Differential response of Central African great apes to hunting pressure across non-protected forests in Gabon

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1 ABSTRACT

Most of the great ape population inhabiting Central African forests live outside of protected areas where human pressures are high. The survival of great apes is uncertain across unprotected areas. It is therefore important for their conservation, to increase information regarding their distribution and assessing the potential effect of human pressure on their abundance across unprotected forests. In the present study, during at least two months, we conducted camera-trap surveys along 10 non-protected forests in Gabon. In each area, we also assessed the hunting pressure through hunting indices. The species accumulation curves suggested that the number of species was saturated for all forested blocs. Chimpanzees were found in all areas whereas gorillas were not found in the areas with high hunting pressure (hunting index > 2 index/Km). Moreover, overall detections of gorillas were less than that of chimpanzees. We investigated the correlation between the relative abundance of each great ape species and hunting pressure index, a significant negative correlation was found between the relative abundance of gorilla ($P < 0.001$, $r = -0.628$). In contrast, a marginal negative correlation between the relative abundance of chimpanzee and hunting index was identified ($P=0.1831$, $\tau = -0.42$). This difference in hunting pressure between the two coexisting great ape species within non-protected shows an urgent need to increase information regarding the distribution of great ape populations in order to update their conservation status across unprotected areas in Gabon.

2 INTRODUCTION

Across protected and non-protected areas, human activities cause an increased proximity between humans and wildlife (Diarrassouba *et al.,* 2019). Most of the time this proximity is unwholesome to wildlife. For many species, human impact, such as hunting, has clearly negative consequences by reducing their abundance, limiting their distribution or affecting population behaviour traits (Leroy *et al.,* 2004; Cronin *et al.,* 2016; Kühl *et al.,* 2019; Tédonzong *et al.,* 2020). Among these species, the sympatric populations of central chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*). The abundance of these Central African great apes is increasingly reduced and their decline continues, as African great apes are a species of international concern for conservation

(Strindberg *et al.,* 2018; Galàn-Acedo *et al.,* 2019). In the absence of major measures to reduce the threats, current trends are expected to continue. Central African (Cameroon, Republic of Congo, Central African Republic, Equatorial Guinea, Gabon and Angola) covers the entire distribution area of two coexisting subspecies of African great apes, the western lowland gorilla and Central African chimpanzee (IUCN, 2014; Strindberg *et al.,* 2018). The entire range of the great apes in Central Africa is now rapidly being converted into agricultural, forestry or mining areas (Laporte *et al.,* 2007; Junker *et al.,* 2012). Great apes are often observed in protected areas, but also within non-protected dominated by agriculture and agroforestry (Junker *et al.,* 2012). Moreover, most of grape ape populations inhabiting central African forests live outside of protected areas where human pressures are high (Tagg and Willie, 2013; Strindberg *et al.,* 2018). The survival of great apes is uncertain across unprotected areas. Several factors such as hunting and the disappearance of natural environments can cause a dramatic decrease in their populations (Dupain *et al.,* 2004; Junker *et al.,* 2012). However, there are few confirmed data on their status, threats to their survival, and conservation prospects for these species across unprotected areas. The disappearance of any species of great apes within any habitat could be a huge loss in terms of biodiversity and ecological role (Abernethy *et al.,* 2013). It is therefore important to increase information regarding the distribution of great ape populations inhabiting unprotected areas in order to develop effective conservation strategies. The social structures and mating strategies of gorillas and chimpanzees differ in resource use despite their coexistence in many forests in Central Africa. Gorillas live in groups up to 11 individuals, dominated by a silverback male and his females and are also characterized by the presence of solitary male living alone (Magliocca *et al.,* 1999; Morgan *et al.,* 2013; Seiler and Robbins, 2020). While chimpanzees live in communities made up of many males and females and ranging from more than 20 individuals (Mitani, 2006; Morgan *et al.,* 2013). This larger social group regularly breaks up into sub-groups of varying size and composition depending on social conditions and the availability of food (Goodall, 1986; Morgan *et al.,* 2013). Gorillas and chimpanzees cover considerable distances, but only chimpanzees exhibit territorial behaviour and defend their resources against other communities (Wilson and Wrangham, 2003; Morgan *et al.,* 2013; Amsler, 2010; Seiler and Robbins, 2020). The different behaviour patterns of these coexisting great apes can lead them to evolve differently in a wide range of dynamic and changing environments. In the present study, we conducted camera-trap surveys and evaluated the hunting pressure across 10 non-protected forests in Gabon. We aimed to obtain reliable information on the potential of these areas, for great ape conservation. Given that the hunting pressure exerted by people living along the study areas, we expected to find low relative abundance of both great ape species.

