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Acoustic behavior, poaching risk, and habitat use in African forest elephants (Loxodonta cyclotis): Insights from passive acoustic monitoring

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ABSTRACT

The African forest elephant (*Loxodonta cyclotis*) is a critically endangered and cryptic species that inhabits the rainforests of Central Africa. Forest elephant populations are severely threatened by poaching for the ivory trade, and an improved understanding of forest elephant behavior and habitat use, and of the anthropogenic pressures that threaten their existence, is essential for conservation of the species. However, their remote tropical rainforest habitat poses logistical constraints on research and makes forest elephants very difficult to observe and study visually. Limited data collection methods have also inhibited our ability to understand the determinants of poaching activity that is driving forest elephants toward extinction. This dissertation addresses forest elephant behavior, ecology, and conservation questions that span multiple scales by capitalizing on the advantages of passive acoustic monitoring (PAM) to detect elephant vocalizations and gunshots. At the finest scale, Chapter 1 examines forest elephant vocal repertoire use at a forest clearing in the Central African Republic and discusses implications for PAM. The different vocalization types of the repertoire varied in the generality or specificity by which they were used by certain age-sex classes of elephants. An understanding of these patterns is important for PAM of forest elephants, as they determine the population (or subset) that is detected and sampled. At the intermediate scale, Chapter 2 examines forest elephant landscape-scale response to individual poaching events detected in a PAM study system. Elephants within 10 km of gunfire events responded to poacher presence (before gunshots were fired) and to gunshots themselves, exhibiting behavioral changes in either vocal activity, site usage, or both. These results suggest that, in addition to the outright killing of targeted individuals, poaching activity affects the general population of elephants across the landscape. At the broadest scale, Chapters 3 and 4 used detections of elephant vocalizations and gunshots to analyze the distributions of forest elephants and poaching events across a 50-sensor PAM grid spanning 1250 km^2 of rainforest in Republic of Congo, for a period of over 3 years. To elucidate the determinants of these distributions, elephant and gunshot detection data were combined with habitat and landscape variables quantified using satellite remote sensing. In Chapter 3, variation in poaching risk depended primarily on factors related to poacher accessibility, such as distance to major rivers and logging roads. These results can guide the allocation of anti-poaching patrol effort to cover high-risk areas at times of increased vulnerability. Chapter 4 examined the habitat resources and anthropogenic pressures (e.g., poaching and logging) that influence forest elephants' use of the landscape. Elephant occurrence probabilities decreased over the 3 years of the study and were seasonally dependent, increasing in the wet season. Ongoing logging activity deterred forest elephants from using nearby sites, but previously logged areas provided important habitat resources. By leveraging remote sensing methods to expand the scale and resolution of data collection, this dissertation aimed to advance our understanding of forest elephant behavior and ecology, and confronted questions that will improve conservation efforts to protect the species from extinction.

ACOUSTIC BEHAVIOR, POACHING RISK, AND HABITAT USE IN AFRICAN FOREST ELEPHANTS (*LOXODONTA CYCLOTIS*):
INSIGHTS FROM PASSIVE ACOUSTIC MONITORING

by

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DISSERTATION

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TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

INTRODUCTION

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

APPENDIX

INTRODUCTION

An introduction to African forest elephants (*Loxodonta cyclotis*) and passive acoustic monitoring (PAM)

The African forest elephant (*Loxodonta cyclotis*; Fig. I.1) is a critically endangered and cryptic species that inhabits the rainforests of Central Africa (Blake & Hedges, 2004; Blanc, 2008). The ivory trade poaching that has decimated elephant numbers across Africa has had devasting consequences for populations of the forest elephant (Blake et al., 2007; Blake & Hedges, 2004; Gobush et al., 2021; Maisels et al., 2013). Between 2002 and 2011, 62% of the entire population and 30% of their geographic range was lost primarily due to poaching (Maisels et al., 2013). In the face of this ongoing threat, the ability to understand forest elephant behavior, landscape and habitat use, and the anthropogenic pressures that threaten their existence is of utmost importance to conserve the species (Blake & Hedges, 2004; Blanc, 2008; Maisels et al., 2013; Thompson, Schwager, & Payne, 2009; Thompson, Schwager, Payne, et al., 2009). However, their dense tropical rainforest habitat poses logistical constraints on research and makes forest elephants very difficult to observe visually (Blake & Hedges, 2004; Wrege et al., 2010, 2012). For this reason, relatively little is known about this species compared to the African savanna elephant (*Loxodonta africana*) and Asian elephant (*Elephas maximus*; Blake & Hedges, 2004). Much of what is known about forest elephants comes from visual observations at naturally occurring forest clearings known as *bais*, where elephants congregate to obtain minerals (Klaus et al., 1998; Turkalo & Fay, 1995) and engage in social interactions (Turkalo & Fay, 1995). However, it is likely that individual elephants spend only a small proportion of their lives in *bais* (Turkalo et al., 2013), where habitat characteristics, social contexts, and elephant behaviors differ from that of the forest proper (Fishlock & Lee, 2013; Hedwig et al., 2019). Therefore, research is needed to elucidate forest elephant behavior and ecology in the forest itself, where they are difficult, if not impossible, to study visually. Historically, these forest-focused (i.e., non-*bai*) studies have relied on dung transects to infer forest elephant presence

(Barnes et al., 1991; Blake et al., 2007; Buij et al., 2007; Hall et al., 1997; Theuerkauf et al., 2001; White, 1994; Yackulic et al., 2011). While useful for certain applications, dung transect methods can suffer from limited spatiotemporal scope and resolution, considerable time and financial costs, inadequate sampling effort, biases, and inaccurate state variable estimates (e.g., abundance estimates; Hedges, 2012; Laguardia, Gobush, et al., 2021).

Limited data collection methods have inhibited our ability to understand not only forest elephant ecology, but also the determinants of poaching activity that threatens the species with extinction. Illuminating the environmental drivers of poaching pressure would benefit forest elephant conservation by facilitating prediction of poaching activity in time and space, and by improving the allocation of anti-poaching patrol effort and the efficacy of intervention (Lavadinović et al., 2021; Moore et al., 2021; Moreto & Lemieux, 2015). However, limited spatiotemporal scope and sampling biases have constrained analyses of poaching activity just as they have for analyses of forest elephant distributions (Doormaal et al., 2021; Gavin et al., 2010; Hedges, 2012; Keane et al., 2011; Moreto et al., 2014). Our limited understanding of forest elephant ecology and of the drivers of poaching pressure remains a hindrance to conservation of the species (Fishlock & Breuer, 2015).

Remote sensing methods offer potential solutions to the challenges impeding the sampling and analyses of forest elephant and poaching distributions. Over the past few decades, the development of remote sensing approaches (e.g., satellite remote sensing) has revolutionized our ability to sample and study ecological phenomena at drastically expanded scales and with higher consistencies than previously possible, thereby extending the range of scientific inquiry (Gillespie et al., 2008; Pfeifer et al., 2012; Roughgarden et al., 1991). Classification and mapping of land cover, vegetation, and/or habitat types, performed on space-borne imagery, can augment ground surveys and greatly improve distributional knowledge of different habitats over ever larger study areas (Duro et al., 2007; Gillespie et al., 2008; Pfeifer et al., 2012). Maps of classified habitats and landscape features (e.g., roads) derived from satellite remote sensing can in turn be integrated into analyses of landscape use patterns of wildlife species (e.g., African forest elephants [Beirne et al., 2021; Mills et al., 2018]) and of patterns of human disturbance (e.g., habitat conversion and illegal hunting [Clements et al., 2014]).

While mapping of study area habitats and landscape features from satellite imagery offers important advantages, the detection of focal animal species is not often possible from space because most species are too small to be resolved (Gillespie et al., 2008) or are obstructed from view. Forest elephants, for example, are hidden from the vertical vantagepoint by the rainforest canopy. In general, a major challenge in ecological research is the detection of species that are cryptic or that inhabit inaccessible areas (e.g., forest elephants and whales; Thompson, 2004). Even for more readily observed species (e.g., birds), it can be difficult to collect data over large spatial and temporal scales, which constrains the range of potential questions that can be addressed with scientific research (Van Parijs et al., 2009; Wiens, 1989). These issues can potentially be remedied by employing another type of remote sensing known as passive acoustic monitoring (PAM; Blumstein et al., 2011; Van Parijs et al., 2009). A variety of taxa, including frogs, birds, fish, insects, and mammals, produce sounds for reasons such as mate attraction, territory defense, navigation, and communication within social groups (Bradbury & Vehrencamp, 2011). Through such sound production, animals leak information into the environment. Biologists can capitalize on that information using PAM, which employs acoustic sensors to record signals from species of interest, from which information about the ecology of the system can be inferred (Blumstein et al., 2011; Van Parijs et al., 2009). Acoustic sensors can be set up and left to record continuously for months or years at a time, drastically expanding the spatiotemporal coverage of data collection (Van Parijs et al., 2009) and facilitating studies in remote, hard-to-access sites (Wrege et al., 2010, 2017). For sound-producing animals, especially those that are cryptic or inhabit remote sites where visual observation is impractical, PAM can partially alleviate the constraints on data collection that limit research potential. In this context, as a remote sensing approach that improves sampling capabilities, PAM is analogous and complementary to the use of satellite imagery; space-borne imagery can be used to quantify large scale phenomena such as habitat patterns across the landscape, while PAM can be leveraged to detect and quantify the distributions of species or activities within those landscapes (Wrege et al., 2017).

To improve our understanding of the elusive, visually-cryptic African forest elephant, which inhabit remote habitats that pose logistical constraints on research, a combination of satellite remote sensing and PAM are a potentially powerful analysis framework. With a PAM approach, forest elephants can be detected across grids of acoustic recorders by their most common vocalization type, known as *rumbles*. Rumbles are composed primarily of very low frequencies (Poole et al., 1988), which attenuate in the environment less rapidly than higher frequencies (Ingard, 1953). This makes rumbles detectable at relatively far distances and thus favorable signals for use in PAM (Thompson, Schwager, & Payne, 2009; Wrege et al., 2017). In addition to rumbles, gunshots from poaching events are readily detectable on PAM recorders (Astaras et al., 2017, 2020; Branch et al., 2022; Wrege et al., 2017). Acoustic detections of rumbles and gunshots can therefore be used to reveal the spatiotemporal distributions of both forest elephants and poaching activity (Wrege et al., 2017). Using statistical models, these distributions can be linked to relevant variables such as habitat features acquired from satellite imagery. By employing these complementary remote sensing approaches, it is therefore possible to illuminate the factors that influence forest elephants' use of the landscape as well as the environmental determinants of poaching pressure.

The overall objective of my dissertation research is to answer forest elephant behavior, ecology, and conservation questions that span multiple scales by capitalizing on the advantages of remote sensing, with a focus on PAM. My chapters incorporate both theoretical and applied research, but my hope is that all the chapters will contribute to the conservation of this critically endangered species. My research covers a broad range of spatial and temporal scales, from direct observations of elephant behavior occurring over a few meters and seconds to multi-year PAM data remotely collected across a 1250 km^2 expanse of rainforest. At the finest and smallest scale, Chapter 1 examines forest elephant vocal behavior at a forest clearing called Dzanga bai in the Central African Republic, and discusses the implications of patterns in their repertoire use for PAM at larger scales. At the intermediate scale, Chapter 2 addresses the question of how forest elephants respond to individual instances of poaching events detected in a PAM study system. At the broadest scale, Chapters 3 and 4 combine PAM and satellite remote sensing to examine factors that influence of the distribution of poaching events and forest elephant habitat use across 1250 km^2 of rainforest in Republic of Congo, for a period of over 3 years. Insights gained at the fine and intermediate scales (Chapters 1 and 2) inform the larger, landscape-scale projects (Chapters 3 and 4), so that certain findings are integrated across chapters and scales.

Our limited understanding of forest elephant ecology and of the drivers of poaching pressure remains a limitation to the successful conservation of the species (Fishlock & Breuer, 2015). This dissertation addresses some of these knowledge gaps not only to advance our basic understanding of forest elephant behavior and ecology, but to do so by confronting specific questions that I hope will improve conservation efforts to preserve the species.

Figure I.1 African forest elephants (*Loxodonta cyclotis*) in Dzanga bai, Central African Republic

CHAPTER 1

Implications of target signal choice in passive acoustic monitoring: An example of age and sex dependent vocal repertoire use in African forest elephants (*Loxodonta cyclotis*)

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Abstract

Passive acoustic monitoring (PAM) is a useful tool for sampling acoustically active animal species, particularly for elusive, visually cryptic species inhabiting remote or inaccessible habitats. Key advantages of PAM are large spatial coverage and continuous, long-term monitoring. In most cases, a signal detection algorithm is utilized to locate sounds of interest within long sequences of audio data. It is important to understand the demographic/contextual usage of call types when choosing a particular signal to use for detection. Sampling biases may result if sampling is restricted to subsets of the population, for example when detectable vocalizations are produced only by a certain demographic class. Using the African forest elephant repertoire as a case study, we test for differences in call type usage among different age-sex classes. We identified disproportionate usage by age-sex class of four call types— roars, trumpets, rumbles, and combination calls. This differential usage of signals by demographic class has implications for the use of particular call types in PAM for this species. Our results highlight that forest elephant PAM studies that have used rumbles as target signals may have under-sampled adult males in this species. The addition of other call types to PAM frameworks may be useful to leverage additional population demographic information from these surveys. Our research exemplifies how an examination of a species' acoustic behavior can be used to better contextualize the data and results from PAM and to strengthen the resulting inference.

Introduction

The methods used to sample animal populations, including how individuals of a species are detected, directly impact the inferences that can be drawn from these data (Thompson, 2004; Williams et al., 2002). Ideally, the sampled population should be identical to the target population to which inference is applied, but this is often not achieved. In many cases the sampled population differs from the target population because sampling effort is restricted to a subset of the target population (Williams et al., 2002). In ornithological research, for example, many studies have relied on the auditory detection of male birdsong. Much of our understanding of avian ecology and distribution therefore derives from what is known about the location of singing/breeding males, and either intentionally or unintentionally disregards females and non-breeding individuals (Buckland, 2006; Burnham et al., 2004; Odom & Benedict, 2018). Such biases must be identified and addressed in statistical methods or when interpreting results.

Passive acoustic monitoring (PAM) is a form of animal population sampling that uses autonomous acoustic recorders to continuously record signals from species of interest and the environment (Blumstein et al., 2011; Sugai et al., 2019; Van Parijs et al., 2009). PAM can drastically expand spatial and temporal coverage of data collection for acoustically active species (Van Parijs et al., 2009), facilitate studies in remote, hard-to-access sites, and provide a solution for sampling elusive, visually cryptic, or rare species and events (Wrege et al., 2010, 2017). As with any form of animal population sampling, potential biases exist that should be considered when choosing signals for PAM (Van Parijs et al., 2009). Acoustic detection methods apply only to the acoustically active individuals of a population. Depending on the species, only a particular demographic class may vocalize, or different classes may use different call types (Marques et al., 2013; Stevenson et al., 2015). Therefore, the demographic specificity or generality of call types should be considered when identifying the most suitable signal used for detection in PAM studies.

When evaluating potential candidate target signals for PAM, practical considerations—source amplitude, propagation characteristics, susceptibility to masking from ambient noise, feasibility of algorithmic detection, etc. (Darras et al., 2016; Ellinger & Hödl, 2003; Llusia et al., 2011)— usually take priority over an examination of the signal's demographic specificity or generality. Target signals in PAM studies are often chosen out of convenience (e.g., they are easily detectable, or they are well established and commonly used in the existing literature) or because they are the only option if little is known about the repertoire and acoustic behavior of the species of interest (e.g., Clark et al., 2010). Indeed, PAM study species are not often readily observed visually, so detailed behavioral data can be difficult to acquire (e.g., cetaceans; Clark et al., 2010). The full repertoire and the degree to which the call types are used differentially by subsets of a population are rarely fully understood or investigated (but see Parks et al., 2011). When obtainable, consideration of such behavioral information is highly advantageous (Parks et al., 2011; Van Parijs et al., 2009; Wood et al., 2020) because it can guide comparison and choice of candidate signals with varying degrees of age-sex specificity and value for PAM. Signals used by a single demographic class (e.g., male breeding song) could be unsuitable if the goal is to make population-level inference, because the sampled and target populations would differ. On the other hand, such a signal provides demographic information in addition to species presence; the age and sex of the calling individual can be inferred. Such signals could be useful as complementary target signals in a PAM study where demographic information is desired (e.g., Matthews et al., 2014).

In many PAM studies, inferences from signal detections are intended to apply to the entire population (e.g., distributional maps or density estimation). A signal used by both sexes and all age classes conveys the advantage of representative sampling from the overall population and provides the most comprehensive data for population-level inference. This is one reason that the North Atlantic right whale (*Eubalaena glacialis*) upcall and African forest elephant

(*Loxodonta cyclotis*) rumble are appropriate target signals for PAM— they are produced by all age-sex classes and therefore presumably sample the acoustic activity of the population as a whole (Davis et al., 2017; Parks et al., 2011; Thompson, 2009). While these types of signals are of great value for PAM, the degree to which such vocalizations are produced proportionally by different age-sex classes is not always examined, limiting the interpretation of PAM results.

Here, we demonstrate how detailed knowledge of vocal behavior can improve demographic inference from PAM studies. We use a case study of the African forest elephant (*Loxodonta cyclotis*), a critically endangered species inhabiting the rainforests of central Africa (Gobush et al., 2021). Forest elephants remain the least studied of the three extant elephant species due in part to their elusiveness and the difficulties posed by their inaccessible and remote habitat (Blake & Hedges, 2004). Given the limitations to direct visual observation in the forest, PAM is one of the best methods for studying the species (Blake & Hedges, 2004; Wrege et al., 2010, 2012). PAM studies of forest elephants have employed only a single call type— the rumble— despite the awareness of a wider repertoire of sound types (Keen et al., 2017; Swider et al., 2022; Thompson, Schwager, & Payne, 2009; Wrege et al., 2010, 2012, 2017). Like many visually cryptic species for which PAM is used, limited data are available on the acoustic behavior and full repertoire use of forest elephants (but see Hedwig et al., 2021; Thompson, 2009). Forest elephants therefore serve as a demonstrative example of the implications of target signal choice in PAM. In this study, we quantify the differential usage of the forest elephant acoustic repertoire by individuals in different age-sex classes. Our results contribute new insight into the interpretation of forest elephant PAM studies that use only rumbles as target signals, and suggest that adding other call types to PAM frameworks could provide additional insight into population demographic information.

Methods

Study site

We collected data from an elevated platform overlooking a 10-ha natural forest clearing called Dzanga bai in Dzanga-Ndoki National Park, Central African Republic (2.963°N, 16.365°E). Dzanga bai provides an opportunity to visually observe the otherwise visually cryptic forest elephants, who congregate in the clearing in large numbers to access mud and water containing dissolved minerals (Klaus et al., 1998) and to engage in social interactions (Turkalo & Fay, 1995). Demographic scans, acoustic recordings, and visual observations took place between 11:00 and 16:30 during two field seasons: December 2018 - February 2019, and February - March 2020.

Demographic scans

To investigate age and sex dependent usage of call types, it was necessary to establish the baseline proportions of elephants of each age-sex class represented within the bai. This controls for differences between demographic classes in their availability to be sampled (Altmann, 1974). On a subset of data collection days (n = 31), we performed scans of the bai in which we assigned individuals to a sex and age class. We limited these scans to elephants within a predetermined sampling area corresponding to the area from which most of our recorded vocalizations originated. The only portions of the bai that were excluded were those so far from the platform that visual observations were unreliable.

Using a simplification of existing aging protocols (Turkalo, 2013), we classified forest elephants into four age classes that correspond to important biological development stages—infant, juvenile, subadult, and adult. We assigned elephants to age classes based on their height relative to their mother’s height, or to the height of a typical adult female if no mother was present. Very young elephants that fit easily under their mother's belly and armpit were classified as infants. At around one year of age, infants transition to juveniles, which were defined as under half mother's height but above mother's belly height. This marks the development of vegetation-eating abilities to supplement nursing. At 5 to 6 years old, elephants attain half the height of their mother, at which point they have likely completely stopped nursing and their behavior becomes more independent. Using this benchmark, individuals that were greater than half the height of their mother, but less than full adult height, were classified as subadults. This subadult category is more inclusive of younger elephants than previous aging rubrics (e.g., Turkalo, 2013), which would categorize some of our smaller subadults (e.g., just over half mother's height) as juveniles/calves. Elephants were classified as adults at the height of a typical adult female— at approximately 20 years of age. We determined the sex of individuals of all age classes except for infants, for which sexing was inaccurate due to inadequate viewing of the small genitalia at a distance.

Because the 31 scan days were distributed over 1.5 months, most of the demographically surveyed elephants were likely unique individuals. However, forest elephants remain around Dzanga bai for an average of 2-3 days per visit (Turkalo et al., 2013), so some individuals were probably included in scans on adjacent days. In this analysis, the sampling unit of interest was not the individual elephant, but rather the demographic structure of the bai population on a given day. Therefore, the minor subset of repeatedly surveyed individuals should not constitute pseudo-replication or distort our calculation of the baseline demographic structure.

We calculated demographic class proportions from the age-sex counts summed (pooled) across the 31 scans. This overall baseline demographic distribution served as a control for variability in sampling availability between classes. The 31 individual demographic scans had been performed every day of data collection during the 2020 field season, but no scans were performed during the first field season (late 2018/early 2019). To verify that our pooled scans represent a stable baseline demographic distribution for Dzanga bai, and to justify applying this baseline distribution to the 2018/2019 field season for which we didn't have demographic data, we (1) examined variation in the demographic structure across the 31 scan days of the second field season, and (2) made comparisons to our preexisting demographic data from Dzanga bai. Using the 'MultinomialCI' package in R (R Core Team, 2022; Villacorta, 2021), we calculated simultaneous 95% confidence intervals for the multinomial proportions of our baseline (pooled) demography distribution (Johnson & May, 2000; Sison & Glaz, 1995). We plotted the proportion of the population (and 95% CIs) represented by each age-sex class. We then overlaid the proportion of each class from each of the 31 individual un-pooled scan days. Next, we reviewed demographic data collected by the Elephant Listening Project at Dzanga bai during previous fieldwork in 2017 and 2018 (prior to our 2018/2019 field season for which we lacked demographic scans). From these earlier data we extracted age-sex class proportion metrics with which to compare and evaluate the baseline demography distribution calculated from our 2020 field season.

Audio recording and visual observations

From the platform overlooking Dzanga bai, we recorded audio continuously with an Earthworks QTC omnidirectional microphone (frequency response: 4Hz-40kHz ± 1dB) and Sound Devices MixPre3 audio recorder (frequency response: 10Hz-80kHz ± 0.5dB), set to 45-55dB re 20µPa, with a sampling rate of 48 kHz and 16-bit resolution. The continuous recordings were accompanied by opportunistic visual observations of vocalizing elephants. While focal follows would result in more complete and potentially less-biased sampling, they do not allow enough rare vocal events to be observed because the rate of vocalization for any given individual elephant is low. However, because there are typically so many elephants in the bai, collective vocal activity of the group is relatively high. Opportunistic sampling (Altmann, 1974) allowed us to capitalize on this overall high vocal activity and collect far more data across the range of vocalizations in the repertoire.

We noted any vocalizations that we observed, almost all of which could be categorized as roars, trumpets, rumbles, or rumble-roars (combinatorial calls *sensu* Pardo et al., (2019); Fig. 1.1). We focused analyses on these four vocalizations because (1) they are discrete, distinguishable call types that can be manually classified (provided high SNR recordings), (2) they make up the vast majority of all the vocalizations produced by forest elephants, and (3) they are produced loudly and frequently enough to be theoretical candidates for target signals in PAM. Occasionally, some roar-like vocalizations, particularly from infants and juveniles, deviated from the stereotypical roar, likely due in part to small body size. Rather than attempt to subjectively classify these as separate call types (e.g., “cries”, “barks”), we instead use “roar” in broad reference to all noisy, broadband vocalizations that lack the clear harmonic structure of call types such as rumbles (Hedwig et al., 2021; Thompson, 2009).

We attributed these vocalizations to individuals on the basis of behavior— open mouth, shaking head and ears, running, repeated sequence of calls by same individual, etc. (Poole et al., 1988; Thompson, 2009)— or by auditory localization if the calling individual was sufficiently spatially isolated from other elephants. We noted the sex and age class of the caller and any other interacting individuals. We also made note of the behavioral context of the vocal event, for which we adapted the behavioral classification system developed by Hedwig et al., (2021). We classified each vocalization into one of eight contexts— affiliation, competition (e.g., displacements from water holes), defensive (e.g., chasing other species; ‘anti-predatory’ *sensu* Hedwig et al., (2021)), sexual, nursing, separation (i.e., distressed searching), alone (non-distressed), and unspecific (see Hedwig et al., (2021) Table 1 for detailed descriptions of behavioral contexts).

Acoustic analysis

Continuous audio spectrograms of observation sessions were made in Raven Pro 1.6 (KLY-CCB, Cornell, 2019). We manually reviewed and annotated the spectrograms with reference to field notes to verify behavioral observations. Any observations that did not match the record of vocalizations revealed by the spectrogram, or that could not be assigned to a particular elephant of known sex and age class, were excluded from subsequent statistical analyses.

Statistical analyses of vocalizations

To determine if certain call types are differentially used by age-sex classes, we compared the numbers of calls emitted by each class to the expected probability based on baseline class proportions within the bai using chi-square goodness-of-fit tests. This was followed by pairwise tests between sexes and adjacent age classes. Infants were excluded from pairwise tests involving sex because we lacked accurate sex data.

To visualize any disproportionate usage of vocalizations across the age-sex classes, we plotted the data in two ways. First, we created standard bar plots from the raw call counts by demographic class, without any demographic correction. Second, we plotted an index that weighed the raw call counts by the proportions, or sampling availability, of each age-sex class within the bai. We calculated this index as the proportion of calls produced by an age-sex class divided by the average proportion of elephants in the baseline population belonging to that class. The index thus corrects for uneven representation of the different demographic classes in the bai.

Values of 1.0 indicate that the proportion of calls recorded from a particular age-sex class is the proportion expected based on that classes' prevalence in the bai. Values greater or less than 1.0 indicate disproportionately more of less usage than would be expected.

Results

Demographic scans

A total of 1809 forest elephants were assigned to age-sex classes over the 31 days we performed the demographic scans in 2020. The different age-sex classes varied substantially in their representation within the bai (Fig. 1.2). However, within-class variation across the 31 scan days was limited. The consistently narrow CIs of the pooled class proportions, and the corresponding pattern of individual scan proportions suggest a stable demographic class structure across our individual scan days (Fig. 1.2). This justified the use of a pooled overall baseline demographic distribution as a control for sampling availability.

The pre-existing demographic data collected in 2017-2018 included fewer demographic classes and used slightly different class criteria. Consequently, we were able to extract population proportion metrics or derivatives thereof (e.g., sex ratios) for only some of our age-sex classes of interest. Over 24 days in 2017, a 5.2 average adult F:M ratio was reported from Dzanga bai, which agrees with the 4.71 (95% CI: 3.49-7.06) ratio from our present study. From data collected in March - May 2018 (n = 32 scan days), we calculated population proportions for adult females (0.308) and infants (0.055; sexes combined). These derived class proportions also fall within the 95% CIs of the baseline demography proportions for the present study (Fig. 1.2). Lastly, a 3F:2M long-term average sex ratio from 20 years of Dzanga bai elephant sightings was reported by Turkalo et al., (2013). This matches our overall F:M ratio of 1.46 across all age classes. These agreements with historical and with 2017-2018 data suggest that we can appropriately apply our 2020 baseline demography distribution to the 2018/2019 field season for which we lack demographic scan data.

Vocalizations

We acoustically recorded and, simultaneously, visually observed 1213 vocalizations attributable to particular elephants within the bai (Table 1.1). The four call types differed in the rate and evenness with which they occurred in different behavioral contexts (Table 1.2). Rumbles were used most often in affiliative and separation contexts but were not uncommon in other contexts. Rumbles were the only call type used in all behavioral contexts and they exhibited the most evenness across contexts. Roars, combination calls, and trumpets were each used in 6 of the 8 contexts. Combination calls occurred primarily in competitive and separation contexts but were somewhat common in association with other behaviors. Roars and trumpets exhibited the most unevenness across and specificity to certain contexts, with roars occurring overwhelmingly in competitive and trumpets in defensive (chasing other species) contexts (Table 1.2).

