

Occupancy and activity of sympatric central chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*) in a multi-use landscape, Campo Ma'an Conservation Area, Southern Cameroon

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Abstract

Occupancy and activity of sympatric central chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*) in a multi-use landscape, Campo Ma'an Conservation Area, Southern Cameroon

Emily Collins

Central chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*) are two endangered great ape species that are sympatric over much of their geographic range. Protecting areas of high conservation value and the development of responsible ecotourism are two main strategies for the continued preservation of these species, and both strategies require up to date knowledge on areas currently occupied by great apes and their activity patterns. The occupancy of chimpanzees and gorillas across three land type designations in a multi-use landscape in Southern Cameroon was assessed and we analyzed whether there was an overlap in species occupancy on the monthly scale. We also tested whether fruit availability or human presence influenced the activity of chimpanzees or gorillas at different locations across the study area. Chimpanzees occupied more sites across the whole study area, with a significant difference among land use types, with the highest proportion of occupied sites being in the National Park. No evidence of spatio-temporal overlap was found between gorillas and chimpanzees on the monthly scale. The probability of either species occupying a site during a given month remained stable under the conditional presence or absence of the other species, suggesting there is neither a positive nor negative interaction between the species. No effect of human presence on the activity levels of either chimpanzee or gorilla was found, although activity analyses were limited to sites where apes

were present. The density of fruiting trees positively influenced the activity of gorillas but had no effect for chimpanzees. This study adds to our understanding of gorilla and chimpanzee occupancy and activity across the CMTOU, which may be useful for further monitoring of both species. Our results are in support of previous work showing the heterogeneous distribution of ripe fruits and preferred feeding resources acting as a mechanism allowing these two sympatric ape species to coexist. This is the first study that we are aware of to simultaneously investigate occupancy and activity of two sympatric ape species across a multi-use landscape.

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1. Introduction

1.1 Current status of wild chimpanzee and gorilla populations and conservation

Central chimpanzees (*Pan troglodytes troglodytes*) and Western lowland gorillas (*Gorilla gorilla gorilla*) are two of Africa's most iconic primates of high conservation priority. The current geographic range of these two great ape subspecies overlap by 97% (Strindberg et al., 2018), encompassing rainforests in six countries: Angola, Cameroon, Central African Republic, Equatorial Guinea, Gabon and the Republic of Congo (IUCN, 2014). This region, referred to as Western Equatorial Africa, harbors 99% of the world's gorillas, and one third of the world's chimpanzees (Strindberg et al., 2018). For decades, great ape populations in Western Equatorial Africa have been undergoing dramatic decline (Maisels et al., 2016; Maisels et al., 2018; Walsh et al., 2003). Threats to great apes can be classified into two groups, direct threats, which remove individuals directly from the population, and indirect threats, which contribute to overall population declines (IUCN, 2014). The three main direct threats to populations of both subspecies are poaching, disease, and habitat loss (IUCN, 2014; Maisels et al., 2016; Maisels et al., 2018; Strindberg et al., 2018). Indirectly, increased human access to once isolated habitat through the construction of roads, an escalating demand for bushmeat, corruption within systems of governance and a lack of law enforcement exacerbate population decline by contributing to direct threats (IUCN, 2014).

Currently, the IUCN lists central chimpanzees as Endangered (Maisels et al., 2016), with the most recent large-scale census across Western Equatorial Africa estimating a total population size of 128,760 weaned individuals [95% confidence interval, 114,208 to 317,039] (Strindberg et al., 2018). Western gorillas are listed as Critically Endangered, with an estimated total population

of 361,919 weaned individuals [95% confidence interval, 302,973 to 460,093] (Strindberg et al., 2018).

Wildlife surveys are an important tool for monitoring populations, providing information on distribution, demography, and species-specific responses to threats. Identifying areas of high conservation priority (specifically, areas harboring high densities of great ape populations), along with developing tailored action plans for each area has been a central goal in the development of the Regional Action Plan for the Conservation of Western Lowland Gorillas and Central Chimpanzees 2015–2025 (IUCN, 2014). Among the high priority landscapes highlighted in this document is the Campo Ma'an region in southwestern Cameroon, harboring a great ape population size of between 2000 and 5000 individuals (IUCN, 2014). The focus of this thesis is on the populations of central chimpanzee and western lowland gorilla located in this region, specifically in the Campo Ma'an National Park and surrounding areas, referred to as the Campo Ma'an Technical Operational Unit (CMTOU).

1.2 Feeding ecology and habitat use in sympatric apes

Our current understanding of the sympatric ecology of gorillas and chimpanzees is that while both species are frugivorous (Head et al., 2011; Head et al., 2012; Yamagiwa and Basabose, 2014), chimpanzees are specialist frugivores while gorillas are generalist folio-frugivores (Head et al., 2011; Oelze et al., 2014). However, gorillas living in lowland forests have been reported to rely heavily on fruits during certain seasons (Doran-Sheehy et al., 2009; Masi et al., 2009) and consume many of the same fruits as sympatric chimpanzees (Morgan and Sanz, 2006). Gorillas and chimpanzees exhibit different preferences for fallback foods (Head et al., 2011; Tédonzong et al., 2019; Yamagiwa and Basabose, 2014), with gorillas consuming high amounts of fibrous, leafy

vegetation when fruit availability is low (Cipolletta, 2003; Head et al., 2011; Doran-Sheehy et al., 2009; Yamagiwa and Basabose, 2014). Chimpanzees have been observed to employ a wider range of foraging practices than gorillas, such as using tools to fish for ants (Yamamoto et al., 2008), algae (Boesch et al., 2017; Matsuzawa, 2019), as well as consuming vertebrate prey including pangolin (*Phataginus tricuspis*), tortoise (Genus *Kinixys*), and small primate species such as red colobus monkey (*Piliocolobus* sp) (Hicks et al., 2019; Newton-Fisher, 2007). Chimpanzees also exhibit greater flexibility in social grouping than gorillas, which may contribute to their ability to persist in searching for ripe fruits during periods of scarcity (Head et al., 2012, Morgan and Sanz, 2007; Yamagiwa and Basabose, 2014). Conversely, gorillas have distinctive digestive physiology in comparison to chimpanzees, including differences in dental topography (Ungar, 1996) and digestive tract function (Remis, 2003; Rogers et al., 2004; Marshall and Wrangham, 2007) which allow them to consume large amounts of herbaceous vegetation to supplement their diet during periods of fruit scarcity.

The heterogeneous distribution of plant species and fruit availability across landscapes shared by both species has been proposed as a primary mechanism allowing the two species to avoid direct competition (Tédonzong et al., 2019; Yamagiwa and Basabose, 2014). As fruit availability changes seasonally (Doran-Sheehy et al., 2009; Oelze et al., 2014; Tédonzong et al., 2019), temporal and spatial shifts in habitat use and different preferred fruit species may facilitate coexistence of the two species at the landscape level (Tédonzong et al., 2019).

1.3 Responses to anthropogenic pressures

Human activity has been shown to effect chimpanzee and gorilla populations differently, with notable variation in species-specific responses to the type and length of disturbance as well

as variation across study sites. After a logging disturbance, chimpanzees will almost exclusively remain or take refuge in adjacent undisturbed regions of forest while gorillas, after the logging has ceased, will preferentially occupy the logged areas (Arnhem et al., 2008, Matthews and Matthews, 2004, Morgan et al., 2018). Changes in forest structure, specifically the loss of large timber species, affect gorillas and chimpanzees differently. Morgan et al. (2019) showed that chimpanzees lowered their nest heights significantly in logged forest, whereas gorilla nest heights remained unchanged in logged versus intact forest. Previously logged forest patches may in fact be opportunistically re-colonized almost immediately by gorillas, while chimpanzee densities have been shown to remain low (Matthews and Matthews, 2004, Morgan et al., 2018). The ability for gorillas to exploit logged forest patches may be in part due to elevated levels of leafy vegetation and clearings for building terrestrial nests (Matthews and Matthews, 2004; Morgan et al., 2019; Stokes et al., 2010). Preferential use of previously logged habitats over other forest types by gorillas occurred even when these areas were in close proximity to villages (Matthews and Matthews, 2004).

