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Fruit Availability Influences Forest Elephant Habitat Use in a Human Dominated Landscape, Campo-Ma'an, Southern Cameroon

Isaac B. Djoko, PhD[1,2], Robert B. Weladji, PhD[1], Alys Granados, PhD[3], Patrick Paré, MSc[4], and Guillaume Body, PhD[5]

Abstract

Background and Research Aim: African forest elephants (*Loxodonta cyclotis*) are critically endangered yet research on factors influencing their resource use is limited in Central Africa. We assessed the influence of fruit availability, land use types, and anthropogenic activity on forest elephant presence and relative abundance in the southwest part of the Campo-Ma'an Technical Operational Unit (CMTOU) to better understand elephant habitat use in human dominated systems and inform elephant management strategies.

Methods: We used 17 camera trap stations and surveyed 17 line transects to monitor forest elephant presence and relative abundance as a function of fruit availability, tree species richness, and land use types. Our study area spanned a gradient of human disturbance and included a National Park (NP), Forest Management Unit (FMU), and Community Land (CL).

Results: Forest elephants were more likely to occur in areas with increased fruit availability and tree species richness. Also, the likelihood of their presence was higher in CL than in FMU and NP. Elephant relative abundance was negatively affected by human activities such as hunting and logging. The relationship between elephant relative abundance and fruit availability was stronger in CL and NP as compared to the FMU. Elephant relative abundance was higher during the rainy season.

Conclusion: Forest elephant habitat use was positively affected by fruit availability across land use types, and negatively affected by human activities in the southwest part of the CMTOU.

Implications for Conservation: Continued monitoring of elephant responses to food availability in CMTOU is warranted to track changes in elephant habitat use. Knowledge of the distribution of fruiting trees consumed by forest elephants may allow managers to predict hotspots of habitat use, and to therefore develop effective management strategies.

Keywords

camera trap, Central Africa, Cameroon, conservation, elephant, endangered species, mammal

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Introduction

Human disturbance can affect food resources available to forest elephants (*Loxodonta cyclotis*) (Mills et al., 2018; Poulsen et al., 2011). The removal of trees for logging or the creation of roads, for example, may lead to the loss of fruiting trees that are important food resources for elephants (Blake et al., 2008). Although forest elephants are generalist herbivores, they show a preference for fruits (Blake & Inkamba-Nkulu, 2004; Campos-Arceiz & Blake, 2011; Ndi et al., 2022; White et al., 1993) which can provide important minerals and influence their habitat use (Rode et al., 2006; Sach et al., 2019). Human disturbance that influences fruit availability could therefore have important implications for elephant behavior (Bush et al., 2020; White et al., 1993) and can lead to a decrease in elephant body condition (Bush et al., 2020; Sach et al., 2019). For example, because there are fewer fruit trees, people and forest elephants have to share trees more frequently and aggressive interactions may occur (Breuer & Ngama, 2020). Also, human activity near fruiting trees may affect elephant movement and food selection if elephants are displaced from or avoid those areas (Breuer et al., 2016; Puyravaud et al., 2019). Fruit availability may vary seasonally and affect elephants' behavior and movement pattern (Branco et al., 2019; Breuer & Ngama, 2020; Mills et al., 2018; Mmbaga et al., 2017).

The critically endangered forest elephant (*Loxodonta cyclotis*) has declined at an accelerated rate in recent decades (IUCN, 2021). Declines are largely due to habitat loss and illegal hunting (Maisels et al., 2013; Poulsen, Koerner, et al., 2017). Protected areas (PAs) are often created as part of conservation strategies where such activities are prohibited but increasing human presence from various projects such as mining, agricultural expansion, urban development, and logging around PAs can still negatively influence wildlife behavior, including elephants (Breuer et al., 2016; Farfán et al., 2019). Elephants frequently roam outside PAs and may become habituated to human presence to varying degrees (Brittain et al., 2020; Granados et al., 2012). In some cases, their proximity to human settlements may lead to conflicts with people, driven by competition for space and resources (Blanc, 2008; Mariki et al., 2015; Thouless et al., 2016). The consequences of such conflict can be serious, often affecting local livelihoods through crop raiding, or the killing of people and/or elephants (Mariki et al., 2015; Tchamba, 1996). Alternatively, elephants may avoid areas used by humans because they may perceive increased risk of mortality, leading to more cryptic behavior (Breuer et al., 2016; Ihwagi et al., 2015, 2018; Wall et al., 2021).

Although human population density is relatively low (~1 inhabitant/km^2, WWF, 2021), throughout the Congo Basin, the expansion of their activities has been shown to threaten biodiversity (Blake et al., 2008, 2007; Breuer et al., 2016; Poulsen, Koerner, et al., 2017; Thouless et al., 2016; Wall et al., 2021). However, few studies have investigated the consequences of anthropogenic disturbances on forest elephants in Cameroon (see Amin et al., 2020; Brittain et al., 2020; Ole, 2011).