3 MATERIALS AND METHODS

3.1 Study sites: The study was conducted within 10 non-protected areas across Gabonese forests, four located in hunting and farming areas, two in mining areas and other four in logging areas (Table 1). Among the hunting and farming areas, Dibwangui (DI) is a village with around 50 people located in the Ngounié province in south-eastern Gabon (Figure 1). The vegetation covering DI area is dominated by secondary forest, which is mainly exploited by local populations for traditional agricultural and hunting purposes. Regarding Bindo (BI), it is a new forest concession of OLAM PALM Gabon intended to increase the surface area of the Makouké palm groves. This forest block is located in Moyen-Ogouué province in the Center-West of Gabon and is covered by a mosaic of plant formations made up of plantations, fallows and young and old secondary forests. The surrounding populations of around 300 people for hunting and farming therefore exploit this forest.

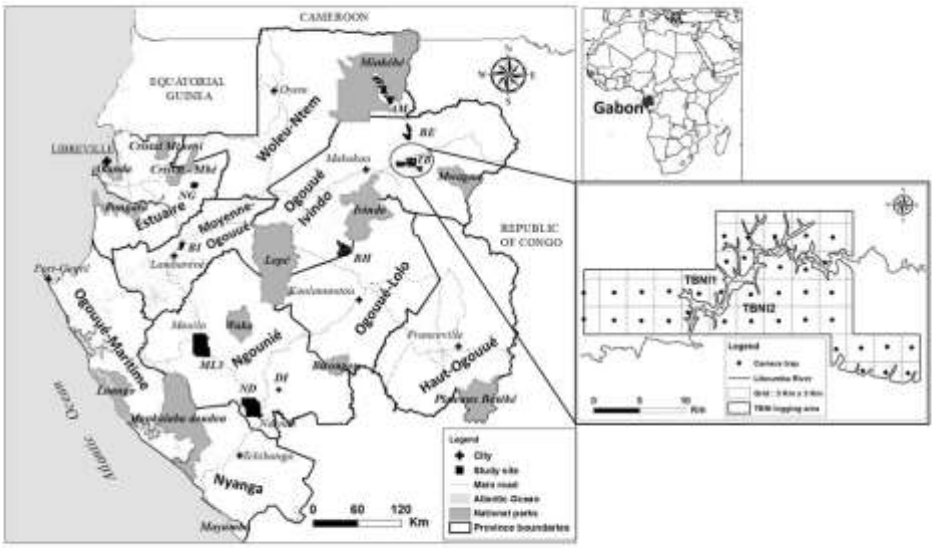

Fig. 1 Location of 10 survey areas across Gabon

Similar to BI forest, Ndendé (ND) and Mouila lot 3 (ML3) forests are OLAM PALM forest concessions located in the Ngounié province in South-Eastern Gabon (Figure 1). These two regions are strongly dominated by shrubby savannas and gallery forests mainly along the rivers. The populations of Ndendé and Mouila cities are around 6300 and 20000 people respectively. They used those forest blocks for hunting and traditional agriculture. Regarding logging areas, Ngoulmendjim (NG) is a part of the SEEF (*Société Equatoriale d'Exploitation Forestière*) logging area located in the Estuaire province in the northeast of Gabon (Figure 1). SEEF is a certified logging company that employs around 200 people and hunting activities are strictly prohibited. The forest in this concession, which belongs to the Monts de Cristal landscape, has been the object of logging since the 1950s (Sunderland *et al.,* 2004). Whereas TBNI (TB) and Bonus Harvest (BH) areas are non-certified logging companies. The TBNI logging area is located in the Ogouué-Ivindo province in the northeast Gabon. Because a wide river has been suggested to limit gene flow in great apes (Bonnin *et al.,* 2023), this site is subdivided into two sub-sites (TB1 and TB2) separated by the Liboumba River whose width varies from 40 to 60 m (Figure 1). The TB1 area is accessible from several villages and is a typical dense forest consisting of young secondary forests, mature secondary forests and swamp forests. This forest is widely used for hunting and farming by the populations. However, the TB2 area, which is on the other side of the river, is a dense evergreen forest consisting of mature and swamp forests. We find marshy clearings made up by streams and ponds supporting aquatic and semi-aquatic vegetation; and are generally crossed by elephants, bush pigs and large antelopes. People rarely access this area to hunt.

