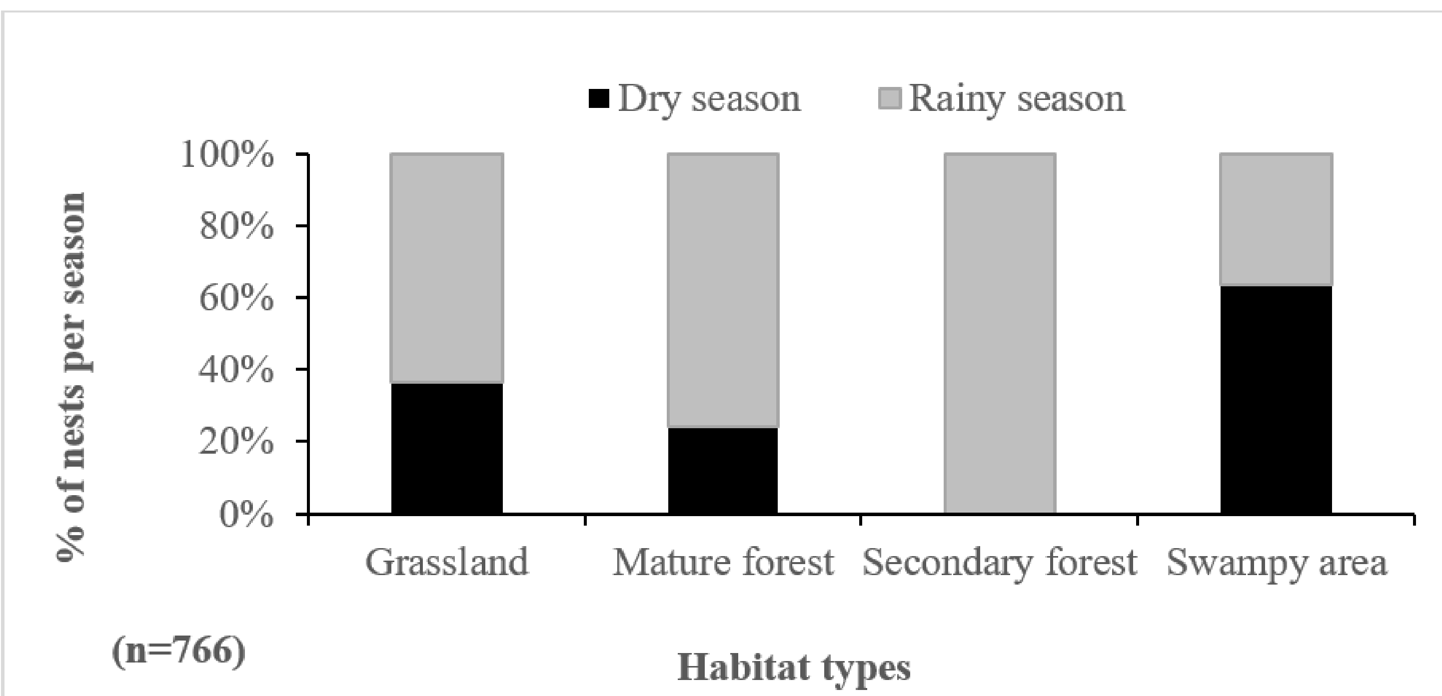

Figure 6

Distribution of nests in various habitat types according to seasons

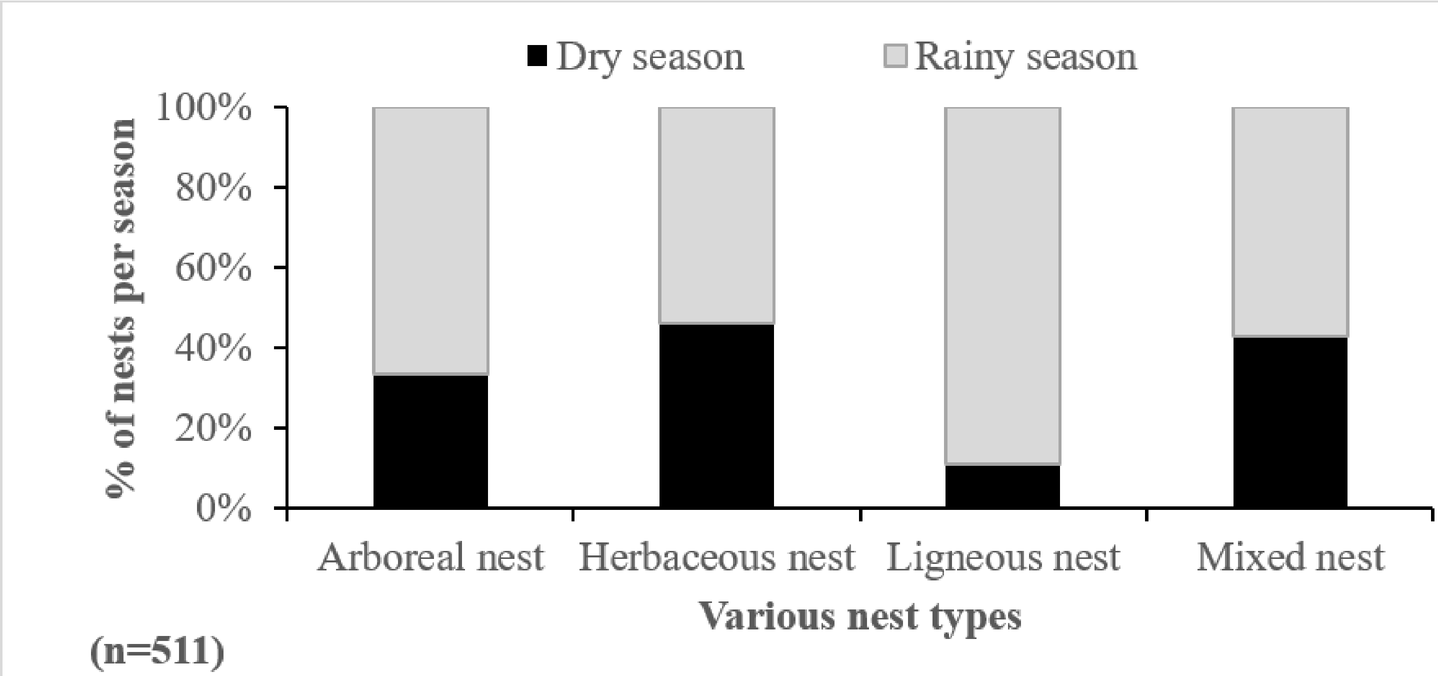

Figure 7

Seasonal variation in nest types constructed by Ebo gorillas