In landscapes shared by both humans and apes, overlap at the site level may occur. Using direct evidence from camera traps, Bersacola et al. (2021) showed that chimpanzees did not avoid humans at the site level, although in general chimpanzee space use showed patterns of avoidance of areas with high human activity, such as villages, and to a lesser degree agricultural areas. Similarly, at the site-level, indirect signs of gorilla activity (nest encounters) have been shown to be inversely correlated with signs of human activity and hunting (Remis, 2000). In the Campo Ma'an forest specifically, chimpanzee densities were essentially doubled in areas with low levels of human activity compared to areas with high levels of human activity (Matthews and Matthews, 2004), corroborating other findings that chimpanzee nest encounter was inversely correlated with

levels of human disturbance (Morgan et al., 2018). Taken together, while both gorillas and chimpanzees may initially avoid areas with high levels of human activity, there is interspecific variation in the effects of disturbances which only become evident over a longer time period.

1.4 Species interactions

Although reports of direct interactions between sympatric chimpanzees and gorillas are rare, during key times of the year important foraging areas may be exploited by both species. For example, a study in Tshibati, Kahuzi-Biega National Park in the Republic of Congo (Basabose and Yamagiwa, 2002) suggests overlap in the use of the same fruiting trees may have occurred during the dry season in a specific forest type (secondary forest), as gorillas primarily foraged in secondary forest regardless of season, and chimpanzees preferentially used secondary forest during the dry season, inferred by the presence of nests. There have also been direct observations of peaceful co-feeding events of both species, i.e., simultaneous foraging for food resources within the same tree (Morgan and Sanz, 2006; Southern et al., 2021; Walsh et al., 2007). Recently published data from a site in the Goualougo Triangle, Republic of Congo (Sanz et al., 2022), showed evidence of complex and long-term social relationships between chimpanzees and gorillas, including both affiliative and non-affiliative interactions between individuals. One instance of lethal attacks on western gorillas by central chimpanzees has also been published (Southern et al., 2021), and authors noted that these events occurred during periods of high dietary overlap and fruit scarcity. While coexistence of these two sympatric apes is largely maintained through dietary divergence (Tédonzong et al., 2019; Yamagiwa and Basabose, 2014) the nature of interspecies group interactions is an area of study which has not been widely researched.

1.5 Purpose of the research

The goal of this study was threefold. Primarily, the purpose was to model chimpanzee and gorilla occupancy across three land use types. The secondary purpose was to study whether there was a correlation between sites occupied by chimpanzees and gorillas during the same time period and if this was affected by fruit availability. The third objective was to test whether availability of feeding resources or levels of human presence influence the activity of each species at the site level. Knowledge on ape occupancy and factors affecting their activity in different regions of the Campo Ma'an Technical Operational Unit may be useful for advancing the possibility of responsible eco-tourism with outcomes beneficial to local communities and the sustained preservation of the biodiversity, including gorillas and chimpanzees.

1.6 Predictions

Based on previous surveys of chimpanzee and gorilla populations in the CMTOU, I predict 1) both chimpanzees and gorillas will occupy the highest proportion of sites in the National Park as well as the Forest Management Unit, to a lesser degree (Nzoo-Dongmo et al., 2015; Matthews and Matthews, 2004), and Community Land will have the least number of sites occupied by gorillas and chimpanzees due to the highest level of human activity occurring in this area. I also predict that 2) co-occurrence of chimpanzees and gorillas at certain sites during times of high fruit availability may arise due to ample foraging opportunities for both (Head et al., 2011; Head et al., 2012; Tédonzong et al., 2019; Yamagiwa and Basabose, 2014). Evidence has shown that interspecies differences in preferred fruits and heterogeneous distribution of feeding resources allow these two species to avoid direct competition (Tédonzong et al., 2019; Yamagiwa and

Basabose, 2014). However, limited evidence also suggests that co-feeding (Southern et al., 2021; Walsh et al., 2007) and direct interspecies interactions do occur (Southern et al., 2021).

Lastly, I predict that 3) gorillas and chimpanzees will be more active at sites with high fruit availability and mean species richness as these areas provide the greatest foraging opportunities (Head et al., 2011; Head et al., 2012; Tédonzong et al., 2019; Yamagiwa and Basabose, 2014) and 4) indirect and direct human signs will be negatively correlated with gorilla and chimpanzee activity (Arnhem et al., 2008, Matthews and Matthews, 2004; Morgan et al., 2018).

2. Materials and Methods

2.1 Study species

The most recent estimate of the total chimpanzee population across the CMTOU is 2199 [1736 –2786] individuals (Nzoo-Dongmo et al., 2015). The southwestern region of CMTOU is designated as National Park and contains the island Dipikar, which harbors the highest density of great apes; 694 [513 - 940] individuals, 1.99 [1.47 – 2.70] individuals per km² (Nzoo-Dongmo et al., 2015). The overall density of gorillas is reported as 0.22 [0.14-0.33] individuals per km², with a total population size of 1000 [661-1514] individuals. The density of gorillas is highest in the southern National Park, Dipikar island region, with 1.25 [0.70-2.23] individuals per km² and 0.10 [0.03-0.35] individuals per km² in the Forest Management Unit. The overall density of chimpanzees is reported as 0.26 [0.20-0.35] individuals per km², with a total population size of 1220 [929-1603] individuals. The highest density of chimpanzees occurs in the National Park, Dipikar island region, with 1.01 [0.71-1.42] individuals per km², and 0.10 [0.06-0.17] individuals per km² in the Forest Management Unit. Neither of the previous surveys included Community Land as a specific land type category for great ape surveys. Currently, details on the specific

ranging patterns and overlap of gorilla and chimpanzee groups within the CMTOU have not been published.

Chimpanzees preferentially nest in mature, closed canopy forest but use other available forest types such as younger, secondary forest occasionally for nesting (Arnhem et al., 2008, Morgan et al., 2006). In contrast, gorillas preferentially nest in younger, secondary forest with more open canopy and denser terrestrial vegetation (Arnhem et al., 2008, Morgan et al., 2006). The variation in preference for mature versus secondary forest may be in part due to the different nest building behaviours exhibited by gorillas and chimpanzees. Both gorillas and chimpanzees build sleeping nests each night from branches and vegetation (Morgan et al., 2019; Sanz et al., 2007); however, chimpanzees tend to build more arboreal sleeping nests while gorillas primarily nest closer to the ground (Morgan et al., 2019; Sanz et al., 2007; Stokes et al., 2010).

Ranging patterns and daily path lengths of gorillas and chimpanzees vary between species, and across locations. Home ranges of western lowland gorillas have been estimated between approximately 10 – 20 km² (Bermejo, 1997; Bermejo, 2004; Cipolletta, 2003; Tutin et al., 1992; Tutin, 1996; Remis, 1997) and may fluctuate seasonally (Cipolletta, 2003; Remis, 1997). Home ranges of central chimpanzee vary between 7 – 59 km² (Martínez-Íñigo et al., 2021, Morgan et al., 2018) and are influenced by group size, interspecific competition, and food availability (Boesch and Boesch-Achermann 2000; Lemoine et al., 2020; Martínez-Íñigo et al., 2021). Both species' home ranges are comprised of a core area with more frequent usage, and a subsequent larger peripheral range which may overlap with other groups (Martínez-Íñigo et al., 2021, Morrison et al., 2020, Remis, 1997). Chimpanzees are known to routinely patrol and defend home range territories (Boesch and Boesch-Achermann 2000; Lemoine et al., 2020), while western gorillas, to a lesser extent, have also shown behavioural patterns consistent with territoriality, including

defensive responses and avoidance of the core areas of other groups (Morrison et al., 2020). It has been suggested that a key difference between the species is that chimpanzees actively defend a geographic area from conspecifics, while gorillas defend their social group (White and Tutin, 2001). As such, gorillas may be more resilient to the destruction of a specific habitat patch (i.e., through logging) as the social group can displace itself to an adjacent habitat patch (Morgan et al., 2018), while chimpanzee groups undergoing forced displacement due to habitat destruction may encounter neighbouring groups actively defending the adjacent territory.