The 351 recorded combination calls included six varieties with differing numbers and orders of rumble and roar components, although the majority were roar-rumbles or rumble-roar-rumbles, which together made up 76% of all combination calls. For the purposes of this analysis, we do not differentiate between the different arrangements.

Statistical analyses

Overall Chi-square goodness-of-fit tests for each of the four call types revealed disproportionate usage across age-sex classes (overall test p-values < 0.0001). However, the patterns of use with age, within and between sexes, differed depending on call type.

Rumbles

We recorded most rumbles from subadult and adult females (Fig. 1.3a top). When considering the baseline proportions of elephants of each age-sex class represented within the bai and available to be sampled, we reveal disproportionate use of rumbles from infants and subadults (Fig. 1.3a middle). The alternating changes in usage between age-classes (sexes combined) are statistically significant (Fig. 1.3a middle; p-values < 0.001). The disproportionate rumble use in subadults is driven by frequent rumble production in females (Fig. 1.3a bottom). While a small, borderline significant ($p = 0.055$) dominance in rumble usage by males occurs in juveniles, usage becomes predominantly female for subadults and adults (Fig. 1.3a bottom; p-values <0.01). For males and females separately, changes in rumble usage between age classes are all statistically significant (p-values < 0.01), except between juvenile and subadult males (Fig. 1.3a bottom; $p = 0.19$).

Roars

Most of our recorded roars were produced by subadults, especially by males (Fig. 1.3b top & middle). Compared with adjacent age classes, the prevalent subadult usage (sexes combined) is statistically significant (Fig. 3b middle; p-values < 0.0001). Roars are predominantly used by males across all age classes, even when accounting for sampling availability differences (Fig. 1.3b bottom). However, this sex difference is statistically significant only for the adult age class, in which roar use is drastically dominated by males ($p < 0.0001$). Significant increases in roar usage between juveniles and subadults exist for both sexes separately (Fig. 1.3b bottom; p-values < 0.0001). The subsequent decrease in female roar production in adulthood is also statistically significant (Fig. 1.3b bottom; $p < 0.0001$). In contrast, adult males maintain disproportionately high roar production.

Combination calls

We recorded the most combination calls from subadult males (Fig. 1.3c top). When accounting for baseline demographic availability differences, combination calls are used disproportionately by infants, juveniles, and subadults; usage then decreases drastically in adulthood (Fig. 1.3c middle; subadult to adult $p < 0.0001$). Across all age classes, combination calls are primarily produced by males, a trend that is statistically significant for adults (Fig. 1.3c bottom; $p < 0.01$). For both males and females separately, the decrease in combination call usage between subadults and adults is statistically significant (Fig. 1.3c bottom; p-values < 0.001).

Trumpets

Trumpets were recorded mostly from subadult elephants (Fig. 1.3d top & middle). Compared with adjacent age classes, the prevalent subadult trumpet production (sexes combined) is statistically significant (Fig. 1.3d middle; p-values < 0.001). Adjusting for availability differences between sexes, these subadult trumpets were produced disproportionately by females (Fig. 1.3d bottom; $p < 0.001$). Apart from the subadult age class, trumpets appear to be used primarily by males, although these sex differences are not statistically significant. For females, the changes in trumpet production between juvenile, subadult, and adult age classes are statistically significant (Fig. 1.3d bottom; p-values < 0.0001).

Discussion

The behavioral contexts in which vocalizations are used is an important consideration in PAM, as this will impact where, when, and how often signals can be detected (Van Parijs et al., 2009). In planning a PAM study for African forest elephants using a single call type, based on our results we would expect to detect the most signals if we targeted rumbles. Rumbles (n = 599) are far more common than the other three call types under consideration (Table 1.1), and also the only call type used in every behavioral context (Table 1.2). In addition to being the least frequent call type in our study (n = 70), trumpets are indicative of only one or two particularly high-emotion contexts, for example when elephants aggressively chase other species such as a giant forest hogs or forest buffalo. Similarly, roars were used overwhelmingly (94%) in the single context of competitive behavior (Table 1.2). We might therefore favor rumbles as a PAM target signal because they are both most common overall and most evenly representative of the range of behavioral states of forest elephants. However, context-specific vocalizations (e.g., roars and trumpets) can provide valuable information if the goals of PAM are to distinguish between the occurrence of such behaviors or to identify and map important forest elephant resources— *bais*, fruiting trees, mud pits, etc.— where competition and roar usage would likely be high.

Our results highlight the importance of considering the demographic specificity of potential PAM signals. The age-sex specificity of a target vocalization determines the subset of the population that is sampled with PAM and must be considered when interpreting monitoring studies. We quantified the age and sex dependent usage of four vocalizations in the forest elephant repertoire. While each call type was used by both sexes and all ages, this usage was notably uneven across demographic classes. Rumble usage transitioned from mostly male in juveniles to predominantly female as age increased (Fig. 1.3a bottom). Roars were produced primarily by males across all ages, and adult females exhibited a pronounced curtailment of roar use compared to subadult females and adult males (Fig. 1.3b bottom). Combination calls were also more often used by males than females, and were more common from younger elephants, with usage decreasing with age for both sexes (Fig. 1.3c bottom). Trumpets showed a slight tendency toward male production except for in subadults, when females notably increased trumpet usage (Fig. 1.3d).

The rumble has been the target signal of choice for PAM of forest elephants (Wrege et al., 2017). Until now, the extent to which rumbles are produced disproportionately by particular age-sex classes has not been explicitly tested. An assumption in PAM of forest elephants has been that the rumbles detected on remote acoustic recorders are mostly from adult females and their small family units, and that adult males have largely gone unsampled (P.H. Wrege, personal communication). The results of the present study generally support this assumption, but also suggest that PAM should detect rumbles from males of other age classes (Fig. 1.3a bottom panel), so males are not likely to go entirely unsampled. While rumbles do exhibit significant differences in usage between demographic classes, their use across all behavioral contexts (Table 1.2; Hedwig et al., 2021) and by both sexes across all ages (Fig. 1.3a bottom), likely moderates the potential unevenness in production across demographic classes. A similar moderating effect may act on combination calls, which are used in almost as many behavioral contexts as rumbles (Table 1.2). Combination calls, however, exhibit disproportionate male usage across all ages and a more pronounced decrease in use with age (Fig. 1.3c middle & bottom). Roars and trumpets also exhibit clear age and sex dependencies, thus unevenly representing certain population subsets. However, the addition of these demographically specific vocalizations into PAM frameworks could help leverage population demographic information from acoustic recordings. Combination calls could provide insight related to the presence of younger age classes, while roars would give greater detection power to adult males that produce rumbles at lower rates than adult females. Roars are produced disproportionately more by adult males than by most other classes, especially compared to adult females (Fig. 1.3b bottom). If competitive interactions involving roars occur frequently enough in the forest (e.g., at fruiting trees, mud pits, etc.), use of roars in PAM could balance the sampled population to match the target population more closely, improving statistical inference. This variability in the age-sex specificity of different vocalizations highlights how the choice of PAM signal determines the population (or subset) that is sampled. Certain vocalizations (e.g., rumbles) more equally represent the demographic classes of a population and provide more comprehensive data for population-level inference, but may still under-sample certain classes (e.g., adult male forest elephants that are unlikely to travel with adult female-led family groups). Vocalizations that exhibit more disproportionate usage among demographic classes (e.g., roars) can provide increased detection of a particular subset of the population.

Once identified, these types of differential rates in signal production can be used to aid interpretation of results or leveraged in the statistical analyses themselves. In a detection/non-detection or occupancy analysis (Mackenzie et al., 2002), the results would apply to the demographic classes that are primarily sampled, not necessarily the population as a whole. For example, an occupancy study on habitat use that employs roars or combination calls as target signals would primarily reveal the habitat use patterns of male forest elephants compared to a study that uses rumbles, which over-represent females. A more sophisticated approach would be to explicitly leverage the age-sex specificity of vocalizations in the statistical models. For example, extensions to basic occupancy approaches, such as multi-state models, can incorporate auxiliary information like age- or sex-specific vocalizations to improve inference (MacKenzie et al., 2018; Wood et al., 2020). In a multistate model, rumbles could be used for one occupancy state, and roars or combination calls for another, thus maximizing the amount of information gleaned from the acoustic record.

In a density estimation framework, the estimator equation can be adjusted to account for sampling bias due to demographic specificity of the target signal. This is possible if the proportion of individuals that vocalize is known, or if call rate, detection probability, or some other multiplier can be adjusted to reflect overall population density rather than the density of vocal individuals only (Marques et al., 2013; Stevenson et al., 2015). In the relatively straightforward example of a fully sex-specific signal (e.g., a vocalization produced only by males), call counts can be combined with estimates of sampling availability and sex ratio to estimate overall population abundance (Driscoll, 1998; Fischer et al., 1997). When the target signal is used by both sexes or across multiple age-classes, more complicated developments of abundance or density estimators may be necessary (e.g., Thompson, Schwager, Payne, et al., 2009). In any case, knowledge of the demographic specificity of potential PAM target signals will facilitate the implementation of acoustic-based density/abundance estimators.

This study focused on identifying potential differences in vocal repertoire use between age-sex classes, to inform PAM studies at the landscape scale. Forest elephants are particularly challenging because, across the landscape, they are highly dispersed and extremely cryptic. Elusiveness and challenges to visual observation are characteristics shared by many species for which PAM is employed (e.g., cetaceans); this is a major justification for implementing a PAM approach. It is therefore not surprising that vocal patterns with respect to demographic classes are poorly understood for many of the species for which PAM is used— it is difficult to observe and document these species' acoustic behavior. In the case of forest elephants, forest clearings (*bais*) provide a unique opportunity to observe and collect data that would be exceptionally difficult in the forest itself. However, these clearings act as social arenas that bring a self-selected portion of the larger population together in much higher densities than in the forest proper. We operate under the assumption that our observation and recording of vocal activity was not biased toward any particular age-sex class. The obvious way such a bias could arise is from differences between age-sex classes in their availability to be observed/sampled (e.g., more adult female than male elephants in the bai; Altmann, 1974). We directly accounted for this potentiality by quantifying the baseline age-sex class structure of the bai population and comparing the observed call frequencies to this demographic "control" (i.e., we controlled for sampling availability). Nevertheless, we recognize that the sub-population of bai visitors might itself be demographically biased with respect to the overall population. This sort of bias may not be entirely ameliorated by our control of sampling availability through quantifying the demographic structure within the bai.

Due to differences in density and context, elephant behavior also likely differs substantially between bai and forest (Hedwig et al., 2019). For example, the tendency of males to disproportionately produce roars may be a consequence of the frequent competition for access to mineral pits in the bai, which could involve more males due to their larger size and predisposition for risk-taking. If such competition is unique to the bai, this result may not apply to the forest in general. On the other hand, the forest harbors resources such as fruiting trees and mud pits that may stimulate similar competitive interactions, in which case our results should transfer to the forest.

This study advanced our understanding of forest elephant repertoire use. However, to fully resolve the discrepancies in call rates between age-sex classes, particularly in the forest itself rather than the bai, biologging acoustic tag studies are needed in which an acoustic recorder is integrated into a collar attached to the elephant. The use of acoustic recording tags to obtain call rates and acoustic behavior data has been successfully demonstrated with other species for which PAM is employed (e.g., cetaceans; Parks et al., 2011, 2019). While elephant collaring is invasive compared to PAM, it is one method to obtain call rates from individual animals and groups in the forest environment. These call rates are an integral component of density estimation equations (Marques et al., 2013) and can also inform occupancy studies by allowing researchers to optimize study design characteristics such as survey length (Bailey et al., 2007; MacKenzie et al., 2018).

Our research exemplifies how examining the acoustic behavior of a focal species can better contextualize the data and results from PAM. The choice of target signal will sometimes introduce a bias toward sampling a particular subset of the population. Call types used more equally across demographic classes will provide more reliable data for population-level inference, as the sampled population more closely reflects the target population. On the other hand, vocalizations that are specific to one sex or age class confer the ability to differentiate specific demographic classes of interest. Researchers should consider the assumptions behind their choice of target signal, and either account for sampling biases accordingly (e.g., adjust statistics or interpretation) or leverage biases to their advantage (e.g., extract demographic or contextual information from recordings). A benefit of the PAM approach is that archived acoustic datasets can be revisited when new information becomes available. Once behavioral data (e.g., demographic specificity of the vocal repertoire) on a species of interest becomes available, previously collected acoustic data can be retroactively analyzed to reveal additional population information and insights.

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Figures and tables

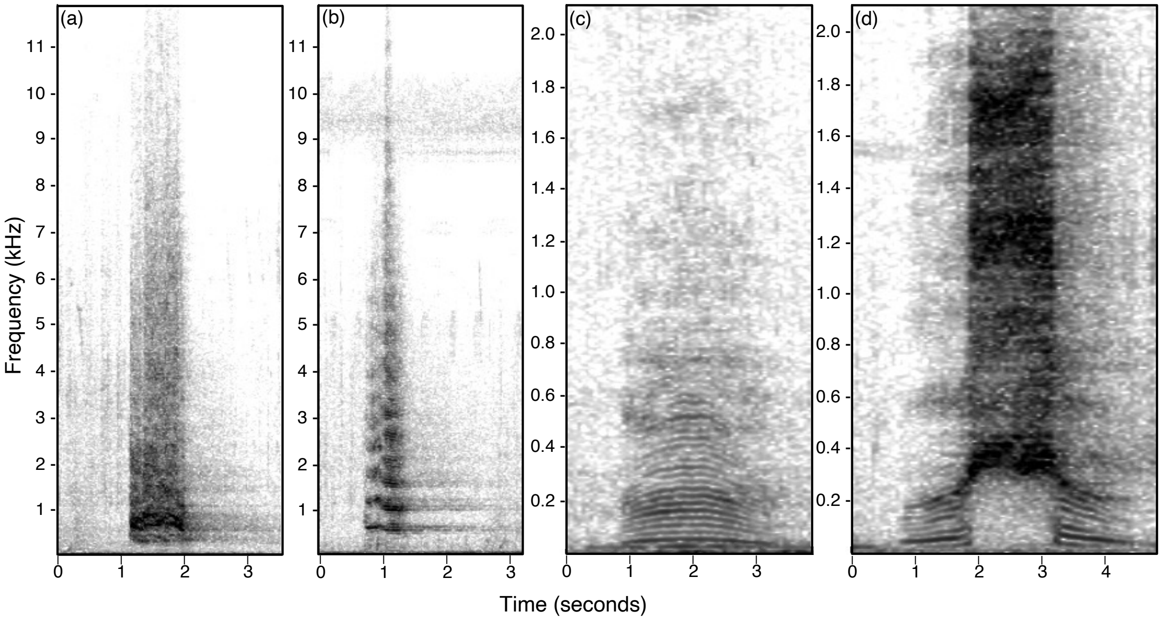


Figure 1.1 Spectrograms of representative examples of the four common forest elephant call types. Roars (a) are noisy broadband vocalizations extending into comparatively high frequencies (Poole, 2011). Trumpets (b) are the quintessential elephant sound, often high-pitched and somewhat tonal, produced by an expulsion of air through the trunk, rather than by the larynx as with the other call types (Poole, 2011). Rumbles (c) are harmonically rich, tonal signals with components near or within the infrasonic range (Poole et al., 1988; Thompson, 2009). Note the change in frequency range between (b) and (c). Combination calls, like this rumble-roar-rumble (d), include at least one rumble and one roar component produced contiguously as a single vocalization (Poole, 2011; Stoeger-Horwath et al., 2007). Spectrograms were made with Raven Pro 1.6 software (KLY-CCB, Cornell, 2019) with 2153-point (for (a) and (b)) and 6022-point (for (c) and (d)) Hamming windows, 90% overlap, and 8192-point discrete Fourier transform. Recording sample rate was 48 kHz.

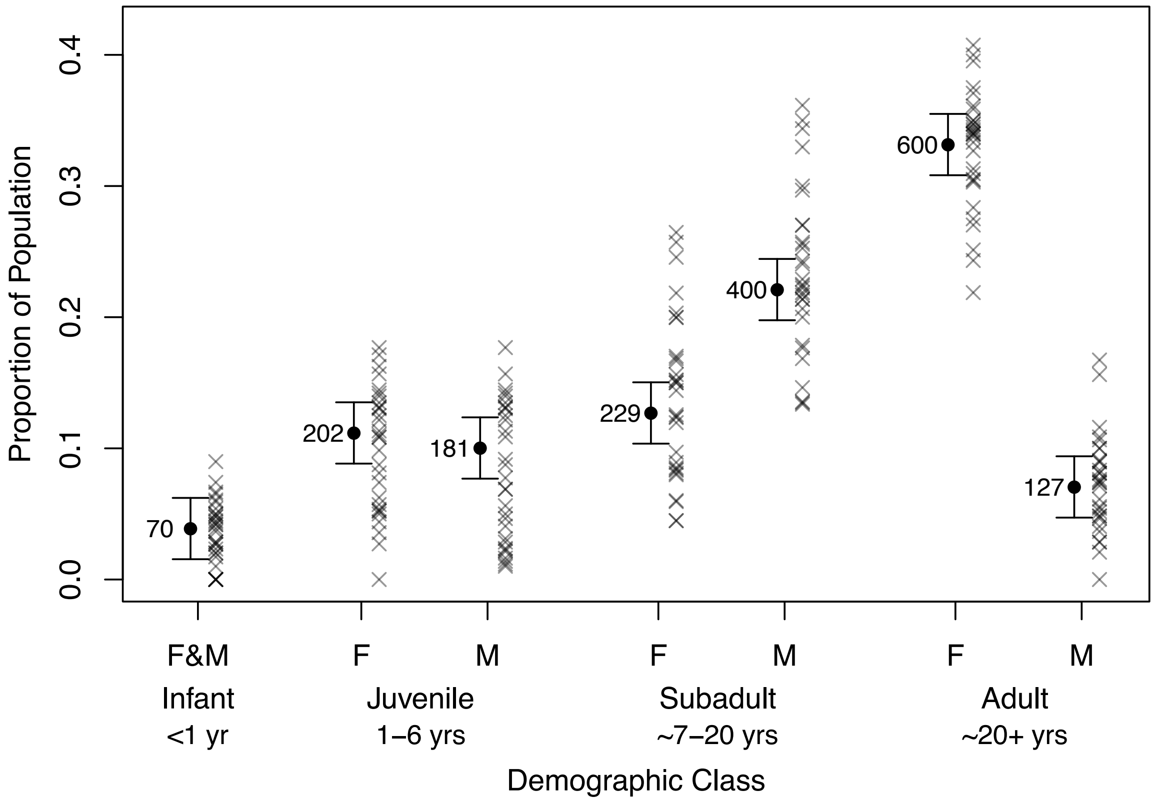
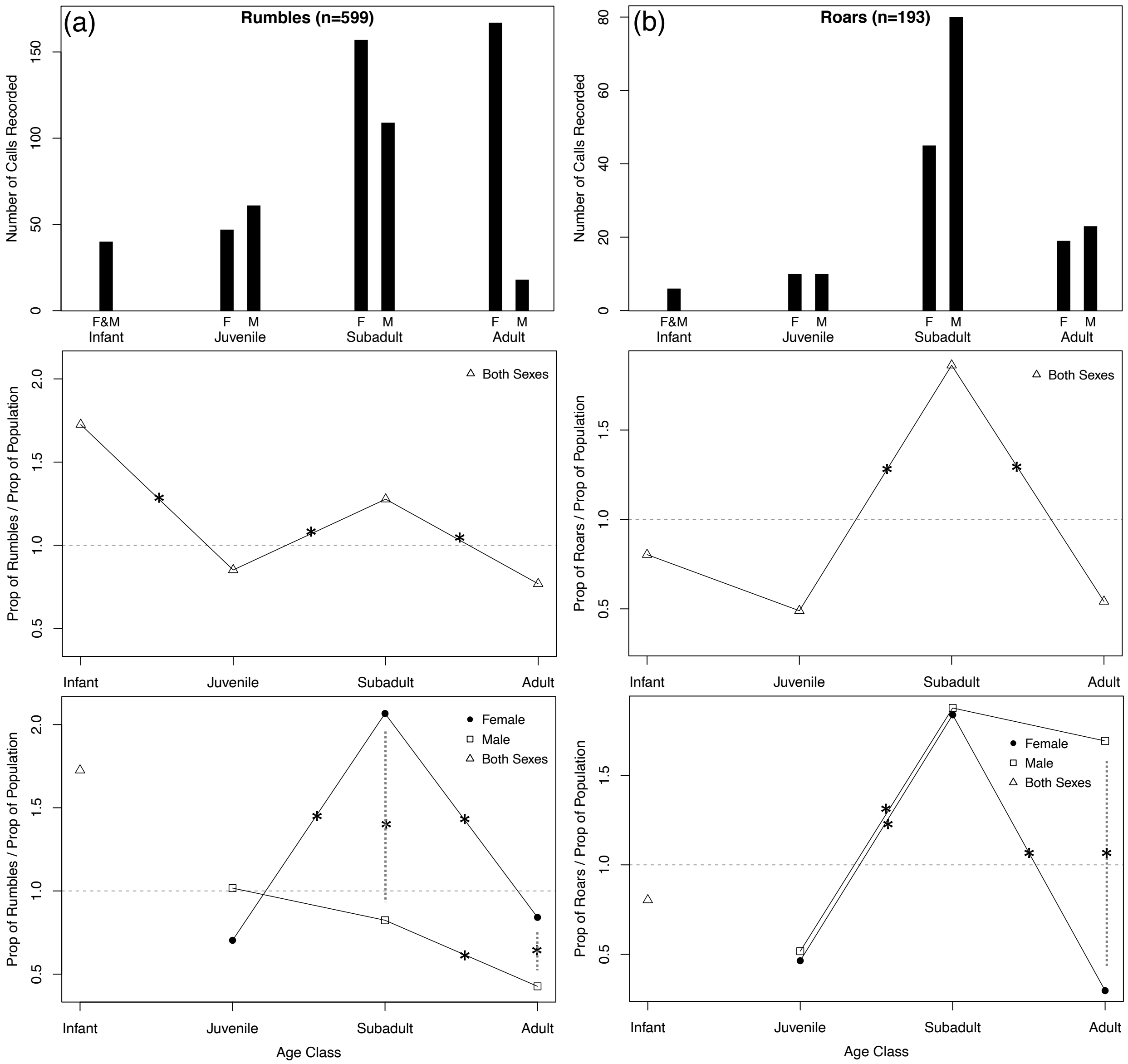


Figure 1.2 We assigned a total of 1809 elephants to age-sex classes over the course of 31 data collection days in 2020 (numbers of elephants of each class is shown). Overall baseline demographic proportions (pooled across 31 scan days) are shown as black circles with multinomial 95% confidence intervals. Individual (un-pooled) scan proportions are shown as adjacent X's.


(a)
Rumbles (n=599)
Number of Calls Recorded
0
50
100
150
F&M
Infant
F M
Juvenile
F M
Subadult
F M
Adult
(b)
Roars (n=193)
0
20
40
60
80
Prop of Rumbles / Prop of Population
Prop of Roars / Prop of Population
Both Sexes
0.5
1.0
1.5
2.0
Infant
Juvenile
Subadult
Adult
Female
Male
Age Class

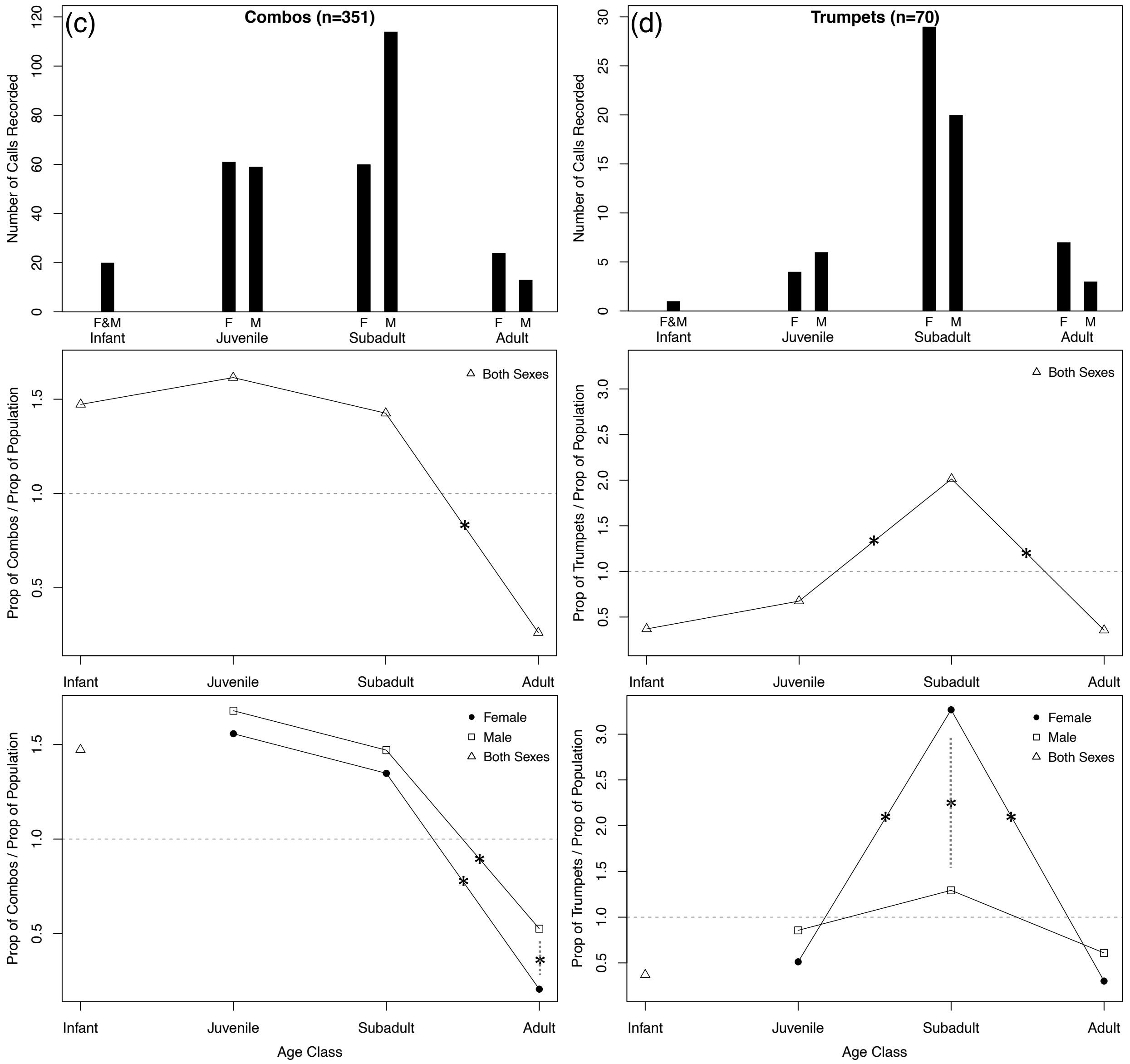


Figure 1.3 The frequency with which (a) rumbles, (b) roars, (c) combination calls, and (d) trumpets were produced by forest elephants of different age-sex classes. Raw call counts (top panels) do not account for baseline differences in the number of elephants in the bai representing each age class (i.e., sampling availability). To employ such a correction, we plotted the proportion of calls from each demographic class divided by the proportion of elephants in the baseline population belonging to that class (middle and bottom panels). Values around 1.0 (horizontal dotted lines) indicate that the proportion of calls from a particular age-sex class is what would be expected given that classes' representation in the bai. Values greater or less than 1.0 suggest disproportionately more or fewer calls than would be expected. Asterisks between sexes of a given age class, or between adjacent age classes of a given sex, indicate statistically significant differences in call type usage (alpha level = 0.05). Approximate ages classes: Infant <1 year; juvenile 1-6 years; subadult 7-20 years; adult 20+ years.

Table 1.1 Numbers of recorded calls (n = 1213) of each type by age-sex class. Aside from the 67 calls from infants (sexes combined), we recorded 630 calls from females and 516 from males.

	Infant	Juvenile		Subadult		Adult		Total
		Female	Male	Female	Male	Female	Male	
Rumbles	40	47	61	157	109	167	18	599
Roars	6	10	10	45	80	19	23	193
Combination	20	61	59	60	114	24	13	351
Trumpets	1	4	6	29	20	7	3	70

Table 1.2 Number of instances in which each call type occurred in different behavioral contexts. We defined contexts based on Hedwig et al., (2021), with minor modifications.

