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Forest elephants modulate their behaviour to adapt to sounds of danger

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The African forest elephant (*Loxodonta cyclotis*) plays a critical role in upholding the Congo Basin's structure and function, a vital area that supports global carbon sequestration. However, between 1990 and 2021, the species' numbers declined by 86%, mainly because of ivory hunting. Owing to their elusive nature in the region's dense rainforests, their responses to human disturbances, such as gun hunting, are not well understood, though the limited studies that have been completed suggest that forest elephants may respond by altering their abundance, distribution and nocturnal activity. Using passive acoustic monitoring (PAM) in and around Nouabalé-Ndoki National Park, Republic of Congo, we assess how gun hunting impacts forest elephant occupancy and night-time vocal activity. Findings reveal that elephant occupancy drops from 0.54 to 0.52 following a gunfire event, a change sustained over 8 days. Additionally, increased gunshots led to a significant rise in the proportion of night-time vocal activity. These behavioural changes can affect forest elephant foraging and reproductive success and their interactions with vegetation, impacting forest growth and function. This study highlights the need for effective conservation strategies to protect the species and their habitats and demonstrates PAMs effectiveness in studying cryptic species in our world's dense, highly biodiverse and life-sustaining tropical forests.

This article is part of the theme issue 'Acoustic monitoring for tropical ecology and conservation'.

1. Introduction

Tropical forests are the richest ecosystems on Earth [1–3], home to about two-thirds of all species [4]. However, they face unprecedented threats from deforestation, infrastructure development, resource extraction, agriculture, overconsumption, population growth and climate change [2,5]. These disturbances significantly impact the forests and the species within them, including invertebrates, reptiles, amphibians, mammals and birds [6]. Effective conservation now critically depends on monitoring wildlife in these areas [7], a challenging task owing to the dense vegetation and cryptic nature of many species that reside in these forests.

Passive acoustic monitoring (PAM) has recently gained recognition as an effective method for monitoring wildlife [8] and collecting and interpreting information on species' diversity, abundance, movement and responses to anthropogenic disturbance [9–13]. PAM is an especially useful monitoring tool as it may considerably expand the temporal and spatial scales at which data can be efficiently collected [14], especially in traditionally inaccessible and remote locations, such as tropical forests, where rare, elusive or cryptic species reside [11,15].

The application of PAM to the study of African forest elephants (*Loxodonta cyclotis*), a cryptic species residing in the Congo Basin, serves as a key example of its benefits for assessing species' communication, activity, behaviour and responses to anthropogenic disturbance [11,15–22]. This critically endangered species has experienced a population decline of more than 80% in the past 93 years [23] owing to habitat destruction, climate change and ivory poaching. Between 2002 and 2011, they lost 30% of their range and 62% of their population, driven by expanding infrastructure, poor governance and increased hunting intensity [24]. Reductions in populations of this keystone species not only have ramifications for the species' existence but for the structure and function of the Congo Basin, the world's second-largest tropical forest that crucially contributes to global carbon sequestration [25]. As architects and mega-gardeners of the rainforest, forest elephants significantly contribute to maintaining the health and diversity of these ecosystems [26].

As architects, forest elephants create natural forest clearings, or 'bais', using their tusks and brute strength to access underground mineral water, benefiting various other species [27–29]. Their paths through the forest, formed by repeatedly stomping down vegetation, act as firebreaks [30] and create transnational networks used by Indigenous communities in Central Africa for travel and resource gathering [31]. As mega-gardeners, forest elephants disperse seeds through their dung over vast areas; they are capable of moving over 2800 km annually throughout their average home range of about 700 km^2 [32]. Their activity crucially promotes the growth of high wood density species [33], so much so that their extinction could decrease carbon stocks by 7%, equivalent to a $43 billion loss in carbon storage services [34]. This exposes the very critical roles that forest elephants play in maintaining diverse, high-carbon tropical forests [26,34].

Poaching severely impacts forest elephant numbers and their ecosystem services, but understanding its effects on their behaviour and life histories is challenging owing to their dense rainforest habitat. Insights from studies on forest elephants' close relative, the African savannah elephant (*Loxodonta africana),* reveal that poaching results in elephants hearing gunshots, encountering poachers and witnessing deaths, prompting them to remain in undisturbed areas. This results in food competition [35], increased rates in aggressive interactions and consequential social and reproductive disruptions [36] and genetic isolation, increasing extinction risks [37]. Elephants exposed to poaching may become more aggressive towards humans, escalating human–elephant conflict [38]. Poaching also skews sex ratios, reduces survivorship and targets older elephants, disrupting social and ecological knowledge [39,40]. The impacts that poaching may have on elephants are varied, meaning that the species may employ diverse temporal, spatial and behavioural strategies to minimize human-induced mortality risk. Savannah elephants respond by increasing flight behaviour, shifting to night-time activity and reducing movement in risky areas [35,41–46].

Research shows that forest elephants respond to human disturbances similarly to savannah elephants. They tend to increase their densities with distance from human activity [47–49] and actively avoid human settlements and roads, with these features directing their distribution more than ecological factors such as the presence of wetlands and fruit [50]. In areas with higher human disturbance, forest elephants move less, have smaller home ranges, are less active during the day and exhibit fewer exploratory movements [51]. Previous research has also shown that forest elephants will avoid the site of a poached elephant carcass for 8 days [52] and increase their nocturnal activity in response to oil exploration [15].

Most studies on forest elephant distribution have used dung sampling methods, revealing that elephants avoid areas with high human activity [47,48,50,53–55]. However, this method is spatially and temporally constrained, often conducted along forest transects, limiting the exploration of forest elephant response at larger spatial scales. Estimating elephant density from dung involves calculating decay rates [56], which vary by habitat type, decomposer abundance and diversity, fruit content and microclimate [57–59], making it complex and site-specific [60,61]. Additionally, dung sampling is less effective for monitoring short-term behavioural changes, such as increased nocturnal activity, because of its costs and required human effort.

Given that existing population monitoring methods, such as dung sampling, have temporal and spatial constraints, there is growing momentum to apply PAM to studying forest elephant responses to anthropogenic disturbance. Using PAM, researchers can collect acoustic data that not only contain information on elephant vocalizations but also signals representing human activity such as gunshots. When applied across large spatial and temporal scales, PAM can provide valuable insight into the broad patterns of elephant vocalizations and gunshot occurrence. However, this data may also be used to explore elephant response to disturbances such as gunshots at finer scales. For example, a study conducted by Swider *et al.* [19] used PAM to examine forest elephant vocal activity throughout the 24 h period following gun hunting events and found that for the first 5 h following the event, vocal activity increased above the control state level, but from hours 6–24, vocal activity dropped below this level. While studies such as this have provided conservation practitioners with valuable insight into forest elephants' vocal response to human activity, knowledge gaps still remain. Primarily, following up on the results of Swider *et al.* [19], it is unknown whether observed changes in numbers of detected elephant vocalizations reflect changes in vocal activity or changes in elephants' use of the landscape (e.g. movement in and out of the area). It is also unclear how long it takes for forest elephant vocal activity/landscape use to return to the control state level, or whether this same population's activity is becoming increasingly more nocturnal in response to gun hunting in the area, as has been demonstrated in other populations responding to human activity [15].