Daily path length for western gorillas have been reported as between 1 – 3 km (Bermejo, 1997; Cipolletta, 2003; Remis, 1997; Tutin et al., 1992; Tutin, 1996). Daily travel distance estimates for central chimpanzee specifically are not currently well reported in the literature; however, daily path length has been estimated to be between 1 – 3.8 km for Eastern chimpanzee (*Pan troglodytes schweinfurthii*) (Green et al., 2020) and between 1 – 4 km for western chimpanzee (*Pan troglodytes verus*) (Herbinger et al., 2001).

2.2 Study site

The study site is the southwest part of the Campo Ma'an Technical Operational Unit (CMTOU) in southern Cameroon (2°10' N/9°50' E and 2°25' N/10°48' E, Figure 1) which comprises a National Park (NP), Forestry Management Unit (FMU) and Community Land (CL). The National Park has the lowest level of human disturbance, with research, tourism, and limited use of non-timber resources and cultural activities by the *Bagyeli* local community. Within Forest Management Units, logging and use of timber products are authorized, as well as research, tourism, and use by local communities. Part of the FMU was declassified in 2019 and converted to palm oil plantations (Djoko et al., 2022). The Community Lands have the highest level of human

disturbance within the CMTOU, with authorization for logging, extraction of non-timber forest products, agriculture, housing, and developmental projects (Djoko et al., 2022). The Campo Ma'an region has high biodiversity, including several endemic plant species (Droissart et al., 2014; Tchouto et al., 2009). In addition to central chimpanzee and western lowland gorilla, the region also harbors other threatened species including African forest elephant (*Loxodonta cyclotis*), leopard (*Panthera pardus*), African forest buffalo (*Syncerus caffer nanus*) and giant pangolin (*Smutsia gigantea*). This region of Cameroon has two distinct dry seasons, June to August and December to February; and two rainy seasons, March to May and August to November (Djoko et al., 2022). Average annual temperature is 25 degrees Celsius and average annual rainfall is between 1670 – 2800 mm (Tchouto et al., 2009).

2.3 Camera Trap Deployment

Remote camera traps (Trophy Cam HD Essential E3 Trail Brown 16 MP 119837C Model, Bushnell, Kansas) were installed in the southwestern region of CMTOU and were active from June 2019 until August 2020. A total of 19 cameras across 17 sites were deployed across the three land types; 7 sites in the NP, 6 in the FMU and 4 in the CL. Seven of the cameras were stolen during the study period, three replacement cameras were installed in new locations, and one camera was moved from its initial location due to humidity. Two sites had two different cameras operational during the study, one set to video capture and one set to photo capture. The distance between camera sites ranged from 1.2 km to 8.8 km. Cameras were placed opportunistically to capture large bodied terrestrial mammals, with assistance from local field guides (Djoko et al., 2022). Cameras were angled horizontally, and camera height was between 80 and 150 cm, with a distance of 5 to 15 meters from target features such as fruiting trees, inactive roads or pathways created by

elephants. In total, nine cameras were installed under fruiting trees, five cameras were placed on elephant paths and five placed on inactive logging roads. Fruiting trees, elephant paths and open travel routes have been proposed as suitable camera trap locations for targeting chimpanzees (Arandjelovic et al., 2014), and may be considered equally accessible for gorillas. As both species have a relatively similar body size, the detection area covered by camera trap motion sensors has been estimated at mean = 9 m², range = 1.5–19.5 m² for both gorillas and chimpanzees (Head et al., 2012). Motion sensors were set to trigger immediately when movement was detected, with a delay of 3 seconds between consecutive photos while movement still occurred. All photos were date and time stamped. To account for bias arising from multiple triggers of the same individual by the same camera, or for inflated detection rates at sites hosting two cameras, all photos or videos of the same species at a site within a 30-minute interval were counted as a single detection event (Meek et al., 2014; Tanwar et al., 2021). Detection events were considered as a single event regardless of the number of individuals detected. The independence interval of 30 minutes has previously been used to estimate the relative abundance index of chimpanzees and gorillas using camera traps (Fonteyn et al., 2021).

2.4 Line transect surveys

Line transects corresponding to each of the 17 camera sites were established to survey tree species, fruit availability and indicators of human presence. Each transect measured 500 meters by 50 meters, for an area of 2.5 hectares covered. All woody tree species with diameters at breast height greater than 20 cm were identified by local botanists, and in cases where identification was not possible, specimens were collected and identified at the Cameroon National Herbarium. Tree species richness was calculated as the total number of woody tree species divided by 2.5 hectares.

Fruit availability in each transect was measured monthly and was calculated as the number of trees bearing ripe fruits divided by 2.5 hectares. Human presence was measured both directly and indirectly. Direct presence was measured by calculating the number of independent captures of humans with the camera traps, using the same 30-minute interval of independence as used for wildlife species. Camera trap images of humans were handled using ethical guidelines outlined by Sharma et al. (2020), including disclosure of camera trap locations to local communities and informing the public that camera trap images of humans would not be published, shared, or used for any purpose besides the current research. Indirect signs of human presence were measured to account for human activity within the transect or camera site that remained undetected by the camera traps. Signs of human presence were measured monthly along transects and included identification of firearm cartridges, evidence of hunting camps, traps, machete cuts on trees, tree stumps, and skidding trails.

2.5 Data analysis

2.5.1 Camera trap images

All camera trap images were processed using Timelapse 2.0 v 2.2.3.5 (Greenberg, 2020). Species name and number of animals were identified manually. Location, date, and time stamps for each image were transferred to the dataset using the Timelapse software and verified manually. Code available from https://github.com/WildCoLab/WildCo_Single_Site_Exploration enabled further processing of the data including the compilation of a dataset representing independent capture events using the 30-minute threshold.

2.5.2 Species occupancy

The purpose of the occupancy modelling was to understand broadly the presence of gorillas and chimpanzees across the three land types of the CMTOU. Occupancy models are useful for obtaining estimates of occupancy while accounting for imperfect detection of a focal species (Mackenzie et al., 2002; Mackenzie and Royle, 2005), which can be a common issue among camera-trap surveys (Sollmann, 2018; McIntyre et al., 2020). The occupancy model also served to test whether positive or negative species interactions occurred between gorillas and chimpanzees while considering imperfect detection of each. The framework of occupancy models considers processes that may influence the detection of a species at site by sampling the same site on multiple occasions. Occupancy modeling uses two main parameters: occupancy probability (Ψ), which may be influenced by ecological processes, and detection probability (p), which may be influenced by biological processes as well as processes related to the accuracy of the observer (Mackenzie et al., 2002; Mackenzie and Royle, 2005). If a species is present at a site, the probability can be described as Ψ , whereas if a species is absent at a site, the probability can be considered as $1 - \Psi$. For every sampling occasion (j) there are three possibilities. Either the site is not occupied by the species ($p=0$), the species is present and detected (probability being p_j), or the species is present but was not detected ($1 - p_j$). Occupancy and detection probabilities are estimated separately and can both be modeled with covariates. As occupancy modelling was originally based on mark-recapture population surveys of closed populations, a central assumption requires that no change in occupancy occurs during the sampling period, referred to as ‘closure’ (Mackenzie et al., 2002; Mackenzie and Royle, 2005; Rota et al., 2009). Both gorilla and chimpanzee are known to alter their range use seasonally, resulting in a high likelihood of their occupancy at a specific site shifting during the 12-month study period. Also, the home range sizes of both species may be large enough to encompass multiple camera sites. To account for this, the data was stacked by month.