The use of camera traps as a wildlife monitoring tool has increased over the last decade in the Congo Basin (Bruce et al., 2018; Djekda et al., 2020; Farfán et al., 2019). Studies seeking to monitor large bodied mammals have largely used interviews or transects and recce to assess species status and population distribution (Amin et al., 2020; Brittain et al., 2020; Nzooh-Dongmo et al., 2015). However, transects and recces are expensive to carry out in large areas and the effectiveness in detecting elusive species may be limited (Burton et al., 2015; Djekda et al., 2020), while camera traps have been shown to be a cost-effective and reliable method for monitoring wildlife communities (Bruce et al., 2018; Djekda et al., 2020), including forest elephant activity pattern and behavior (Ngama et al., 2016, 2018). Camera traps have been used by researchers to monitor large bodied mammal including forest elephants in the Dja Faunal Reserve, southeast Cameroon (Bruce et al., 2018; Farfán et al., 2019), also part of Congo Basin, like Campo-Ma'an National Park. Understanding how forest elephant use habitat in Campo-Ma'an, particularly in areas where camera trap surveys have not been done and where human wildlife conflict is growing, can inform management decisions to set up strategies for coexistence.

Here, we quantified the influence of fruit availability, land use types, and human activity on forest elephants in Campo-Ma'an Technical Operational Unit (CMTOU), Cameroon. Our study area spanned a gradient in human accessibility and disturbance (a National Park (NP), Forest Management Unit (FMU), and Community Land (CL)). The FMU is a forest concession run by a certified timber company for wood extraction primarily but where some wildlife conservation measures were implemented, a requirement for maintaining their certification. These conservation measures included anti-poaching activities carried out by the company and park rangers. Specifically, we explored whether the forest elephant habitat use varied between land use types in the CMTOU. We expected human activities to negatively affect forest elephants' relative abundance, which should be highest in the park, where human activity is restricted (Supplementary Table S1). Elephant habitat use can be negatively associated with intensive logging which causes forest fragmentation and facilitate access to poachers by creating roads in previously inaccessible areas of the forest (Amin et al., 2020; Blake et al., 2008; Breuer et al., 2016). Further, elephants may avoid areas of high poaching intensity (Breuer & Ngama, 2020) and may increase their walking speed when passing through such areas (Ihwagi et al., 2018). Human–elephant conflict may result in elephant range contraction or range shift if they are extirpated from areas where conflict occurs (Breuer et al., 2016; Breuer & Ngama, 2020; Wall et al., 2021).

Elephants make movement choices based on nutritional needs (Sach et al., 2019). Accordingly, larger fruits may better attract forest elephants as they contain more nutrients. However, whether forest elephant habitat use is influenced by fruit size needs to be explored further. Because forest elephants feed on fruits (Blake & Inkamba-Nkulu, 2004; Ndi et al., 2022) and their movement is driven by their nutritional needs, habitat use could be influenced by fruit size (Sach et al., 2019). Indeed, the uneven distribution of fruit trees as well as the difference in nutritional values may favor the choice for large fruits. Therefore, we determined fruit size from existing literature in order to assess whether they affected forest elephant presence and abundance. Finally, we tested the influence of tree species richness and fruit availability on elephant presence and relative abundance, expecting a positive relationship because greater species richness may offer more feeding options (Mills et al., 2018; Neupane et al., 2019). Moreover, high tree species richness in a limited space may provide elephants with a greater diversity of minerals they require for their metabolism (Rode et al., 2006; Sach et al., 2019).

Methods

Study Area

This study took place in the southwest part (~75 000 ha) of the CMTOU (770 000 ha), Cameroon (2°10' N/9°50' E and 2°25' N/10°48' E, Figure 1). The CMTOU is a mosaic of three land use types, including Campo Ma'an National Park (CMNP, 264 000 ha), a Forest Management Unit (FMU) where timber extraction has been ongoing since 2000, and a multipurpose Community Land area (CL) where farming, use rights for domestic purposes (hunting, fishing, artisanal logging of wood, and gathering), housing, and infrastructures are permitted (MINFOF, 2014). CMNP is a state-managed strict protected area where access for purposes other than research and tourism are prohibited, except for the *Bagyeli* (an indigenous community) in well-defined areas to allow the perpetuation of their cultural heritage. Within the past two decades, the FMU (n°09025) was selectively logged for commercial tree species, estimated at about 0.23–0.28 tree/ha (Tchiofo-Lontsi et al., 2019) (e.g., *Lophira alata and Erythrophleum ivorense*) before being partially declassified in 2019 for conversion to palm oil plantation. Existing roads and bridges were abandoned in the FMU because logging companies were no longer active. Most are now used by Camvert-SA, an industrial palm oil plantation company covering 60 000 ha of the declassified part of the FMU.