This study aims to understand the impact of hunting on forest elephants in and around Nouabalé-Ndoki National Park, Republic of Congo, by examining their responses at two different scales. Using PAM, we first assessed changes in forest elephant occupancy over 8 days following gun hunting events compared to control events, hypothesizing that gunfire would affect occurrence probability differently across days. A period of 8 days was chosen based on the Stephan *et al.* [52] study conducted in Nouabalé-Ndoki National Park, which found that it took forest elephants 8 days to return to the site of a poached elephant carcass. Additionally, we investigated whether the proportion of night-time calling activity changes in response to gun hunting and examined the influence of habitat, season, protection status and distance to the nearest mainstem river. Based on previous research conducted on both savannah and forest elephants, we predicted that increased gunfire would correlate with a higher proportion of night-time calling activity [42,46]. We also expected that open forest habitats, characterized by sparse canopy, greater light penetration into the understory and increased visibility, would be linked to a greater proportion of night-time calling activity [17]. Additionally, we hypothesized that proximity to rivers would decrease the proportion of night-time activity because of higher hunting frequency [62], while unprotected areas would exhibit a higher proportion of night-time activity [41–44,63]. Lastly, we predicted that the proportion of night-time calling would increase during the wet season owing to the species' reduced hearing range in rainfall.

2. Methods

(a) Study area

The Sangha Trinational Protected Area is composed of four national parks across three Central African countries including the Dzanga-Sangha and Dzanga-Ndoki National Parks in the Central African Republic, Lobéké National Park in Cameroon and Nouabalé-Ndoki National Park in the Republic of Congo. Nouabalé-Ndoki National Park sits at the core of the Ndoki Forest, which is found between 1.5° to 3° N and 16° to 17° E and is mainly composed of monodominant *Gilbertiodendron dewevrei* forest, mixed species forest on *terra firma* and swampy forest [64–66]. The forest experiences a minimum mean monthly temperature of 21.1°C and a maximum of 26.6°C and an average annual rainfall of 1694 mm [66].

(b) Acoustic data collection and processing

Nouabalé-Ndoki National Park offers a unique opportunity to explore forest elephant activity owing to the presence of a landscape-scale acoustic grid managed by the Elephant Listening Project and the Wildlife Conservation Society Congo Program. Acoustic data were collected from a grid of 50 SWIFT acoustic recorders, designed and manufactured by the K. Lisa Yang Center for Conservation Bioacoustics, which were deployed within and around the park in October 2017 (figure 1). Each acoustic recorder was randomly placed within each of the systematic 25 km^2 grid cells stratified across the landscape of the study area, which ultimately covers an area of 1250 km^2. Each unit was suspended approximately 7–10 m high on an appropriate tree branch and was left to record continuously for 3–4 months. At the end of this period, the unit was revisited, the SD card and batteries were replaced for the next recording period and the data were downloaded. The sound data collected from the recorders were stored on 256 GB SD cards as 16-bit WAV files using an 8 kHz sampling rate. The microphones for SWIFT recorders are omnidirectional and can detect rumbles within 0.5-0.6 km of the recorder [17] and gunshots within 2.5 km of the recorder (A. Verahrami, unpublished data from 2021).

To identify elephant and gunshot signals in the sound recordings, we used an elephant rumble detection algorithm [67] and gunshot detection algorithm [11]. For the purposes of this study, only rumble detections that exceeded a likelihood threshold of 0.4 and gunshot detections above 0.53 were tagged and then manually reviewed using RAVEN PRO [68] to confirm the classification.

(c) Exploring broad temporal patterns of forest elephant vocal activity and hunting activity

All confirmed rumbles recorded between 15 December 2017 and 30 December 2020 were averaged across hours of day and week of year to illustrate the broad temporal patterns of the population's vocal activity across this period of time. Rumbles that occurred between hours 0–5 and 18–23 were classified as occurring at 'night' and between hours 6–17 as occurring in the 'day', following the patterns of dawn and dusk in the equatorial forests.

All confirmed gunshots recorded between 24 November 2017 and 25 January 2021 were grouped into gunshot events, with gunshots that occurred within 1 h of each other at the same recording site being grouped into the same event. The sampling period used to explore the temporal patterns of rumbles was different than the sampling period used to examine hunting activity owing to the availability of gunshot and rumble data that had been previously manually reviewed by the Elephant Listening Project (i.e. the gunshot data had two additional months of gunshot detections manually reviewed compared to the rumble data). Once gunshot events were created, we noted that the number of gunshots in a given single event could range from one to 58 gunshots and subsequentially divided all events into classes of hunting pressure intensity based on their number of gunshots. 'Low' intensity events ranged from 1 to 5 gunshots, 'medium' intensity events ranged from 6 to 13 gunshots and 'high' intensity events ranged from 23 to 58 gunshots. The 'intensity' of gunshot events was categorized in this way to attempt to infer more information on the 'type' of hunting that was occurring in each gunshot event. For example, based on anecdotal evidence that author A.V. obtained from ecoguards in Nouabalé-Ndoki National Park, it is probable that low-intensity events represent subsistence hunting activity where non-automatic firearms are discharged at most, five times over the duration of the event by a hunter who is probably hunting smaller wildlife for bushmeat. Alternatively, high-intensity events that are characterized by more frequent gunshots within the duration of the event imply that automatic firearms are probably being used to hunt larger, typically more endangered, wildlife such as forest elephants. Events were also classed by whether they occurred during the day or night. Hours 6–17 were also classified as 'day', and hours 0–5 and 18–23 were also classified as 'night'.