This step was taken to mitigate bias that may have arisen due to violation of the closure assumption and resulted in each site used for the occupancy model relating to both to a geographic and temporal identifier (i.e., a specific camera location during a specific month, grouped as one 'site'). The dataset was then divided into four sampling occasions (SOs) per month (Crunchant et al., 2020), resulting in each camera location having between 8 - 48 SOs (median = 36). Detection history for each species were compiled as separate matrices using binary values (0 = non-detection, 1 = detection). To estimate occupancy and detection probability in accordance with the stacked study design, a single-season occupancy model was used, applying the function 'occuMulti' from the package 'unmarked' (Fiske and Chandler, 2011) in R Studio (R Studio Team, 2022). To assess goodness of fit of the model, the parametric bootstrap procedure 'parboot' function (MacKenzie and Bailey, 2004) from the package 'unmarked' (Fiske and Chandler, 2011) was used, with no evidence of lack of goodness of fit ($p > 0.05$).

2.5.3 *Species activity*

A generalized linear mixed model (GLMM) was used to test the influence of environmental and anthropogenic variables on the activity of chimpanzees and gorillas. A separate model was conducted for each species, using the total number of independent detections per month at each site as the response variable, with the total number of trap days per month at the site (a measure of the effort) used as an offset term. The number of independent camera trap captures of a species can be considered as an index of species activity at a given site, and therefore may be used to investigate if habitat covariates contribute to variation in the activity of a focal species (Sollmann, 2018). Photos or videos of the same species within a 30-minute interval at the same site were considered as independent captures (Meek et al., 2014; Tanwar et al., 2021). The independence

interval of 30 minutes has previously been used to estimate the relative abundance index of chimpanzees and gorillas using camera traps (Fonteyn et al., 2021). The main effects tested consisted of a categorical variable (land use type), and four continuous variables (fruit tree density, mean species richness, indirect human signs, and human trapping rate). Continuous covariates were standardized to have a mean of 0 and standard deviation of 1. Because our response variable was a count type of data, the GLMM was fit using a negative binomial family with log link function. For the final model, we used backward selection, dropping each sequential predictor failing to meet an alpha of 0.2. To account for unexplained heterogeneity between camera locations, and lack of spatial independence between detections recorded every month for the same location, camera trap stations (Sites) were modeled as a random intercept (Djoko et al., 2022; Popescu et al., 2014). For each respective model, sites which had no detections of the focal species during the entire study were removed from the analysis.

3. Results

The camera trap survey included a total of 4168 camera trap days between June 2019 to May 2020, with 107 total independent detections of chimpanzee at 12 sites, and 38 independent detections of gorillas at 7 sites (Table 1, Figures 2-3). Notably, the number of camera locations varied across land types, with only 894 trap days across 4 sites in Community Land, compared to 1845 trap days across 6 sites in the Forest Management Unit, and 1429 trap days across 7 sites in the National Park (Table 1).

The occupancy model showed the estimated detection probability for chimpanzee was 0.276 [95% confidence interval (CI), 0.195 to 0.375] and 0.297 [95% CI, 0.161 to 0.484] for gorilla (Table 2). Using a single-species model, the predicted proportion of sites occupied each month (ψ)

for chimpanzee was 0.792 (95% CI, 0.463 to 0.944) in the National Park, 0.249 (95% CI, 0.131 to 0.423) in the Forest Management Unit and 0.131 (95% CI, 0.041 to 0.347) in the Community Land (Table 3). Chimpanzee occupied a higher proportion of sites in the National Park compared to Community Land ($p < 0.001$, Table 4) and compared to the Forest Management Unit ($p = 0.002$, Table 4). Chimpanzee occupancy between Community Land and Forest Management Unit was not significantly different ($p = 0.288$). Predicted occupancy for gorilla was 0.136 (95% CI, 0.053 to 0.306) in the National Park and 0.167 (95% CI, 0.074 to 0.334, Table 3) in the Forest Management Unit. There was no significant difference between gorilla occupancy in National Park and Forest Management Unit ($p = 0.713$, Table 4).

The multi-species occupancy model showed the marginal occupancy (occupancy probability across sites every month) was 0.417 (95% CI, 0.303 to 0.548) for chimpanzee and 0.117 (95% CI, 0.040 to 0.227) for gorilla (Table 5). No significant interaction was found between chimpanzee and gorilla occupancy under the null model, and the occupancy estimates of both gorilla and chimpanzee remained relatively similar under the conditional presence or absence of the other species (Table 5). No significant effect of fruit level on occupancy was shown for either species, and the interaction between chimpanzee and gorilla was also non-significant when modeling fruit availability as a covariate (Table 6). Covariates influencing detection probability for both species were assumed to be constant for all models and across all sites [$p(\cdot)$].

The generalized linear mixed model showed no effect of fruiting tree density, mean tree species richness, direct evidence of human presence or indirect evidence of human presence on chimpanzee activity at a site, using independent chimpanzee capture events as the response variable (all $p > 0.05$, Table 7). However, land use type had a significant effect on chimpanzee activity, with a smaller number of capture events in the Community Land as compared to National

Park ($p = 0.015$, Table 7, Figure 4) and Forest Management Unit ($p = 0.039$, Table 7, Figure 4). There was no significant difference in chimpanzee activity between National Park and Forest Management Unit (Tukey's test, $p = 0.785$). The GLMM showed no influence of land type, mean tree species richness, direct evidence of human presence or indirect evidence of human presence on gorilla's activity at a site, using independent gorilla capture events as the response variable (all $p > 0.05$, Table 8). Density of fruiting trees positively influenced the activity of gorillas at the site level ($p = 0.01$, Table 8, Figure 5).

4. Discussion

The results of the occupancy model showed that chimpanzees occupied a greater proportion of sites each month in the National Park compared to the Forest Management Unit and Community Land. The generalized linear mixed model showed that chimpanzee activity was significantly greater in the National Park and the Forest Management Unit compared to Community Land, with no significant difference between the National Park and Forest Management Units. The apparent incongruity of these two results may be explained by the response variables used in each respective model; the occupancy model uses a binary presence or absence value for occupancy at a site, while the response variable for activity may be considered more nuanced as it considers the number of capture events at a given site. Therefore, although proportion of sites with chimpanzees present every month may have been greater in National Park than the other two land use types, there was significantly greater activity, measured as monthly capture events, at sites within both the National Park and Forest Management Unit compared to Community Land.

Gorillas were not detected at any sites in Community Land during the study period, and there was no significant difference in gorilla activity between the National Park and Forest Management Unit. Taken together, the marked absence of gorillas from the Community Land and the significantly greater activity of chimpanzees in the National Park and Forest Management Unit compared with Community Land confirms our prediction 1, that areas with highest human activity may provide less suitable habitat for chimpanzees and gorillas. This matches with previous literature showing that levels of human activity are important predictors in habitat suitability for chimpanzees and gorillas (Bersacola et al., 2021; Ginath Yuh et al., 2020; Matthews and Matthews, 2004, Strindberg et al., 2018). For example, a study in Lobéké National Park, South-East Cameroon showed hunting pressure was predicted to contribute 21% and 23% for gorilla and chimpanzee habitat suitability, respectively (Ginath Yuh et al., 2020). Although high levels of human activity may not directly lead to hunting pressure, the construction and maintenance of roads and trails may indirectly facilitate greater access for any human activities in the area, including hunting. Notably, gorillas were present at fewer sites than chimpanzees, and overall detections of gorillas were less than half that of chimpanzees. Although the population sizes for both great ape species are similar across the CMTOU (Nzoo-Dongmo et al., 2015), the probability of capturing either species using camera traps would likely be affected by species-specific factors such as foraging behaviour, ranging patterns and social group dynamics. Chimpanzees have been described as being more persistent in searching for ripe fruits (Head et al., 2012, Morgan and Sanz, 2006; Yamagiwa and Basabose, 2014) while gorillas tend to consume more widely available terrestrial vegetation when fruits are scarce (Head et al., 2011; Doran-Sheehy et al., 2009; Yamagiwa and Basabose, 2014). As such, if chimpanzees are ranging to forage over greater distances than gorillas, they are more likely to be present at a greater number of camera sites during

the study period. Moreover, the fission-fusion social grouping dynamic of chimpanzees (Yamagiwa and Basabose, 2014) versus the generally more stable gorilla social groups (Bermejo, 2004; Morrison et al., 2020) may result in greater dispersion of individual chimpanzees within the study area and thus lead to detections at a greater number of camera sites. Therefore, interpretation of differences in species occupancy across the CMTOU should be considered under this context. However, detection probability (p) estimated by the occupancy model was found to be very similar for both species (0.276 and 0.297 for chimpanzee and gorilla, respectively) providing the opportunity to model occupancy of these species together while avoiding the possibility of disparities in detection leading to bias in the results.