	Rumbles	Roars	Combination	Trumpets	All Call Types
Affiliation	198	1	24	3	226
Competition	78	181	145	3	407
Defensive	5	0	0	47	52
Sexual	8	1	0	1	10
Nursing	24	4	37	0	65
Separation	178	4	124	12	318
Alone	86	0	14	0	100
Unspecific	22	2	7	4	35

CHAPTER 2

Passive acoustic monitoring reveals behavioural response of African forest elephants to gunfire events

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Abstract

African forest elephants (*Loxodonta cyclotis*) are a critically endangered and visually cryptic species that inhabits Central African rainforests. Using a 1250 sq-km grid of 50 acoustic sensors in Republic of Congo, we investigated the landscape-scale behavioural response of forest elephants to poaching events. We detected eight automatic weapon fire events over 1.5 years of recording (2017—2019). We examined detections of elephant vocalizations across grid sites within 10 km of the gunfire events in the 48 hours surrounding the gunfire, and in paired 48-hour control periods free of gunfire. Fewer vocalizations were detected before gunfire events than during control periods, suggesting elephants show behavioural responses to poacher presence before any shots are fired. Immediately following the gunfire events a significant increase in elephant calls was detected, which may indicate increased communication to facilitate group cohesion and movement. Elevated call levels dropped to lower-than-baseline rates after several hours, suggestive of a sustained response. These patterns indicate forest elephants respond to both poacher presence and to gunfire events themselves. As these patterns may reflect behaviours that mediate population processes, conservation strategies should account for the potential of poaching to impact populations via indirect effects on non-target elephants in the area.

Keywords

African forest elephant, Rumble, Endangered species, Gunfire, *Loxodonta cyclotis*, Passive acoustic monitoring, Poaching, Vocalizations

Introduction

While African forest elephants (*Loxodonta cyclotis*) have few natural predators, poaching is analogous to predation and constitutes a grave threat to this critically endangered species (Blake & Hedges, 2004; Gobush et al., 2021; Maisels et al., 2013). It is unclear how forest elephants that are not killed by poaching respond to poaching pressure, although there is evidence that they change visitation patterns to forest clearings when local levels of elephant poaching are high (Fishlock, 2010; Maisels et al., 2015; Vanleeuwe et al., 1997). Studies have also revealed that forest elephants respond to human disturbance by temporarily (e.g., for several months) changing their distribution (Rabanal et al., 2010) and becoming more nocturnal (Wrege et al., 2010). However, studies of poaching effects have relied on proxies of poaching pressure, such as distance to access roads, rivers, or human settlements. These proxies serve as explanatory variables in models that include a measure of animal response as the response variable (e.g., animal abundance increases with distance to access road, which serves as a proxy of poaching pressure; Barnes et al., 1991, 1997; Blake et al., 2007, 2008; Hall et al., 1997; Laurance et al., 2006; Maisels et al., 2013; Yackulic et al., 2011). These studies have shown that forest elephants engage in risk avoidance behaviour including avoidance of roads, which researchers often interpret as avoidance of perceived poaching pressure (Blake et al., 2007, 2008; Yackulic et al., 2011). Unfortunately, these proxies do not consistently reflect levels of poaching pressure. Sometimes they are unsubstantiated and lack ground-truthing to confirm their correlation with actual poaching levels (Blake et al., 2008). Even when ground-truthing does exist, the relationship between proxy values and poaching levels is inconsistent and hard to generalize; Blake et al., (2007) found that signs of forest elephant poaching decreased with distance to the nearest road, while Laurance et al., (2006) found no relationship between hunting pressure and distance to roads.

Passive acoustic monitoring (PAM) offers an avenue to explore poaching impacts on wildlife more directly. PAM draws inference from autonomous acoustic sensors that can continuously record signals from species of interest and the environment (Blumstein et al., 2011; Van Parijs et al., 2009). In a PAM context, poaching pressure can be directly quantified by counting the number of gunshots detected at acoustic sensors (Astaras et al., 2017; Wrege et al., 2017). This allows poaching impacts on landscape use and other behaviours to be investigated directly— a major improvement over indirect proxies such as distance to roads. Poaching attempts and behavioural responses can be detected and quantified using the record of acoustic data.

Insights from the field of conservation behaviour indicate that studying such responses can contribute to the conservation of endangered species (Berger-Tal et al., 2016; Berger-Tal & Saltz, 2016; Blumstein & Fernandez-Juricic, 2004). Detectable patterns in vocal activity can reflect underlying behaviours that mediate population processes such as immigration, emigration, survival, and reproduction. Quantifying such behaviours can therefore inform population management and conservation (Berger-Tal et al., 2016; Berger-Tal & Saltz, 2016; Blumstein & Fernandez-Juricic, 2004). Forest elephants may abandon areas with high poaching pressure, thereby forsaking otherwise high-quality habitat. This would mean that in addition to directly killing elephants, poaching could have indirect population-level consequences (Blumstein & Fernandez-Juricic, 2010; Frid & Dill, 2002). A first step in exploring such indirect population effects is to test whether forest elephants respond in a detectable way to individual poaching events. Anecdotal evidence suggests that forest elephants reduced their use of a forest clearing following gunfire (personal observation), and temporarily avoided a poached conspecific carcass (Stephan et al., 2020). Other than these examples, to our knowledge no one has systematically investigated forest elephant response to individual poaching events on any scale. For those elephants that are not directly killed but that witness or hear the event at a distance, do gunshots elicit an acoustically detectable response?

There are several reasons to expect changes in vocal behaviour in response to poaching events, particularly in the use of rumble vocalizations. Rumbles are harmonically rich vocalizations with frequency components near or within the infrasonic range (i.e., below 20 Hz; Poole et al., 1988; Thompson, 2009). Rumbles are used in a variety of contexts, including group cohesion and movement coordination (Leighty et al., 2008; Poole et al., 1988). After a poaching incident, elephants might increase rumble production to coordinate the reunion of family units following separation, or movement away from the dangerous area. Alternatively, rumbles could function as alarm signals that propagate information away from the disturbance, as demonstrated in the alarm calls of a variety of taxa (Caro, 2005; Hollén & Radford, 2009). We unite these possibilities and refer to this as the 'coordination' hypothesis— due to the disruptive nature of poaching attempts, rumble production increases following the events.

A contrasting possibility would be fewer rumbles following a poaching attempt than before. Forest elephants could immediately abandon the area and redistribute to less dangerous locations, resulting in an absence of elephants and their vocalizations. We refer to this as the 'abandonment' hypothesis. Alternatively, elephants could reduce their vocal activity without leaving the area. Reducing vocalization to avoid detection by predators is a tactic shared among many taxa (Parks et al., 2019; Ruxton, 2009). As poaching is the closest thing to predation that forest elephants experience, they may respond to poaching activity in a similar manner. We refer to this as the ‘crypsis’ hypothesis. We used a PAM approach to test these hypotheses that forest elephants respond to poaching events in a way that is acoustically detectable.

Methods

Data Acquisition

A grid of 50 acoustic sensors was established in Nouabalé-Ndoki National Park (NNNP), Republic of Congo, by the Elephant Listening Project (ELP, KLY-CCB, Cornell) in collaboration with the Wildlife Conservation Society (Fig. 2.1). Sounds were recorded continuously between December 2017 and May 2019 using acoustic recorders (Koch et al., 2016) with a sampling rate of 8 kHz and 16-bit resolution. The grid covers an area of 1250 km^2 (mean inter-sensor distance of 5.5 km [SD=1.4]), with portions extending into an adjacent forestry concession. Batteries were replaced and data were retrieved from the sensors approximately every four months. Controlled experiments conducted near a ranger training site in the same forest indicate that gunshots are detected at distances of at least 2 km from the sensors. We used a template-based detector algorithm trained on recorded gunshots to search the continuous audio dataset for gunfire (see Wrege et al., 2017 Appendix S3 for detector details). The algorithm’s putative gunshot detections were then manually reviewed via spectrographic and auditory analysis by experienced personnel. During this process, all false positive gunshot detections were removed from the dataset. For confirmed gunshots, we manually inspected spectrograms to verify that no additional missed gunshots occurred within 24 hours of the focal shot(s). We aggregated any shots occurring within 30 minutes of one another into ‘gunfire events’, because these would likely represent a single hunting or elephant poaching attempt. Gunfire events were each detected at a single sensor only, which we defined as the gunfire event site. From December 2017 through May 2019, we detected eight automatic gunfire events (Fig. 2.2a), each at a different site and date (Fig. 2.1). From our interviews with anti-poaching patrol teams in NNNP and nearby national parks, we have high confidence that automatic weapon fire (e.g., AK47) events represent attempted elephant kills, whereas single-action weapon fire likely includes illegal hunting of other species. While single action hunting events were more common (we detected over 50 during the study period), we limited analyses to the eight automatic weapon fire events to focus on elephant poaching per se, rather than illegal hunting in general. This also allowed us to focus on events that would most likely elicit a behavioural response (automatic weapon fire events contain many gunshots; Fig. 2.2a). Anticipating that the number of gunshots in the events might influence elephant response, we quantified the intensity of each event as the number of individual rounds fired.

The presence of elephants near a gunfire event site was indicated by detection of their rumble vocalizations (Fig. 2.2b). Rumbles are a favorable signal for this purpose because they are the most common vocalization and are used by both sexes and all age classes (Poole et al., 1988; Stoeger et al., 2014). These signals are also well-suited for PAM due to their low frequencies, which are less prone to environmental attenuation than higher frequencies (Ingard, 1953), allowing a greater detection range than other signal types. Our previous detection distance experiments indicate that we can detect rumbles at a range of 500-600 m, corresponding to a detection area of approximately 0.79-1.13 km^2 around each of the grid's 50 sensors. We used an automated detector algorithm to extract rumbles from the continuous audio dataset. This algorithm is based on a feature extraction and classification system and uses time- and frequency-domain features to provide a likelihood that a detected signal is an elephant rumble (Keen et al., 2017). We manually reviewed the detector output to confirm detections and remove all false positives from the dataset. We evaluated detector performance by manually reviewing spectrograms from a subset of the continuous audio data to find all existing rumbles. Comparing this to the detector output for the same period, we calculated the average proportion of existing rumbles found by the detector to be 75%.

For each gunfire event, we included rumbles from all sensor sites within 10 km of the event site. This resulted in clusters of five to fifteen sensors analyzed for each event (mean 9.1 sensors per event cluster; Fig. 2.1). This decision was based on review of several forest elephant GPS collaring studies, which found that while forest elephants are capable of higher speeds, mean daily travel distances and/or displacements are between 1 and 9 km (Blake, 2002; Blake et al., 2008; Kolowski et al., 2010; Mills et al., 2018). Including sensors out to 10 km from the poaching site afforded us high confidence of detecting behaviours of elephants that were exposed to or aware of the poaching event. As we were uncertain of the timescale over which a response might occur, we included elephant calling activity occurring within 24 hours before and after each gunfire event. We predicted that any potential response would be most pronounced and detectable in the period immediately following each event.

To establish a baseline of elephant vocal activity in the absence of any gunfire, we established one 48-hour control period for each of the eight event clusters, during which no gunshots of any kind were detected (single-action or automatic). For each control, we quantified rumble detections at all sites in the cluster, so that each control utilized the exact set of sensors as its corresponding gunfire event. This controlled for spatial variation in elephant abundance across the grid sites and promoted comparability between gunfire and control periods. We centered each control period three days prior to its corresponding gunfire event, at the exact same time of day as the gunshots. However, for some events this interval had to be shifted longer to avoid data gaps at particular sensors (maximum interval: 10 days). We kept this interval short to minimize any effect of seasonal change in elephant abundance and promote comparability between control and gunfire events, rather than to uphold any assumption of individual-level closure— we expected individual elephants to move freely between sites (turnover of individuals).

Statistical modeling

Initial GLMMs: comparison to baseline activity

Having accounted for the elephant rumbles in the 48-hour periods centered on each gunfire event and in the 48-hour control periods free of gunfire, we first implemented a modeling strategy to detect potential elephant responses to gunfire events, and to determine if responses differ from baseline activity. Our design improved upon simpler spatio-temporal sampling designs (e.g., baseline, before-after, simple Before-After-Control-Impact [BACI], etc.) by including multiple control and impact sites (n = 8 clusters of 5-15 sites), and by incorporating a "staircase" structure (Walters et al., 1988) in which treatments and control periods are staggered through time rather than all occurring simultaneously. These design features remedy the issues associated with simpler designs— namely, the inability to isolate treatment effects from potentially confounding random events, due to a lack of spatial replicates and temporal staggering (Underwood, 1992, 1994; Walters et al., 1988).

We expected any initial response to such dramatic events to be immediate— within several hours of the gunfire. However, we also wanted to accommodate the potential for a sustained response, perhaps with different temporal or behavioural characteristics than the immediate response. We divided the 24-hour period after the gunshots into an 'immediate' (hours 1 to 5) and a 'sustained' (hours 6 to 24) interval, each of which was paired to the corresponding interval from before the gunfire (hours -1 to -5 and -6 to -24, respectively). We located the division between the two intervals based on qualitative patterns noticed during initial data exploration. We chose a non-overlapping ‘sustained’ interval— hours 6 to 24 rather than hours 1 to 24— so that the measurement of potential sustained effects would be unconfounded by immediate responses. We matched each of these two intervals to a corresponding model to test for an immediate and sustained behavioural response. We constructed generalized linear mixed-effects models (GLMMs) using the ‘glmmTMB’ package (Brooks et al., 2017) in R (R Core Team, 2022). The response variable was the rumble count at each sensor (site) for each of the eight gunfire events and eight control periods (n = 294 counts). Note that rumble counts were made at each of the five to fifteen sensors within 10 km of the gunshot site, not just the sensor at which the gunfire was detected. We included *event ID* as a random effect to control for these repeated measures (multiple sensors within an event cluster). We included *distance* of each sensor to the gunshot detection sensor to account for potentially stronger responses closer to the poaching sites. Our predictor variable of major interest— *period*— defined the time intervals over which rumbles were counted at each sensor. For the ‘immediate’ model, we defined *period* as the five hours before vs. after the gunshots, and the analogous intervals from control periods. We incorporated *period* as a fixed effect with three levels (before, after, control) to detect any responses to gunfire and to contrast this with baseline activity. Using an information theoretic framework (Burnham & Anderson, 2002), we compared a *period* X *distance* interaction model to a null model and to simpler main effects models. To account for zero inflation in the rumble count data, we specified all GLMMs as hurdle models with truncated negative binomial distributions. These two-part models allow the probability of zero-counts and non-zero counts (conditional abundance) to be modeled independently (Mullahy, 1986). We explored modeling both components as a function of *period*, *distance*, and/or their interaction. However, the zero-inflation (zero-count) component consistently fit the data best as a function of a constant intercept. We therefore structured the zero-inflation component as intercept-only for all GLMMs, while modeling the conditional component with the variables described above (see Table 2.1 for candidate model structure). We followed this same strategy for the 'sustained' model, but with *period* defined as -24 to -6 hours before and 6 to 24 hours after the gunshots (and the analogous intervals from control periods).

We controlled for the influence of natural diel vocalization patterns on our measurement of elephant response in three ways. First, we centered the control periods at the exact time of day that the gunshots occurred in the corresponding gunfire events. Second, we implemented 'sustained' models whose intervals extended ±24 hours from the time of the gunshots, so that any natural diel rumble patterns would be encapsulated by both the before and after periods. Lastly, we compared the times of the eight gunfire events to control period rumbles and to a model fit to these baseline rates (Fig. 2.S1), confirming their unbiased distribution.

Subsequent GLMMs: event variability

Focusing only on the before-after data from gunfire events (no control periods), we examined how the 'immediate' behavioural response was influenced by event intensity, measured as the number of gunshots comprising each event. We included the *number of gunshots* as a fixed effect, as well as its interaction with *period* and *distance*. Our relatively small sample size and the zero-inflated nature of the data would not accommodate a 3-way interaction between all three variables. The interaction between *period* and *number of gunshots* was of most interest because it represented our hypothesis that elephants would respond to gunfire events in a way that varied with event intensity. We compared this model to a null model and to other candidate models with 2-way interactions and/or main effects only (see Table 2.S1 for candidate model structure). We again included '*event ID'* as a random effect. We implemented this modeling strategy for the 'immediate' period only, as our aim was to elucidate the short-lived behavioural response immediately following gunfire (see Results).

We therefore represented the 'coordination' and 'abandonment'/'crypsis' hypotheses as candidate models for comparison, and allowed for variation in response due to event intensity (number of gunshots), distance, and time relative to the gunfire ('immediate' vs. 'sustained' intervals). Variables that we accounted for but did not include in the final modeling framework are presented in 2.S1 Text. We used an information theoretic approach for model selection and parameter estimation to arbitrate between these competing hypotheses, while accommodating the null hypothesis of no response. Model selection and inference proceeded according to Akaike's Information Criterion and model weights (Burnham & Anderson, 2002). Finally, to visualize the temporal characteristics of any responses, we plotted rumbles over time. We divided the 48-hour gunfire events into 1-hour bins and for each bin we summed the rumbles across all sensors for each event cluster.

Results

The gunfire events contained on average 34.3 gunshots (SD=27.9; range: 7-81) and had a median duration of 2.5 minutes (mean: 8.5; range: 0.17-33.7). A total of 516 elephant rumbles were detected for use in analyses, 187 (36%) during gunfire events and 329 (64%) during control periods. The temporal distribution of these rumbles relative to gunfire events varied substantially (Fig. 2.3a), but generally there were more rumbles following a gunfire event than preceding it. This pattern was especially prominent during the five hour 'immediate' intervals (Fig. 2.3b).

Initial GLMMs: comparison to baseline activity

There was no support for an influence of *period* or *distance* in the zero-inflation model component, so this was structured as intercept-only for all models (Table 2.1). The probability of zero rumbles on a single sensor during a given period was 0.92 (inverse logit of 2.47) for the 'immediate' and 0.81 (inverse logit of 1.46) for the 'sustained' interval (Table 2.2). For the conditional (non-zero count) model component, during the 'immediate' interval, the *period* + *distance* model ranked definitively higher than the other candidate models (Table 2.1)—strong support that variation in rumble counts was influenced by *period* and *distance*. Rumbles per sensor were lower before gunfire events compared to control periods ($\beta_{\text{periodBef}}$ estimate < 0; p = 0.016; Table 2.2; Fig. 2.4a), and higher after gunfire events than before (p = 0.006; Fig. 2.4a). Rumble counts increased with distance from the poaching event site/sensor (β_{distance} estimate > 0; p = 0.013; Table 2.2; Fig. 2.5). For the 'sustained' interval, the *period* model ranked the highest, but was followed by the null and *period* + *distance* models within 2 AIC units (Table 2.1). Rumble counts did not differ between before and after gunfire periods (*period* model before-after p = 0.976; Fig. 2.4b). However, rumble counts from both before and after gunfire periods were significantly (or marginally significantly) lower than in control periods ($\beta_{\text{periodBef\&Aft}}$ estimates < 0; Table 2.2; Fig. 2.4b). *Distance* was far less important in the 'sustained' period (p = 0.782; Table 2.2).

Subsequent GLMMs: event variability

The zero-inflation component was structured as intercept-only for all models (Table 2.3). The probability of zero rumbles on a single sensor during a given period was 0.91 (inverse logit of 2.33; Table 2.4). For the conditional component, while no model unambiguously outperformed all others, there was strong support for the influence of both *period* and *number of* *gunshots* on elephant response—these two variables composed the two top-ranked models (Table 2.3). The *period* + *number of gunshots* additive model ranked highest according to AIC, followed by the *period* X *number of gunshots* interaction model and other candidates within 2 AIC units (Table 2.3). The four top-ranked models (within 2 AIC units of the top model) make similar predictions. All four predict a higher number of rumbles per sensor in the 5-hour period after the gunfire events than before ($\beta_{\text{periodAft}}$ estimates > 0; Table 2.4). Three of the four top models predict rumbles to increase with the number of gunshots composing the events (β_{shots} estimates > 0; Table 2.4). According to the second-ranked interaction model, the effect of *period* is strengthened as the number of gunshots constituting an event increases ($\beta_{\text{periodAft*no. gunshots}} = 0.02$; Table 2.4). This trend is corroborated in rumbles summed across all sensors of the individual event clusters, where post-gunfire rumble counts increase more drastically for events characterized by many gunshots (Fig. 2.6; note that the summed rumbles visualized here differ from the GLMMs, which used rumble counts at each sensor). There was some support for an effect of *distance*, with rumble counts increasing with distance from the poaching event site/sensor (β_{distance} estimates > 0; Table 2.4).

Discussion

We reveal two behavioural responses of forest elephants to poaching activity. The two responses each exhibit a distinct pattern of elephant vocalizations. Each response occurs at a different time (before versus after gunfire) and presumably results from a different aspect of poaching activity (poacher presence versus gunfire).

The first discovery of this study is a reduction in rumble vocalizations when poachers are in the vicinity, even before any gunshots are fired. The pattern of overall higher rumble counts in control periods compared to before-gunfire periods pertained to both ‘immediate’ and ‘sustained’ interval data (Fig. 2.4ab; Table 2.2). *Period* is an important variable in the top models for both intervals, where significant or marginally significant differences exist between control and before-gunfire rumble counts (Fig. 2.4ab; Table 2.2). This suggests that forest elephants may be responding directly to the presence of poachers in the forest. As poachers move into an area, elephants may reduce their vocalization rate (‘crypsis’), move away in avoidance (‘abandonment’), or some combination of the two. The potential impact of these different behavioural responses on elephant ecology could be significant. From a survival perspective, acoustic crypsis would not be effective because poachers do not use elephant vocalizations to locate (and then kill) them, but the behaviour might be a more general response to fear. Abandonment could affect access to important resources and shift the distribution of elephants on the landscape, potentially increasing competitive interactions. Unfortunately, PAM has difficulty separating these alternatives because the absence of vocalizations does not necessarily mean the animals are not present.

This study also found an acute but short-lived response to gunfire characterized by increased rumbles immediately after gunfire, followed by a decrease to lower-than-baseline rumble counts after several hours (Fig. 2.4). In the initial GLMMs comparing gunfire and control period activity, the superiority of the *period* + *distance* model over all other candidate models for the ‘immediate’ interval suggests that this response represents a legitimate departure from baseline activity (Fig. 2.4a; Tables 2.1 & 2.2) and from normal diel variation in call rate (Fig. 2.S1). The spike in vocalizations following gunfire is apparent (Fig. 2.3b).

The subsequent GLMMs of only gunfire event data provide further evidence of this response. The highest-ranked models all contain the *period* variable (Table 2.3) and provide evidence of increased vocalization following gunfire ($\beta_{\text{periodAft}}$ estimates > 0; Table 2.4). We can appropriately draw inference from the top four models (ΔAIC < 2), as their cumulative AIC weight equals 0.67 (Tables 2.3 & 2.4), and the remaining models in the candidate set received substantially less support (Table 2.S1). These models support the 'coordination' hypothesis—due to the disruptive nature of poaching events, rumble production increases afterward in accordance with an elevated need for communication and coordination. This may be indicative of the important role that rumble vocalizations play in group cohesion. Alternatively, rumbles following a poaching event could be alarm signals, propagating information regarding the disturbance away from the focal site.

We also provide evidence that this response to gunfire is partially dependent on event intensity. Three of the four top models predict rumbles to increase with the number of gunshots, and there was some evidence that events characterized by more gunshots resulted in more drastic increases in rumbles from before to after periods (Table 2.4). When rumbles are summed across all sensors for each event cluster, the influence of the number of gunshots on elephant response is apparent (Fig. 2.6). Multi-shot events might be associated with attacks on larger groupings of elephants, resulting in higher numbers of traumatized individuals communicating with the population. Alternatively, events involving only a few shots might be less detectable at a distance and could go unnoticed or misinterpreted by elephants far from the poaching site.

Some of the variability in response is likely due to the distribution of elephants in the vicinity prior to the gunfire events, irrespective of the number of gunshots fired. We are less likely to detect a response if very few elephants are in the area when the poaching attempt occurs. An important element of future analyses will be to explore baseline changes in elephant distribution at varying time scales and with all 50 sensors of the grid. This highlights one of the major tradeoffs involved with PAM— while it allows continuous data collection on otherwise unachievable spatial and temporal scales, the amount of data and effort required for extracting signals of interest can be enormous.

Another issue related to the unknown elephant distribution is the potential for systematic bias in elephant abundance between gunfire and control periods. As poaching necessarily occurs where and when elephants are present, the gunfire event periods could be more likely to have elephants present, and in higher abundance, compared to control periods in which elephant presence is not a given. However, given that the majority (64%) of all rumbles occurred during control periods, such a bias is highly unlikely in our dataset. In general, our sampling strategy of using identical clusters of sensors for control periods and gunfire events, separated by a short time interval, was designed to control for variation in elephant abundance.

The observed changes in calling behaviour immediately following gunfire likely involve elephants not directly targeted but that hear the gunshots, as well as more distant individuals that learn of the disturbance through communication. As mentioned above, multi-shot events could theoretically expose more individuals directly to poaching trauma, which in turn could trigger elevated vocalization rates. However, we do not believe the activity of directly targeted elephants to underlie the responses we have discovered, for three reasons. Forest elephants generally move in family groups of two to three individuals, or solitarily in the case of bulls (Fishlock et al., 2008; Morgan & Lee, 2007; White et al., 1993). For a given poaching attempt, we therefore do not expect there to be numerous escaping elephants that could contribute to a vocal response. Second, rumbles were never detected simultaneously with gunfire, and only once was a rumble vocalization identified within five hours after gunfire at the poaching site itself. Third, during the 'immediate' interval, *distance* featured prominently in the top model of the initial GLMMs

(Table 2.2)—rumble counts were higher at sensors farther away from the gunfire site than at nearby sensors (Fig. 2.5). Therefore, detected responses to gunfire involve elephants distributed throughout the area around the poaching attempts (within approx. 10 km), but not necessarily directly targeted individuals that experienced the poaching attempt firsthand.

Compared to the immediate post-gunfire vocal activity, we observe a very different pattern in the ‘sustained’ interval. Following the high vocal activity immediately after gunfire, rumble counts drop to levels that are similar to pre-gunfire periods, and significantly lower than control periods (Fig. 2.4b; Table 2.2). This indicates that the initial vocal increase in response to gunfire is short-lived and is followed by a sustained response of lower-than-baseline vocal activity. Again, calling frequency could be low because individuals have relocated to other potentially less dangerous areas (‘abandonment’) or because they have restricted acoustic communication (‘crypsis’). Our current sampling and analysis scheme does not allow us to illuminate the mechanism underlying the sustained reduction in vocalization.

This study generated useful findings and implications for continued PAM research on African forest elephants. We now know that we can detect an acute but short-lived behavioural response to individual poaching attempts that would be unobservable through any other means. We know that we can expect this response to be characterized by increased elephant vocal activity immediately following gunfire events, whereas previously we may have expected the opposite (reduced vocal activity). This is followed by a reduction in calls to below baseline rates, indicating a sustained response. We have also revealed a reduction in elephant vocalizations while poachers are in the vicinity, before any gunshots are fired. These contrasting before-after patterns will be helpful in developing future PAM sampling schemes investigating forest elephants and poaching. An important next step is to look at longer time scales and ask, for example, whether forest elephants abandon otherwise high-quality habitat because of continued or intermittent poaching pressure.

The implications of this research for the conservation of African forest elephants are substantial. Together, the response patterns suggest that poaching attempts influence the behaviour of non-target elephants in the vicinity. While the acute behavioural changes appear short-lived, we provide some evidence of a sustained response. We reveal increases and decreases in vocal activity, lending support to both the ’coordination’ and the ‘abandonment’/’crypsis’ hypotheses, with their associated behaviours each dominating at a different point in time. If these behaviours incur costs and occur in many individuals, they may manifest as population-level consequences by influencing the vital processes of survival, reproduction, immigration, and emigration. In addition to the outright killing of target individuals, our study suggests that poaching has indirect consequences for non-target forest elephants which should be considered by future conservation strategies.