The CMTOU is rich in biodiversity with many threatened species (e.g., leopard *Panthera pardus*, western lowland gorilla *Gorilla gorilla*, forest elephant, chimpanzee *Pan troglodytes*, giant pangolin *Smutsia gigantea*, and African forest buffalo *Syncerus caffer nanus*). This area is also subject to wood logging, dam and port constructions, and agro-industrial plantations. Small scale farms also occur in and around the conservation area, making the CMTOU a hotspot of human-elephant conflict due to the high concentration of forest elephants in some parts of the CMTOU (MINFOF, 2014; Nzooh-Dongmo et al., 2015).

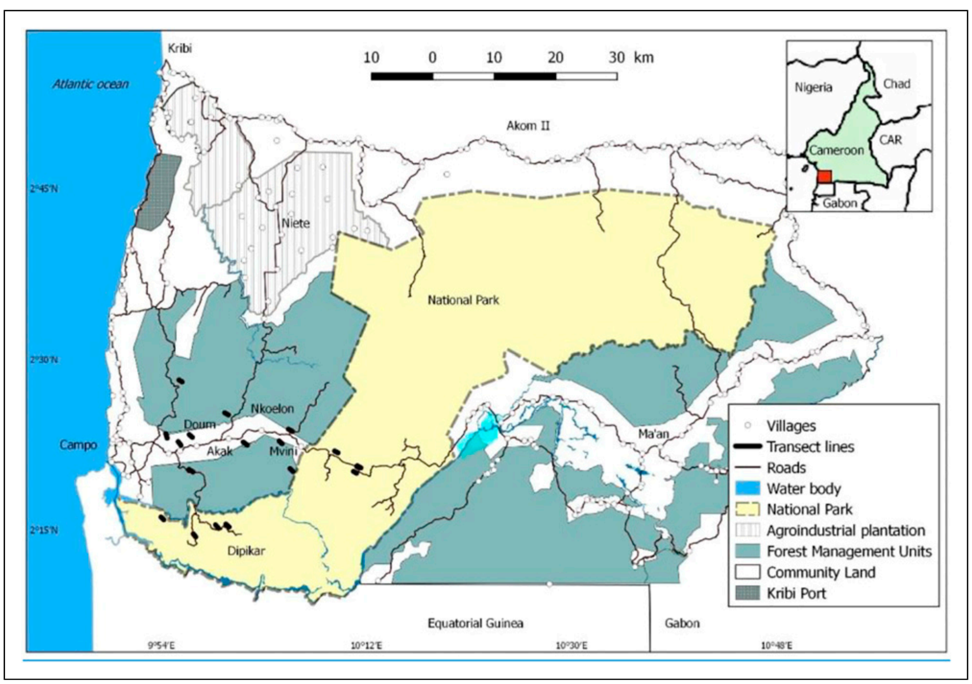

Figure 1. Campo-Ma'an Technical Operational Unit, Cameroon, displaying the main land use types (Forest Management Units, Community Land, National Park, and Agroindustry) as well as the transect lines (along which the camera traps were located).

There are 2297 vascular plant species here, of which 29 species are endemic to CMTOU (Tchouto, 2004). There are two dry seasons (June to August and December to February) and two rainy seasons (March to May and August to November). Mean annual precipitation ranges between 1700 and 2800 mm, while the altitude goes from 0–500 in the west lowland to 400–1100 m toward east side. Although the area has been described as water rich with many rivers and swamps (MINFOF, 2014; Tchouto, 2004), some of them may be seasonal, with elephants relying on these temporary water sources at various times of the year (Beirne et al., 2020; Mills et al., 2018). In the CMNP, four forest clearings (bais) and a salt lick, reported as places that forest elephants like to visit (Blake & Inkamba-Nkulu, 2004; Breuer & Ngama, 2020), have been monitored for ecotourism in CMNP (Forje et al., 2020; MINFOF, 2014).

Data Collection

Camera Trapping. We deployed 19 Bushnell camera traps (Trophy Cam HD Essential E3 Trail Brown 16 MP 119837C Model, Bushnell, Kansas) in southwestern Campo-Ma'an. Deployment was stratified between land use types (6 cameras stations in the FMU, 4 in the CL, and 7 in the NP). Four stations were located on inactive timber skidding trails originally created for wood logging about 22 years ago, five were on paths created and maintained by forest elephants, and eight were under or near fruiting trees. Camera placement was chosen based on expert knowledge of a team of field assistants (hunters and wood logging workers) with the goal of maximizing detection of forest elephants when present at camera trap location. Distance between adjacent camera traps ranged between 1.2 km and 8.8 km. Camera traps were active 24 hours/day between June 2019 and May 2020. Because two sites hosted two camera traps each, we dropped data from two camera traps and report only data from 17 camera traps stations and corresponding transects (transect methods detailed below). Camera stations were visited approximately every 30 days to replace SD cards and batteries. Camera traps were not rotated within strata and seven camera traps had been stolen, three of which were replaced. Another camera trap was moved from its initial location because of problems with humidity. Cameras were set at 80–150 cm height, angled horizontal, and approximately 5–15 m away from target features (e.g., roads and fruiting trees). The quiet period (i.e., the trigger delay between consecutive photos) was set to 3 seconds. Camera trap photos were date and time stamped. We used an independence interval of 30 min for species at the same camera trap station (Chakraborty et al., 2021; Deith & Brodie, 2020; O'Brien et al., 2003; Tudge et al., 2022). Photos with multiple individuals of the same species at the same camera trap station on the same time frame was considered a single detection event (Chakraborty et al., 2021).