Although gorillas and chimpanzees co-occurred at certain sites when independent detections were pooled over the entire study period (Table 1), the multi-species occupancy model failed to detect a significant correlation between chimpanzees and gorilla occupancy of the same sites during the same month (Table 5, $p = 0.821$). The probability of either species occupying a site during a given month remained stable under the conditional presence or absence of the other species, suggesting there is neither a positive nor negative interaction between the species. There was also no significant occupancy interaction between the species when fruit availability was modeled as a covariate (Table 6, $p = 0.509$), thus refuting prediction 2. Although co-feeding and direct interspecies interaction has been observed (Southern et al., 2021; Walsh et al., 2007), our study does not show a significant proportion of sites were occupied by both species during the same month. This supports the current understanding that heterogenous distribution of fruit availability and interspecific differences in preferred fruits facilitates co-existence of gorillas and chimpanzees, allowing them to partition their access to resources spatially and temporally (Tédonzong et al., 2019; Yamagiwa and Basabose, 2014). It may be of interest to compare these

results with other populations of sympatric apes living in habitats with varying degrees of suitable habitat and fruit resources available for both species.

The activity of chimpanzees at the site level was not influenced by fruit availability or mean species richness, failing to support prediction 3 for this species. The failure of our results to show fruit availability influencing activity of chimpanzees may indicate that chimpanzee foraging resources are dispersed across the landscape and therefore activity was not significantly different between various sites with differing levels of fruit availability. Moreover, our index of fruit availability was measured across the entire transect (2.5 ha) while our activity estimate was based off data from a single camera location within the transect. Therefore, it is possible that chimpanzees present within a given transect were simply not detected by our camera trap. It is also worth noting that our cameras were set at a height of 80-150 cm, and therefore may not have detected chimpanzees foraging for fruits higher up in the canopy. Direct human activity at the site level did not influence the activity of chimpanzees, matching with previous findings that there is no spatial partitioning between humans and chimpanzees at the site level (Bersacola et al., 2021). Indirect human signs, such as evidence of hunting along the transect, did not significantly affect chimpanzee activity. However, this finding should be interpreted with caution as we excluded all sites with no chimpanzee activity from the analysis, and therefore some of the sites with the highest levels of indirect signs of human activity may not have been considered.

Gorilla activity at the site level was positively and significantly influenced by fruit availability, partly supporting prediction 3 for this species, and highlighting the importance of fruit as an important food resource for lowland gorillas (Head et al., 2011; Head et al., 2012; Tédonzong et al., 2019; Yamagiwa and Basabose, 2014). Mean species richness did not have a significant effect on gorilla activity, suggesting that availability of ripe fruits is a more important predictor of

activity than the richness of fruiting tree species, and that gorillas shift their habitat use with the seasonal availability of ripe fruits (Doran-Sheehy et al., 2009; Oelze et al., 2014; Tédonzong et al., 2019). The home ranges of gorillas often overlap with one or more gorilla groups (Doran-Sheehy et al., 2009; Morrison et al., 2020), which could result in detections of gorillas from multiple groups at sites with high fruit availability. As chimpanzees exhibit high levels of territoriality (Boesch and Boesch-Achermann 2000; Lemoine et al., 2020), activity at a site may be limited to one group, and therefore impact the overall number of chimpanzee detections and the reported influence of fruit availability on activity when comparing the two species.

Indirect signs of human presence did not influence gorilla activity at the site level, although this finding should be interpreted with caution, as the sites where no gorillas were present were excluded from the analysis. This led to the removal of all sites in Community Land, which have the highest level of human disturbance. Consequently, the total absence of gorillas from these zones of high human activity could be interpreted as revealing an effect of human disturbance on gorilla activity, comparable with other findings (Morgan et al., 2018; Remis, 2000). Direct signs of humans at a site, evidenced from the camera trap data, also had no effect on gorilla activity. These results may suggest that, like chimpanzees, no spatial partitioning between humans and gorillas occur at the site level. Alternatively, human presence at a site never occurred simultaneously with gorilla presence, therefore the presence of humans at the site may not prevent gorillas from using the area at a different time. There is also an ongoing gorilla habituation project in the southwest region of the National Park, where many of the gorilla detections occurred. Therefore, it is worth considering that some of these gorillas have become accustomed to certain levels of human presence within their preferred habitats.

Importantly, no detailed information has been published on the home ranges of gorilla and chimpanzee groups in the area, therefore it is unknown whether the locations of any of the camera sites coincided with known territories of either species. To date, research on site-level spatial overlap between sympatric apes has involved studies on habituated or semi-habituated groups (Southern et al., 2021, Walsh et al., 2007), providing authors with a better understanding of interspecies range overlap than was available for our current study.

The continued preservation of gorillas and chimpanzees (Figure 6) relies on a concerted effort to effectively manage protection of their habitats, facilitated by accurate knowledge of their current distribution, resource use, and reactions to habitat disturbances (Forje et al., 2021; IUCN, 2014; Maisels et al., 2016; Maisels et al., 2018; Strindberg et al., 2018). The development of eco-tourism has also been suggested to be an ethical and sustainable way to protect habitats without disadvantaging local communities (Borrini-Feyerabend et al., 2004; Forje et al., 2021), and relies equally on knowledge of population distribution and activity. Here, we show the occupancy of the two ape species across the different regions of the CMTOU and highlight both the importance of the National Park and Forest Management Unit as suitable habitat for gorillas and chimpanzees, and the importance of ripe fruits in the diets of lowland gorillas. The results show a general avoidance of areas of high-level human activity by both species, although among the sites that were frequented by chimpanzees and gorillas, human presence did not significantly affect activity levels. This in part supports previous findings that chimpanzees may balance foraging trade-offs within landscapes shared with humans (Bersacola et al., 2021). Taken together, this information provides insight on gorilla and chimpanzee occupancy and activity patterns across the CMTOU which may be beneficial for informing future long-term research, conservation and responsible eco-tourism opportunities in the area.

5. Tables and Figures

Table 1. Independent captures of chimpanzee and gorilla across all three land types. National Park (NP), Community Land (CL) and Forest Management Unit (FMU).

Land type	Site name	No. of camera days	No. of independent chimpanzee captures	No. of independent gorilla captures
CL	CL B	172	0	0
CL	CL Biba	320	3	0
CL	CL Doum	347	1	0
CL	CL Nkoadjap	55	0	0
Total CL		894	4	0
FMU	FMU Essokie	297	1	3
FMU	FMU Kribi	376	0	0
FMU	FMU Limite Parc	229	17	15
FMU	FMU Mvini	336	2	0
FMU	FMU Nkoelon	320	15	2
FMU	FMU Route Dipikar	287	0	2
Total FMU		1845	35	38
NP	NP A	99	0	0
NP	NP B	193	7	1
NP	NP Bauge	365	44	14
NP	NP C	83	3	0
NP	NP Camp C	83	1	0
NP	NP Dipikar E	302	8	0
NP	NP Dipikar Eb	304	5	1
Total NP		1429	68	16

Table 2. Estimated detection probabilities for chimpanzee and gorilla from single-species occupancy models.

Detection Probability (p)				
Model: $\psi(\cdot) p(\cdot)$	Predicted	SE	lower	upper
<i>Chimpanzee</i>	0.276	0.046	0.195	0.375
<i>Gorilla</i>	0.297	0.085	0.161	0.484

Table 3. Summary of single-species occupancy models showing predicted proportion of sites occupied by chimpanzee (a) and gorilla (b) over 12 months in each land type; National Park (NP), Community Land (CL) and Forest Management Unit (FMU).