Acknowledgements

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Data Availability

The acoustic data used in this study is archived and freely available in the form of sound files accessible via Amazon Web Services Open Data Sponsorship Program: https://registry.opendata.aws/elp-nouabale-landscape/ (Elephant Listening Project, 2021)

Figures and tables

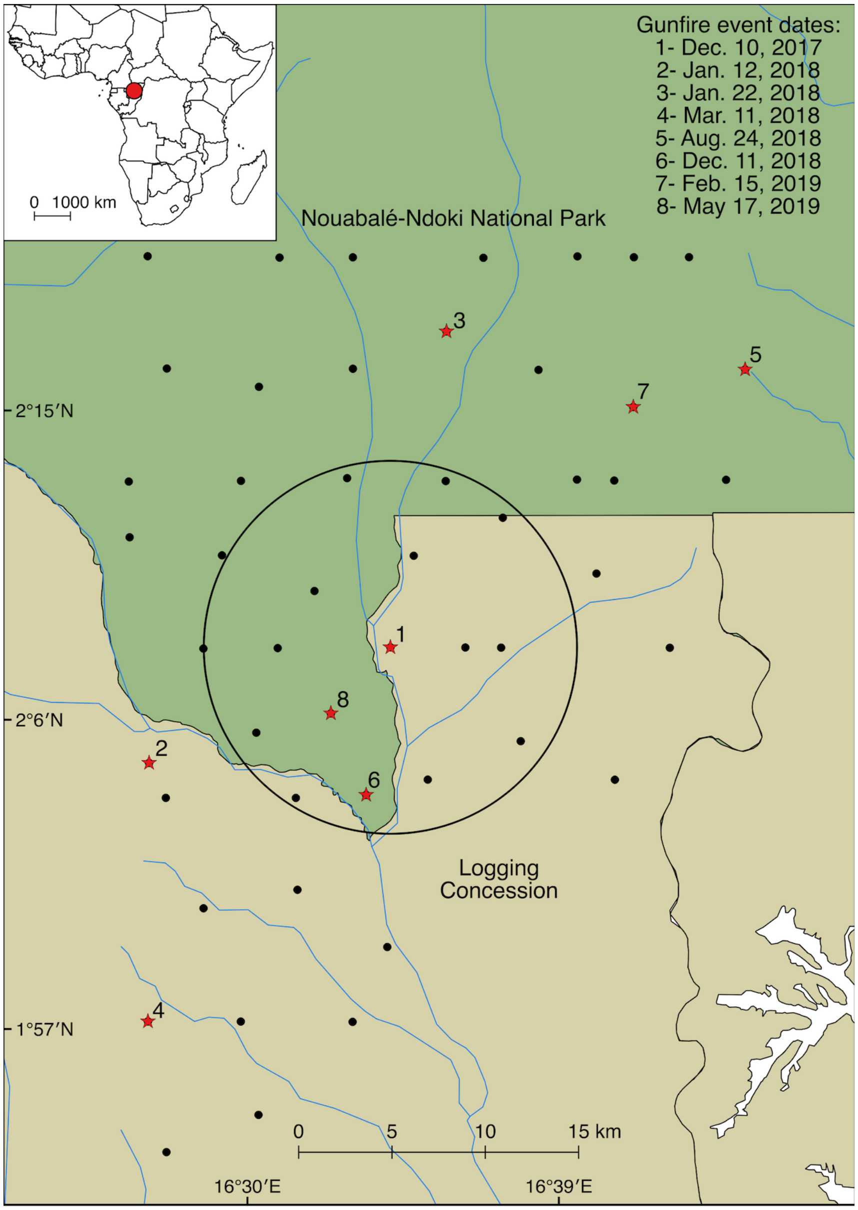


Figure 2.1 Map of the 50-sensor study grid, spanning portions of Nouabalé-Ndoki National Park (NNNP) and the adjacent forestry concession. Black dots indicate sensors and red star symbols indicate the eight sensors at which automatic weapon fire events were detected, numbered chronologically by event date. The circle centered on gunfire site/event one is an example of the 10 km distance within which rumble counts from all sensors were analyzed with GLMMs for a given event. The red dot in the inset panel indicates the location of the study area in Republic of Congo in central Africa.

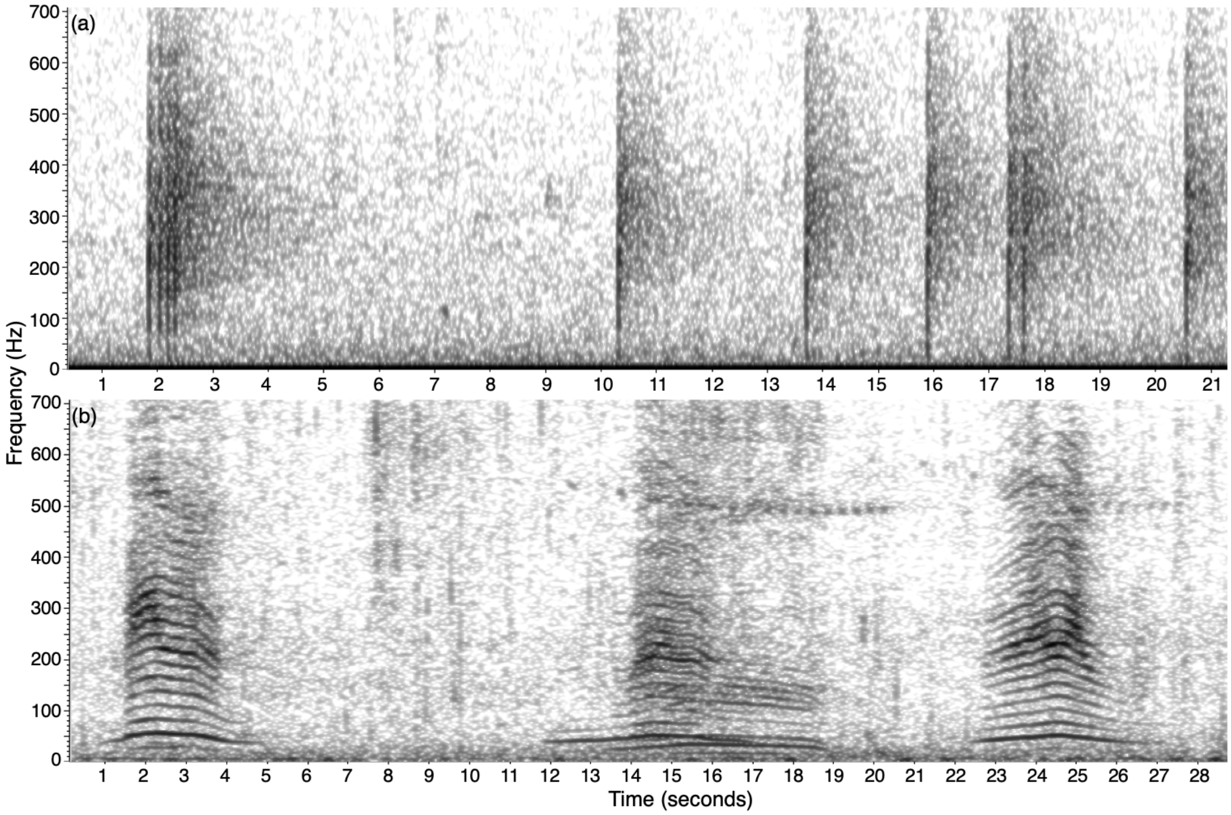


Figure 2.2 Spectrogram of (a) a portion of an automatic weapon fire event, zoomed in on a burst of four shots fired in rapid succession, followed by several 1- and 2-shot segments, and (b) a series of forest elephant rumble vocalizations, including two overlapping rumbles from different individuals (at 12-19 seconds). Spectrograms made with Raven Pro 1.6 software (Raven Pro, KLY-CCB, Cornell, 2019) with 1040-point (130-ms) and 2300-point (288-ms) Hamming windows (for (a) and (b), respectively), a 90% overlap, and a 4096-point discrete Fourier transform.

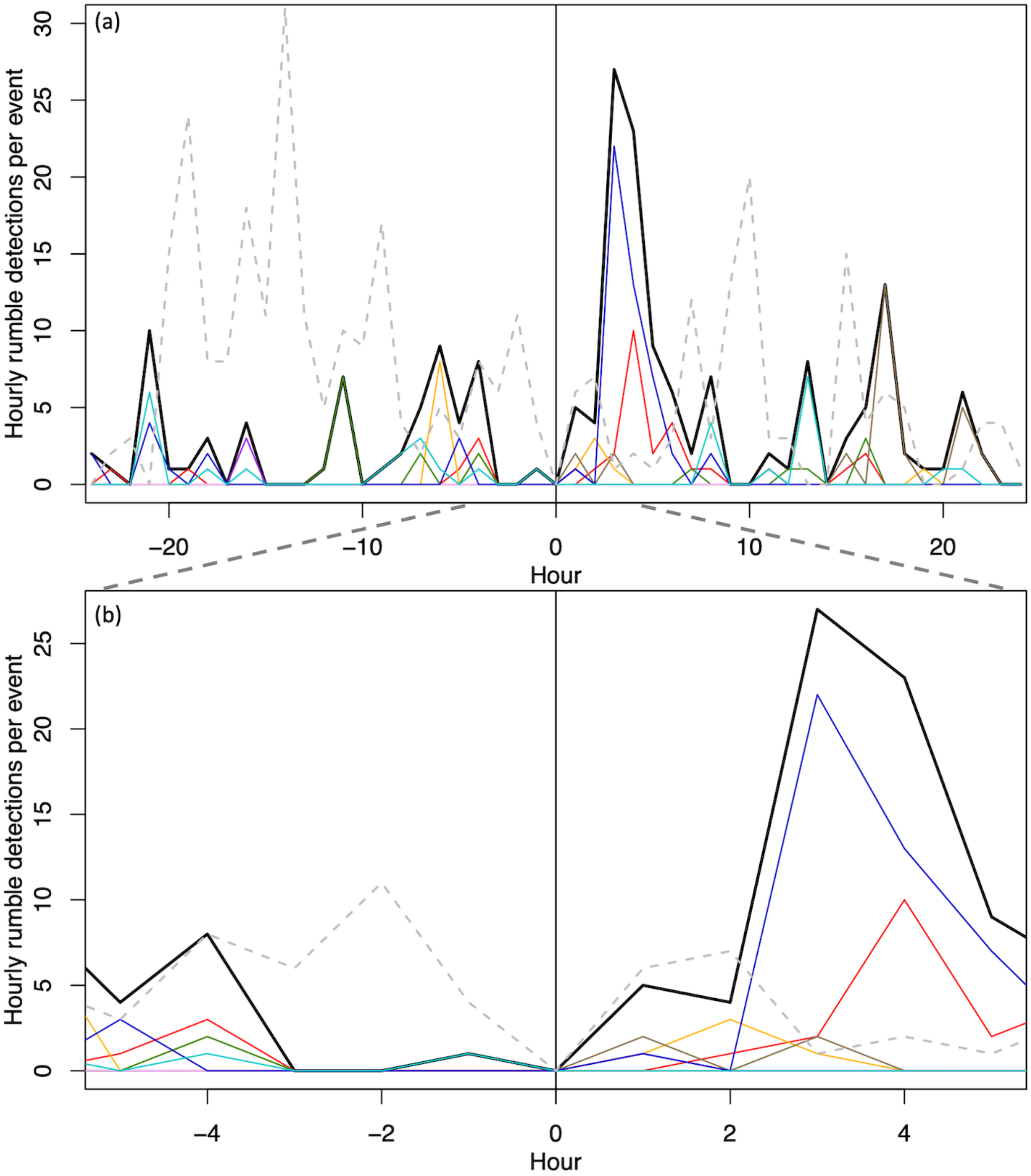


Figure 2.3 The total number of elephant rumbles per hour, summed across all sensors of each event cluster, for (a) the entire 48-hours centered on each gunfire event, and (b) the 'immediate' interval of ±5 hours from each gunfire event. The black vertical line at hour zero is the instance of the gunfire. The coloured lines represent these sums for each independent gunfire event. The thick black line represents rumbles summed across all eight gunfire events. The dashed grey line represents rumbles summed across all eight control events.

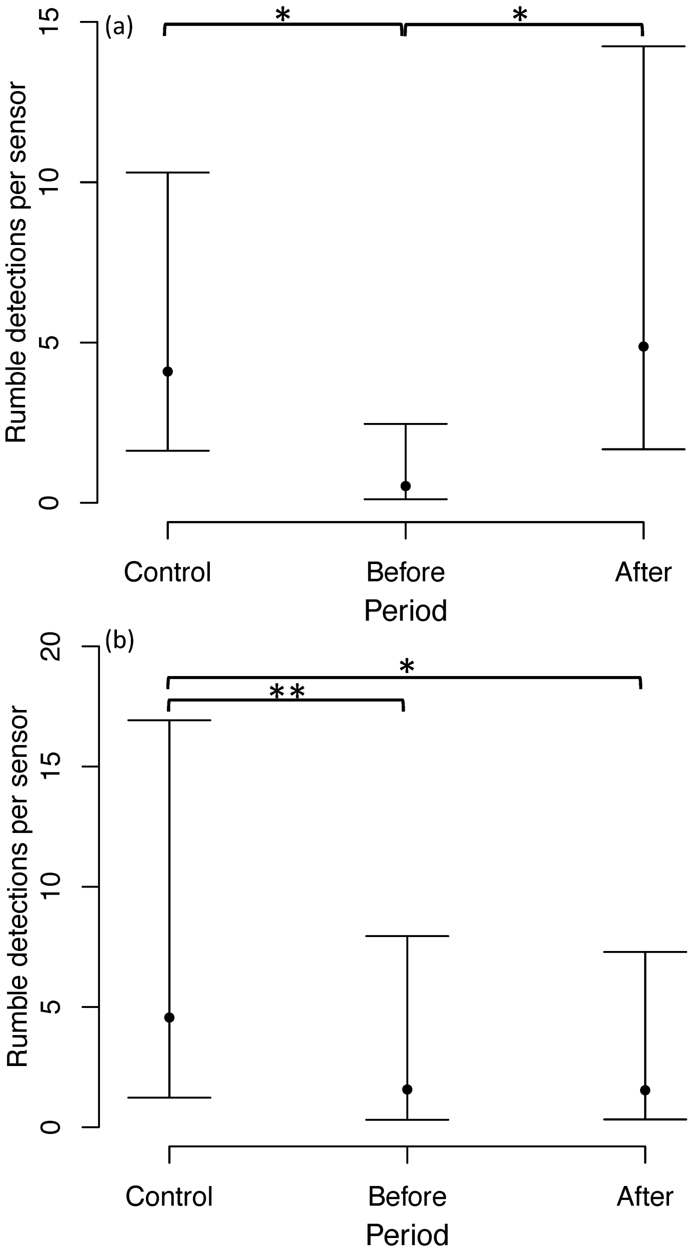


Figure 2.4 Initial GLMM predictions from the top models of the (a) 'immediate' and (b) 'sustained' intervals. Error bars represent 95% confidence intervals. * indicates $p \leq 0.05$ and ** indicates $p = 0.077$.

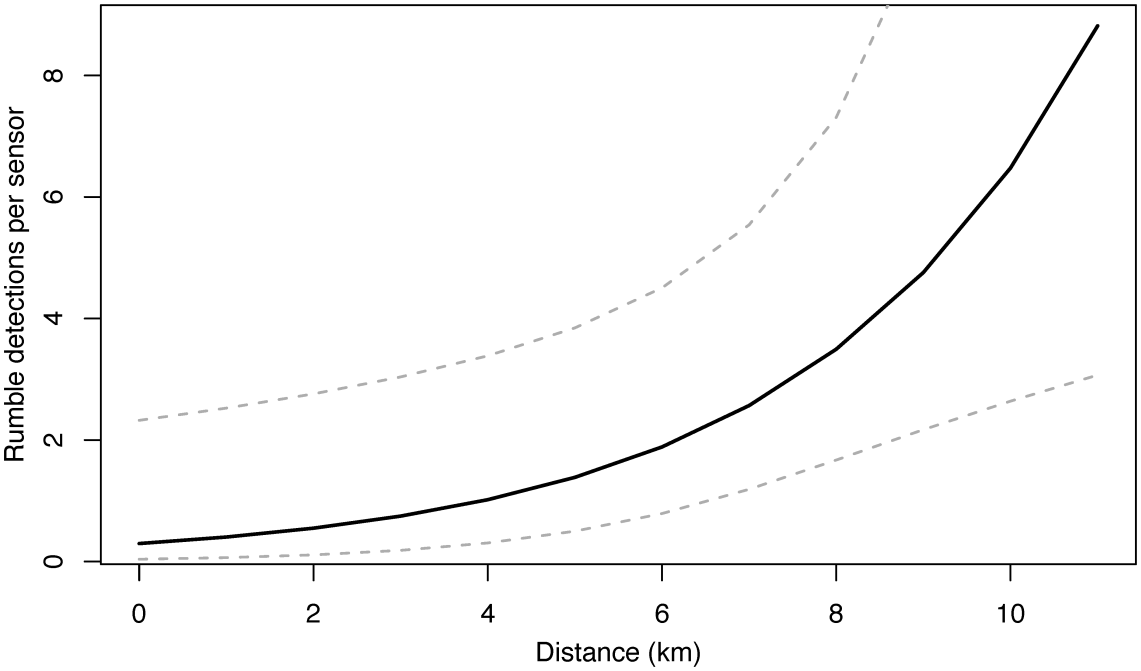


Figure 2.5 Initial GLMM predictions for the ‘immediate’ interval top model *period* + *distance*. Marginal means of predicted rumbles per sensor are averaged over the three periods (control, before, and after) and shown as a function of distance from the gunfire event site/sensor. Dashed grey lines indicate 95% confidence intervals.

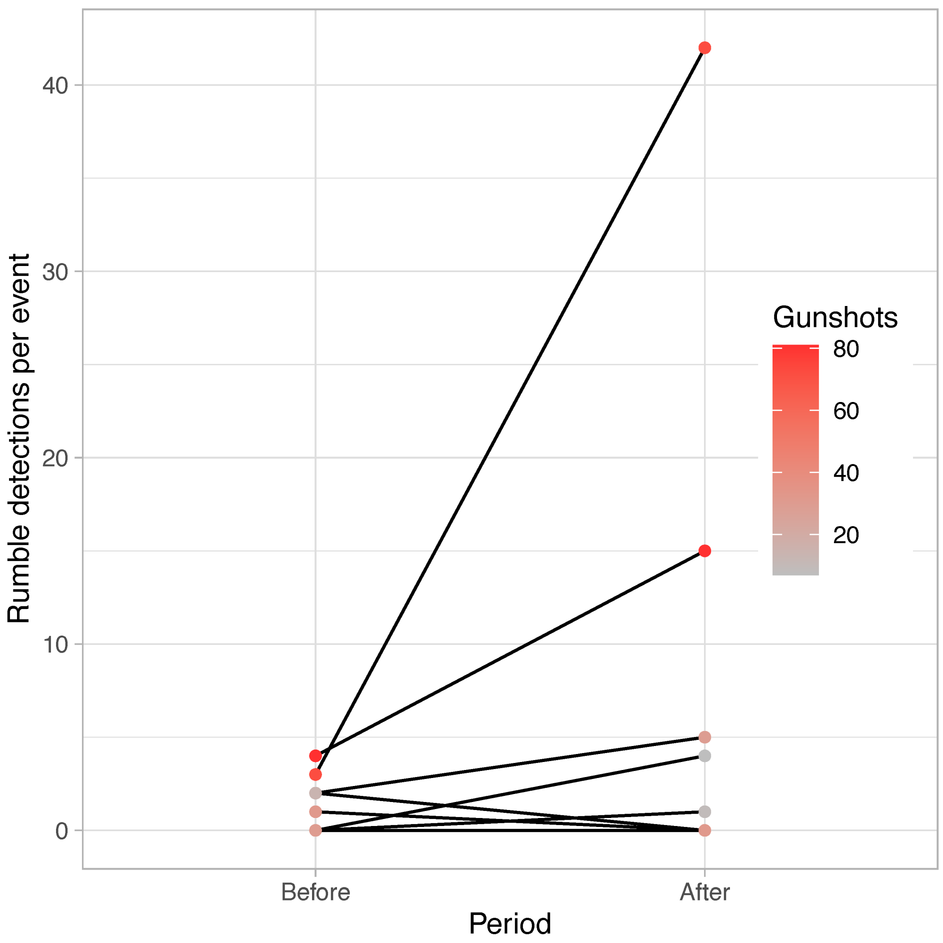


Figure 2.6 Elephant rumbles for the eight individual gunfire events, summed across all sensors of an event, for the 'immediate' interval of ±5 hours from the gunshots. Note that these summed rumbles on the y-axis differ from the GLMMs, which used rumbles per sensor.

Table 2.1 Summary of initial GLMMs predicting counts of elephant rumbles per sensor in the 'immediate' and 'sustained' intervals around gunfire events, ranked by AIC. In the initial GLMMs, the models compare rumble counts from before gunfire, after gunfire, and control periods, and consider distance from the poaching event site/sensor. All candidate models include a random effect for *event ID*.

Interval	**Conditional Component**	**Zero-Inflated Component**	**# Parameters**	**Log-likelihood**	**AIC**	**ΔAIC**	**AIC Weight**
Immediate	*per+dist*	*intercept*	7	-131.86	277.73	0	0.62
	distance	*intercept*	5	-135.22	280.45	2.7	0.16
	*per*dist*	*intercept*	9	-131.61	281.23	3.5	0.11
	period	*intercept*	6	-135.01	282.02	4.3	0.07
	intercept (null)	*intercept*	4	-137.77	283.54	5.8	0.03
Sustained	*period*	*intercept*	6	-290.28	592.57	0	0.42
	intercept (null)	*intercept*	4	-292.65	593.30	0.7	0.28
	per+dist	*intercept*	7	-290.25	594.49	1.9	0.16
	distance	*intercept*	5	-292.63	595.27	2.7	0.11
	*per*dist*	*intercept*	9	-289.94	597.89	5.3	0.03

Table 2.2 Initial 'immediate' and 'sustained' interval GLMM parameter estimates, standard errors (in parentheses), and *p*-values for candidate models within 2 AIC units of the top model for each interval. Estimates and SEs are on the link scale of the GLMMs (conditional component = truncated negative binomial with log link; zero-inflation component = binomial with logit link). While the contrast is not shown, before and after periods differed significantly for the 'immediate' interval (*p* = 0.006; more rumbles after) but not for the 'sustained' interval (*period* model *p* = 0.976). All models include a random effect for *event ID*.

Interval	**Model**	**Conditional Component Parameter Estimates**				**Zero-Inflated**
		Intercept	**Period (=Before)**	**Period (=After)**	**Distance**	**Intercept**
Immediate	*per+dist*	1.41(0.47) p=0.003	-2.06(0.86) p=0.016	0.18(0.67) p=0.795	0.31(0.12) p=0.013	2.47(0.22) p<0.001
Sustained	*period*	1.52(0.67) p=0.023	-1.07(0.60) p=0.077	-1.09(0.56) p=0.050	-	1.46(0.15) p<0.001
	null	0.60(1.42) p=0.672	-	-	-	1.46(0.15) p<0.001
	per+dist	1.54(0.67) p=0.021	-1.09(0.61) p=0.074	-1.13(0.57) p=0.049	0.03(0.09) p=0.782	1.46(0.15) p<0.001

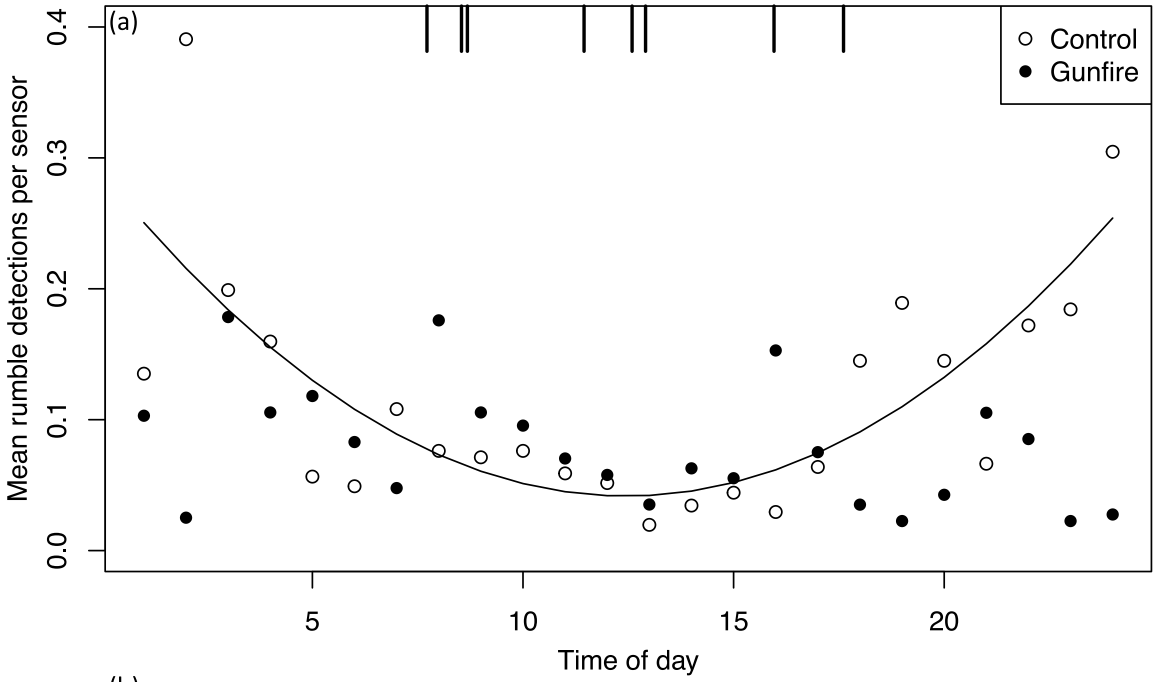
Table 2.3 Summary of candidate set of subsequent GLMMs, which used gunfire event data only and considered the influence of *period*, event intensity (*number of gunshots*) and *distance* from the gunfire event sensor/site. Models predict counts of elephant rumbles per sensor in the 'immediate' period, ±5 hours from the gunshots. All models include a random effect for *event ID*. Models composed of combinations of variables that received very little support (model weights ≤ 0.05) have been excluded from the table (the full candidate set can be found in Table 2.S1).

Conditional Component	**Zero-Inflated Component**	**# Parameters**	**Log-likelihood**	**AIC**	**ΔAIC**	**AIC Weight**
per + shots	*Intercept*	6	-70.66	153.32	0	0.25
*per*shots*	*Intercept*	7	-70.12	154.24	0.9	0.16
per + dist	*Intercept*	6	-71.22	154.44	1.1	0.14
per + shots + dist	*Intercept*	7	-70.39	154.78	1.5	0.12
*per*shots + dist*	*Intercept*	8	-69.94	155.89	2.6	0.07
intercept (null)	*Intercept*	4	-76.13	160.27	7.0	<0.01

Table 2.4 Parameter estimates, standard errors (in parentheses), and *p*-values for the four top candidates of the set of subsequent GLMMs, ranked by ΔAIC and model weight. Models predict elephant rumble counts per sensor for the 'immediate' interval, ±5 hours from the gunshots, and consider the influence of *period*, event intensity (*number of gunshots*) and *distance* from the gunfire event sensor/site. Estimates and SEs are on the link scale of the GLMMs (conditional component = truncated negative binomial with log link; zero-inflation component = binomial with logit link). All models include a random effect for *event ID*.