Line Transects. From each camera trap station, a transect was established (Appendix S1) for a total of 17 transects (each 500 m x 50 m, covering 2.5 ha). Along each line transect, tree species richness (number of species of trees/ha) was surveyed once, and fruit availability was surveyed monthly. Transects were delimited with markers and all woody tree species, whether bearing fruits or not, with diameter at breast height (1.3 m above ground) ≥ 20 cm, were identified. Local, common, and/or scientific names were used to identify specimens to at least the genus level by local botanists. Where specimens could not be identified in the field, they were collected and later identified at the Cameroon National Herbarium.

Fruit availability was measured monthly, as the number of trees bearing ripe fruits (hereafter fruiting trees). In all, 42.5 ha were covered monthly. For most of the tree species, fruiting period lasts about a month (Chapman et al., 1994). In Congo Basin, most trees are tall enough for their fruits to be out of reach to forest elephants. For example, *Saccoglottis gabonensis* may fruit at 45 m height (White, 1994) so forest elephants mostly access the fruits that fall on the ground. The total number of trees with ripe fruits in each line transect during each monthly visit was used to estimate fruit availability (trees/ha) (Chapman et al., 1994). For each line transect, fruit availability was estimated by dividing the total number of trees with ripe fruits counted during each monthly survey by transect area (i.e., 2.5 ha). The average sizes of fruits from identified fruit trees were later obtained from the Plant Resources of Tropical Africa website (https://www.prota4u.org/database/).

Signs of human activity on transects were measured directly and indirectly. Direct signs of human activities were identified as humans from camera trap images and included research team or park staff.

To account for imperfect detection of human activity at camera trap stations (humans present but not detected by the camera trap), indirect signs of human activity were measured from line transects as frequency in which firearm cartridges, traps, signs of machetes cuts on vegetation, evidence of hunting camps, wood skidding trails, and tree stumps resulting from logging were detected each month.

Ethics

Village meetings were organized during which we presented our authorization letter to the village chief and any community member upon request. Human images from camera traps were processed according to ethical guidelines suggested by Sharma et al. (2020). For example, community members were informed about our work and were involved with camera trap location selection and set up. They were also informed that their privacy would be respected and none of their images would be transferred to park staff for prosecution nor would they be published. Field assistants were contacted directly by our research team and were paid daily for their work.

Data Analysis

We were interested in testing the effects of several anthropogenic and habitat covariates on two response variables: 1) elephant presence and 2) elephant relative abundance at each station. Elephant presence was modeled per month as a binary response (presence or absence) at each camera station. Independent detections of elephants were used as an index of elephant abundance, determined as

$$N \times 100/A,$$

where N is the number of independent detection events at a station during a month, and A is the total number of camera trap days (Chakraborty et al., 2021; O'Brien et al., 2003). We also used this equation to determine relative abundance of humans. Camera trap images were processed using Timelapse 2.0 v 2.2.3.5 (Greenberg, 2020). We used indirect signs of human activity to assess the monthly density of human activities in different land use types. Density was calculated as the total number of indirect signs of human activity, divided by transect area (2.5 ha) each month. All types of human activity signs were weighted equally in the analyses.

Analyses were performed separately for elephant presence and for elephant relative abundance. As there are no strong knowledge on the form of the relation between the response variables and our explanatory variables, we allowed non-linear relations to be considered, which we combined with a mixed modeling approach to overcome pseudo replication within sites, by using generalized additive mixed model (GAMM). Accordingly, we tested the effects of anthropogenic variables (direct human activity, indirect human activity, and land use types), habitat covariates (seasonality, fruit availability, tree species richness, distance to nearest water source, and average size of fruits (cm)) on elephant presence, and relative abundance using GAMM. Seasonality was modeled as categorical variable with four levels: rainy season, short rainy season, short dry season, or dry season. We also sought to test for the interacting effects between covariates to better understand whether, for example, elephant responses to fruit availability was influenced by land use types or season (Mills et al., 2018). Camera trap station ID was modeled as a random intercept in each model to account for repeated sampling within individual stations.

We used backward variable selection for both models, by sequentially dropping the single term with the highest non-significant *p*-value from the models and re-fitting, until all terms were significant (https://rdrr.io/cran/mgcv/man/gam.selection.html). Terms present in interaction terms could not be removed until the interaction term was removed (Supplementary Tables S2 & S3).