Concerning mining areas, Belinga (BE) and ACM Minkebe (AM) are located in the Ogooué-Ivindo province, in the northeast of Gabon (Figure 1). BE is a vast iron ore deposit under exploration whereas AM is a gold exploration area. The forests covering both sites are mainly mature dryland forests at an altitude of 450-1000 m. Gold panning camps are widespread in both areas. The establishment of gold panning camps is regularly associated with intense exploitation of wildlife (Lahm, 1993).

3.2 Camera trapping surveys: The surveys were carried out between June 2012 and July 2023 (table 1). Before setting camera traps, each study area was previously stratified in grids (from 0.75 km x 0.75 km to 3 km x 3 km grids) covering the entire target area. The camera traps were therefore placed 100 m around the center of each grid. However, when the center of a grid was outside the prospecting area, the camera was not placed. Within ND and ML3 mosaic forests, to avoid sunlight, we placed the cameras at the forest edge or in small fragments of forest within the savannah. The precise positioning of the cameras was determined by the presence of trees suitable for placing cameras and the presence of animal tracks. We placed at least 18 camera traps by forest block and each was mounted around 50 centimetres above the ground on a tree without baits. The cameras were angled parallel to the ground. For each survey, we programmed the cameras to "camera mode," which enables the capture of photos and designated that 3 should be recorded. Because gorillas sometimes can stay for several hours in front of the same camera, the data were filtered to exclude photos of the same species at the same station within a period of 1 hour to make sure that the events were independent (Tobler *et al.,* 2008; Hegerl *et al.,* 2017).

3.3 Hunting survey: Information on the development and nature of hunting in each forest block was collected during the installation of camera traps. To optimize information on hunting, one researcher and 3 field assistants collected hunting index along the recces-transects on a strip of 4 m, 2 m on either side of the line of march, in order to make them comparable. We used a global positioning system (GPS) to locate the hunting paths, snare trails, and hunting camps.

Additionally, we used photos captured by camera traps showing hunters with guns or animal carcasses. Following Laurence et al. 2008, we recorded an index of hunting pressure for each area based on signs of hunting activities: 1, old trail or abandoned hunting camp; 2, trap or gun shell; 3, fresh trail or active snare trap; 4, gunshot heard or photos captured by camera traps showing hunter with gun or hunter with animal carcass. These data were collected throughout the study area and then summed to form a single composite value for each forest block.

3.4 Data analysis: We identified the animal species in the photos following the nomenclature of Kingdon *et al.,* (2013). We were unable to discriminate *Cephalophus ogilbyi* and *C. callipugus*; and *Genetta cristata* and *G.servalina*. In the present study, we treated the two red duikers and the two genets as single species. All statistical analyses were performed using R version 1.3.1093 (R Core Team, 2022). P values less than 0.05 were considered statistically significant (*$*P<0.05$; $**P<0.01$; $***P<0.001$). To examine whether the number of recorded species reached an asymptote, we plotted a species accumulation curve, using Kindt's exact method in the R package "vegan" (Oksanen *et al.,* 2007). We drew separate accumulation curves for each study site. We calculated the hunting index (the cumulative number of indices/the-total number of kilometres travelled) for each forest block. Then we calculated the mean capture rate (the number of photos/1,000 camera days) of gorillas and chimpanzees for each study site as an abundance index (Nakashima *et al.,* 2013). Additionally, comparison between the abundance index of great ape species within each study were assessed using Student's t test. Finally, to examine the effect of hunting index on the relative abundance of each great ape species, the correlations between the abundance index of gorillas and chimpanzees as well as the index of hunting observed in each site were assessed through Person correlation and linear regression analysis.