Model	**ΔAIC (weight)**	**Conditional Component Parameter Estimates**					**Zero-Inflated**
		Intercept	**Period$_{\text{Aft}}$**	**Shots**	**Distance**	**Per$_{\text{Aft}}$*Shots**	**Intercept**
per + shots	0 (0.25)	-0.28(0.58) *p*=0.627	1.92(0.55) *p*=<0.001	0.03(0.01) *p*=0.009	-	-	2.33(0.29) *p*<0.001
*per*shots*	0.9 (0.16)	0.08(0.61) *p*=0.893	1.46(0.67) *p*=0.029	0.01(0.02) *p*=0.506	-	0.02(0.02) *p*=0.296	2.33(0.29) *p*<0.001
per + dist	1.1 (0.14)	-0.51(0.68) *p*=0.451	2.01(0.67) *p*=0.003	-	1.03(0.50) *p*=0.040	-	2.33(0.29) *p*<0.001
per+shots+ dist	1.5 (0.12)	-0.35(0.60) *p*=0.562	1.92(0.56) *p*<0.001	0.02(0.02) *p*=0.180	0.40(0.59) *p*=0.490	-	2.33(0.29) *p*<0.001

Supplemental material



(b)

Model	R-squared	Intercept	TOD	TOD^2
Rumble detections ~ TOD + TOD^2	0.59	0.289(0.04) $p<0.001$	-0.040(0.01) $p<0.001$	0.002(0.0003) $p<0.001$

Figure 2.S1(a)We plotted the mean number of control period rumbles per sensor for each hour of the day (open circles). We fit a quadratic linear model with the form *Rumbles ~ TOD + TOD^2* to this baseline data (black line). The model summary is provided in (b). We compared this baseline rumble curve to the times of day of the eight gunfire events (rug at top of figure). The gunfire event times are evenly distributed with respect to the inflection point of the rumble curve, with events falling on either side. Therefore, we conclude that natural diel rumble patterns are unlikely to systematically bias our measurement of vocal response to gunfire events. We plotted the mean number of gunfire event rumbles per sensor for comparative purposes (filled circles).

Table 2.S1 Full candidate set of subsequent GLMMs, which used gunfire event data only and considered the influence of *period*, event intensity (*number of gunshots*) and *distance* from the gunfire event sensor/site. Models predict counts of elephant rumbles per sensor in the 'immediate' period, ±5 hours from the gunshots. All models include a zero-inflated component as a function of a constant intercept and a random effect for *event ID*.

Conditional Component	**No. Par.**	**LL**	**AIC**	**ΔAIC**	**AIC Weight**
per + shots	6	-70.66	153.32	0	0.25
*per*shots*	7	-70.12	154.24	0.9	0.16
per + dist	6	-71.22	154.44	1.1	0.14
per + shots + dist	7	-70.39	154.78	1.5	0.12
*per*shots + dist*	8	-69.94	155.89	2.6	0.07
*per*dist*	7	-71.18	156.36	3.0	0.05
period	5	-73.24	156.49	3.2	0.05
*dist*shots + per*	8	-70.28	156.56	3.2	0.05
*per*dist + shots*	8	-70.34	156.68	3.4	0.05
shots	5	-73.91	157.81	4.5	0.03
distance	5	-74.57	159.15	5.8	0.01
dist + shots	6	-73.80	159.60	6.3	0.01
intercept (null)	4	-76.13	160.27	7.0	<0.01
*dist*shots*	7	-73.78	161.55	8.2	<0.01

Appendix 2.S1 Accounting for ‘nuisance’ variables

Initial GLMMs: comparison to baseline activity

We did not include a variable for logging in the candidate models. Much of the logging area is now inactive concession that was logged over 7 years prior to the start of our study, so this would not impact our detected responses. Only one of the eight gunfire events (event 1; Fig. 2.1) occurred within the active portion of the concession, where selective logging was restricted to relatively small areas at any given time. Instead of including a variable for this one event, we checked logging data to verify that no logging activities overlapped or interfered with our measurement periods for that event.

Subsequent GLMMs: event variability

It is possible that event duration (time over which gunshots were discharged) could reflect event intensity, and therefore have an effect similar to the number of gunshots. Because we expected duration and number of shots to effect elephant response in similar ways, and because these two variables were correlated ($r = 0.36$, $p < 0.001$), we chose to include only number of shots in the final suite of candidate models. We made this decision after modeling both variables and determining that number of shots explained more variation in the data in an information theoretic framework.

CHAPTER 3

Evaluating the environmental determinants of the distribution of elephant poaching and bushmeat hunting using passive acoustic monitoring

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Abstract

Poaching and bushmeat hunting are major causes of diminishing wildlife populations and global biodiversity loss. The ability of conservation efforts to combat these activities, through law enforcement patrols for example, is limited by our understanding of the determinants of where and when poaching occurs. Much of the research on the drivers of poaching has focused on scales and variables that are not relevant to prediction and intervention at the landscape scale. Furthermore, the opportunistic and biased data collected by patrols themselves are unsuitable for robust statistical analyses and inference. In this study, we examined the proximate environmental determinants of the distribution of poaching and bushmeat hunting in a national park and adjacent logging concessions in Republic of Congo. We employed a passive acoustic monitoring (PAM) framework to systematically collect unbiased data amenable to statistical inference on the determinants of the distribution of gunfire events. Over 3.25 years of recording starting in late 2017, we detected 86 gunfire events across a grid of 50 acoustic recorders. We analyzed the spatiotemporal distribution of these events as a function of covariates pertaining to the hypotheses that poaching/hunting risk is determined by accessibility (e.g., distance to rivers and roads), deterrence (e.g., patrol effort), target species abundance (e.g., relative abundance of forest elephants), or a combination thereof. Distance to major rivers and its interaction with season emerged as the most influential determinant of gunfire event risk, with lower risk characterizing sites farther from rivers, especially during the dry season. Other covariates that explained the distribution of gunfire events included habitat, ongoing logging activity, and proximity to permanent roads and temporary logging roads. Increased local patrol effort only slightly reduced the risk of gunfire events in the TTE analysis. However, a potential effect of patrol effort on overall gunfire event rates became apparent at broader scales across the entire study area.

Protected area designation and the relative abundance of elephants were among the uninformative predictors. Overall, variation in risk was determined primarily by accessibility to potentially exploitable areas. Our results can be used to guide and optimize the allocation of patrol effort to high-risk areas at times of increased vulnerability. Our study exemplifies how a PAM approach can be used to overcome the limitations of biased data collection common to studies in this field.

Introduction

Poaching, often defined as the illegal killing, taking, or harvesting of protected wildlife, is an issue that spans local to international and global scales, and is associated with an equally extensive array of social, political, economic, and environmental drivers (Burn et al., 2011; Hauenstein et al., 2019; Lavadinović et al., 2021). It is a phenomenon that detrimentally affects wildlife populations, species and population management goals, human safety, and conservation efforts worldwide (Haenlein & Smith, 2017; Lavadinović et al., 2021). While poaching is commonly associated with megafauna such as elephants and rhinos, it encompasses the illegal taking of any protected species, making it a worldwide phenomenon that is not limited to particular taxa (Lavadinović et al., 2021). It includes, for example, illegal bushmeat hunting of diverse species (although not all bushmeat hunting is illegal, e.g., local hunting; Lavadinović et al., 2021; Poulsen et al., 2009). Overhunting for bushmeat has reduced wildlife populations and caused local extinctions of numerous species throughout the global tropics (Corlett, 2007; Fa et al., 2002; Milner-Gulland & Bennett, 2003; Peres & Palacios, 2007). The overharvesting of wildlife is one of the most widespread and leading causes of local extinctions and of the global decline in biodiversity (Fa et al., 2002; Milner-Gulland & Bennett, 2003; Vié et al., 2009).

Poaching associated with the ivory trade has severely impacted populations of all three extant elephant species (two in African, one in Asia; Aryal et al., 2018; Blake & Hedges, 2004; Maisels et al., 2013; Wittemyer et al., 2014). Since 1979, African elephant (*Loxodonta* spp.) populations have suffered an estimated overall reduction of 72% (Chase et al., 2016; Jackson, 2013; Robson et al., 2017). Recent evidence suggests that while elephant poaching rates have fluctuated over the past few decades, rates remain high and are increasing in some areas (Chase et al., 2016; Underwood et al., 2013; Wittemyer et al., 2014). Research that has considered the two African elephant species independently has revealed that poaching has decimated populations of the critically endangered African forest elephant (*Loxodonta cyclotis*; Blake & Hedges, 2004; Gobush et al., 2021; Maisels et al., 2013). Between 2002 and 2011, 62% of the entire population and 30% of their geographic range was lost primarily due to poaching (Maisels et al., 2013).

Conservation efforts to combat poaching and illegal bushmeat hunting often employ anti-poaching patrols as a primary wildlife law enforcement tool (Dobson et al., 2019; Hilborn et al., 2006). Effective law enforcement patrols have been identified as a crucial factor for the successful conservation of large mammal species in particular (Bruner et al., 2001; Hilborn et al., 2006; Tranquilli et al., 2012). Inadequate law enforcement, by contrast, can result in rapid losses in biodiversity (Peres & Terborgh, 1995; Tranquilli et al., 2012). Patrols are often tasked with protecting large expanses of terrain with limited resources (Peres & Terborgh, 1995; Plumptre et al., 2014). Insufficient personnel and monetary resources, ineffective management, and lack of evidence-based decision-making frameworks can reduce the ability of patrol effort to provide adequate protection for vulnerable species and areas (Gavin et al., 2010; Hilborn et al., 2006;

Keane et al., 2011; Plumptre et al., 2014). Research that provides guidance on the allocation of resources and optimization of patrol effort is therefore of high value (Moore et al., 2018, 2021).

Understanding the drivers of poaching and bushmeat hunting would aid conservation by allowing prediction of when and where poaching will occur, facilitating intervention. Studies on determinants of poaching and illegal hunting have often been on regional, national, multinational, or global scales to reveal political and socioeconomic drivers of poaching pressure (e.g., corruption, political stability, poverty, GDP; Burn et al., 2011; Hauenstein et al., 2019; Lavadinović et al., 2021). Studies that illuminate such drivers can potentially inform high-level strategy to address poaching but are less useful for tactical, on-the-ground interventions and apprehension of poachers. To improve the efficacy and optimize the use of available conservation law enforcement resources, more research is needed that examines the environmental predictors of when and where poaching occurs at the proximate or landscape scale (Lavadinović et al., 2021; Moreto & Lemieux, 2015). Far fewer studies focus on the predictor variables of poaching and bushmeat hunting at this scale (e.g., ecological drivers *sensu* Lavadinović et al., (2021); Moreto & Lemieux, 2015). In a systematic review of the illegal hunting literature, Lavadinović et al., (2021), found that the majority of studies worldwide focus only on the resulting environmental impacts. Only a small percentage of studies explore the determinants underlying the distribution of illegal hunting, a better understanding of which would facilitate prediction of illegal hunting activity in time and space (Lavadinović et al., 2021; Moreto & Lemieux, 2015). Of this limited research, many studies have discernable limitations. Some studies have used proxies of the likelihood of poaching events (e.g., distance to access roads and human settlements) and investigated their impacts on animal populations (Barnes et al., 1991, 1997; Blake et al., 2007, 2008; Hall et al., 1997; Laurance et al., 2006; Maisels et al., 2013; Yackulic et al., 2011), while fewer studies investigate the proximate determinants of poaching pressure itself (see Burn et al., 2011; Zafra-Calvo et al., 2018). Some studies have found that signs of poaching and bushmeat hunting decrease with distance from roads (Blake et al., 2007; Branch et al., 2022), while others indicate that hunting pressure decreases with distance to villages and logging camps, but not with distance to roads (Laurance et al., 2006). The distribution of poaching pressure may therefore be determined by some, but not all, types of access points into wildlife species habitat.

The influence of logging activity, which provides access to remote forests through the construction of temporary logging roads, has also been implicated in increased levels of bushmeat hunting (Poulsen et al., 2009, 2011). Rates of poaching and illegal hunting should also be dependent on the frequency or intensity of anti-poaching patrols (Doormaal et al., 2021; Moreto et al., 2014; Wrege et al., 2017), which in turn can correlate with the degree of land protection (e.g., national parks vs. forest concessions). Temporal trends of elevated hunting levels prior to major holidays have also been documented in various systems (Astaras et al., 2017, 2020; Moreto & Lemieux, 2015; Viollaz et al., 2021). It is also possible that poachers and bushmeat hunters simply seek out areas where the abundance of target species is high (Ferreguetti et al., 2018; Matos et al., 2020). A more thorough investigation that simultaneously evaluates the variety of potential determinants of poaching and bushmeat hunting pressure is warranted. As some of these factors are likely context dependent, more location-specific studies are also necessary. Such knowledge would advance conservation efforts by informing anti-poaching patrols and potentially allowing prediction of when and where poaching attempts will occur (Lavadinović et al., 2021; Moreto et al., 2014).

To achieve such goals, another major issue must be addressed. Perhaps the biggest limitation of research on poaching and hunting drivers to date is that data are usually not collected in a manner suitable for statistical analyses and scientific inference (Gavin et al., 2010; Hedges, 2012; Keane et al., 2011). As noted, proxies such as distance to hunter access points often serve as indices of poaching pressure in lieu of quantification of poaching attempts per se (Barnes et al., 1991, 1997; Blake et al., 2007, 2008; Hall et al., 1997; Laurance et al., 2006; Maisels et al., 2013; Yackulic et al., 2011), in part due to the extreme difficulties of observing actual poaching attempts. When evidence of actual poaching events is observed, it is typically opportunistically collected by anti-poaching patrol personnel and takes the form of elephant carcasses, signs of poacher activity (e.g., camps), or the poachers themselves (Moreto et al., 2014). Such opportunistic data poses challenges to statistical analyses as it is rarely systematically collected with the characteristics required for statistical inference, namely randomness and replication (Doormaal et al., 2021; Gavin et al., 2010; Keane et al., 2011). Instead, patrols often travel opportunistic and biased routes based on ease of access, prior knowledge, informant tips, and previously detected poaching events (Doormaal et al., 2021; Gavin et al., 2010; Johnson et al., 2016; Keane et al., 2011). Furthermore, the amount and quality of the data recorded by patrols is affected by the patrolling efforts themselves (e.g., the amount of terrain covered), and is therefore not an objective reflection of the actual distribution of poaching events (Hedges, 2012; Moreto et al., 2014). In summary, much of the data has been biased and unsuitable for inclusion in predictive models (Gavin et al., 2010; Keane et al., 2011). It is in part this constraint that has limited the ability to elucidate the drivers of poaching pressure that in turn could be used to inform anti-poaching efforts and predict poaching activity.

We employ a data collection approach that remedies these shortcomings, co-opting a technique usually used to study animals— passive acoustic monitoring (PAM)—to detect and investigate gunshots from poaching. PAM uses acoustic sensors capable of continuously recording environmental sounds, including vocalizations from species of interest such as African forest elephants (Wrege et al., 2017), over large areas of landscape. Acoustic signals from human activity and disturbance, such as gunshots from poaching, can also be detected with PAM (Astaras et al., 2017, 2020; Branch et al., 2022; Wrege et al., 2017). PAM thus presents a unique and novel way to study the determinants of the distribution of poaching activity with (1) a more direct quantification of poaching levels (rather than an indirect proxy), (2) a temporal and spatial resolution unachievable by previous means (e.g., walked transects in search of hunter signs; Astaras et al., 2017, 2020; Wrege et al., 2017), and (3) a systematic and unbiased data collection scheme characterized by elements of random sampling and replication, all of which facilitate statistical inference.

We used a grid of acoustic sensors deployed across the rainforest landscape in northern Republic of Congo to detect instances of poaching and bushmeat hunting, and to explore the spatial and temporal variables that influence their distribution. We hypothesized that the level of poaching and hunting activity across the landscape, quantified as the number of gunfire events detected over time, would be determined by three major factors—accessibility, deterrence, and target species abundance. To explore these hypotheses, we constructed models with spatial and temporal predictor variables associated with accessibility (e.g., distance to access points), deterrence (e.g., patrol effort), and animal abundance (e.g., elephant vocalization detections), and confronted the models with data collected with a PAM approach.

Methods

Data acquisition

In late 2017, a grid of 50 acoustic recorders was established in northern Republic of Congo by the Elephant Listening Project (ELP, KLY-CCB, Cornell) in collaboration with the Wildlife Conservation Society (WCS). The grid covers 1250 km^2 (mean inter-sensor distance of 5.5 km [SD = 1.4]) of Nouabalé-Ndoki National Park (NNNP) and adjacent forestry concessions (Fig. 3.1). Acoustic recordings were made continuously between November 2017 and January 2021 using Swift recorders (Koch et al., 2016) with a sampling rate of 8 kHz and 16-bit resolution. Batteries were replaced and data were retrieved from the recorders approximately every 4 months. Controlled experiments near a ranger training site in the same forest revealed that gunshots can usually be detected at distances of at least 2 km from the recorders. A template-based detector algorithm trained on recorded gunshots was used to search the continuous audio data for gunfire (see Wrege et al., 2017 Appendix S3 for detector details). Putative gunshots identified by the algorithm were then manually verified via spectrographic and auditory analysis by experienced personnel. All false-positive gunshot detections were removed from the dataset. For confirmed gunshots, we manually examined spectrograms to verify that no additional gunshots had occurred within 24 h of the detected focal shot(s). We aggregated any shots occurring within 1 hour of one another into ‘gunfire events’, which would likely represent a single elephant poaching or bushmeat hunting attempt. The gunfire events were each detected at a single recorder only, which we designated the gunfire event site. Automatic weapon fire events likely represented attempted elephant kills, whereas single-action weapon fire could include both elephant poaching and bushmeat hunting of other species (Swider et al., 2022).

Time-To-Event (TTE) Analysis

We analyzed detected gunfire events in a time-to-event (TTE) framework with Cox proportional hazards (Cox PH) models extended for recurrent events (multiple events per site). For the TTE analysis, study onset was set to December 15, 2017— the date at which all recorders across the grid were deployed and continuously recording. In 2020, our acoustic record was interrupted by complications from the Covid-19 pandemic, resulting in an approximately 2-month data gap starting in June 2020. We therefore set the end of the TTE analysis to April 30, 2020, before this interruption occurred. We measured time to gunfire events in days since study onset (December 15, 2017).

Although the PAM approach allowed for near-continuous monitoring, some recording gaps were expected given such a long recording period and many recorders. Many of the 50 recording sites experienced at least some recording interruptions due to routine equipment maintenance, battery failures, and equipment malfunctions. Such gaps in the otherwise continuous acoustic record are potentially problematic for time-to-event analyses. Jolani et al., (2021) present a useful review of such "missing outcome" scenarios in TTE analyses and compare several methods for resolving the issue. They suggest multiple imputation— often considered the gold standard for management of missing data— as the least biased method for dealing with missing outcome data. We decided against imputation because gunfire events were so rare that (1) we would not be comfortable introducing an unobserved "fake" gunfire event into a missing data period, and (2) imputation would likely predict event non-occurrence anyway. We therefore chose the method of assuming event non-occurrence for the missing periods in our recordings. When events of interest are frequent, this method can introduce considerable bias (Jolani et al., 2021). However, given the rarity of gunshots, the probability of a gunfire event occurring at a site while the recorder was not functional is small. While we acknowledge that this approach could slightly lower our overall estimates of gunfire event rates, it should not influence the comparison of covariate effects on gunfire event risk.

Occasionally, recorder malfunctions resulted in longer gaps in recording, at which point we censored the TTE data. To determine a systematic length threshold for censoring, we used the overall rate of events per site to calculate the time interval over which the probability of an event occurring would reach 0.05. This turned out to be approximately one month: for any sites experiencing a recording gap longer than one month, we right-censored the data at the time of recorder malfunction.

We included both time-independent and time-dependent covariates, the latter of which we quantified over monthly intervals. Our predictor variables pertained to our hypotheses that poaching and bushmeat hunting risk is determined by poacher accessibility to a given area, factors that deter poaching, target species abundance, or a combination of these factors (Table 3.1). All distance-related variables were quantified using QGIS software (*QGIS 3.22*, 2022).

Accessibility-related covariates

We expected roads to influence the accessibility of different sites, and therefore the degree of gunfire event risk. In our study area, both permanent roads and ephemeral logging roads could influence variation in accessibility. Permanent roads exist to the east, south, and west of the region of the national park where our acoustic grid was located (Fig. 3.1). We measured the distance of each site to the nearest permanent road, also including a major logging road that was in use during most of the study period.

Temporary logging roads potentially contribute to the accessibility of study sites and the national park in general. Logging roads permeate both logging concessions of our study area, in some instances extending to the park border. Logging roads are “closed” and cease to be maintained once logging of a particular zone of the concession is complete. Over the course of several years, these are progressively invaded by secondary growth, but nonetheless could potentially facilitate access by foot travel. The old logging concession contained roads closed for over a decade, but road remnants were still visible on Landsat 8 imagery taken in 2017-2021. In the operational concession, roads were actively built and used from study onset until September 2019. Almost all the logging roads in the operational concession had been built prior to study onset, although a small network was added in association with ongoing logging activity in 2017-2019 (see below). We attempted to capture the potential differences in accessibility in these two areas with alternative specifications of the strata: sites within 2 km or inside of either concession, versus within 2 km or inside of only the operational concession. Sites in the NP (other than those within 2 km of logging concessions/roads) constitute another level of the variable, as no roads extend past the NP border (Table 3.1; Fig. 3.1). We also compared alternative specifications of this covariate by grouping sites according to the hard boundaries of the strata, rather than within a 2-km buffer (Table 3.1; Fig. 3.1).

Aside from road-related accessibility, logging activity per se could increase levels of illegal hunting because logging workers may engage in bushmeat hunting themselves, and logging vehicles are sometimes used to transport hunters and collected bushmeat (Poulsen et al., 2009; Robinson et al., 1999). We included a binary, time-varying covariate for whether logging activity— clearing logging roads, felling trees, moving downed trees to logging roads, and transportation out of the concession— was ongoing within 2 km of recording sites (Table 3.1). These activities occurred near some sites of the operational concession from study onset to September 2019. Data on these activities were provided by the logging company, *Congolaise Industreille des Bois* (CIB). Because logging activity likely drives away elephants (see Chapter

4) and bushmeat species (Poulsen et al., 2011), the expected effect on gunfire events could be positive (due to increased hunting associated with logging personnel) or negative (due to reduced target species abundance; Table 3.1).

Rivers also potentially contribute to the accessibility of hunting locations (Ferreguetti et al., 2018), facilitating travel in two ways. Some watercourses are passable by pirogue, local wooden canoes capable of navigating shallow water. The depth and navigability of rivers varies between wet and dry seasons, but in general the mainstems of the Ndoki and Guoalougo rivers can support such travel. Watercourses, large and small, can also increase accessibility via the elephant trails that are often located adjacent to them. These riverine trails (Blake, 2002) tend to be well traveled by elephants, resulting in wide open paths that can greatly ease foot travel for humans. We defined two river covariates: distance to nearest mainstem of the Ndoki or Guoalougo rivers (relevant to pirogue travel), and distance to nearest mainstem or primary tributary (relevant to foot travel; Table 3.1; Fig. 3.1). Distances were measured using GIS watercourse layers. These layers were created by manual tracing of digital elevation models and confirmed with on-the-ground GPS mapping performed during routine maintenance of the acoustic grid. Because navigability should vary with rainfall, we also included a seasonality interaction term with each month categorized as wet (>60 mm of rain) or dry (<60 mm of rain) (Beck et al., 2018). Rainfall data were collected continuously throughout the study at four weather stations in and around the acoustic grid study area; millimeters of rain per month were averaged across the four stations. To accommodate a potential time lag in the effect of rainfall, we also compared models with the interaction terms fit with the seasonal status (wet vs. dry) of the previous month (Table 3.1). The Cox PH models in our analysis predict risk of poaching activity as a function of time and of relevant covariates by comparing the numbers of detected gunfire events between sites that differ in their covariate values. Because seasonality is collinear with time and static across all sites, the Cox PH models could not accommodate a main effect of season. We therefore explore the potential effect of rainfall in a separate analysis (see *Non-TTE analyses* below).

Deterrence-related covariates

Our main deterrent-related covariate of interest was anti-poaching patrol effort, which we quantified as total monthly foot patrol distance (kilometers) using GPS tracks of patrol routes provided by WCS. For the TTE analysis, we calculated total monthly foot patrol distance at each site using two spatial scales— within 2 km and 10 km of the recorder location (Fig. 3.2; Table 3.1). These represent the effect of patrol effort acting either at a very local scale in an immediate manner (i.e., poachers detecting and avoiding rangers in the forest), or acting in a broader regional sense (i.e., poachers monitoring overall levels of patrol effort and planning activities accordingly). We imposed an *a priori* constraint on patrol effort parameter values, allowing only negative effects on the risk of gunfire events. To accommodate the possibility of a lag time in the effect of patrol effort, we also fit and compared models with patrol effort values from the previous month.

The other deterrence-related covariate of interest was overall level of protection: national park versus concessions. This variable is also pertinent to road-facilitated accessibility (Table 3.1). To reflect protection, we included this categorical variable with the 2 levels specified as NP versus both concessions (old and operational) combined. To reflect operational road-related accessibility, we re-specified the levels to differentiate between the presence of absence of operation logging roads (operational concession vs. NP and old concession combined). During model comparison, support for models with the former specification would indicate either nominal protected status or access to roads of any condition are important, but not operational roads or logging activity per se. Alternatively, support for models with the latter specification would suggest operational logging activity and associated newer roads are important, but not nominal protected status or old road remnants. In this way, comparing models with alternative specifications of covariate levels could potentially arbitrate between competing hypothesized determinants of gunfire event risk (Table 3.1).

Target species abundance covariates

While accessibility and deterrence were our hypotheses of interest, we needed to account for a null hypothesis that the distribution of detected gunfire events reflects the distribution of animals (i.e., poachers and bushmeat hunters use areas of high target species abundance, independently of accessibility or deterrence; Ferreguetti et al., 2018; Matos et al., 2020). As a proxy for forest elephant abundance, we included a standardized metric of elephant detections at each recording site (Table 3.1). We also compared models with a 1-month lag for this covariate, to accommodate the possibility of increased poaching activity at sites with high elephant abundance in the previous month. The presence of forest elephants near each site was indicated by detection of their rumble vocalizations. Rumbles are an appropriate signal to use as a proxy for elephant abundance because they are the most common vocalization and they are used by both sexes and all age classes and in many behavioral contexts (Chapter 4; Hedwig et al., 2021; Poole et al., 1988; Stoeger et al., 2014; Thompson, 2009). Previous detection distance experiments indicate that we can detect rumbles at a range of 500–600 m, resulting in a detection area of approximately 0.79–1.13 km^2 around each of the 50 recorders. An automated detector algorithm based on a feature extraction and classification system (Keen et al., 2017) was used to extract rumbles from the continuous audio data set. For 3 randomly selected days per week, the detector output was reviewed to confirm putative rumble detections and remove false positives from the data set. Using the 3 verified days per week, site-specific mean rumble detections per day were calculated over monthly intervals (Table 3.1).

We also quantified habitat type around each of our recording sites, under the premise that target species abundance or diversity varies with habitat (Poulsen et al., 2011). Using Landsat 8 satellite imagery paired with ground truth locations obtained during WCS foot surveys, we performed a supervised classification of habitat type across our study area (Appendix). We classified pixels into 3 categories: 1) forest composed of mixed tree species, 2) monodominant forest composed of *Gilbertiodendron* sp., and 3) an "open" class that included river floodplain with sparser canopy than upland forest (or no canopy), open-canopy swamps, open water, aquatic vegetation and grasses, and forest clearings. In NNNP, fruit tree density, a potentially important indicator of animal food resources, is highest in *terra firma* mixed forest compared to *Gilbertiodendron* monodominant forest and lowland habitats (e.g., our "open" class; Blake, 2002). The proportion of mixed species forest around each site is therefore an indicator of resource availability, making it a potential proxy for animal abundance or diversity. This is especially pertinent in the wet season because more tree species, and the highest proportion of individual trees, fruit during the months of highest rainfall (Blake, 2002). Within the 2-km radius gunshot detection range around each of the 50 recorders, we calculated the percentage of forest pixels that were classified as mixed forest (Appendix). We also included a seasonality interaction term with each month categorized as wet or dry (Table 3.1).

While greater proportions of mixed forest around each site could reflect animal resources and abundance and therefore increase the risk of gunfire events, it could also potentially influence site accessibility, with the opposite effect. Mixed forest understory is often thick and difficult to penetrate, reducing accessibility and likely hindering successful hunting attempts because lines of sight are heavily interrupted. *Gilbertiodendron* monodominant forests, by comparison, generally have much more open understories (Blake, 2002), facilitating both accessibility by foot travel and presumably the targeting of animals. If the proportion of mixed species forest acts on the risk of gunfire events by reducing accessibility rather than increasing target species abundance, we anticipated that it would have a negative effect on the rate of detected gunfire events.

While we included distance to river covariates primarily as measures of site accessibility, these metrics could correlate with animal abundance as well. This is especially plausible during the dry season, when river mainstems and larger tributaries serve as water sources after smaller streams throughout the forest have dried up. These covariates therefore pertain also to the target species abundance hypothesis in addition to accessibility (Table 3.1).