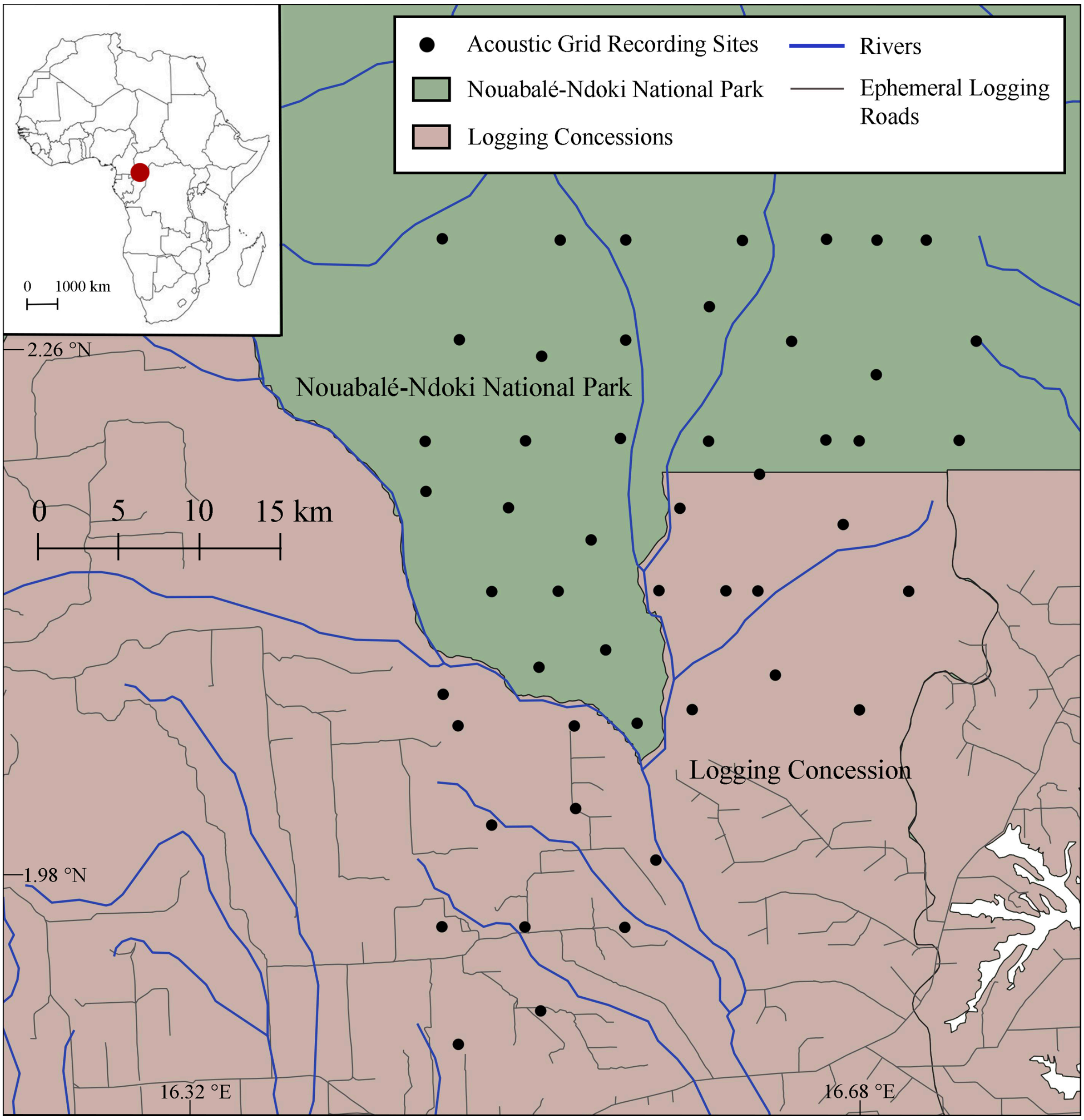

Figure 1. A map of the study site depicting the grid of 50 acoustic recorders, located in portions of Nouabalé-Ndoki National Park and adjacent logging concessions. Rivers are shown in blue, and ephemeral logging roads are shown in grey. The red dot in the insert map corresponds with the approximate location of the study site in the northern Republic of Congo.

(d) Occupancy analysis

To examine how forest elephant vocal activity and/or landscape use changes across the 8 days following a gun hunting event, a dataset of rumbles and gunshots recorded throughout 80 days of sound recordings taken between 28 November 2017 and 3 October 2018 was used. From these recordings, 8421 confirmed rumbles and 112 confirmed gunshots were found from 5018 unique site-date recordings.

Gunshots that occurred within 1 h of each other and that were recorded at the same recording site were grouped into 'events', resulting in 42 gunshot events. For each gunfire event, we compiled detection histories (i.e. records on whether an elephant was detected or not) for multi-season occupancy models for all sites within 10 km of and including the gunfire event site (following [19]). We also ensured that no other gunfire events occurred within the subsequent 8-day period following the gunfire event across all sites relevant to that event. This sampling approach resulted in the sampling period noted above and in clusters of 5–15 sites (i.e. acoustic recorders) analysed for each event (mean 9.4 sites per event). Gunfire events only occurred at 27 sites, but since data from sites within 10 km of the event site were also included, all 50 sites from the acoustic monitoring grid are represented in the dataset for this analysis. After each gunfire event, we examined the 8 days immediately following and designated a primary period (i.e. season; $n = 8$), which was divided into four 6 h secondary sampling periods. Any number of recorded rumbles during a secondary sampling period indicated forest elephant presence.

To establish a baseline of elephant activity, for each gunfire event, we defined a corresponding 8-day control period that was set three to five weeks prior to the gunfire event at the same recording site as the associated gunfire event, resulting in 42 control events. Control periods used the exact same cluster of sites as their corresponding gunfire events, controlling for spatial variation in elephant abundance across the PAM grid sites and ensuring comparability between gunfire and control periods. We ensured that no gunfire events occurred at any sites relevant to the control event within the 8-day control period as well as during the 8-day period preceding the start of the control event. Control period detection histories were compiled in the same manner as those for gunfire events. This method of including multiple control and impact sites (multiple clusters of 5–15 sites) and of staggering control and treatment periods through time rather than simultaneously is a powerful approach for isolating effects of interest from potentially confounding random events [69–71].

We compiled a candidate set of nine multi-season occupancy models that reflected our *a priori* hypotheses about how forest elephants would respond to gunfire events, either through changes in landscape/site use (represented by the occurrence probability component of the models) or changes in vocal activity (probably reflected in the detection probability component of the models). The fixed effects of interest included 'GunEvent' (whether a gunfire event had occurred as opposed to a control period) and its interaction with 'day' (primary periods 1–8). In the global model, both the occurrence and detection probability components were modelled as a function of the interaction between GunEvent and day. This represents the hypothesis that elephant site use or vocal activity would be different (reduced) following gunfire events than during control periods, but that it would change over the eight subsequent days, perhaps returning to baseline levels (e.g. elephants abandon but then resume use of sites within 8 days). We also modelled occurrence and detection as a function of the GunEvent main effect only, representing the hypothesis that post-gunfire site use or vocal activity would differ from control periods, but would not change over the subsequent 8 days (e.g. elephants do not resume site use within 8 days). The nine candidate models differed in whether the occurrence and detection components incorporated the GunEvent × day interaction, the GunEvent main effect only or an intercept only (null model). In the occurrence and detection components of all candidate models, we included event ID as a random effect to control for the fact that a cluster of multiple sites was analysed for each gunfire event and control period.