Predicted Occupancy by Land Type (ψ)				
Model: $\psi(\text{land type}) p(\cdot)$	Predicted	SE	lower	upper
<i>(a) Chimpanzee</i>				
NP	0.792	0.125	0.463	0.944
CL	0.131	0.073	0.041	0.347
FMU	0.249	0.076	0.131	0.423
<i>(b) Gorilla</i>				
NP	0.136	0.062	0.053	0.306
FMU	0.167	0.065	0.074	0.334

Table 4. Results of occupancy model across all land types for chimpanzee (a) and gorilla (b). National Park (NP), Community Land (CL) and Forest Management Unit (FMU). Reference level is NP.

Occupancy by Land Type				
Model: $\psi(\text{land_type}) p(\cdot)$				
	Estimate	SE	Z value	p-value
<i>(a) Chimpanzee</i>				
(Intercept)	1.340	0.759	1.770	0.078
land_typeFMU	-2.441	0.784	-3.121	0.002
land_typeCL	-3.230	0.940	-3.442	<0.001
<i>(b) Gorilla</i>				
(Intercept)	-1.845	0.525	-3.517	0.001
land_typeFMU	0.239	0.649	0.368	0.713

Table 5. Summary of multi-species occupancy model showing predicted marginal (a) and conditional (b) occupancy probabilities across entire study area. Marginal occupancy predictions for each species are irrespective of the occupancy status of the other species at a site. Conditional occupancy predicts the occupancy of one species conditional to the occupancy status of the other species at a site. Occupancy interaction (c) represents the probability that a site will have both species present during the same month.

Model: $\text{chimp}\psi(.) \text{gorilla}\psi(.) \text{chimp:gorilla}\psi(.) p(.)$				
	Predicted	SE	lower	upper
(a) Marginal Occupancy				
<i>Chimpanzee</i>	0.417	0.065	0.303	0.548
<i>Gorilla</i>	0.117	0.040	0.071	0.227
(b) Conditional Occupancy				
<i>Chimpanzee (+Gorilla)</i>	0.458	0.174	0.140	0.790
<i>Chimpanzee (-Gorilla)</i>	0.412	0.077	0.286	0.556
<i>Gorilla (+Chimpanzee)</i>	0.128	0.082	0.047	0.361
<i>Gorilla (-Chimpanzee)</i>	0.109	0.053	0.038	0.230
(c) Occupancy Interaction (logit scale)				
	Estimate	SE	Z value	p-value
<i>[Chimpanzee:Gorilla]</i>	0.185	0.817	0.227	0.821

Table 6. Summary of multi-species occupancy model using fruiting tree density as an occupancy covariate.

Model: $\text{chimp}\psi(\text{fruit_level}) \text{gorilla}\psi(\text{fruit_level}) \text{chimp:gorilla}\psi(\text{fruit_level}) p(\cdot)$				
	Estimate	SE	Z value	p-value
Occupancy (logit scale)				
<i>Chimpanzee</i>				
(Intercept)	-0.349	0.299	-1.164	0.244
fruit_level	-0.012	0.330	-0.036	0.971
<i>Gorilla</i>				
(Intercept)	-2.072	0.508	-4.079	<0.001
fruit_level	0.130	0.573	0.226	0.821
<i>[Chimpanzee:Gorilla]</i>				
(Intercept)	-0.069	0.864	-0.080	0.937
fruit_level	0.485	0.733	0.661	0.509

Table 7. Coefficient estimates of the results from generalized linear mixed model (GLMM) of chimpanzee capture events (response variable). R^2 (marginal/conditional) = 0.469/0.498, negative binomial family and logit link function, theta estimation = 0.50. National Park (NP), Community Land (CL) and Forest Management Unit (FMU). The reference level for Land Type is CL. Estimates for significant terms (noted in bold) are from the reduced model.

Explanatory variable	Estimate	SE	CI	Z value	p-value
(Intercept)	-6.151	1.192	0.00 – 0.02	-5.160	<0.001
Land type [FMU]	2.707	1.309	1.15 – 195.04	2.068	0.039
Land type [NP]	3.130	1.282	1.85 – 281.89	2.442	0.015
Fruit tree density	0.270	0.252	0.80 – 2.15	1.074	0.283
Mean species richness	0.380	0.274	0.85 – 2.50	1.386	0.166
Indirect human signs	0.265	0.275	0.76 – 2.24	0.963	0.336
Human trapping rate	-1.346	1.309	0.02 – 3.38	-1.029	0.304

Table 8. Coefficient estimates of the results from generalized linear mixed model (GLMM) of gorilla capture events (response variable). R^2 (marginal/conditional) = 0.252/0.252, negative binomial family and logit link function, theta estimation = 0.24. National Park (NP) and Forest Management Unit (FMU). The reference level for Land Type is FMU. Estimates for significant terms (noted in bold) are from the reduced model.

Explanatory variable	Estimate	SE	CI	Z value	p-value
(Intercept)	4.301	0.499	0.00 – 0.02	-8.622	<0.001
Land type [NP]	-0.793	1.282	0.09 – 2.32	2.442	0.342
Fruit tree density	1.0441	0.4035	1.29 – 6.26	2.588	0.010
Mean species richness	-0.587	0.357	0.28 – 1.12	1.386	0.100
Indirect human signs	0.428	0.400	0.70 – 3.36	0.963	0.285
Human trapping rate	0.362	0.447	0.60 – 3.45	0.809	0.418

Figure 1. Campo-Ma'an Technical Operational Unit, Cameroon, showing the main land use types (Forest Management Units, Community Land, National Park and transect lines (along which the camera traps were located).