Continuous covariates were standardized to have a mean of 0 and standard deviation of 1, to facilitate comparison of their effects on elephant presence or relative abundance. The smoothing parameter of the model was set to be k = 4 for all variables. The elephant presence model was run with a logistic link function. Elephant relative abundance was fit using the Tweedie family with log link function. Covariates were tested for multicollinearity using Variance Inflated Factor (VIF) using car package (Fox & Weisberg, 2019). GAMMs were run using MGCV package version 1.8–38 (Wood, 2021) with the maximum likelihood method. When significant differences were found among different levels of a variable, we changed the reference level to be able to compare all pairs. All statistical analyses were performed using R v. 4.0.2 (R Core Team, 2020), with a 95% level of significance.

Results

Our camera trap survey included a total of 4510 camera trap days with elephants being detected on 159 of those days (see Supplementary Table S4). In all, 375 ha were surveyed for fruit availability and for tree species richness in line transects.

Forest Elephant Presence

As compared to Community Land (CL), forest elephant presence was significantly lower in Forest Management Unit (FMU) ($p = 0.037$; Table 1, Figure 2a) and National Park (NP) (p = 0.004; Table 1, Figure 2a), whereas they occurred similarly in FMU and NP (p = 0.088, Figure 2a). Forest elephant presence was positively associated with tree species richness ($p < 0.001$, Table 2, Figure 2b) and distance to the nearest permanent river ($p = 0.004$, Table 2, Figure 2c). There was a significant interaction between fruit availability and land use types ($p < 0.001$, Figure 2d–f). Indeed, elephant presence in FMU was significantly and positively associated to fruit availability ($p = 0.005$, Table 2, Figure 2e), while fruit availability had no effect on elephant presence in CL or NP (all $p > 0.05$, Table 2, Figure 2d, Figure 2f).

Forest Elephant Relative Abundance

Forest elephant abundance was lower in the FMU than in the CL and NP (both $p < 0.001$) but similar between CL and NP ($p = 0.136$, Table 3, Figure 3a). Seasonality influenced forest

Table 1. Coefficient estimates of the results from generalized additive mixed model (GAMM) of elephant presence (response variable). R^2(adj) = 0.223, deviance explained = 25.3%, binomial family and logit link function, maximum likelihood (ML) = 68.485, scale estimation = 1, n = 150. The reference level is CL. Significant coefficient estimates are noted in bold.

Explanatory variable	Estimate	SE	Z value	*p*-value
Intercept	0.500	0.539	0.759	0.448
Land use type FMU	−1.643	0.788	−2.086	**0.037**
Land use type NP	−2.55	0.888	−2.878	**0.004**

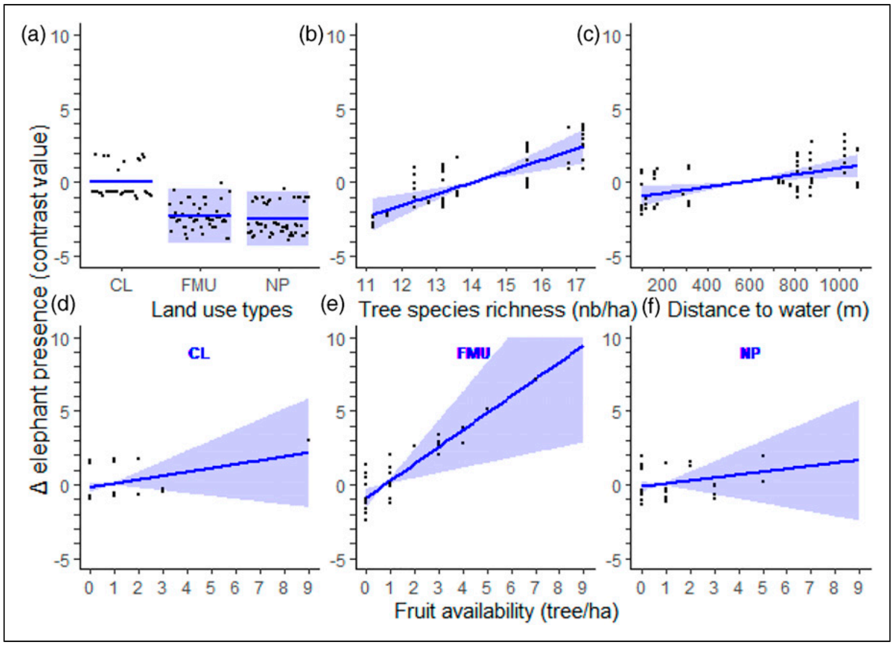

Figure 2. Relationship between forest elephant presence (contrast values of partial residuals) and land use types (a), tree species richness (number of species/ha) (b), distance to the nearest permanent river (m) (c), and the interaction between land use types and fruit availability (tree/ha) (d–f), Model estimates are based on generalized additive mixed effect model regression model. The parametric variable was land use types (CL, FMU, NP) and the non-linear variables were distance to the nearest permanent river (m), tree species richness (tree/ha) and the interaction between land use types and fruit availability (tree/ha). 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.