We implemented the occupancy models in a Bayesian context using the 'spOccupancy' package [72] in R [73]. We used vague normal priors for both occurrence and detection coefficients. To assess the fit of all candidate models, we performed posterior predictive checks using both the Freeman–Tukey and chi-squared fit statistics to calculate Bayesian *p*-values (low values reveal lack of fit; [72,74]). We used the widely applicable information criteria (WAIC; [75]) as a criterion for Bayesian model comparison and calculation of model weights.

(e) Night-time calling activity analysis

To examine changes in night-time calling activity in response to gun hunting, the proportion of night-time calling activity was compared between 47 days with gunshots and 47 control days using recordings collected between 16 December 2017 and 23 December 2020. From these recordings, 301 confirmed rumbles and 137 confirmed gunshots were found from 94 unique site-date recordings. Gunfire events were created by grouping together gunshots that were recorded within 1 h of each other at the same recording site. The 24 h period over which elephant rumbles were compiled into 'night' and 'day' categories began immediately following the end of the gunfire event, and we ensured no other gunshots occurred within this 24 h period. For control events, the 24 h period over which rumbles were compiled was set to begin exactly 3 days prior to the gunfire event and at the same recording site, and we ensured no gunshots occurred within this 24 h period as well.

Within the 24 h periods, rumbles were compiled into 'day' and 'night' categories based on the pattern of an 'elephant day'. An elephant day, as outlined in Wrege *et al*. [16], is the 24 h period beginning at 6.00 on one day and ending at 5.59 the next consecutive day. Formatting the data into elephant days is useful for the interpretation of forest elephant activity as previous research at bais has shown that forest elephants are the most active at night between 16.30 and 6.30, meaning that their 'days' end closer to 6.00 in the morning rather than at midnight [76]. An elephant day is then divided into 12 h day (6.00–17.59) and 12 h night (18.00–5.59) [16,77] to follow the patterns of dawn and dusk in the equatorial forests. Once rumbles were compiled into 'night' and 'day' categories and to calculate the proportion of night-time calling activity, we divided the total number of rumbles that occurred in the night by the total number of rumbles that occurred during the 24 h period that immediately followed the end of the gunfire or control event.

The total number of gunshots recorded for each 24 h period was also calculated and used as a predictor in the model. Additional covariates include protection status (whether the recording site was located in a protected area or a logging concession), season (defined below), proportion of open forest (defined below) located within 600 m of the recording site, distance between the recording site and the nearest mainstem river and an interaction between protection status and the number of gunshots. Recording site and event pair were also included as random effects in the model in order to control for any unknown variability associated with specific recording sites or event pairs (e.g. hunting and/or elephant presence might be higher at some sites versus others).

To determine the season, long-term seasonal trends based on rainfall data collected by the Goualougo Triangle Ape Project in the Goualougo Triangle of Nouabalé-Ndoki National Park, which falls approximately in the centre of the acoustic grid, were used. The trends revealed that the dry season (<60 mm of rainfall per month) occurs between December and February. The distance between each recording site and the nearest mainstem of the Ndoki or Goualougo River (whichever was closest) was measured using geographical information system watercourse layers. Layers were created by manually tracing digital elevation models and were then confirmed with on-the-ground global positioning system mapping conducted during routine acoustic grid maintenance. A random forest classifier was created for habitat classification and had an overall accuracy of 0.91 and a Kappa coefficient of 0.86 [62]. For the open forest class, the model had a producer's accuracy and user's accuracy of 0.94. Using the classifier, the proportion of open forest within 600 m of each recording site was then quantified. Open forest includes habitats associated with water such as river floodplains with sparse or open canopy, open canopy swamps, open water (rivers), aquatic vegetation and grasses and bais and other small clearings known as 'eyangas' [62].

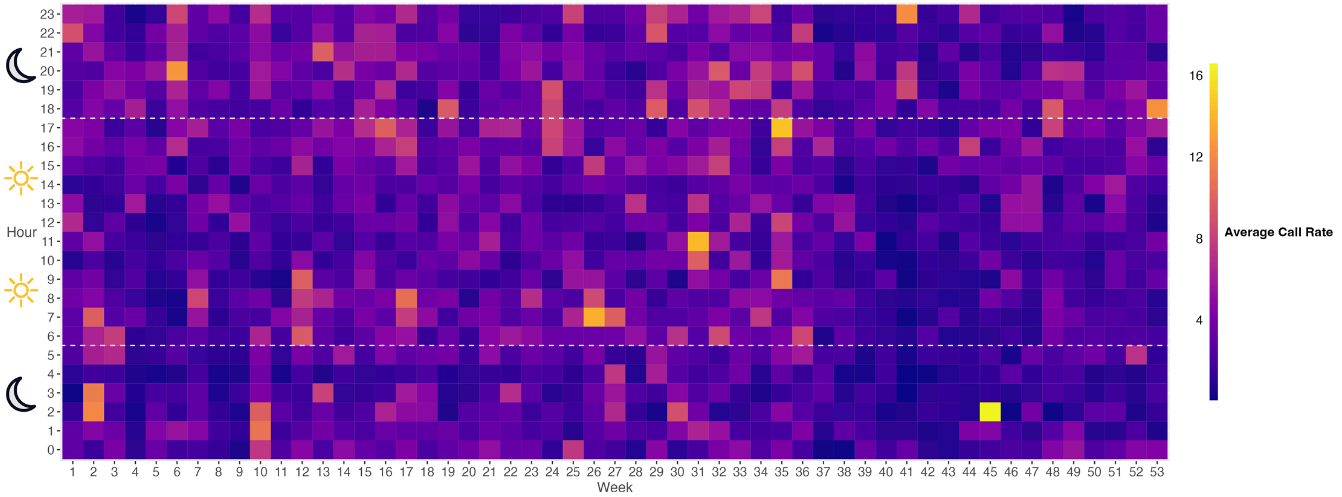

Figure 2. Average forest elephant call rate by week of year (*x*-axis) and hour of day (*y*-axis), compiled from acoustic data collected in and around Nouabalé-Ndoki National Park, Republic of Congo between December 2017 and December 2020. Brighter colours correspond with higher call rates. Horizontal white dashed lines mark the transition between 'night' and 'day', with night occurring between hours 0–5 and 18–23 and day occurring between hours 6–17, following the patterns of dawn and dusk in the equatorial forests. As seen from the figure, forest elephant call rates are generally higher at the beginning of the year than at the end, with the highest vocal activity occurring towards the middle of the year. We also note that across each week, calling activity typically occurred at similar rates throughout the night and day.