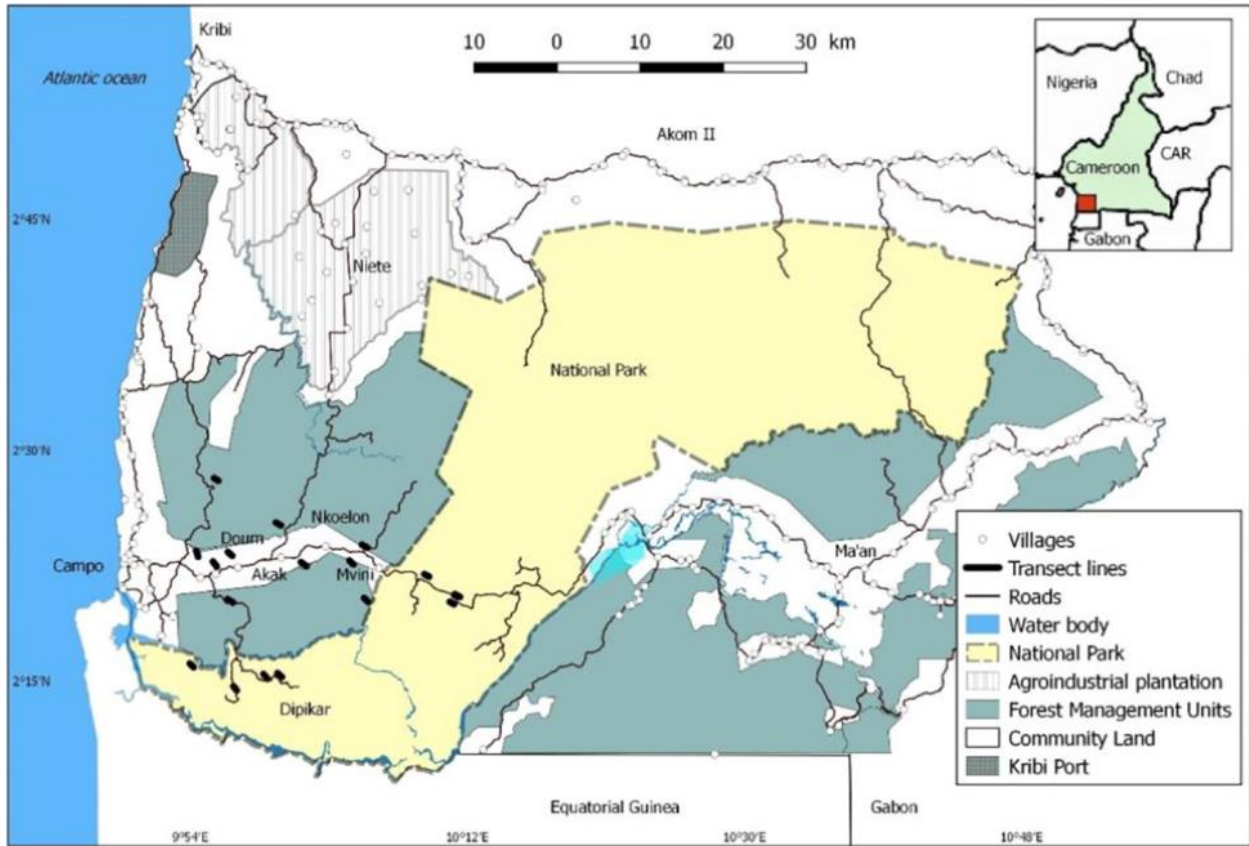


Figure 2. Map of independent captures of chimpanzee across the three land types of CMTOU from June 2019 to May 2020. National Park (NP), Community Land (CL) and Forest Management Unit (FMU).

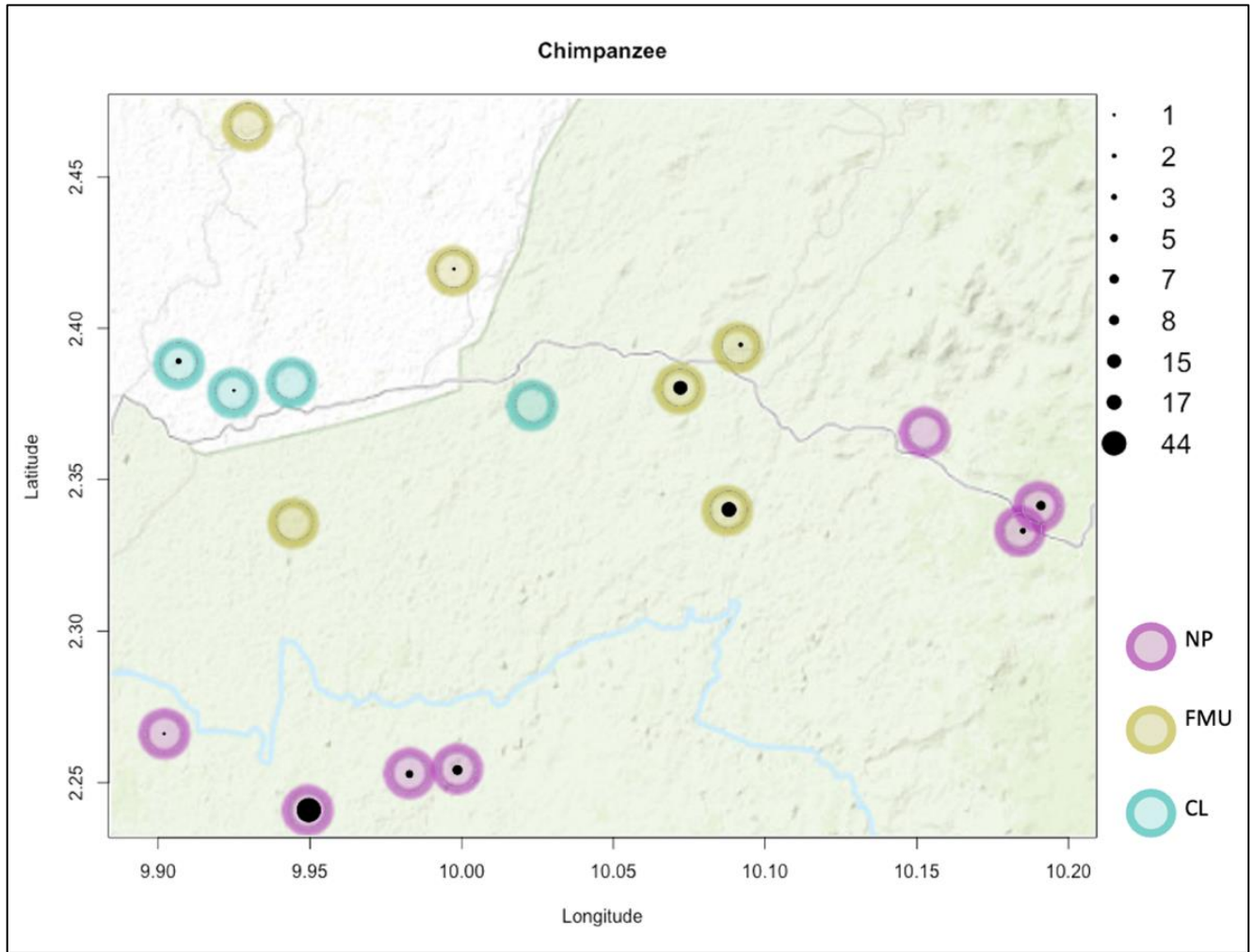


Figure 3. Map of independent captures of gorillas across the three land types of CMTOU from June 2019 to May 2020. National Park (NP), Community Land (CL) and Forest Management Unit (FMU).