Table 2. Approximate significance of smooth terms of the results of generalized additive mixed model (GAMM) of elephant presence (response variable). Edf = effective degree of freedom for the model terms, Ref. df = estimated residual degree of freedom. (R^2(adj) = 0.223, deviance explained = 25.3%, binomial family and logit link function, maximum likelihood (ML) = 68.485, *n* = 150. Significant coefficient estimates are noted in bold.

Explanatory variable	χ^2 test	Ref. df	edf	*p*-value
Species richness	16.485	1	1	**< 0.001**
Distance to perennial water	8.419	1	1	**0.004**
Fruit availability: Land use type CL	1.299	1	1	0.254
Fruit availability: Land use type FMU	7.872	1	1	**0.005**
Fruit availability: Land use type NP	0.619	1	1	0.431

Table 3. Coefficient estimates from generalized additive mixed model (GAMM) of elephant relative abundance (response variable). R^2(adj) = 0.468, deviance explained = 54.1%, Tweedie family (power parameter *p* = 1.583) with log link function, maximum likelihood (ML) = 138.61, scale estimation = 2.093, *n* = 45, (see method for model). The reference levels are CL and short dry season. Significant estimates are noted in bold.

Explanatory variable	Estimate	SE	t value	*p*-value
Intercept	3.189	0.485	6.576	**< 0.001**
Land use type FMU	−1.750	0.463	−3.777	**< 0.001**
Land use type NP	−0.548	0.359	−1.528	0.136
Dry season	0.541	0.512	1.057	0.298
Rainy season	1.196	0.427	2.799	**0.008**
Short rainy season	0.730	0.486	1.504	0.142

elephant relative abundance, ($p < 0.001$). Indeed, elephant relative abundance was higher during rainy season than in the short dry season ($p = 0.009$, Table 3, Figure 3b) but was similar for all other seasons (all $p > 0.05$, Figure 3b). Also, elephants were less abundant at camera trap stations where direct human activity was high ($p = 0.017$, Table 4, Figure 3c). There was a significant interaction between fruit availability and season ($p < 0.001$; Table 4, Figures 3d–f) as well as between fruit availability and land use types ($p < 0.001$; Table 4, Figures 3g–j). Elephant relative abundance increased with fruit availability in CL ($p < 0.001$, Table 4, Figure 3d) and NP ($p < 0.001$, Table 4, Figure 3f) but not significantly in FMU ($p = 0.252$, Table 4, Figure 3e). The relationship between fruit availability and elephant relative abundance changed according to seasons (Table 4, Figure 3g–j), with the