4 RESULTS

4.1 Hunting effort: The hunting effort was highly variable between survey sites (Table 1). The site subject to the lowest hunting effort was the TBNI2 (TB2) dense evergreen forest very distant, whereas the most intensely hunted site, Dibwangui (DI), had a hunting effort more than twice greater. All sites were subject to both gun hunting and trapping. Trapping was the most frequently used method, with a mean effort across the 10 survey sites of 0.89 indices/km and 0.45 for gun hunting efforts.

4.2 Camera trap surveys: Sampling was conducted over a total of camera days comprised between 1142.2 and 2342.72 camera-days (Table 1). During the study periods and across all study sites, elephants broke 60 cameras (18.18%), chimpanzees 16 (4.84%) and 8 (2.42%) cameras were stolen. For all forest blocks where we conducted camera trap surveys, the species accumulation curves having reached asymptote (Figure 2a, b, c, d, d, e, f, g, h, i). Therefore, the abundance index of the two great ape species was different among study sites. Except for two sites (NG** and TB2**) where the abundance index of gorillas was significantly higher than that of chimpanzees, chimpanzee abundance index was significantly higher than gorilla abundance index throughout other study sites (BE*, BI**, AM***, TB1*, ML3*** and BH**).

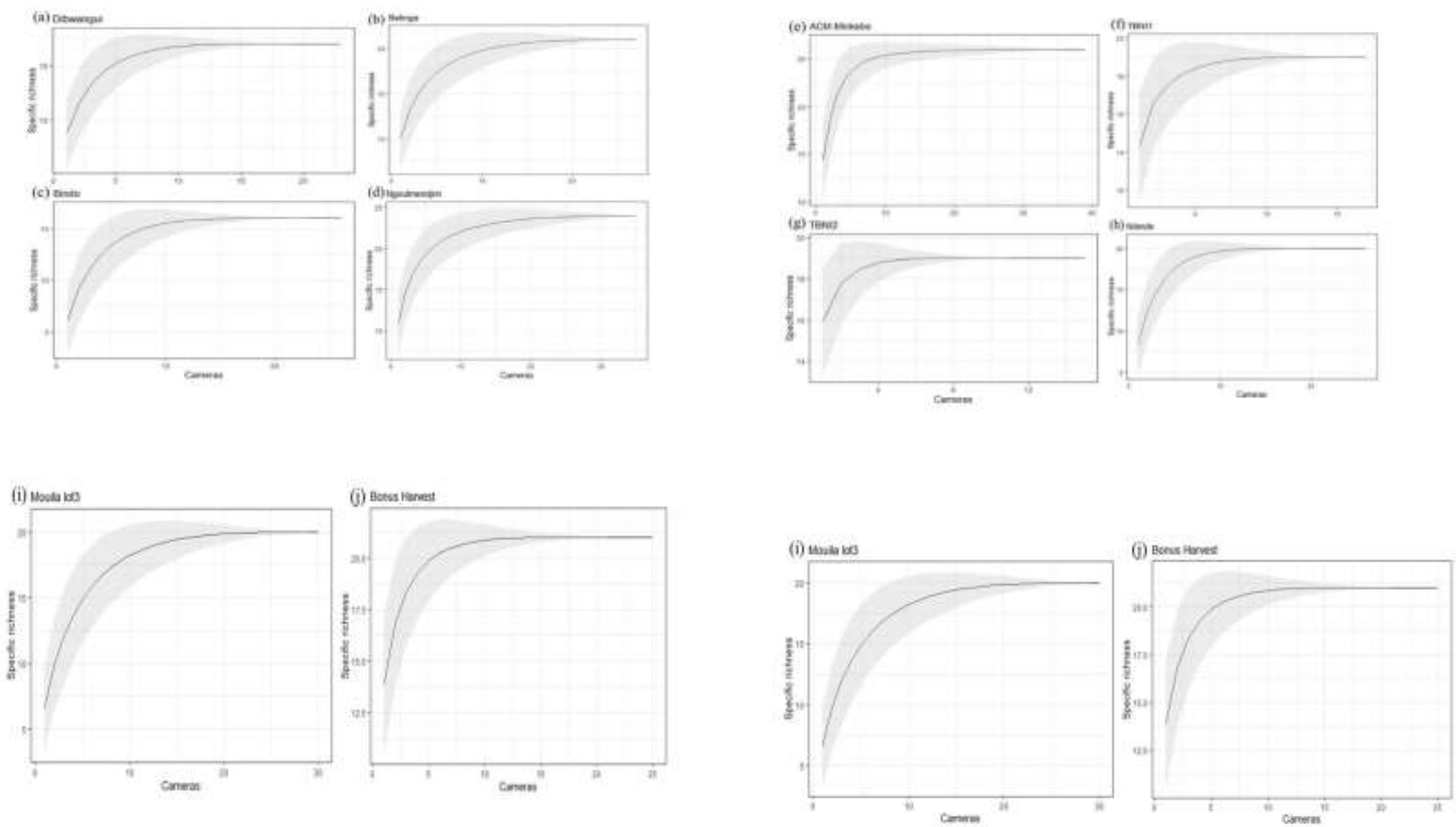