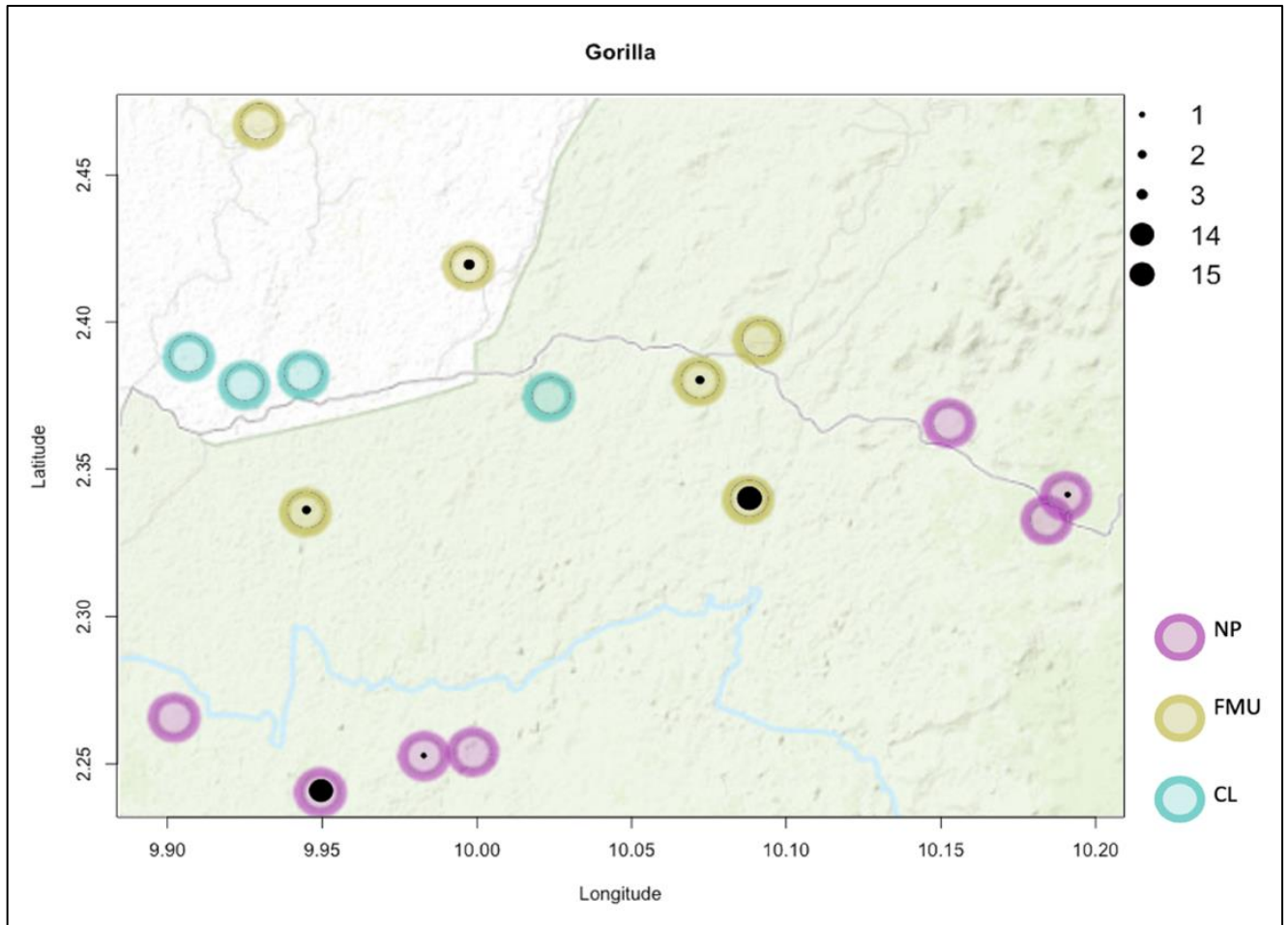


Figure 4. Chimpanzee capture events by land use type. Model estimates are based on generalized linear mixed effect model. Camera station was modeled as the random effect and the contrast method was used to scale the response, hence the negative values in the Y-axis. National Park (NP), Community Land (CL) and Forest Management Unit (FMU).

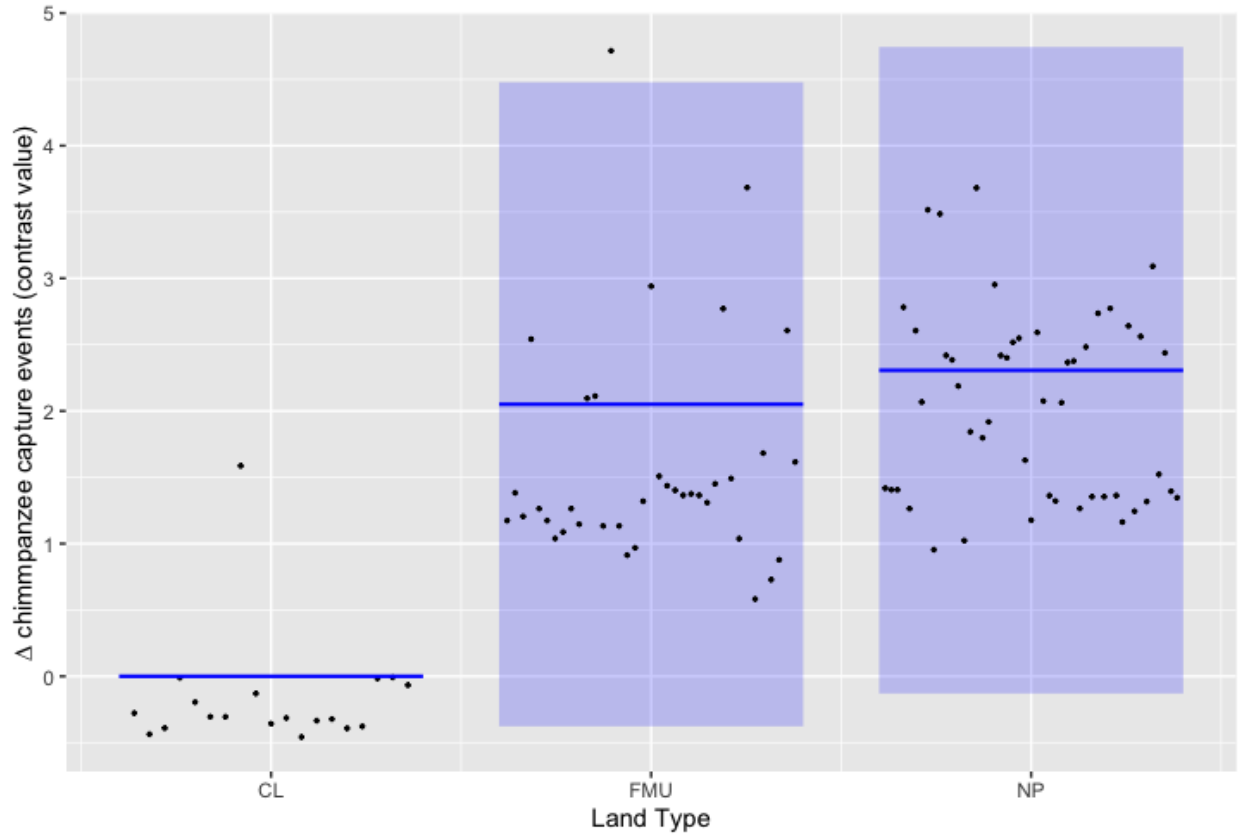


Figure 5. Relationship between gorilla capture events (contrast values of partial residuals) and fruit availability (number of trees bearing ripe fruits/ha). Model estimates are based on generalized additive mixed effect regression model. CT station was modeled as the random effect and the contrast method was used to scale the response, hence the negative values in the Y-axis.

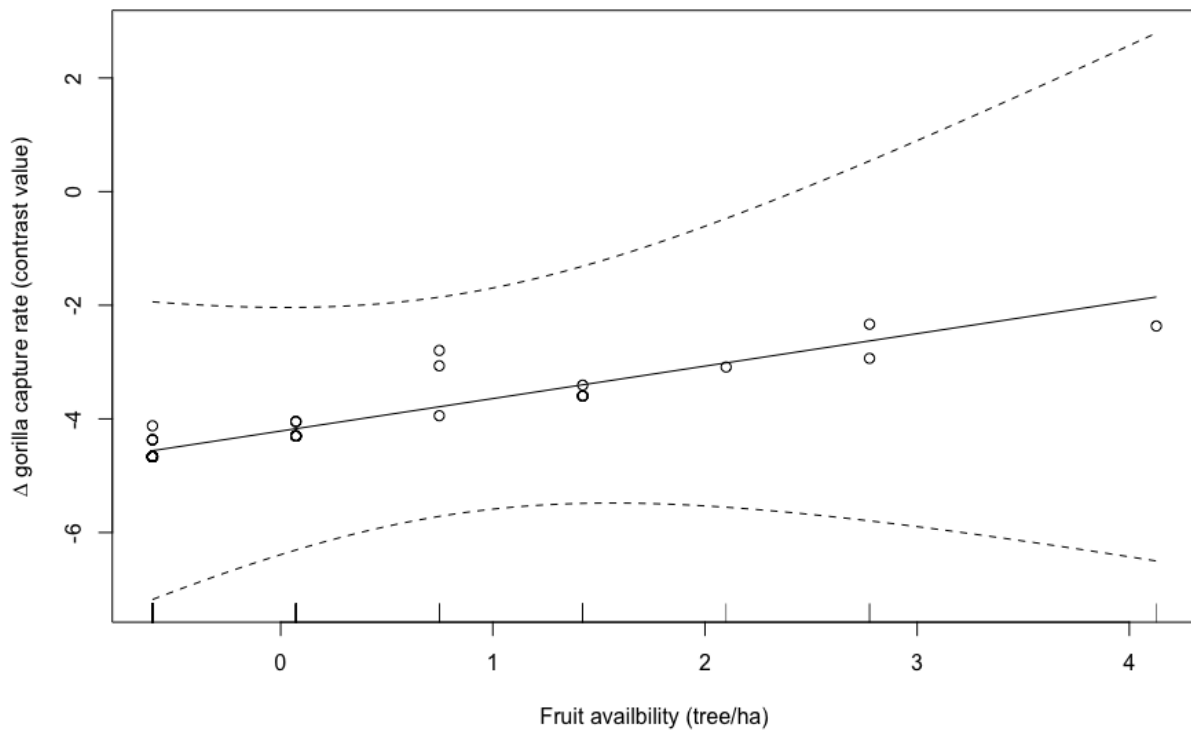


Figure 6. Sample camera trap images of chimpanzees (top) and gorillas (bottom) from the Campo-Ma'an Conservation Area, Cameroon.



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