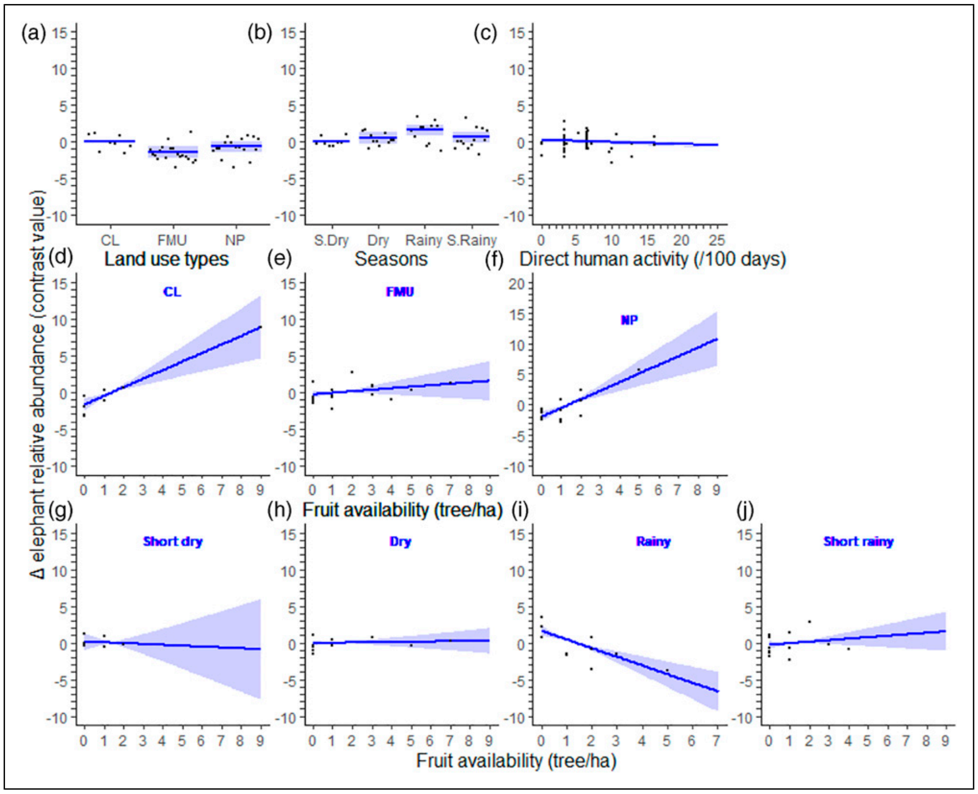

Figure 3. Relationship between forest elephant relative abundance (contrast value of partial residuals) and land use types (a), seasons (b), human activity rate (/100 days) (c), and interactions between fruit availability (tree/ha), and land use types (d–f), fruit availability and seasons (g–j). Model estimates are based on generalized additive mixed model regression model. Parametric terms were land use types (CL, FMU, and NP) and seasons (dry, short rainy, short dry, and rainy) and non-linear terms were human camera trapping rate, the interactions between seasons and fruit availability, and between fruit availability and land use types.

Table 4. Approximate significance of smoothing terms of the results of generalized additive mixed model (GAMM) of elephant relative abundance (response variable). edf = effective degree of freedom for the model terms, Ref. df = estimated residual degree of freedom. (R^2(adj) = 0.468, deviance explained = 54.1%, Tweedie family (power parameter p = 1.583) with log link function, maximum likelihood (ML) = 152.01, scale estimation = 2.093, n = 45, (see method for the model). Significant coefficient estimates are noted in bold.

Smoothing terms	edf	Ref. df	F test	*p*-value
Fruit availability: Short dry season	1.001	1.001	0.500	0.484
Fruit availability: Short rainy season	0.002	0.004	0.045	0.989
Fruit availability: Dry season	1.015	1.030	0.734	0.400
Fruit availability: Rainy season	1.007	1.013	23.036	**< 0.001**
Fruit availability: Land use type CL	1.003	1.005	16.486	**< 0.001**
Fruit availability: Land use type FMU	1.009	1.018	1.327	0.252
Fruit availability: Land use type NP	1.013	1.025	22.114	**< 0.001**
Direct human activity	1.053	1.103	6.361	**0.017**

relationship being negative in the rainy season (p = 0.027, Table 4, Figure 3i).

Discussion

Both elephant presence and relative abundance were positively influenced by fruit availability, suggesting that the pattern of habitat use by forest elephants is driven, in part, by the availability of the fruits they consume. However, elephant local abundance decreased in long rainy season when they are more scattered due to the diversity and the spread of food resources. In our study area, fruits availability is seasonal, and habitat use is influenced by tree species richness which is patchily distributed in all land use types. Direct human activity was negatively related to elephant relative abundance, suggesting that human and forest elephants may avoid each other although they spatially overlap in the southwest part of the CMTOU. Our results highlight the importance of fruits for forest elephants, similar to other findings that fruit availability is an important driver of habitat use by forest elephants (Blake, 2002; Blake & Inkamba-Nkulu, 2004; Bush et al., 2020; Mills et al., 2018; Poulsen, Rosin, et al., 2017; White, 1994).

Contrary to our expectations, the likelihood of elephant presence was higher in the CL than the FMU and the NP, whereas their relative abundance was negatively related to direct human activities dominated by wood logging and hunting. During periods of logging, human disturbances (noise from machinery, felling of trees, creation of tracks, etc.) are particularly high, and forest elephants may avoid overlapping with those areas, especially if human are present. This suggests that, if intensified, certain types of human activity may have a strong influence on elephant habitat use in our study area as has been already reported elsewhere (Poulsen et al., 2011; Puyravaud et al., 2019). This presence of forest elephants in CL may suggest a trade-off between risk of mortality associated with human presence and access to food resources in secondary forest (CL and FMU). Indeed, areas subject to human-induced habitat disturbances, such as cropping lands in the CL and wood logging in FMU provide feeding opportunities for forest elephants (Breuer & Ngama, 2020; Grantham et al., 2020; Poulsen et al., 2011). Elephants frequently occurred in the FMU and in the CL where they feed along the dead-end skidding trails in logging concession and human food crops as also shown in Gabon (Breuer & Ngama, 2020; Mills et al., 2018; Ngama et al., 2018). However, our results are contrary to the study by Tudge et al. (2022) that did not detect forest elephants, reported to be rare (Brittain et al., 2022), in some community forests around Dja Biosphere Reserve in southeast Cameroon where human activity is greater (Amin et al., 2020; Poulsen, Koerner, et al., 2017). In our study area, the risk of elephants being killed by farmers in CL might be reduced because rangers frequently patrol this southwest area of the CMTOU which is where the conservation head office is located. In contrast, the east side of the park is not patrolled to the same extent and may be perceived by elephants as less safe. Previous studies have noted a low density of large mammals in this part of the CMTOU as a result of human disturbances (Eyebe et al., 2012; Matthews & Matthews, 2006). Also, signs of human presence (hunting, machete cut, trail, and gathering) have been on the rise in the FMU and to a lower extent the NP (Nzooh-Dongmo et al., 2015). Indeed, in NP and FMU, images of poachers with hunting tools were frequently detected and the theft of five of our camera traps occurred inside the NP. The removal of our camera traps by some people was presumably to cover up illegal activities. As mentioned earlier, human activities are permitted in the CL (MINFOF, 2014). In southeast Cameroon, Dancer (2019) found that parks are targeted by poachers; the lack of funding usually does not allow for permanent surveillance by rangers compared to FMU. Therefore, the lack of detection of forest elephants in community forests which is part of the CL in the southeast of Cameroon as reported by Tudge et al. (2022), suggest that, compared to our study