Fig. 2 Species accumulation curves for the 10 survey areas. (a) Dibwangui, (b) Belinga, (c) Bindo, (d) Ngoulmendjim, (e) ACM-Minkebe, (f) TBNI1, (g) TBNI2, (h) Ndende, (i) Mouila lot3 and (j) Bonus Harvest. The black line represents the mean accumulation curve of species whilst the lighter shading shows on standard deviation around this mean using Kindt's exact method (Oksanen et al. 2007).

4.3 Effect of hunting pressure on great ape relative abundance: We conducted camera trap surveys within 10 non-protected areas whose hunting index varies from 0.14 to 2.92 indices/Km. Chimpanzees were detected in all sites, while gorillas were not detected in 3 sites (DI, BI and ND) with higher hunting pressure index (Table 1). When we investigated the correlation between the hunting index and the abundance index of each great ape species, a significant negative correlation was found between the hunting index and the abundance index of gorillas (P < 0.001, τ = –6.63; Fig. 3a), whereas, a marginal negative correlation was found between the hinting index and the abundance index of chimpanzee (P=0.1831, τ = –0.42; Fig. 3b).

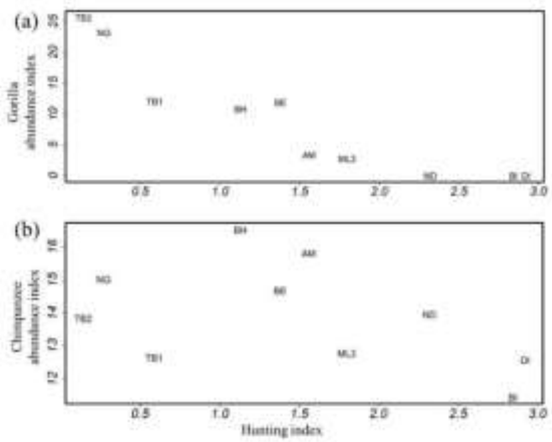

Fig. 3 Correlation between each great ape abundance index and hunting index across survey areas. (a) Western lowland gorillas and (b) central chimpanzees. The correlation between the parameters were assessed through Person correlation analysis, n = 10.