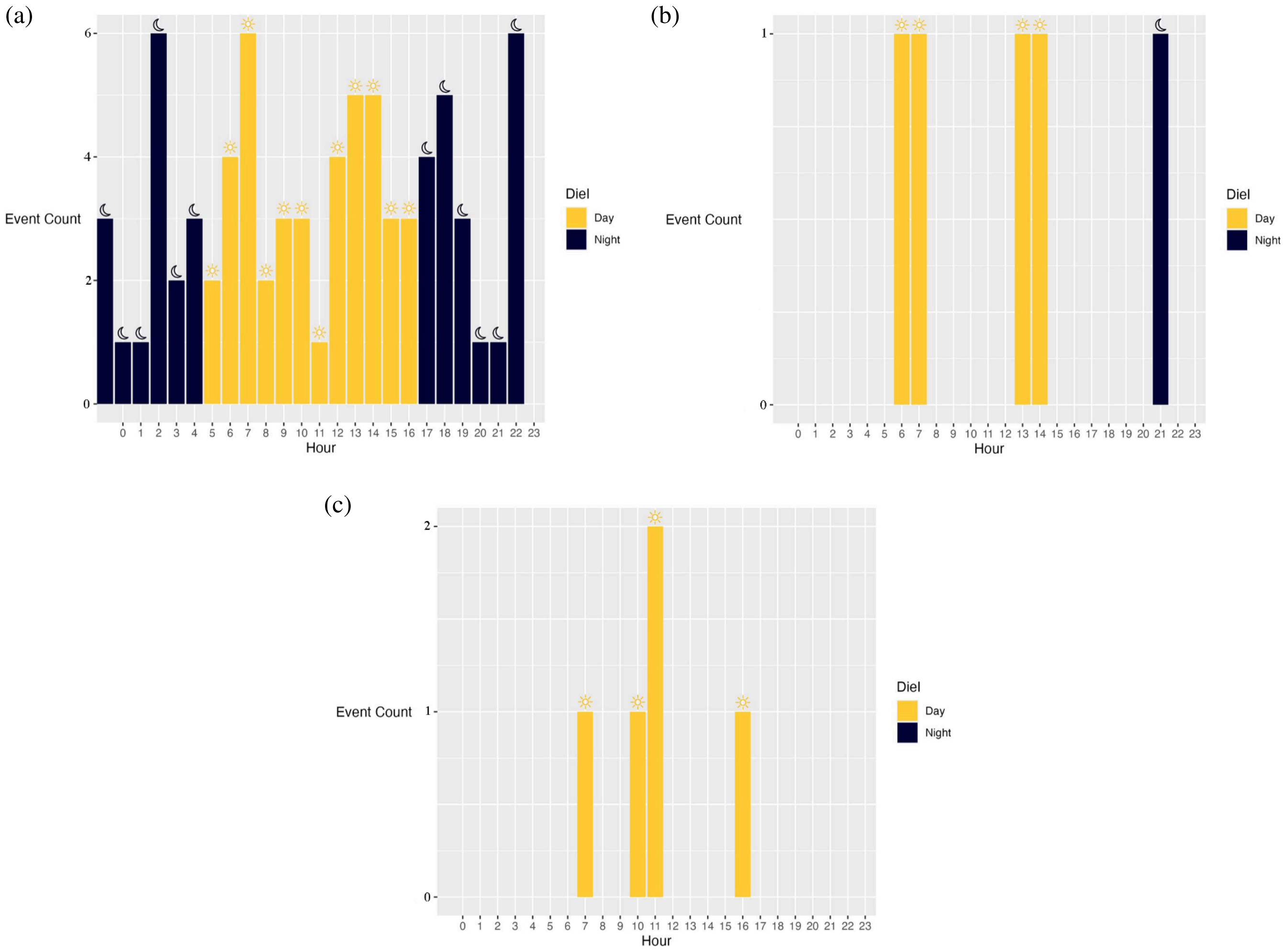

Figure 3. (a) Count of low hunting pressure gun events (1–5 gunshots within the event) recorded across an acoustic grid located in and around Nouabalé-Ndoki National Park, Republic of Congo between 2017 and 2021. We note that low-hunting pressure events occur throughout both day and night. (b) Count of medium hunting pressure gun events (6–13 gunshots within the event) recorded across an acoustic grid located in and around Nouabalé-Ndoki National Park, Republic of Congo between 2017 and 2021. We note that medium hunting pressure events occur most often during the day. (c) Count of high hunting pressure gun events (23–58 gunshots within the event) recorded across an acoustic grid located in and around Nouabalé-Ndoki National Park, Republic of Congo between 2017 and 2021. We note that high-hunting pressure events occur only during the day. Note: an 'event' consists of gunshots that were recorded within 1 h of each other on the same recording unit; hours 0–5 and 18–23 correspond with 'night', and hours 6–17 correspond with 'day', following the patterns of dawn and dusk in the equatorial forests.

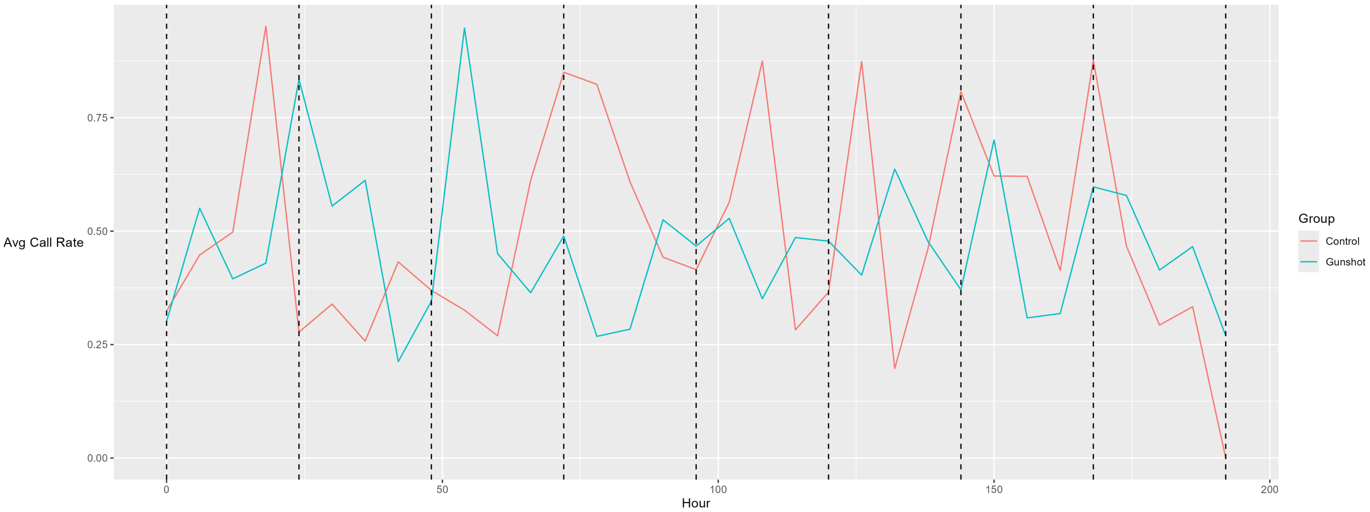

Figure 4. Average forest elephant call rate throughout the 8 days following a gunshot and control event. The dashed vertical lines divide the *x*-axis into individual 'days'.