Figure 4. Sample camera trap images of forest elephants from the Campo-Ma'an Conservation Area, Cameroon.

area, the pressure on forest elephants might be low enough to allow them to occur in all land use types. Also, forest elephants were detected at least once every month in each land use types. This continued presence suggests that forest elephants are year-round residents, with enough food resources to sustain themselves, contrary to elephants elsewhere for which seasonal migration may be driven by fruit availability (White, 1994). Forest elephant habitat use is tied to fruiting phenology (Blake, 2002; White et al., 1993) and elephant presence was more tightly related to fruiting in FMU where, on average, fruit availability was higher. Fruit availability peaked in the long rainy season. The effect of the variation in fruit availability between long and short rainy seasons on elephant relative abundance was marked between September and October, which is also the period when logging activity peaked and reports of crop raiding by elephants were highest (Ole, 2011).

The distance to nearest permanent water sources correlated positively with the presence of forest elephants (Figure 2c) ranging from 100 to 1090 m. This result contradicts our prediction that distance to perennial rivers had no effect on elephant presence as the area has been reported water rich. However, it corroborates the pattern reported in Gabon where elephants move farther from perennial water sources during wet seasons in response to the reduced limitation of water supply (Mills et al., 2018).

Our findings illustrate the ability of elephants to become habituated to some level of human disturbance, yet also highlight the need to monitor forest elephants in CL and FMU because their presence could lead to conflicts with humans (Breuer & Ngama, 2020; Puyravaud et al., 2019). Repeated crop raiding has been previously documented in this area and led to retaliatory killing of elephants (PNCM, 2017).

Implications for Conservation

Tree species richness and fruit availability affected forest elephant presence and relative abundance. Indeed, forest elephant (Figure 4) presence was associated with fruit availability, some of which fruit trees are present in all land use types (e.g., *Sacoglottis gabonensis*) with spatial and seasonal variations in fruit production. Such variability represents a significant change in fruit availability for forest elephants who rely on them for food. We found forest elephants occurring mostly in CL, especially during harvesting period which corresponds to the period when farmers also reported incidence of crops raiding. During that period, farmers are afraid of encountering forest elephants and may make fewer visits to the forest where they normally go to gather fruits and other non-timber forest products (MINFOF, 2014; Ole, 2011). This indicates that forest elephants might have familiarized themselves to using the multipurpose land in our study area as feeding site.

Even though people are prohibited from entering the NP, we noted frequent human presence, highlighting the need to strengthen the enforcement of laws forbidding their entry. Increased presence of park rangers in NP and FMU will be critical for the persistence of forest elephants in the study area as this can help to reduce the illegal killing of wildlife in the area. Besides increased patrolling, there is also a need to simultaneously increase engagement with local people and developing income-generating activities (e.g., beekeeping and chili farming) for them, other than hunting, and to create mechanisms that allow them to benefit from the park. For example, law enforcement can be accompanied with a push-pull like strategy, typically used to control unwanted animal in agricultural lands (Cook et al., 2017), which over time, create attractive feeding conditions for forest elephants in the NP and FMU where they could be more secure (Neupane et al., 2017). This push-pull strategy may consist of planting fruiting trees known to be preferred by elephants in order to favor their movement in the NP and FMU, away from edges (pulling strategy), while progressively cutting some fruiting trees (not those commonly consumed by human) in or close to CL around farms following an approved and well-tested method. A similar approach has been proposed to mitigate human–elephant conflict in Nepal (Neupane et al., 2017).

Our study also highlights the value of using camera traps for monitoring wildlife and the need to establish long-term research in the whole CMTOU. Palm oil plantations are predicted to overtake logging as one of the main forms of landscape disturbance in the study area. Therefore, predicting the potential impacts of large scale agro-industrial farms on forest elephants is crucial for the development of effective management and conservation strategies.

Supplemental Material

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Data Availability Statement

The data that supports the findings of this study will be made available upon request.

Permissions

We conducted this study using permissions from (1) the Animal Ethics and Care certificate provided by Concordia University (Protocol number 30003983), (2) the authorization n°3212/L/MINFOF/SETAT/SG/DAG/SDPSP of June 8th, 2019, and (3) the research protocol reviewed and approved by the Ministry of Forestry and Wildlife of Cameroon through the Campo-Ma'an National Park Conservator prior to carrying out the experiment.

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Supplemental Material

Supplemental material for this article is available online.

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