Cox PH model structuring and comparison

We implemented recurrent event Cox PH models with the 'survival' package (Therneau, 2023) in R (R Core Team, 2022), using the counting process formulation of Andersen & Gill (1982). The data were clustered by site and a robust variance estimator was used to account for correlation between events at the same site (Andersen & Gill, 1982; Therneau & Grambsch, 2000). The relative rarity of gunfire events constrained our ability to construct and compare extensive global models, models with many covariates, or models with multiple interaction terms. Our approach was to compile a candidate model set by composing sub-models of 6 or fewer covariates, structured in ways that could potentially arbitrate between competing hypotheses. Where alternative specifications of the same general predictor were possible (e.g., distance to nearest mainstem vs. distance to nearest mainstem or primary tributary), only one was allowed in a particular candidate model. For numerical variables, we included only uncorrelated pairs of covariates ($r < 0.6$; Hebblewhite et al., 2014; Petracca et al., 2019) in models simultaneously. The four spatial categorical covariates, indicated by asterisks in Table 3.1, were related variations of a common strata system that each used an alternate specification of levels, and were thus highly correlated with one another (chi-sq. p-values < 0.01). We included only one such covariate in each candidate model, while holding our *a priori* combinations of numerical predictors constant. We evaluated support for candidate models using AIC_c and model weights (Burnham & Anderson, 2002), and considered for inference only models within 2 AIC_c units of the highest ranked model. We verified that these candidate models met the proportional hazards assumption using scaled Schoenfeld residuals (Grambsch & Therneau, 1994). We present the hazard ratios (HRs) of all covariates included in this set of top models for their potential predictive value. Model averaging was not appropriate due to the constraints we imposed when structuring sub-models— not all covariates were allowed to appear simultaneously in all candidate models. Therefore, we use the most parsimonious model containing each covariate to report effect sizes (HRs) and produce figures; for most covariates, this was the highest ranked model in the top model set.

Non-TTE analyses

Some variations of time-dependent covariates of interest had identical values for all sites and therefore could not be used to arbitrate between candidate Cox PH models. We explored these variables independently from the TTE analysis by plotting and fitting curves to the data. These variables included monthly rainfall, monthly patrol effort across the entire study area, the influence of Christmas and New Year's (with the expectation of elevated bushmeat hunting in preparation for the holidays), and the influence of an anti-poaching ranger training program that occurred in early 2018. For exploring the potential effect of monthly rainfall, which could influence the accessibility of the acoustic grid study area in general, millimeters of rain per month were averaged across four weather stations, as previously described. Total monthly patrol effort was measured as kilometers of foot patrols across the entire acoustic grid study area, delineated by a convex hull using a 2-km buffer around the outer sites (Fig. 3.2). In testing for a holiday effect, we compared gunfire event detection rates in the 2 months leading up to Christmas and New Year's (November and December of each year) to event rates of non-holiday months. To illuminate the apparent decrease in rate of poaching and bushmeat hunting events over the course of the study, especially in relation to the 2018 ranger training program, we fit a generalized linear model (GLM) to the monthly gunfire events detected across the entire study grid, using a Poisson distribution.

Results

From November 2017 to January 2021, we detected a total of 86 gunfire events (Fig. 3.3) composed of both automatic (e.g., AK47; n = 8) and single-action (n = 78) weapon fire. The total number of events at each site ranged from 0 to 10 (mean = 1.72; SD = 1.73). The monthly rate of gunfire event detection decreased over the 3.25 years of the study (Fig. 3.4). We tested recorder functionality and confirmed that this trend was likely not a result of decreasing functionality or sensitivity of the recorders over time.

TTE (Cox PH) analysis

Of the 86 total gunfire events, 75 were included in the TTE analysis (Dec. 15, 2017 – April 30, 2020); 11 events were excluded because of study period truncation and interval censoring due to recording interruptions. No model unambiguously outperformed all others, as indicated by AIC_c and model weights (Table 3.2). Thirteen candidate models appeared in the set of top models (within 2 AIC_c units of the highest ranked model). All 13 top models included distance to river mainstem and its interaction with seasonality (wet vs. dry months), revealing this as the most influential covariate in determining illegal hunting activity (Table 3.2). Risk of gunfire events decreased as distance to rivers increased (1st ranked model $\text{HR}_{\text{Dist. to river mainstem}}$ = 0.811; Table 3.2; Fig. 3.5a), and this effect was weaker in wet months (Fig. 3.5a).

Proportion of mixed forest received the next highest amount of support, appearing in 11 of the 13 top models (Table 3.2). Sites with lesser percentages of mixed forest cover had greater risks of gunfire events than sites dominated heavily by mixed forest (1st ranked model $\text{HR}_{\text{Prop. mixed forest}}$ = 0.202; Table 3.2; Fig. 3.5b). Distance to permanent roads and ongoing logging activity also received substantial support, appearing in 4 and 5 of the top models, respectively (Table 3.2). The risk of gunfire events was slightly higher for sites farther from permanent/semi-permanent roads (1st ranked model $\text{HR}_{\text{Dist. to road}}$ = 1.056; Table 3.2; Fig. 3.5c). Ongoing logging activity within 2 km in any given month substantially reduced the risk of gunfire events compared to sites and months without such activity (2nd ranked model $\text{HR}_{\text{current logging activity}}$ = 0.353; Table 3.2).

Covariates that received less support, appearing in 2-3 of the top models, included concurrent-month patrol effort at the 10-km scale and the categorical variables of whether sites were within 2 km of either logging concession/roads or within 2 km of the operational concession/roads only (Table 3.2). According to the highest ranked model, sites within 2 km of either concession (and their associated logging roads) were at a higher risk of gunfire events ($\text{HR}_{\text{Within 2km either concession}}$ = 1.696; Table 3.2). The hazard curves in Fig. 3.5a-c were produced using the highest ranked model and sites greater than 2 km from either concession for prediction.

Identical curves are produced when using sites within 2 km, but the expected number of events is 1.696 times higher, indicating substantially increased risk with proximity to either old or operational concessions and their logging roads. An increase in risk was also suggested for sites within 2 km of the operation concession only (3rd ranked model $HR_{\text{Within 2km operation concession}}$ = 1.952; Table 3.2). The amount of anti-poaching patrol effort within 10 km in the concurrent month slightly reduced the risk of gunfire events, with HRs of 0.994-0.995 (Table 3.2). Patrol effort within 2 km had a similar effect but was included in only one of the top models and thus considered less influential (Table 3.2).

Finally, the interaction of proportion of mixed forest with seasonality (wet vs. dry month) appeared in only one model of the top model set (Table 3.2). This model suggests the influence of proportion of mixed forest, which reduces risk of gunfire events, is not as strong in the wet months (i.e., risk is reduced less in the rainy months; Table 3.2). Covariates not listed in Table 3.2— the protection and logging strata variables, distance to nearest mainstem or primary tributary, mean elephant detection rate, and previous month patrol effort— were not among the top candidate models and are not considered supported.

Non-TTE analyses

Total monthly gunfire event detections across the entire acoustic grid decreased with sequential month from study onset (GLM $\beta_{\text{SequentialMonth}} = -0.07$ (log link scale), $p < 0.0001$; Fig. 3.6). Monthly gunfire events peaked in early 2018, when patrol effort was low because rangers were undergoing a training program (Figs. 3.6 & 3.7 top). Following this period, total monthly gunfire events decreased steadily and then remained low (Figs. 3.6 & 3.7 top panel). However, when plotted as a function of monthly total patrol effort across the entire study area, monthly gunfire event rates exhibited no apparent relationship with patrol effort (Fig. 3.7 bottom).

Similarly, monthly gunfire event rates lacked a clear relationship with monthly rainfall (Fig. 3.8). The slope of linear models fit to the data did not differ from zero (*p*-values of 0.52 and 0.96 for patrol effort and rainfall, respectively). Splines fit with smoothing parameters of 0.9 further indicate a lack of discernable trends. The monthly rate of gunfire events in the two months prior to Christmas and New Year's (November and December) did not differ from other months (p = 0.63), although unbalanced sample sizes (pre-holiday months versus other months) likely influenced the accuracy of standard errors and our ability to detect an effect.

Discussion

In this study we employed a PAM approach to systematically collect unbiased data on poaching and bushmeat hunting activity, in a manner amenable to statistical inference. We identified landscape-scale environmental predictor variables that can be used to identify areas (and seasons) at higher risk of poaching and bushmeat hunting activity. Our results can inform and potentially increase the efficacy of anti-poaching efforts, which are tasked with patrolling and protecting vast areas with often limited resources. Guided by models and covariates with predictive potential, patrol effort could be adapted to increase the probability of intervening with or deterring poaching and illegal bushmeat hunting activity.

The most influential determinant of poaching risk was distance to nearest river mainstem (Ndoki and Goualougo rivers), and its interaction with season (wet versus dry months; Table 3.2). The risk of poaching and bushmeat hunting decreased with distance from main rivers (Fig. 3.5a), lending support to our hypothesis that rivers provide poachers with a means of accessing exploitable areas. The influence of mainstems but not of primary tributaries is consistent with the idea that poachers navigate the main watercourses by pirogue, but tributaries are likely too small or shallow. The importance of rivers in our analysis is consistent with research from Brazil that found distance to water— used as a proxy for site accessibility— to be one of the most influential variables for predicting the distribution of poaching activity (Ferreguetti et al., 2018). While rivers have received less attention than roads as potential avenues for poacher access, our results contribute to the evidence that watercourses are influential determinants of illegal hunting activity that should be considered more thoroughly in future research.

An alternate explanation for the effect of higher risk near rivers is that potentially high elephant abundance near water provides more opportunities for poachers. We do not consider this to be the likely cause of the distance to river effect, however. We included average rumble rates at each site as a proxy for the relative abundance of elephants, in order to accommodate the "null" hypothesis that poaching risk reflects variation in elephant abundance, regardless of accessibility or deterrence factors. The elephant abundance covariate received no support, as indicated by its absence from the top model set. This suggests the effect of rivers on poaching risk involves access rather than the distribution of forest elephants.

While we could account for the relative abundance of elephants, we had no method of estimating the relative abundance of bushmeat species, other than through indirect habitat covariates. It is plausible that animal abundance correlates with distance to rivers, and that sites closer to rivers experience more hunting due to higher densities of common bushmeat species. This could explain why distance from rivers reduced the risk of gunfire events more drastically in the drier months (Fig. 3.5a). In the dry season, when small streams throughout the forest have dried up, animals may be attracted to habitat near the major watercourses, creating profitable hunting sites near rivers. In the rainy season, when small streams are plentiful throughout the forest, animal populations may be more dispersed, thereby curtailing the effect of distance to rivers on the distribution of gunfire events (Fig. 3.5a). However, many bushmeat species in the study area (e.g., duikers, monkeys; Poulsen et al., 2011) are territorial. We therefore might not expect any seasonal shifts in the distribution of bushmeat species with respect to watercourses. In research conducted near our study area, Poulsen et al. (2011) found that the abundance of many common bushmeat species varied with forest type and other habitat characteristics, but the analysis did not include distance to rivers as an explanatory variable. Regardless of the mechanism behind the effect of distance to rivers— accessibility versus target species abundance— our results can be used to inform conservation efforts. For example, patrol effort could be adapted to cover vulnerable locations near major watercourses at times of elevated risk.

Proportion of mixed forest also emerged as an important environmental determinant of the distribution of gunfire events. Sites composed of higher percentages of mixed forest were at a lower risk of poaching and bushmeat hunting (Fig. 3.5b). This contrasts with our hypothesis that high fruit availability in mixed forests would result in high target species abundance and predispose such sites to hunting. However, these results support the alternate hypothesis that mixed forest sites are less suitable for hunting because the dense understory inhibits foot travel (accessibility) and presumably also the successful targeting of animals. Different stands of mixed forest vary in their understory characteristics and the ease through which they can be travelled, however. Where there are large or numerous elephant trails, mixed forests can be traversed just as easily as open-understory *Gilbertiodendron* forests. The importance of mixed forest as an influence on site accessibility therefore remains unclear.

Another consideration is that *Gilbertiodendron* forests are usually located adjacent to rivers and thus often contain well-travelled riverine elephant trails (Blake, 2002). These monodominant forests were the other major forest type included in our habitat classification

(Appendix). Accordingly, sites characterized by low proportions of mixed forest often had relatively high proportions of *Gilbertiodendron* habitat. If the open understories or riverine trails of the *Gilbertiodendron* forests result in higher rates of poaching and bushmeat hunting, either through increased accessibility or target species abundance, this could have contributed to the low hazard ratios estimated for mixed forest sites, simply because they lack the *Gilbertiodendron* habitat type. Regardless of the specific mechanism underlying the mixed forest effect, our results show that habitat type can shape the distribution of poaching and bushmeat hunting activity.

Increasing distance to permanent roads had the unanticipated effect of increasing the risk of gunfire events. This contrasts with previous research that found elevated poaching/hunting activity closer to roads (e.g., Blake et al., 2007; Branch et al., 2022). Anti-poaching rangers are often stationed at multiple outposts located along the permanent roads of our study area, so distance to nearest road likely correlates with distance to nearest ranger outpost. It is not surprising, then, that sites farther from ranger outposts experience more gunfire events, where poachers and bushmeat hunters are less prone to apprehension (e.g., Moore et al., 2018). Mapping the exact locations of these outposts and including a distance to nearest outpost covariate in the modeling framework will be a useful next step in teasing apart the influence of road-related accessibility versus ranger-related deterrence. If small satellite stations and outposts reliably deter poaching and bushmeat hunting activity in their vicinities, expanding the distribution of these outposts could be an effective way to prevent poaching (Moore et al., 2018) without necessarily increasing the distances covered by mobile foot patrols. This could be an attractive option if resources for patrolling protected areas are limited.

To assess the effects of ongoing logging activity, we determined the months in which logging roads were cleared and trees were actively felled, moved to the nearest logging road, and transported out of the operational concession. During these active time periods, sites within 2 km of these activities experienced substantially reduced risks of gunfire events (HRs of 0.348 to 0.389; Table 3.2). This was initially surprising in light of previous evidence that logging workers sometimes engage in bushmeat hunting and aid in the transportation of hunters and bushmeat products (Poulsen et al., 2009; Robinson et al., 1999). However, in the operational concession of our study area, CIB was expected to operate according to the requirements established with certification by the Forest Stewardship Council (FSC). Among other things, FSC certification requires the logging company to control illegal hunting by employees, monitor changes in fauna, and ensure the protection of endangered species (FSC, 2014). The decrease in gunfire event risk associated with ongoing logging activity may indicate that CIB was effective in its regulation of employee hunting activity. However, at sites and times when logging activity was not ongoing, risk of gunfire events at sites within and nearby the logging concessions was high compared to sites deeper in the national park. Any potential poaching deterrence resulting from CIB management was short lived and constrained to only sites in close proximity to ongoing logging activity, rather than throughout the entire concession.

Another explanation for the risk-reducing effect of ongoing logging is that the habitat disturbance associated with these activities drives animals out of the vicinity (Poulsen et al., 2011), thereby diminishing the hunting prospects at these sites. In Chapter 4, I show that ongoing logging activity is one of the most important variables that influences the distribution of forest elephants, significantly reducing the probability of elephant occurrence at nearby sites. These activities should therefore reduce successful hunting prospects in the vicinity, whether the target species are elephants or bushmeat species. This explanation is further supported by the fact that gunfire event risk was reduced at these sites only during times of ongoing logging activity. By comparison, sites that were in or within 2 km of the logging concessions, irrespective of the timing of ongoing logging activity, experienced higher overall risk at all times compared to sites farther from the concessions (HRs of 1.384 to 1.952; Table 3.2). Therefore, while ongoing logging activity may curtail concurrent poaching and hunting, the baseline risk at sites within or in close proximity to concessions is higher in general. The system of temporary logging roads likely facilitates access and predisposes these areas to exploitation by poachers and bushmeat hunters. Interestingly, designation as protected area— and the deterrence value that it theoretically imparts— did not influence the risk of gunfire events. This lends further support to the hypothesis that risk is determined primarily by accessibility related to logging roads, rather than nominal level of protection. Our results suggest that even older, non-operational logging roads facilitate accessibility, as the highest ranked model and 2 others in the top model set suggest increased risk at sites in or within 2 km of the either concession (old or operational; HRs of 1.384 to 1.696; Table 3.2). Still, proximity to operational logging roads, which are less overgrown and more easily traveled, had a greater effect of increasing risk, as expected (HRs of 1.706 to 1.952; Table 3.2). Conservation efforts would benefit from a thorough investigation of the rate at which ephemeral logging roads succumb to forest succession, and how these changes determine accessibility and poaching/hunting activity in the impacted areas.

We provided limited evidence in the TTE analysis of a deterrence effect in the form of anti-poaching patrol activity. Increasing patrol effort, quantified as the total distance of foot patrols travelled each month, resulted in slightly reduced risk of gunfire events in the concurrent month— ongoing patrols appear to be a mild deterrent to poaching activity in our study area. This effect of patrol effort was more influential at the 10-km scale than at the 2-km scale (the 10-km covariate appears in more candidate models; Table 3.2). These results suggest that patrol effort has less influence at the local, immediate scale (i.e., deterrence in the form of avoidance of rangers by poachers in the forest). Rather, patrol effort seems to deter poaching in a more regional sense, potentially because knowledge of increased protection discourages poachers from exploiting broader areas that receive more thorough patrol coverage. Given the small effect sizes, and the inclusion of these covariates in only a few of the top models (Table 3.2), we are reluctant to draw much inference about the efficacy of patrol effort from the results of our TTE analysis. However, a potentially important effect of patrol effort emerges when considering the overall trends in total monthly gunfire events in relation to patrol activity and training (Figs. 3.6 & 3.7 top). Grid-wide patrol effort was reduced in early 2018 because rangers were undergoing an extensive training program and spending less time on field patrols (Fig. 3.7 top). During this period of reduced patrol effort, the rate of gunfire event detections was higher than any other period of the study, which provides an indication of what might be expected if law enforcement patrols were removed from the system (Figs. 3.6 & 3.7 top). When patrol effort returned to normal levels following the training period, the rate of gunfire events decreased (Fig. 3.7 top), suggesting that poaching and bushmeat hunting activity in our study system is indeed influenced by patrol effort. Furthermore, following the ranger training period, gunfire event rates remained at low levels for the remaining years of the study (Figs. 3.6 & 3.7 top). This may indicate that the ranger training in early 2018 was effective and improved the capabilities of patrols to deter illegal hunting activity. While hopeful, this evidence is circumstantial, and the relationship between grid-wide gunfire event rates and overall patrol effort remains unclear (Fig. 3.7 bottom). Our results suggest that patrol effort exerts an influence at some spatial and temporal scales but not others. The scale at which patrols are most effective needs to be examined with continued research, including analyses with finer temporal resolutions and higher sample sizes (i.e., more detected gunfire events). Improving our understanding of patrol effort as a determinant of the distribution of poaching activity will be fundamental in optimizing the allocation of conservation law enforcement resources.

We examined monthly rainfall independently from the TTE analysis, as a potential determinant of overall accessibility to the study area and thus the distribution of gunfire events. We found no evidence of constrained poaching or bushmeat hunting activity in the rainy seasons (Fig. 3.8), as would be expected if accessibility were impeded by extensive swamp and inundated forest areas. While the interaction between distance to rivers and seasonality (wet vs. dry months) was an important result of the TTE analysis (Fig. 3.5a; Table 3.2), monthly rainfall considered alone does not appear to influence the rate of gunfire events detected across the entire PAM grid (Fig. 3.8). Bushmeat hunters may overcome any wet season obstacles because the need to provide food or income through bushmeat hunting is constant year-round. Alternatively, elucidating the effects of rainfall may require analyses that include both spatial and temporal dimensions, rather than temporal considerations alone. This would explain the importance of season in the TTE analysis (Fig. 3.5a) which examined variation across space (sites) and time, but the absence of a rainfall effect when considering the entire study area without spatial partitioning (Fig. 3.8). A potentially informative next step would be to map seasonally inundated forests throughout the study area and examine gunfire detections in these areas as a function of season.

While this study focused on landscape scale environmental determinants of poaching and bushmeat hunting, we also accounted for the potential socioeconomic influence of national holidays. It has been suggested that poaching and bushmeat hunting activity is higher in the months preceding Christmas and New Year’s, as people attempt to accumulate food or monetary resources in preparation for the holidays (Astaras et al., 2017, 2020; Moreto & Lemieux, 2015; Viollaz et al., 2021). While we found no evidence of this phenomenon, our ability to detect a trend was limited by an unbalanced sample size of relevant months (pre-holiday months versus all other months). These potential patterns would likely be more effectively studied by pairing a PAM study with measures of bushmeat products entering local households and markets (e.g., Poulsen et al., 2009).

The overall number of gunfire events detected across the acoustic grid each month was highest toward the beginning of the study in 2018 and decreased over the subsequent 3 years of recording. While increased patrol efficacy resulting from the ranger training program may be partly responsible, the causes and significance of this trend remain unclear. Poachers often monitor conservation law enforcement effort closely (WCS, personal communication), and it is plausible that knowledge of the acoustic grid study spread through local poaching networks and is also acting as a deterrent. While speculative, this is consistent with growing evidence that research activity can deter illegal hunting (Branch et al., 2022; Junker et al., 2017). In NNNP, poachers may be concentrating activities farther north in the national park to avoid detection. A logical extension of this analysis would be to compare our gunfire event detection trend to evidence of poaching activity collected by patrols throughout the rest of the national park, including north of the study area. Examining patrol data collected over the same period could illuminate whether regional poaching rates are truly declining or if the distribution of gunfire events is simply shifting locally. However, as discussed previously, analysis and interpretation of patrol data requires caution if it has been collected in a manner unsuitable for common statistical approaches.

Using PAM to systematically collect spatiotemporal data on gunfire events, this study allowed poaching and bushmeat hunting activity to be statistically analyzed without the limitations imposed by opportunistic and biased data collection common to much of the research in this field. We provide evidence of environmental variables that influence the distribution of poaching and bushmeat hunting in NNNP and adjacent logging concessions. Our results suggest that the distribution of gunfire events is likely affected by a combination of the hypothesized categories of determinants— accessibility, deterrence, and target species abundance. However, the accessibility hypothesis received the most support and from our perspective is the most useful predictor of poaching and hunting activity. Proximity to major rivers and its interaction with season emerged as the most reliable variable explaining variation in risk of gunfire events. We suggest that patrol effort be adaptively adjusted by season to cover vulnerable areas near major watercourses. Our results also indicate that habitat and ephemeral logging concession roads influence accessibility to potentially exploitable sites, and that these roads may facilitate access long after they have been "closed" and become non-operational to logging companies. We suggest that conservation efforts use these results to estimate site-specific accessibility and guide the allocation of patrol coverage accordingly, rather than considering factors such as designation of protected area status alone. We advocate for continued research using PAM or other robust methods to systematically collect unbiased data on poaching and bushmeat hunting activity. These data will solidify our understanding of the environmental determinants of these activities, facilitate prediction of when and where they will occur, and aid conservation efforts in their intervention.

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Figures and tables

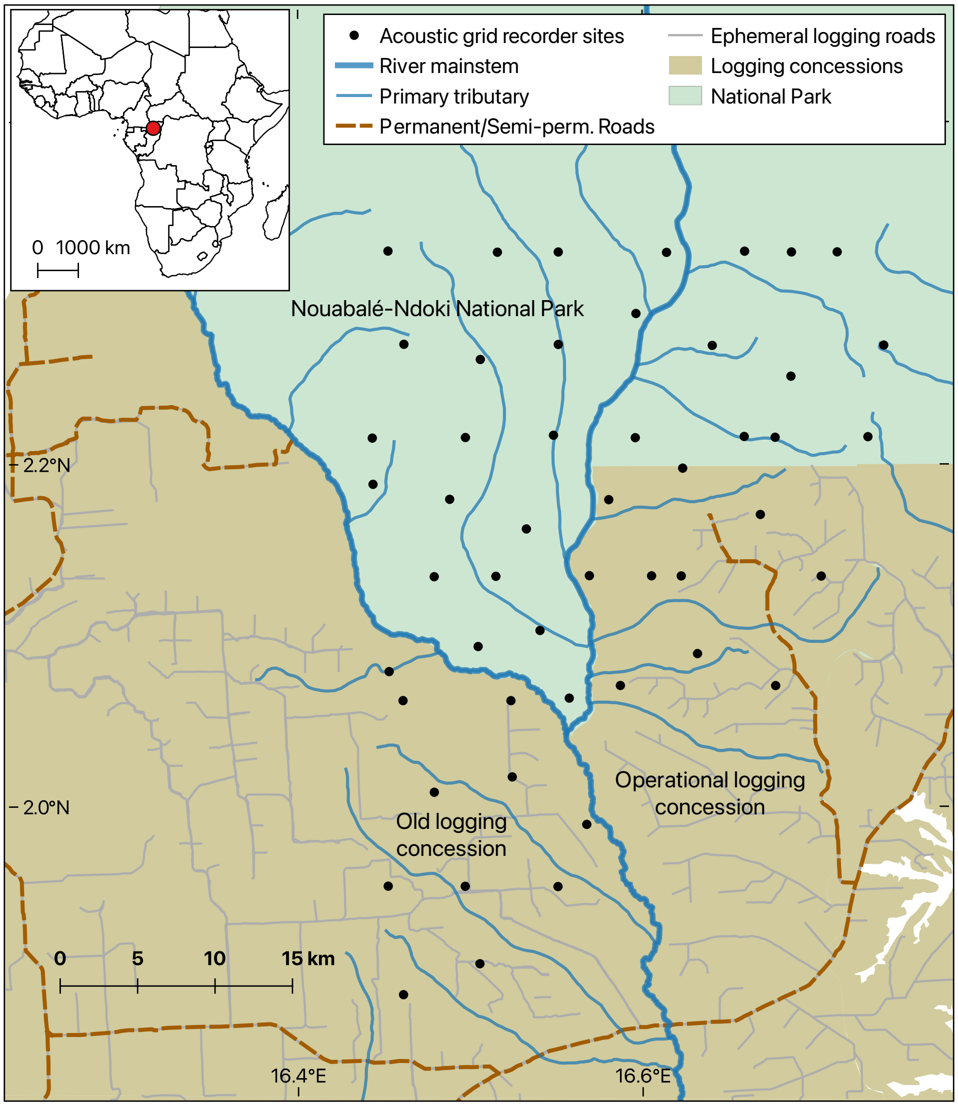

Figure 3.1 The grid of 50 acoustic recorders, covering portions of NNNP and adjacent logging concessions. The "old" concession, west of the Ndoki river, was selectively logged prior to 2010. The "operational" concession, east of the Ndoki and Goualougo rivers, was selectively logged during the years of the study, from 2017 to 2019. River mainstems, primary tributaries, and permanent/semi-permanent roads are shown, indicating potential avenues of access for poachers and bushmeat hunters. Ephemeral logging roads (shown in grey) are more navigable in the operational logging concession compared to the old concession, where only remnants remain. No roads of any kind exist in the national park. The red dot in the inset map shows the approximate location of the study area in northern Republic of Congo in central Africa.