Regression models were used and fitted to a binomial family as the response variable is a proportion. Models were developed using the glmmTMB R package [78]. The most parsimonious model among candidate models was chosen based on the corrected Akaike Information Criterion (AICc) [79] and using the AICcmodavg [80] package in RStudio v. 2023.03.0. Using the DHARMa R package [81], we also checked the assumptions of the top models to avoid overfitting and to ensure the validity of the conclusions drawn from the model selection process. Model diagnostics for our three top models indicated good performance (electronic supplementary material, appendix S1, figures S1–S3). Plots were created in R [73] using built-in base functions, as well as functions from ggplot2 (v. 3.3.2 [82]).

3. Results

(a) Exploring broad temporal patterns of forest elephant vocal activity and hunting activity

We found that forest elephant call rates were generally higher during the beginning of the year, peaking mid-year, with similar rates of activity during the day and night (figure 2). By contrast, higher-intensity gun hunting activity was most common during the daytime (figure 3a–c).

(b) Occupancy analysis

For control events, the average daily forest elephant call rate was 0.50 with a minimum daily call rate of 0.27 and a maximum of 0.63. For gunfire events, the average daily call rate was 0.47 with a minimum daily call rate of 0.39 and a maximum of 0.56 (see figure 4 for an illustration).

Four of our candidate models were moderately supported (model weights >0.10), and others had some support (table 1). Given that no particular model unambiguously outperformed all others (model weights ranged from 0.014 to 0.273; table 1), we chose to model average predictions from all candidate models to estimate occurrence probability of forest elephants in the presence and absence of gunfire events.

Occurrence probabilities were lower following gunfire events (0.52) than during control periods (0.54) and remained relatively stable over the 8-day period (figure 5a), demonstrating that there is a slight reduction in the population's use of sites within 10 km of the gunfire event. For occurrence probability, the average value for any of the 8 days following a gunfire event never increases to the level of any of the average values of the 8 days following a control event (figure 5a; electronic supplementary material, appendix S1, table S1), revealing that forest elephant occurrence probability does not return to 'baseline' within the 8-day period examined. During the first few days following gunfire events, detection probabilities were slightly lower than during the initial days of control periods; gunfire event and control period detection probabilities converged around day five (figure 5b; electronic supplementary material, appendix S1, table S2).

(c) Night-time calling activity analysis

Three models were well-supported (ΔAICc <2; [83]), with all models including effects of the number of gunshots and season (table 2). Our top model also included a positive effect of the proportion of open forest within 600 m of the recording site. Our second best-supported model was the same as the first, excluding the effect of proportion of open forest. Our third best-supported model included the same effects as our top model but additionally contained the effect of protection status of the forest and the interaction effect between protection status and the number of gunshots. The most parsimonious model was used to interpret results from the data.

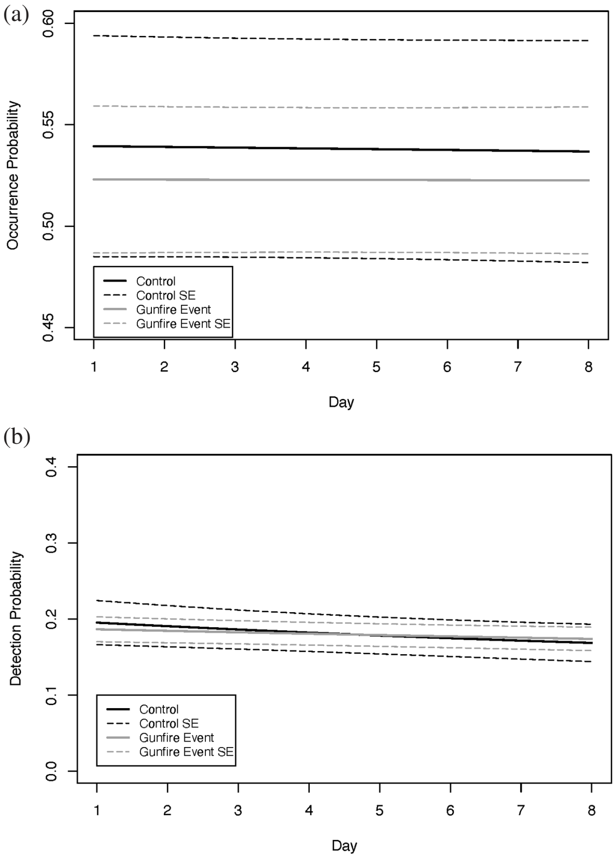

Figure 5. (a) Occurrence probability and associated s.e. plotted over the 8-day period for both gunfire and control events, and (b) detection probability and associated s.e. plotted over the 8-day period for both gunfire and control events.

Table 1. Output of nine candidate models for the occupancy analysis.

rank	occupancy fixed covariates	detection fixed covariates	occ. and det. random effect	WAIC	ΔWAIC	weight
1	GunEvent	—	event ID	9874.914	0	0.273
2 (null)	—	—	event ID	9875.515	0.601	0.202
3	—	GunEvent × day	event ID	9875.799	0.885	0.175
4	—	GunEvent	event ID	9876.377	1.464	0.131
5	GunEvent	GunEvent × day	event ID	9877.062	2.148	0.093
6	GunEvent	GunEvent	event ID	9877.692	2.778	0.068
7	GunEvent × day	—	event ID	9879.328	4.414	0.030
8	GunEvent × day	GunEvent	event ID	9880.806	5.892	0.014
9 (global)	GunEvent × day	GunEvent × day	event ID	9880.911	5.997	0.014

Table 2. Output from the top four candidate models for the night-time calling activity analysis, with the top three models falling within ΔAICc <2. (Note that all models had [+ (1|Site)] and [+ (1|Pair)] included as random effects for 'site' and 'pair', respectively.)

model rank	model description	AICc	ΔAICc	AICc weight	log-likelihood	d.f.
1	NumShots + PropOpen600 m + Season	121.75	0.00	0.23	−54.39	6
2	NumShots + Season	122.77	1.02	0.14	−56.04	5
3	NumShots + PropOpen600 m + Season + Protection + NumShots*Protection	122.95	1.20	0.13	−52.63	8
4	NumShots + PropOpen600 m + Season + Protection	123.78	2.03	0.08	−54.24	7