Table 1: Summary of study site characteristics

Sites	Area (Km^2)	Data collection periods	Grid design	Cameras/functional cameras	Camera days	Gorilla abundance index	Chimpanzee abundance index	Hunting index
Dibwangui (DI)	18	August–September 2017	0.75km x 0.75km	26/19	1142.20	0	12.58	2.92
Belinga (BE)	35	January – March 2023	1km x 1km	32/27	1565.61	11.88	14.68	1.38
Bindo (BI)	44	January –March 2018	1km x 1km	38/26	1498.61	0	11.45	2.84
Ngoulmendjim (NG)	42	August–October 2017	1km x 1km	40/32	1915.42	23.22	15.02	0.27
ACM Minkebe (AM)	226	April – July 2023	2km x 2km	54/40	2342.72	3.41	15.62	1.56
TBNI 1 (TB1)	194	June – September 2021	3km x 3km	18/16	1490.18	11.28	12.65	0.58
TBNI 2 (TB2)	172	June – September 2021	3km x 3km	18/15	1325.49	25.65	13.84	0.14
Ndendé (ND)	288	July – October 2012	3km x 3km	30/20	1563.42	0	13.96	2.32
Mouila lot3 (ML3)	396	June – September 2012	3km x 3km	38/26	1776.56	2.814	12.78	1.80
Bonus Harvest (BH)	426	April – July 2022	3km x 3km	36/25	2184.12	10.86	16.52	1.13

5 DISCUSSION

5.1 Abundance of great apes across study sites: In the present study, gorillas were present at fewer sites than chimpanzees, and overall detections of gorillas were less than that of chimpanzees. These findings are consistent with those of previous studies that have demonstrated that overall abundance of chimpanzees is higher than that of gorillas across differential sites within Central African forests (Furuichi *et al.,* 1997; Tagg *et al.,* 2011; Strindberg *et al.,* 2018; Collins, 2022). Traits such as long life, low reproduction rate, late maturation and long inter-birth interval, high infant and juvenile mortality and complex social behaviour might contribute to explain the high abundance of chimpanzees compared to gorillas through most of the study sites. For both chimpanzees and gorillas, adult female give birth once every four to six years and only three or four over her entire lifetime (Hill *et al.,* 2001; Robbins *et al.,* 2004). However, infant mortalities, one the first and third year, are higher in gorilla populations (42.9% and 22-65% (Robbins *et al.,* 2004)) than in chimpanzee populations (20% and 10% (Hill *et al.,* 2001)). This low child survival rate makes difficult for gorillas to recover from population declines.

Moreover, we investigated the abundance index of chimpanzees and gorillas across several sites and during different periods using camera traps. Species-specific factors such as as foraging behaviour, ranging patterns and social group dynamics can affected the probability of detection through camera traps. Chimpanzees are well known for their territorial behaviour (Wilson and Wrangham, 2003; Seiler and Robbins, 2020). During boundary patrols and forage, chimpanzees are ranging over greater distances than gorillas (Amsler, 2010; Seiler and Robbins, 2020). Therefore, in most study sites, the probability of camera traps to detect them might be higher during each study period (Collins, 2022). Additionally, as suggested by Collins (2022), the fission-fusion social grouping dynamic of chimpanzees (Yamagiwa and Basabose, 2014) versus the generally more stable gorilla social groups (Morrison *et al.,* 2020) may result in greater dispersion of individual chimpanzees within each study area. Furthermore, chimpanzees are fruit-eating species and most of the time, they are foraging for finding ripe fruits (Morgan and Sanz 2006; Head *et al.,* 2012; Yamagiwa and Basabose, 2014) while gorillas tend to consume more widely available terrestrial vegetation when fruits are scarce (Head *et al.,* 2012; Yamagiwa and Basabose, 2014). All of these activity patterns might lead the detections of chimpanzees at a greater number of camera sites.