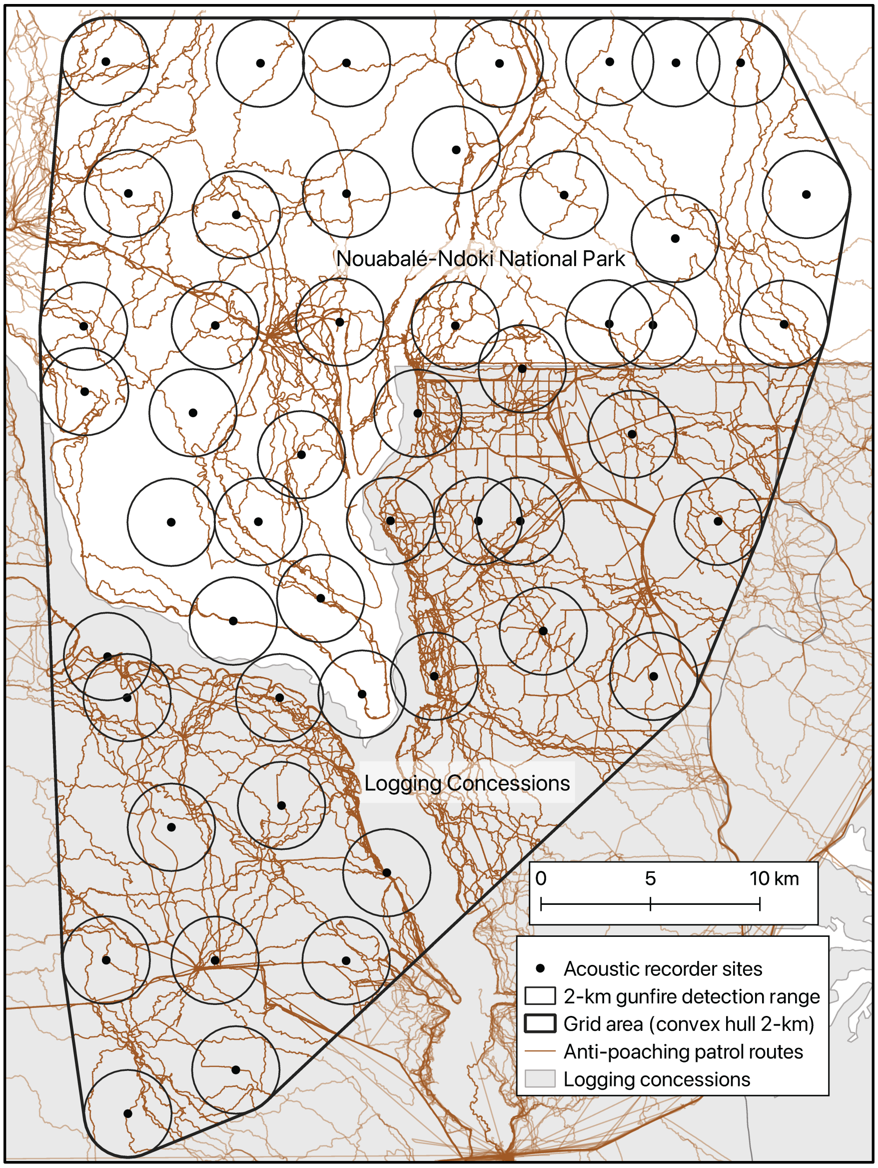

Figure 3.2 Anti-poaching patrols conducted from 2017 to 2021 covered both the national park and adjacent logging concessions. We quantified patrol effort— an expected deterrent of poaching and bushmeat hunting activity— on multiple spatial scales. For site specific measurements (TTE analysis), we used the total distance (km) of foot patrols per month within a 2-km radius (black circles) and a 10-km radius (not shown) from each recorder site (black dots). We also quantified monthly patrol effort across the entire study grid, defined by a convex hull with a 2-km buffer around the outer sites.

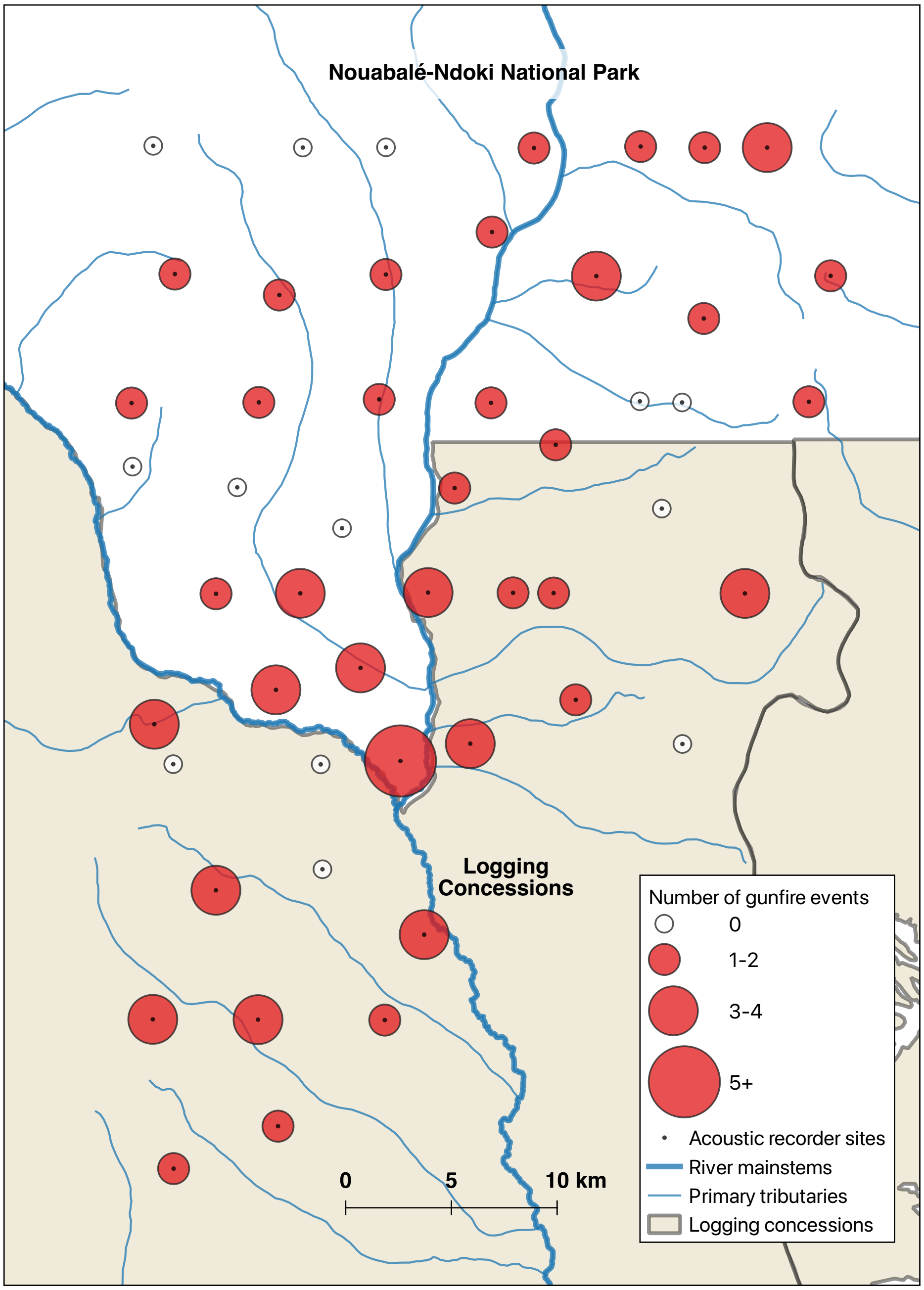

Figure 3.3 We detected a total of 86 gunfire events across the 50-sensor PAM grid over a 3.25-year period starting November 2017. The diameter of the red circles indicates the total number of gunfire events detected at each site, which ranged from 0 to 10 (mean = 1.72; SD = 1.73). At 13 of the 50 recorder sites, no gunfire events were detected (unfilled circles).

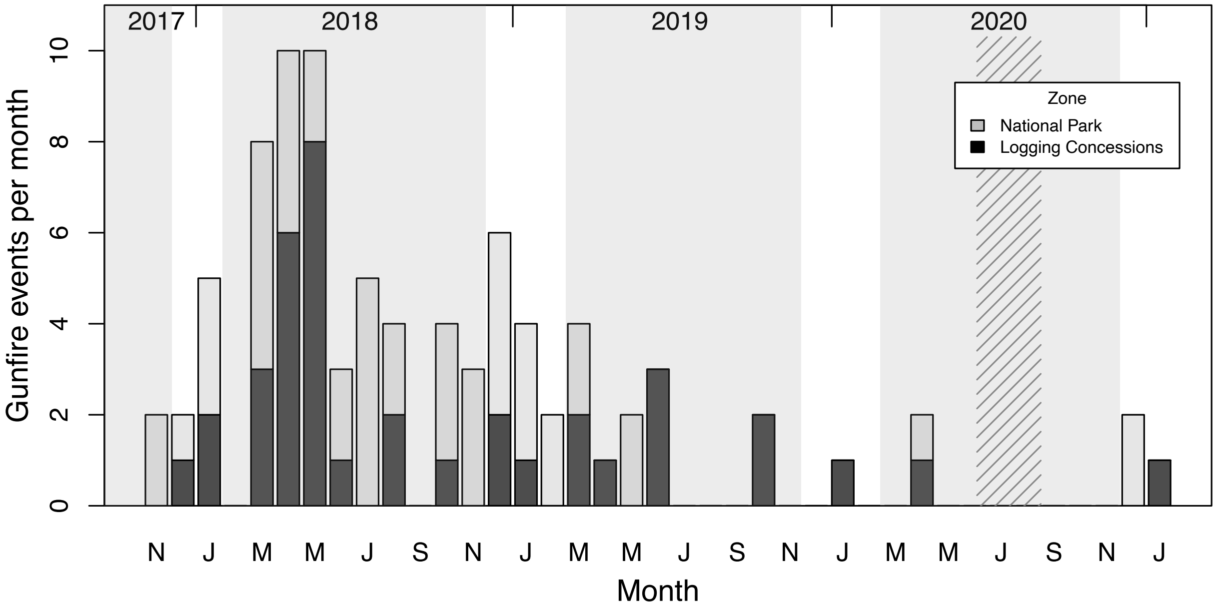

Figure 3.4 Monthly gunfire events across all 50 recorders of the PAM study grid, differentiated by national park recorders (grey portions of bars) and logging concession recorders (black portions of bars). Years are indicated between tick marks at the top of the figure. Grey background areas indicate rainy seasons, defined as months receiving more than 60 mm of rain. The region of diagonal hash lines indicates an approximately 2-month period in 2020 during which recording was interrupted due to the Covid-19 pandemic.

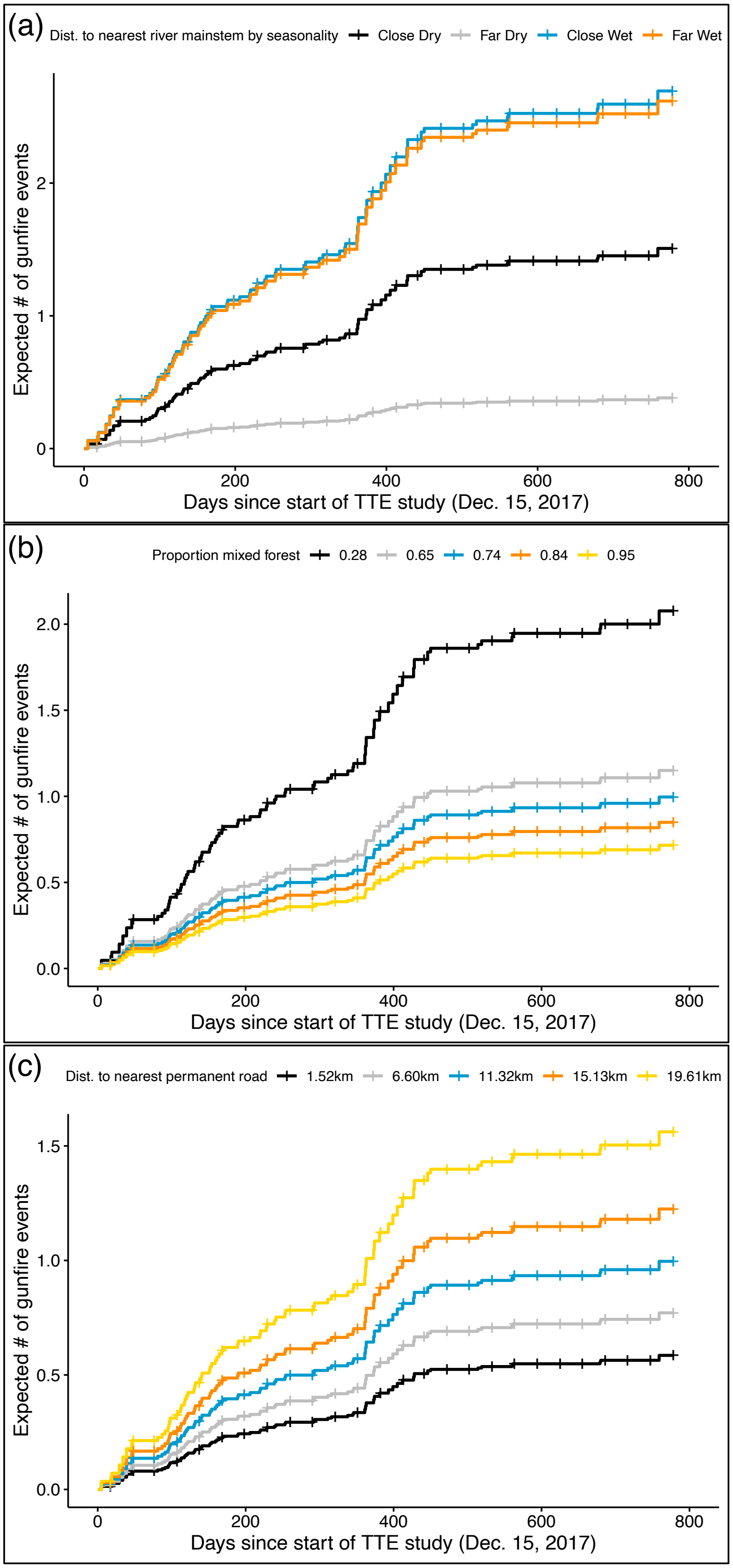
(a)
Dist. to nearest river mainstem by seasonality
Close Dry
Far Dry
Close Wet
Far Wet
Expected # of gunfire events
0
1
2
0
200
400
600
800
Days since start of TTE study (Dec. 15, 2017)
(b)
Proportion mixed forest
0.28
0.65
0.74
0.84
0.95
Expected # of gunfire events
0.0
0.5
1.0
1.5
2.0
0
200
400
600
800
Days since start of TTE study (Dec. 15, 2017)
(c)
Dist. to nearest permanent road
1.52km
6.60km
11.32km
15.13km
19.61km
Expected # of gunfire events
0.0
0.5
1.0
1.5
0
200
400
600
800
Days since start of TTE study (Dec. 15, 2017)

Figure 3.5 The expected number of gunfire events (which can be interpreted as risk) as a function of time since the start of the TTE study (Dec. 15, 2017). Risk of gunfire events was greater for sites closer to river mainstems than for sites farther away, but the magnitude of this effect was reduced in wet months (a). Risk was greater for sites whose forested area was characterized by lower proportions of mixed forest (b). Risk was greater for sites farther from the nearest permanent/semi-permanent road (c). The highest-ranked model was used to predict all curve values. The numeric covariates of the model that were not the focus of each panel were held at their average values, while percentile values were used for the focal covariate. For (a), distance values of 2.83 km (25th percentile) and 9.39 km (75th percentile) were specified for close and far sites respectively. For (b) and (c), the five specified proportions or distances were the 0th, 25th, 50th, 75th, and 100th percentile values of the variable. The predicted curves are shown for sites farther than 2 km from either concession (categorical variable included in highest ranked model). Identical curves are produced when using sites within 2 km from either concession (not shown), but the expected number of events is 1.696 times higher, indicating that close proximity to the concessions and their logging roads increases risk of gunfire events.

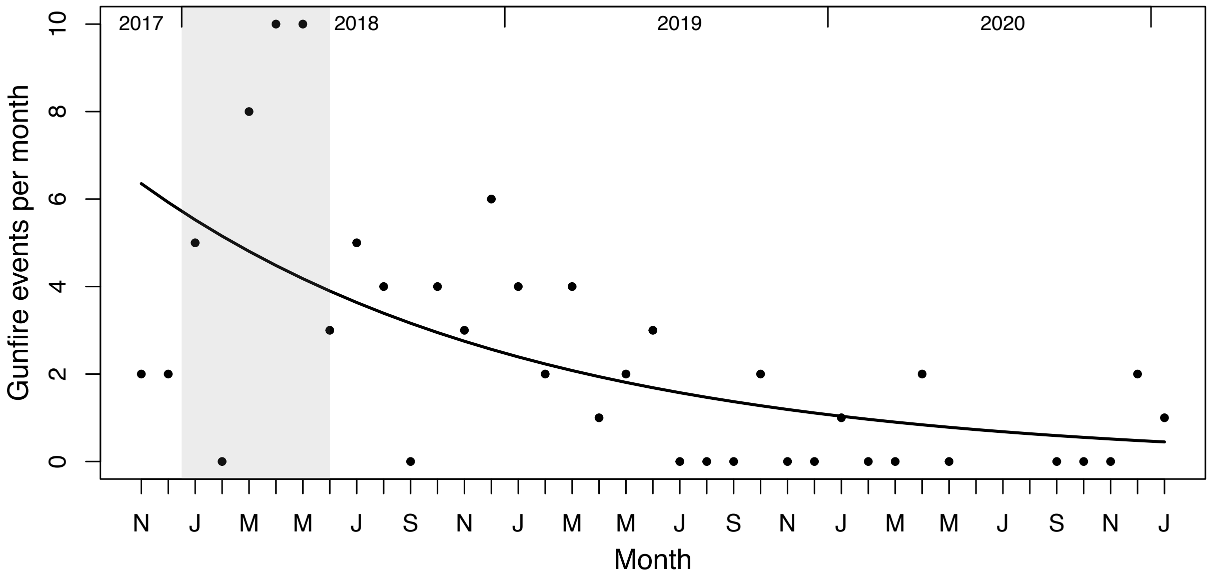

Figure 3.6 The total monthly gunfire events detected across all sensors of the PAM grid decreased over the study period from late 2017 to early 2021, as indicated by a GLM (Poisson distribution) fit to the monthly gunfire event count data ($\beta_{\mathrm{SequentialMonth}} = -0.07$ (log link scale), $p < 0.0001$). The grey shaded area indicates a period in early 2018 when grid-wide anti-poaching patrol effort was reduced because rangers were undergoing an extensive training program.

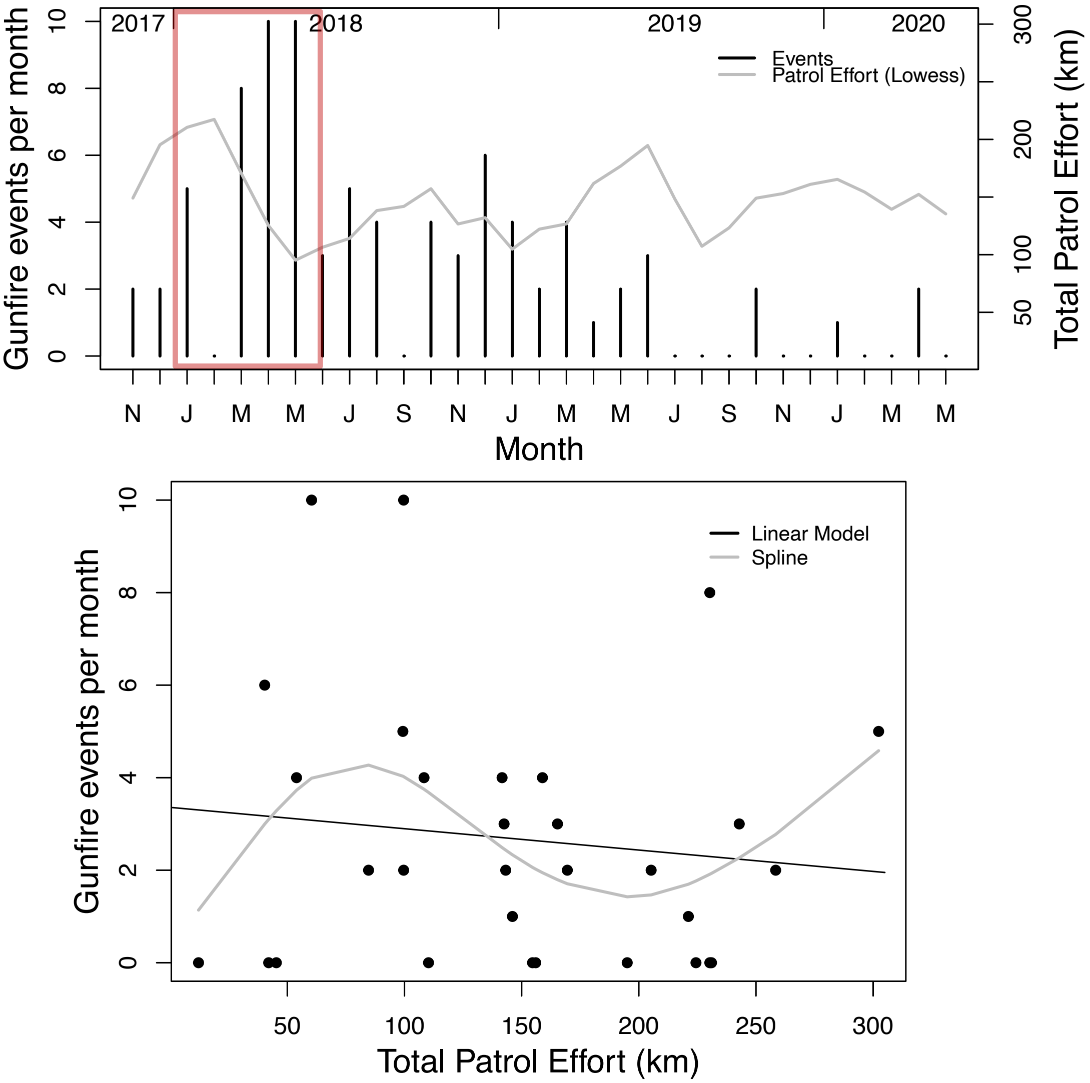

Figure 3.7 Gunfire events and total patrol effort (Lowess curve; smoothing parameter of 0.13) across the entire grid study area, from Nov. 2017 to May 2020, after which data collection was interrupted due to the Covid-19 pandemic (top panel). Patrol effort was substantially reduced in early 2018 (indicated by the red box) when rangers underwent an extensive training program. After this training period, monthly gunfire event detections exhibited a decreasing trend over the remainder of the study (see Fig. 3.6). When taken out of chronological context, the number of monthly gunfire events exhibited no clear relationship with total patrol effort (bottom panel). The slope of a linear model fit to the data did not differ from zero ($p = 0.52$). A smoothing spline fit to the data confirms the absence of a clear trend (smoothing parameter of 0.9).

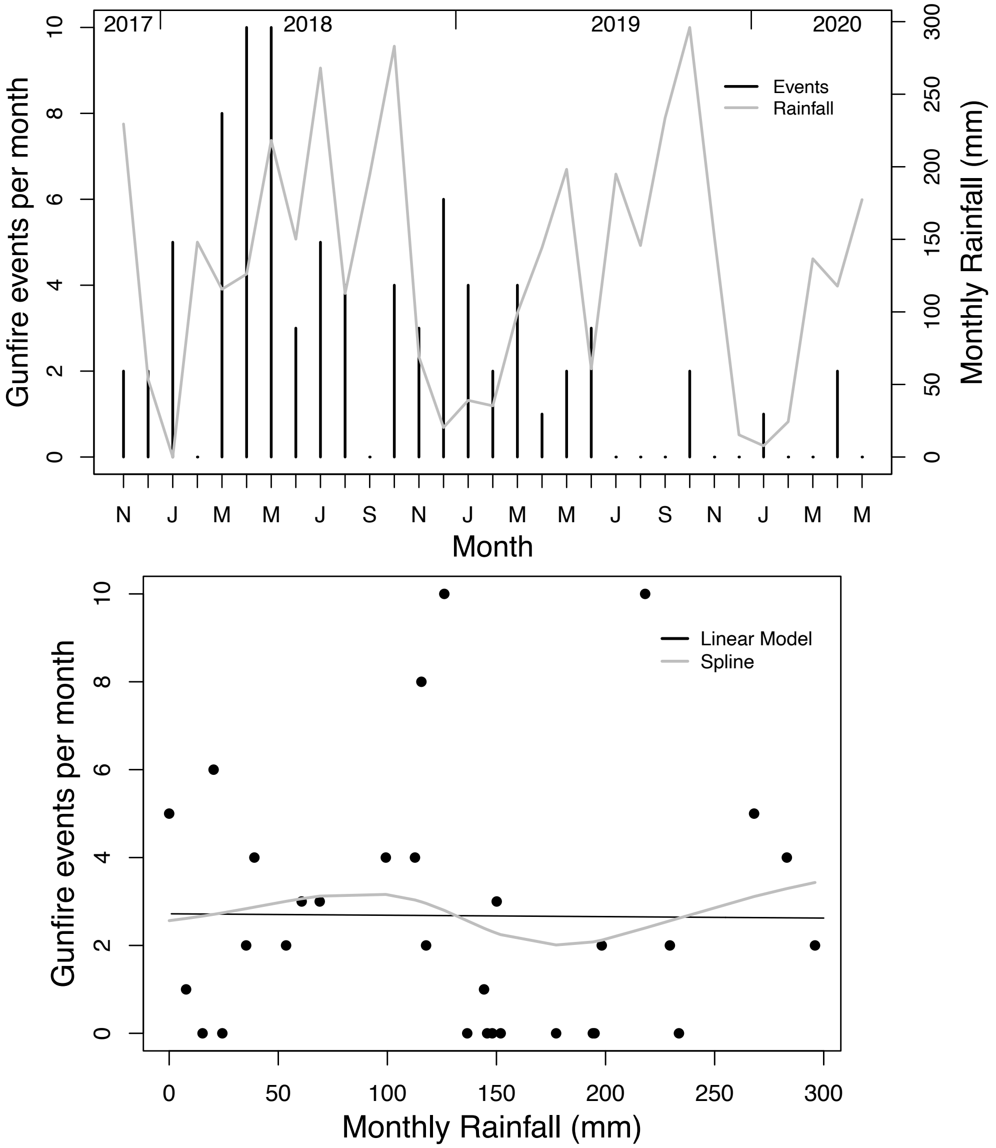

Figure 3.8 Gunfire events and monthly rainfall from Nov. 2017 to May 2020 (top panel). The number of monthly gunfire events exhibited no clear relationship with rainfall (bottom panel). The slope of a linear model fit to the data was not significantly different from zero ($p = 0.96$). A smoothing spline fit to the data confirms the absence of a trend (smoothing parameter of 0.9).

Table 3.1 Specifications of the general predictor variables used in the TTE modeling framework. Each general predictor and its alternative specifications represent one of the hypotheses that the distribution of gunfire events is determined by accessibility, deterrence, or target species abundance. Our predictions for the effect of each covariate on the risk of gunfire events are displayed in the last column.

Hypothesis	General Predictor		Specifications	Predicted effect
Accessibility	Roads		Distance to nearest permanent road	-
			Within 2 km of operational logging roads (yes/no)*	+
			Within 2 km of any logging roads, old or operational (yes/no)*	+
		Ongoing logging activity	Operational logging/roads stratum, 2 levels (operational concession vs. NP and old concession)*	+/-
			Ongoing logging activity (tree felling and transport) within 2 km, by month (yes/no)[a]	either
	Rivers		Distance to nearest river mainstem[a]	-
			Distance to nearest mainstem or primary tributary[a]	-
			Distance to nearest mainstem X Season (wet vs. dry month)[a]	-
			Distance to nearest mainstem or primary tributary X Season (wet vs. dry month)[a]	-
Deterrence	Patrol effort		Montly patrol effort within 2 km (distance of foot patrols travelled)	-
			Montly patrol effort within 10 km (distance of foot patrols travelled)	-
	Overall protection		Protection, 2 levels (NP versus either concession)[b]*	-/+
Target Species Abundance	Elephant abundance		Mean elephant rumble detection rate, by month	+
	Animal resources (proxy for abundance)		Proportion of mixed species forest[b]	either
			Proportion of mixed species forest X Season (wet vs. dry month)	+

* = spatial categorical covariates that are variations of a common strata system

[a] = can also influence animal abundance

[b] = can also influence accessibility

Table 3.2 Set of top candidate models (within 2 AIC$_c$ units of highest model) ranked according to AIC$_c$. No model in the top set unambiguously outperformed the others, indicated by low delta AIC$_c$ values and model weights. Hazard ratios (HRs) are provided for each of the covariates included in the models. HRs greater than 1.0 indicate that the effect of the covariate is to increase the risk of gunfire events. HRs less than 1.0 indicate a risk-reducing effect. HRs closer to 1.0 indicate weaker effect sizes than those farther from 1.0. (Note: HRs have a different interpretation for interaction terms and reflect the ratio of effect size differences between factor levels). Some covariates appeared in many or all the top models, indicating substantial support as predictors of poaching and bushmeat hunting risk. Some covariates listed in Table 3.1 did not appear in any of the top models and are thus not considered supported.