In line with our predictions, the proportion of night-time calling activity was positively associated with the number of gunshots (β = 1.3741, standard error (s.e.) = 0.4956, z = 2.7727; figure 6a) and the proportion of open forest (β = 5.3412, s.e. = 2.5846, z = 2.0665; figure 6b). However, contrary to our prediction on season, the wet season was negatively associated with the proportion of night-time calling activity (β = −3.9529, s.e. = 1.4632, z = −2.7015; figure 6c). To confirm the reliability of using the

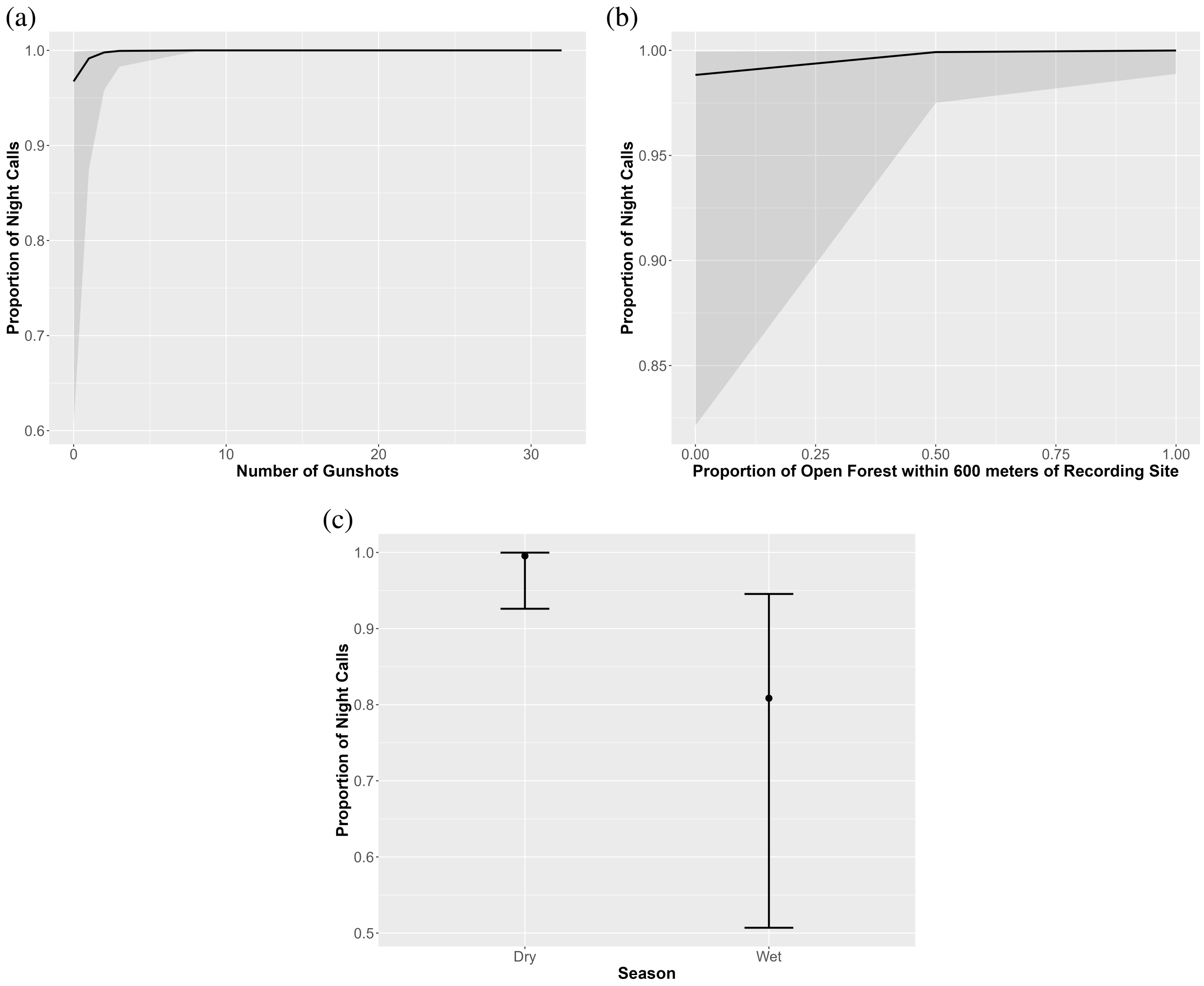

Figure 6. Positive association between the proportion of night calls and (a) number of gunshots, (b) proportion of open forest within 600 m of the recording site, and (c) dry season, as predicted by the best-supported model.

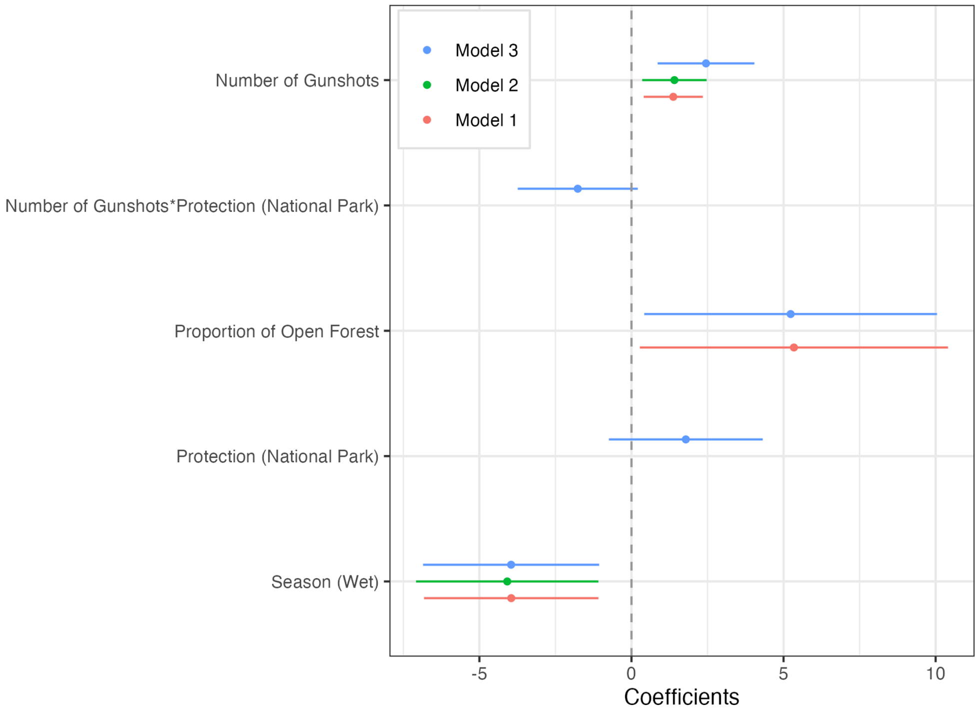

Figure 7. Estimates of coefficients and s.e. for each variable included in the top three models.

first top model to interpret results, we examined the effect of protection found only in the third top model and noted a slightly higher proportion of night-time calling activity in logging concessions compared to the national park, though the difference was small (0.004), and the confidence intervals overlapped significantly (electronic supplementary material, appendix S1, table S3 and figure S4). Estimates of coefficients and s.e for all predictors included in the top three models can be seen in figure 7.