5.2 Effect of hunting pressure on great ape populations: This study provides a broad assessment of the differential effect of hunting on the abundance of a wide range of Central African great apes. We have shown clear differences in the relative abundance of the two coexisting great ape species in response to variable hunting effort. Central chimpanzees (*Pan troglodytes troglodytes*) are the most widely distributed and least sensitive to hunting pressure, whereas western lowland gorillas (*Gorilla gorilla gorilla*) show a very strong response to hunting pressure. Prior to our research, in order to assess the impact of hunting on the abundance of chimpanzees and gorillas inhabiting Central African forests, most studies were conducted using line transect method based of dung and nest counts (Kano and Asoto, 1994; Rist *et al.,* 2009; Strindberg *et al.,* 2018; Ginath *et al.,* 2020). Although, most results are more likely to reflect the negative effects of bushmeat hunting on both coexisting great apes, chimpanzees (*Pan troglodytes*) have suggested to be most resilient to agricultural expansion and can persist in mosaic habitats alongside rural farming communities (Hockings and McLennan, 2016; Garriga *et al.,* 2018; Bersacola *et al.,* 2021; Collins, 2022). In contrast of gorillas which are the largest-bodied species among Central African great apes, are generally most sensitive to hunting (Tutin, 2001; Fa and Brown, 2009). Furthermore, gorilla abundance has been suggested to be inversely correlated with human disturbance including hunting in the Dzanga Sangha Dense Forest Reserve, Central African Republic (RDS) (Remis, 2000). The susceptibility of single species to hunting depends on its ecological specialization, its ability to avoid predation and its ability to reproduce (Linder *et al.,* 2011). Although it is difficult to consider the history of hunting in different sites, we assume that the current abundance of different species is affected by the past levels of hunting pressures (Jerozolimski and Peres, 2003; Rist *et al.,* 2009). The western lowland gorillas appear to be very sensitive even to low levels of hunting because of particular social behaviors traits in contact with human. Most of the time, gorillas always show aggression as a first reaction when they encounter human (Cipolletta, 2003, Blom *et al.,* 2004). Some individuals, like the silverback males, are particularly aggressive and attack people unexpectedly in the forest (Tutin, 2001; Cipolletta, 2003). In addition, gorillas are most often curious and tend to ignore observers, especially when they are on trees (Blom *et al.,* 2004). Furthermore, in Central Africa, gorillas are not only hunted for meat, but also as trophies. Gorilla skulls are most often found among several notable houses (Cousins, 1975). Those behavioural traits and exotic use put gorillas at risk of more being hunted. In contrast with gorillas, our results show that Central African chimpanzees appear to be less sensitive to hunting. This result is similar with that of Kano and Asato (1994) who described that the density of chimpanzees was higher near the village than that of gorillas (Table 5 in Kano and Sato, 1994). Several potential behavioural treats may explain the observed patterns. In contact with humans, chimpanzees can exhibit a high level of behavioural diversity. Tutin and Fernandez (1991) documented the behavioural responses of chimpanzees to humans in the Lope Reserve, Gabon. The most common responses were immediate departure by flight, approach/wait for another before moving away from the observer, and stealthy retreat. They rarely exhibited hide, ignore, charge, or curiosity, which might be increase the risk of being hunted. Moreover, chimpanzees have been suggested to be very intelligent among great apes and can communicate to report the danger to other members within the community (Dezecache *et al.,* 2019). The members living in an area with high hunting pressure could develop an alarm that signals the presence of hunters or the location of traps within their territory. Furthermore, within several sites with various conflicts between chimpanzees and humans, they are often observed only when people are not common (Gašperšič and Pruetz, 2011). Therefore, chimpanzees can forage in forests subject to hunting pressure while avoiding being further targeted by hunters.

6 CONCLUSION

For sustainability, declines in biodiversity highlight the need to develop strategies for species monitoring particularly in Central Africa. Acquiring new information regarding the distribution and the impact of anthropogenic activities on great ape populations is important for their conservation. We have shown that the effect of hunting pressure is different among the coexisting great apes inhabiting non-protected areas in Gabon. Consequently, gorillas appear to be more susceptible to hunting than chimpanzees. This difference shows an urgent need to increase information regarding the distribution of great ape populations in order to update their conservation status across unprotected areas. Furthermore, this information may be beneficial for the future monitoring of western lowland gorillas and central chimpanzees outside of national parks in Gabon.

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CONFLICTS OF INTEREST

The authors declare that they have no competing interests.

AUTHORS'CONTRIBUTIONS

AOEF, MNR and NA designed the project. AOEF, MNFL, MB and OEJP collected camera trap data and conducted species identification from camera trap photos and videos. AOEF, OEJB and BM performed the data and AOEF wrote the manuscript.

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