4. Discussion

Our results show how forest elephants are being impacted by gun hunting, revealing that both occurrence and detection probabilities were slightly lower following gunfire events compared to control periods. Additionally, the proportion of night-time calling activity was positively associated with the number of gunshots and the proportion of open forest, while the wet season had a negative impact.

Our findings directly expand on a previous study demonstrating changes in forest elephant call rates in the 24 h following gunfire events [19]. Swider *et al*. [19] acknowledged that the observed decline in elephant call detections may reflect elephants' shift in landscape use away from the disturbance or a reduction in vocal activity. In the present study, we employ an occupancy approach in an effort to differentiate between changes in landscape use versus changes in vocal activity. Occupancy models contain separate model components for occurrence and detection probabilities so that estimates of species occurrence are not confounded by potential changes in the probability of detecting the species [84]. The occupancy approach allows us to potentially disentangle changes in elephant landscape use from changes in vocal activity because shifts in landscape use should primarily influence the occurrence model component while changes in vocal activity are likely to manifest in the detection model component (call rates will impact the probability of acoustically detecting a vocal species). By analysing additional gunfire events and expanding the analysis period of Swider *et al*. [19] to cover an 8-day period following gunfire events, we sought to determine the duration of any shifts in landscape use and/or vocal activity. While we found no clear pattern in model-averaged detection probabilities (figure 5b), we revealed a slight difference in occurrence probabilities between gunfire and control events (figure 5a). Although this difference was minor, our findings demonstrate a prolonged shift in forest elephant landscape use away from gunfire event sites for more than 8 days (i.e. occurrence probabilities did not return to control levels during the 8 days under investigation). This suggests that the 8-day period with which we chose to explore forest elephant response was not long enough to capture the return of their behaviour to the control state.

Changes in forest elephant occupancy may impact the species' interactions with vegetation, affecting trophic dynamics [85] and forest growth and function, ultimately eroding carbon storage services [86]. Similar to savannah elephants, forest elephants might congregate in safer areas, leading to superabundance and vegetation damage [87,88]. Forest elephants are attracted to mast fruiting events [65,89,90], but a decrease in their use of these areas may reduce their foraging and ranging behaviours, affecting body conditions and associated biological processes. Changes in forest elephant occupancy in certain areas of the forest may also increase human–elephant conflict in areas where the population feels more secure, negatively affecting the species' conservation [91].

Results of the proportion of night-time calling activity analysis indicate that, as we predicted, forest elephants increase the proportion of their night-time calling activity as gun hunting intensifies, consistent with previous studies that have examined fear-based responses of both savannah [41–45] and forest elephants [16]. In line with our prediction on habitat, we also found that as the proportion of open forest increases, so does the proportion of night-time calling activity, supporting the findings of previous research which has demonstrated that forest elephant activity is strongly nocturnal in open forest areas [17]. This behaviour is probably owing to the population's increased visibility to hunters in this habitat, which allows more light through the canopy and consists of a more open forest structure. Counter to our prediction, we found that the dry season was associated with a higher proportion of night-time calling activity, possibly because elephants spend more time near water sources in the dry season [54,62], making them more vigilant in these areas with higher hunting activity. While we did not find an effect of distance to the nearest mainstem river on the proportion of night-time calling activity, which is further supported by previous research [66], it is possible that this effect is being masked by the effect of the dry season. Future research may explore if there is an interaction effect between season and distance to the nearest mainstem river in order to investigate whether this may be the case. We also did not find an effect of protection status of the forest on the proportion of night-time calling activity as we had originally predicted. We note that up until 2020, gunshots were recorded both in and out of the national park, indicating that it is possible that the effect of increased protection was not captured by this dataset. However, the combined efforts of conservation practitioners working in Nouabalé-Ndoki National Park have resulted in no gunshots being detected across the acoustic grid since 2021. While this means that we may not have the data to further explore the effects of protection status on nocturnal activity, this is a compelling example of successful conservation for this critical species and the biodiversity that depends on them. Moreover, the results from our investigation into the broad temporal patterns of forest elephant vocal activity and hunting activity provide compelling examples of how PAM may be used to provide conservationists with information on the broad patterns of wildlife and human activity in the areas they are working to protect.

Although gun hunting has decreased in and around Nouabalé-Ndoki National Park, it persists elsewhere in forest elephants' range, potentially affecting night-time calling activity widely. Vocalizations are crucial for maintaining group cohesion in dense forests [92], and shifts in vocal activity to the night-time may disrupt social behaviours like meeting family members or finding mates, impacting population size [36]. The risk of being near hunters (i.e. death) drives elephants to adopt avoidance strategies, including temporal niche partitioning. However, these shifts in vocal activity may alter the important intraspecific interactions that occur between individuals. For example, in savannah elephants, rumbles allow individuals to communicate information about their identity [93], their emotional state [94,95] and external threats that they may be aware of [96]. In forest elephants, changes in vocal activity in social settings such as bais, where elephants share information and establish social and ecological traditions [97], may consequentially impact their biology, sociality and cognition.

The results of this study have provided insight into how forest elephants are responding to gun hunting, having implications for their monitoring and conservation [91]. The demonstrated shifts in their behaviour provide evidence that non-target elephants in the vicinity of gunfire events are also affected, shifting their vocal activity to the night and sustaining changes in their local habitat use for at least 8 days following gun hunting. Reductions in safe spatial and temporal niches may have ramifications for the species' population size, genetic fitness, group cohesion and the social learning and relationships that are vital for their survival. These reductions may also influence forest structure and reduce our planet's ability to sequester carbon [34] if the Congo Basin's mega-gardeners and architects choose to depart vital parts of the forest and compress into more secure areas.

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Data accessibility. The datasets and code for both analyses can be found online via Zenodo [98].

Supplementary material is available online [99].

Declaration of AI use. We have used AI-assisted technologies in creating this article.

Authors' contributions. A.V.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; C.S.: conceptualization, formal analysis, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing; F.B.-D.B.: data curation, methodology, resources, validation, writing—review and editing; P.J.F.M.: data curation, methodology, resources, validation, writing—review and editing; O.J.S.: data curation, methodology, resources, validation, writing—review and editing; D.H.: funding acquisition, methodology, project administration, resources, supervision, validation, writing—original draft, writing—review and editing; S.B.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests. We declare we have no competing interests.

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