Model rank	Hazard Ratios for Model Covariates (95% CI)										Assessment Metrics				
	Dist perm road	Dist river mainstem	Dist river mainstem* Wet months	Current logging activity	Patrol 10km current month	Patrol 2km current month	Prop mixed forest	Prop mixed forest* Wet months	Within 2km either concession	Within 2km operational concession	# par	logLik	AICc	ΔAICc	Weight
1	**1.056** (0.994, 1.122)	**0.811** (0.680, 0.968)	**1.228** (1.011, 1.491)				**0.202** (0.025, 1.632)		**1.696** (0.849, 3.386)		5	-277.492	565.853	0.000	0.147
2		**0.791** (0.650, 0.962)	**1.244** (1.011, 1.532)	**0.353** (0.104, 1.197)			**0.316** (0.036, 2.776)				4	-279.042	566.655	0.802	0.098
3	**1.074** (0.971, 1.189)	**0.810** (0.678, 0.967)	**1.228** (1.008, 1.495)							**1.952** (0.586, 6.505)	4	-279.239	567.050	1.196	0.081
4		**0.794** (0.651, 0.969)	**1.240** (1.007, 1.526)	**0.348** (0.105, 1.149)							3	-280.375	567.087	1.234	0.079
5		**0.785** (0.650, 0.949)	**1.242** (1.015, 1.521)		**0.994** (0.986, 1.003)		**0.275** (0.031, 2.415)				4	-279.278	567.128	1.274	0.078
6		**0.788** (0.650, 0.955)	**1.243** (1.012, 1.527)	**0.389** (0.113, 1.338)	**0.995** (0.987, 1.003)		**0.287** (0.034, 2.450)				5	-278.159	567.187	1.334	0.075
7		**0.789** (0.651, 0.956)	**1.243** (1.013, 1.526)				**0.304** (0.032, 2.846)				3	-280.477	567.291	1.438	0.072
8		**0.788** (0.650, 0.955)	**1.249** (1.015, 1.538)	**0.354** (0.107, 1.178)			**0.086** (0.010, 0.767)	**6.399** (0.513, 79.808)			5	-278.276	567.423	1.569	0.067
9		**0.796** (0.665, 0.953)	**1.230** (1.011, 1.496)				**0.265** (0.030, 2.327)		**1.406** (0.749, 2.640)		4	-279.438	567.448	1.595	0.066
10		**0.793** (0.665, 0.946)	**1.229** (1.012, 1.491)		**0.994** (0.986, 1.003)		**0.246** (0.031, 1.955)		**1.384** (0.752, 2.546)		5	-278.337	567.544	1.690	0.063
11		**0.783** (0.644, 0.952)	**1.253** (1.019, 1.540)	**0.368** (0.107, 1.261)		**0.947** (0.861, 1.041)	**0.297** (0.034, 2.589)				5	-278.344	567.558	1.704	0.063
12	**1.069** (0.978, 1.169)	**0.806** (0.675, 0.962)	**1.233** (1.012, 1.502)				**0.383** (0.075, 1.966)			**1.706** (0.663, 4.392)	5	-278.429	567.728	1.874	0.057
13	**1.034** (0.981, 1.090)	**0.793** (0.654, 0.963)	**1.246** (1.014, 1.532)				**0.281** (0.030, 2.613)				4	-279.631	567.834	1.981	0.055
null												-286.95	573.908	8.055	NA

CHAPTER 4

The influence of habitat resources and anthropogenic disturbance on the landscape use of African forest elephants (*Loxodonta cyclotis*) in Nouabalé-Ndoki National Park, Republic of Congo

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Abstract

Knowledge of species distributions in space and time is crucial for understanding a species' basic ecology and for facilitating the protection of important sites and habitats for conservation. This is particularly important for endangered species like African forest elephants, who are influenced not only by habitat resources but also by anthropogenic pressures such as poaching and logging. Our knowledge of forest elephant behavior and ecology is relatively limited, in part due to difficulties imposed by their remote rainforest habitat. Many forest elephant studies have been limited in spatiotemporal scope by the constraints of methods such as dung transects. Others have focused only on a narrow selection of predictor variables or included only anthropogenic pressures while disregarding the habitat characteristics that also shape forest elephant distributions. There is a need for more comprehensive research that includes a diversity of variables and expands the spatial and temporal scales of data collection. In this study, we simultaneously examined anthropogenic- and resource-related determinants of forest elephant landscape use. We used a passive acoustic monitoring (PAM) approach to broaden the scale of data collection beyond what is achievable with many other methods. Over 3.25 years of continuous recording, we detected thousands of elephant rumble vocalizations across a grid of 50 acoustic recorders, covering 1250 km^2 of rainforest landscape in northern Republic of Congo. We used Bayesian multi-season occupancy models to investigate covariates hypothesized to influence forest elephant landscape use, including both habitat resources and anthropogenic disturbances such as poaching pressure, which we quantified by acoustically detecting gunshots across the PAM grid. Important relationships that emerged included an overall declining trend in forest elephant occurrence in the study area over the 3.25 years of recording; higher occurrence probability in the wet seasons, potentially indicative of seasonal movements in and out of the

study area; and a deterrent effect of ongoing logging activity that reduced occurrence probability. We provide some evidence that sites previously disturbed by selective logging constitute habitat that is just as important as undisturbed protected areas. Poaching activity did not appear to impact elephant use of the landscape at the temporal scale and resolution of our analysis. Our results contribute to our understanding of forest elephant behavior and ecology, although more data and research are needed to confirm some of our proposed relationships and effects. As our understanding of the determinants of forest elephant distributions improves, we hope that findings such as these will be integrated into the adaptive management of conservation efforts (e.g., patrol effort) and anthropogenic activities (e.g., logging), to minimize disturbance and more effectively protect this critically endangered species.

Introduction

A major goal of the ecological subdisciplines focusing on habitat use and spatial distribution is to identify the particular habitat types that are most suitable for a species, with the goal of understanding the basic ecology of the species or of predicting important habitat for conservation purposes (Blumstein & Fernandez-Juricic, 2010; Stamps, 2009). Knowledge of species' distributions in space and time is critical in that it enables decision making about which resource patches, habitats, and/or landscapes to prioritize for protection (Blumstein & Fernandez-Juricic, 2010; Cooke, 2008). This is particularly important for endangered species such as elephants, whose use of the landscape is influenced not only by habitat resources but also by devastating anthropogenic activities such as poaching (Blake et al., 2008; Yackulic et al., 2011). While considerable attention has been paid to the landscape and habitat use of African savanna elephants (*Loxodonta africana*, e.g., Martin et al., 2010; Western, 1975; Western &

Lindsay, 1984), there are fewer analogous studies with African forest elephants (*Loxodonta cyclotis*), in part due to the logistical constraints and difficulty of observation in their dense rainforest habitat. Those studies that do exist have focused on the effects of human disturbance while placing less emphasis on natural environmental covariates (e.g., Barnes et al., 1991, 1997; Blake et al., 2007, 2008; Hall et al., 1997; Laurance et al., 2006; Maisels et al., 2013; Yackulic et al., 2011; but see Blake, 2002; Buij et al., 2007; Morgan & Lee, 2007; Theuerkauf et al., 2001 as exceptions), apart from relating elephant movement to fruiting trees (Blake & Inkamba-Nkulu, 2004; Short, 1981, 1983; White, 1994) and bai mineral deposits (Blake & Inkamba-Nkulu, 2004; Turkalo et al., 2013; Turkalo & Fay, 1995; Vanleeuwe & Gautier-Hion, 1998). Furthermore, the vast majority of studies have relied on dung transects to infer forest elephant presence (Barnes et al., 1991; Blake et al., 2007; Buij et al., 2007; Hall et al., 1997; Theuerkauf et al., 2001; White, 1994; Yackulic et al., 2011). While useful for certain applications, dung transect methods often suffer from limited spatiotemporal scope and resolution, considerable time and financial costs, inadequate sampling effort, and biased or inaccurate state variable estimates (e.g., abundance estimates; Hedges, 2012; Laguardia, Gobush, et al., 2021). Therefore, there is a need to simultaneously evaluate the effects of both resource-based (e.g., dominant vegetation type) and disturbance-based (e.g., degree of poaching pressure) covariates that influence forest elephant landscape and habitat use, and to do so over a larger spatial and temporal extent, which is possible using methods such as passive acoustic monitoring (PAM) rather than relying on dung transects. We still do not adequately understand forest elephant habitat use or how it is influenced by human activities (Fishlock & Breuer, 2015). We do not know which types of habitat will be crucial for sustaining forest elephant populations (Fishlock & Breuer, 2015), or to what degree elephants will survive along gradients of increasing anthropogenic disturbance (Kolowski et al., 2010).

Forest elephant habitat use can be examined in the framework of optimal foraging theory, which suggests that animals should choose feeding locations and food sources that maximize their average rate of energy intake, which in turn should increase fitness (Charnov, 1976; Pulliam, 1974; Stephens & Krebs, 1986). When available, foragers should opt for more profitable resource patches or food items, all other things being equal (Lima & Dill, 1990; Pulliam, 1974; Stephens & Krebs, 1986). Forest elephants take advantage of a variety of food sources including grass, leaves, bark, roots, and stems (Blake, 2002; Short, 1981), but fruit from fruiting trees is their preferred food when available, likely due to its higher energetic and nutritional payoff (Blake, 2002; Blake & Inkamba-Nkulu, 2004; Short, 1981, 1983; White, 1994). In NNNP, fruit availability tracks precipitation, with the most tree species and the highest proportion of individual trees fruiting during the months of highest rainfall (Blake, 2002; Groenenberg et al., 2016). Fruit tree density is highest in *terra firma* mixed-forest upland sites of NNNP (Blake, 2002), which might be expected to serve as important habitat, particularly during the wet season. However, in drier periods when fruit is scarce, the higher-quality leafy browse near wetlands and rivers, or in secondary forests previously disturbed by logging, may attract forest elephants to swampy lowland or previously disturbed sites (Blake, 2002; White, 1992). Hence, the importance of habitat types and particular sites may change seasonally for forest elephants (Buij et al., 2007; Eggert et al., 2014) like it does for savanna elephants, in which seasonal movements to track water sources and areas of high grass productivity are well documented (e.g., Western, 1975).

The basic optimal foraging framework can be amended to include situations of foraging under predation risk or disturbance (Brown & Kotler, 2004; Frid & Dill, 2002; Gilliam & Fraser, 1987; Lima & Dill, 1990), which is arguably the default state for most species, as most species serve as prey for at least some others (Lima & Dill, 1990). While foraging under predation risk, animals must balance their need for food and safety, a task that is particularly pertinent and difficult when high-quality feeding areas are also the most dangerous. This trade-off can be optimized by monitoring changes in risk over time and selecting sites that provide adequate energy acquisition without intolerable exposure to predators or disturbance (e.g., by minimizing the ratio of predation risk to net energy intake; Brown & Kotler, 2004; Frid & Dill, 2002; Gilliam & Fraser, 1987; Lima & Dill, 1990). While forest elephants have few natural predators, poaching by humans is analogous to predation and constitutes a grave threat to individual animals and the persistence of the species as a whole (Blake & Hedges, 2004; Blanc, 2008; Maisels et al., 2013). Studies that have sought to understand the effects of poaching pressure on forest elephants have often relied on proxies of poaching risk, such as distance to nearest access roads. These studies have shown that forest elephants engage in risk avoidance behavior including avoidance of roads, which has been interpreted as avoidance of poaching pressure (Blake et al., 2007, 2008; Yackulic et al., 2011). It may be that forest elephants are actively avoiding areas with high poaching pressure and therefore forsaking otherwise high-quality habitat that is made unsuitable by human activity. This could lead to reduced energy intake and reproductive rates and associated population level consequences (Blumstein & Fernandez-Juricic, 2010; Frid & Dill, 2002). Our understanding of these potential effects would benefit from research methods such as PAM, where poaching pressure can be measured directly by counting the number of gunshots detected at acoustic recorders distributed across the landscape.

An advantage of the PAM approach is that the more straightforward quantification of poaching pressure allows the effects of these activities on elephant habitat use to be measured in a direct manner (Astaras et al., 2017, 2020).

The impact of logging activity on forest elephants has received less attention than that of poaching, although forest elephants seemingly avoid human activity in general (Barnes et al., 1991; Blake et al., 2008; Buij et al., 2007). There is considerable evidence that animals perceive and respond to non-lethal human disturbance and predation risk in the same way, and thus disturbance may result in the same trade-offs between foraging efficiency and maintenance of adequate safety as does predation risk per se (Frid & Dill, 2002). The reason that non-lethal human disturbance stimuli and predation risk are interchangeable in the optimal foraging framework is that both elicit behavioral responses that divert energy away from maximizing foraging efficiency (Frid & Dill, 2002). Therefore, in addition to altering their landscape use in response to poaching pressure, forest elephants may also forsake high-quality habitat because of logging activity. On the other hand, temporary access roads created in logging concessions result in an increase in secondary re-growth of leafy browse, which may be attractive to forest elephants, particularly during the drier months when fruit is less available at undisturbed mixed forest sites (Blake, 2002; White, 1992). Therefore, one might expect reduced elephant landscape use at sites with ongoing logging activity, but increased use of previously logged sites where human activity has returned to low levels, but perhaps only when fruit availability at undisturbed mixed forest sites is low.

We implemented a PAM approach to collect data on forest elephant and gunfire event distribution over 3.25 years in NNNP and the adjacent logging concessions in northern Republic of Congo. We analyzed forest elephant detection/non-detection data with multi-season occupancy models to examine the environmental variables that influence forest elephant use of the landscape. These variables pertained to either anthropogenic disturbance (e.g., poaching and logging pressure) or habitat resources (e.g., forest type). We anticipated that the effects of these different covariates would change between the wet and dry seasons due to the shifting importance of elephant food resources (Table 4.1). In particular, we expected prevalent use of mixed forest habitat in wetter months and a shift to usage of previously disturbed sites with abundant browse in the drier months, depending on the spatiotemporal distribution of poaching and logging activity.

Methods

Acoustic data acquisition

Forest elephant detection data were collected with a PAM approach, using a grid of 50 acoustic recorders established in Nouabalé-Ndoki National Park (NNNP), Republic of Congo, and the adjacent logging concessions (Fig. 4.1). Acoustic grid and recording details are provided in Swider et al., (2022) and in Chapters 2 & 3. The grid covered 1250 km^2 (mean inter-sensor distance of 5.5 km [SD = 1.4]) and recorded continuously from November 2017 to March 2021. Recorder sites belonged to one of 3 different strata: the national park (29 sites), the old concession that was selectively logged prior to 2010 (11 sites), and the operational concession, selectively logged throughout the study until September 2019 (10 sites; Fig. 4.1).

The presence of forest elephants at each site was indicated by detection of rumble vocalizations. Rumbles are an appropriate signal to use for detection because they are the most common vocalization and they are used by both sexes and all age classes and in many behavioral contexts (Chapter 4; Hedwig et al., 2021; Poole et al., 1988; Stoeger et al., 2014; Thompson, 2009). Their low frequencies also make them favorable for PAM because they are less susceptible to environmental attenuation than higher frequency vocalizations (Ingard, 1953). Previous detection distance experiments indicate that we can detect rumbles at a range of 500-600m, resulting in a detection area of approximately 0.79-1.13 km^2 around each of the 50 recorders (Fig. 4.1). An automated detector algorithm based on a feature extraction and classification system (Keen et al., 2017) was used to extract rumbles from the continuous 3.25-year audio data set. For 3 randomly selected days per week, the detector output was manually reviewed to confirm putative rumble detections and remove false positives from the data set. To evaluate detector performance, spectrograms of 267 days throughout the study period were manually reviewed to establish a "truth" dataset of identified rumbles. We compared these data to the reviewed detector output for the same days and found the average percentage of existing rumbles identified by the detector per day to be 68.6%.

Modelling approach

We analyzed elephant detection/non-detection data and covariates that we hypothesized to influence forest elephant distribution (see below) with Bayesian multi-season occupancy models using the 'spOccupancy' package (Doser et al., 2022) in R (R Core Team, 2022). We used months as primary sampling periods (the "seasons" of multi-season models *sensu* Mackenzie et al., 2003; MacKenzie et al., 2018), starting with January 2018, as this was the first full month that all acoustic recorders of the grid were installed and recording continuously. We included all months through March 2021, except for June-September 2020 (data collection interrupted by Covid-19 pandemic) and January-February 2021 (interruptions due to equipment malfunctions). This resulted in 33 months used as primary sampling periods. We used the 3 random days per week for which the detector output had been manually verified to compile 12 days per month with which to estimate detection probability (i.e., to serve as secondary sampling periods or "surveys" *sensu* Mackenzie et al., 2003; MacKenzie et al., 2018). Therefore, each primary sampling period (month) included 12 survey days, 3 of which were randomly allocated to each week, so that sampling covered the duration of each month. One or more rumbles detected within the 24 hours of each survey indicated forest elephant presence. Throughout the 3.25 years of recording, equipment failures resulted in at least some gaps in recording at most sites. Therefore, sites occasionally had fewer than 12 surveys each month, or in some cases lacked data for a given month entirely. Occupancy modeling is a flexible approach that can accommodate such missing or unbalanced surveys (Doser et al., 2022; MacKenzie et al., 2018). We compared models with different combinations of covariates representing the effects of anthropogenic disturbance and habitat resources on forest elephant landscape use, while accounting for variables that could impact the probability of detecting forest elephants (Table 4.1).

Anthropogenic disturbance covariates

We used the PAM grid to detect gunshots from poaching and bushmeat hunting activity (Chapter 3), an anticipated determinant of forest elephants' use of the landscape (Swider et al., 2022). Controlled experiments near a ranger training site in the same forest revealed that gunshots can usually be detected at distances of at least 2 km from the recorders. A template-based detector algorithm trained on recorded gunshots was used to search the continuous audio data for gunshots (see Wrege et al., 2017 Appendix S3 for detector details). Putative gunshots identified by the algorithm were then manually verified via spectrographic and auditory analysis by experienced personnel. All false-positive gunshot detections were removed from the dataset. For confirmed gunshots, we manually examined spectrograms to verify that no additional gunshots had occurred within 24 hours of the detected focal shot(s). We aggregated any shots occurring within 1 hour of one another into ‘gunfire events’, which would likely represent a single elephant poaching attempt. The gunfire events were each detected at a single recorder only, which we designated the gunfire event site. Automatic weapon fire events likely represented attempted elephant kills, whereas single-action weapon fire could include both elephant poaching and bushmeat hunting of other species (Swider et al., 2022). We quantified poaching/gun-hunting covariates using all detected events because (1) we are unable to definitively differentiate between elephant poaching and bushmeat hunting events, and (2) gunshots may contribute to elephants’ perception of risk and use of the landscape irrespective of the species that is targeted (i.e., non-lethal disturbance stimuli; Frid & Dill, 2002). We included two versions of the poaching/hunting pressure covariate in the occupancy models— number of events in each primary period, and cumulative number of events having occurred since study onset (Table 4.1). These represent the potential of forest elephants avoiding sites with currently high poaching risk or avoiding sites with historically high poaching risk over the course of the study.

In addition to poaching activity, we expected logging activity to be an anthropogenic disturbance that would deter forest elephants from using affected sites. Variability in logging activity is correlated with protected area designation in our study system (logging concession versus national park). To capture broad scale variability in logging pressure (and protected status), we included the stratum to which each site belonged as a covariate (Fig. 4.1). We specified the levels of this variable in alternate ways to arbitrate between multiple hypotheses (Table 4.1). To reflect protection, we specified 2 strata to differentiate between NP and concession (old and operational combined). During model comparison, support for models with this specification would indicate that protected status is important, or that selective logging results in habitat changes that in turn affect elephant distribution. To reflect the potential effect of operational logging per se, we re-specified the 2 strata to differentiate between the presence or absence of operational logging (operational concession vs. NP and old concession combined). Support for models with this specification would suggest that operational logging activity influences forest elephant distribution, but not the protected status of sites or logging-induced habitat changes per se. In the final version, we specified all 3 strata separately: national park, old concession, or operational concession (Table 4.1). Support for models with this specification would indicate that operational logging activity, protected status, or logging imposed habitat changes could all be important.

To explore the potential effects of selective logging at a finer spatiotemporal resolution, we mapped variability in ongoing logging activity using data provided by the logging company, *Congolaise Industreille des Bois* (CIB). These activities included clearing temporary logging roads, felling trees, moving downed trees to the nearest logging road, and transporting trees out of the concession. We included a binary, time-varying (monthly) covariate for whether these activities were ongoing within 600 m of recorder sites (Table 4.1; 600 m is our estimated detection range for forest elephant rumbles). This covariate allowed us to account for the potential of forest elephants to adjust site usage in accordance with selective logging activity in a more immediate, localized, and dynamic manner than could be reflected by the strata covariates (discussed above).

Habitat resource-related covariates

Our main habitat covariate of interest was the amount of mixed species forest that characterizes the sites across the grid, and the potential interaction with season. The amount of mixed forest should reflect the availability of fruit— an indispensable component of the forest elephant diet— because fruit tree density in NNNP is highest in mixed forest compared to other habitats (Blake, 2002). This is especially pertinent in the wet season when fruiting rates are highest (Blake, 2002). Using Landsat 8 30-m resolution satellite imagery paired with ground truth locations obtained during Wildlife Conservation Society foot surveys, we performed a supervised classification of habitat type across our study area (Appendix). We classified pixels into 3 categories: 1) forest composed of mixed tree species, 2) monodominant forest composed of *Gilbertiodendron* sp., and 3) an "open" class that included river floodplain with sparser canopy than upland forest (or no canopy), open-canopy swamps, open water, aquatic vegetation and grasses, and forest clearings. Within a 600-m radius around each of the 50 recorders, we calculated the percentage of pixels that were classified as mixed forest (Appendix). We included a seasonality interaction term with each month categorized as wet (>60 mm of rain) or dry (<60 mm of rain) (Beck et al., 2018). Rainfall data from four weather stations in and around the acoustic grid were averaged to determine season. With the exception of February 2018 (wet), rainy season was March-November and dry season December-February of each year. Seasonality of primary period was included as a main effect on occurrence and as an interaction with proportion of mixed forest (Table 4.1).

While we anticipated mixed forest and corresponding fruit availability to be important in the wet season, a shift of resource use may occur in the drier months. We hypothesized that increased browse resources associated with secondary succession in logging concessions may attract forest elephants to these previously disturbed sites in the dry season when fruit is limited. To accommodate this potentiality, we included an interaction of seasonality (wet versus dry months) with the logging strata covariates discussed previously (Table 4.1).

Other resource-related covariates included distance to the nearest river mainstem (Ndoki and/or Guoalougo rivers), and distance to the nearest *bai* or *eyanga* (Table 4.1)— clearings with resources that are attractive to forest elephants (Klaus et al., 1998; Turkalo & Fay, 1995). Distances were measured on GIS layers of watercourses, using QGIS software (*QGIS 3.22*, 2022). These layers were created by manual tracing of digital elevation models and confirmed with on-the-ground GPS mapping that we implemented during routine maintenance of the acoustic grid.

Lastly, preliminary analyses indicated that forest elephant raw occupancy estimates (uncorrected for detection) had declined throughout the study period (see Results Fig. 4.2). To account for this possibility, we included primary sampling period itself as a continuous covariate that would reveal any linear trends in occupancy (site use) over time (Table 4.1).

Detection covariates

We accounted for three variables that could potentially influence the detection probability for forest elephants in our study system. Unlike occurrence covariates, which can vary only by site and primary period, detection probability covariates can also vary survey to survey (Doser et al., 2022; MacKenzie et al., 2018). Swider et al. (2022) (Chapter 2) showed that forest elephants likely alter their acoustic behavior in the 24 hours before or after gunfire events. We therefore included a site-specific binary detection covariate for whether a gunfire event had occurred within two days of any survey day (Table 4.1). Other factors that can interfere with the acoustic detection of forest elephants are rain and thunder, which are characterized by low frequency sound in the same range as elephant rumble vocalizations. Using the weather stations for which we had the most consistent data over the course of the study, we calculated the average daily rainfall over weekly intervals, and included these values as a detection probability covariate that could vary between surveys of different weeks (Table 4.1). Lastly, we allowed a random effect for primary sampling period that would accommodate differences in detection probability among the months of the study (Table 4.1), due to changes in forest elephant abundance in the grid area over time, for example.

Model structuring and comparison

As a criterion for Bayesian model comparison, we used the Widely Applicable Information Criteria (Watanabe, 2010). In addition to WAIC, we compared candidate models based on their predictive performance, using deviance calculated via k-fold cross-validation (CV; Hooten & Hobbs, 2015). By using different subsets of the data for model fitting (training) and validation (testing), this deviance metric measures a model's out-of-sample predictive performance and is another criterion by which to compare candidate models (Hooten & Hobbs, 2015). We used vague normal priors— the default values provided by the 'spOccupancy' package— for occurrence and detection coefficients (Doser et al., 2022). To account for potential spatial autocorrelation among the 50 grid sites, we compared 2 structures for each candidate model. In the spatially explicit version, we used recorder site UTM coordinates to include a spatial random effect using an 'exponential' covariance model. We compared this to a simpler version in which we included a non-spatial random effect for site.

We started the model selection process by constructing global models that included all the occurrence covariates previously described. Three versions of the global model were possible, corresponding to the 3 alternate ways in which we specified the strata covariate that represented level of protection and/or logging concession (indicated by asterisks in Table 4.1). We used these global models to then determine the best structure for the detection probability model component, which we subsequently held constant for the rest of the model selection process. After identifying the best-performing global model, we compared it to simpler models in which one occurrence covariate was removed at a time (sometimes the excluded main effect was part of an interaction term, in which case the interaction was also excluded). For some covariates, removal from the global model clearly reduced model performance, resulting in higher values for both WAIC and deviance in the reduced model. This indicated that the excluded covariate was important. In other cases, WAIC remained relatively unchanged (e.g., delta WAIC < 0.5), but deviance decreased substantially, suggesting better performance without the excluded variable; covariates responsible for these changes in metrics were deemed uninfluential. After establishing each covariate's importance by running models with each one removed at a time, we re-ran the global model with the uninfluential covariates removed to arrive at the final model. The WAIC and deviance from 4-fold CV identified this final model as the best candidate model. To assess the Goodness-of-fit of the final model, we performed posterior predictive checks using the Freeman-Tukey fit statistic to calculate a Bayesian *p*-value (low values indicate lack of fit; Doser et al., 2022; Kéry & Royle, 2015).

Results

PAM detection data

From January 2018 to March 2021, we detected a total of 28,381 elephant rumbles across the 50 acoustic recorder sites and 33 months (each containing 12 survey days). Of the 19,800 possible surveys (50 sites * 33 months * 12 survey days), we had data for 17,816 (90%). The 10% of survey days for which we lacked data (e.g., due to recorder malfunctions) were "NAs" in the occupancy model detection history. Of the 17,816 useful surveys, forest elephants were detected in 3862 (21.7%) and undetected in 13,954 (78.3%). Preliminary plotting of detections indicated that forest elephant raw occupancy estimates (uncorrected for detection) had declined throughout the study period (Fig. 4.2). This justified the inclusion of primary sampling period itself as a covariate that could reveal any linear trends in occupancy over time. Plotted rumble detections from dry season months (December and January) and wet season months (July and August) from 2018 and 2019 suggested a shifting distribution between seasons (Fig. 4.3).

We detected a total of 86 gunfire events composed of both automatic (e.g., AK47; n = 8) and single-action (n = 78) weapon fire. The total number of events at each site ranged from 0 to 10 (mean = 1.72; SD = 1.73) (Ch. 3 Fig. 3.3). As covariate values, gunfire events per primary period (month) ranged from 0 to 3, and cumulative gunfire events since study onset ranged from 0 to 10.

Habitat resource quantification

We achieved an overall accuracy of 0.92 with the supervised classification of habitat types using Landsat 8 satellite imagery, and similar per-class accuracies (Appendix Table A.1). The proportion of mixed species forest within 600 m of recorder sites ranged from 0.15 to 0.93 (Appendix Fig. A.3). Distances from recorder sites to nearest river mainstems ranged from 0.70 km to 15.59 km (mean = 6.35 km). Distances to nearest clearings (*bais* and *eyangas*) ranged from 0.69 km to 24.52 km (mean = 10.74 km).

Model selection

For the spatial autocorrelation component, the simpler non-spatial models consistently outperformed the more complex spatially explicit models, indicating spatial random effects were unnecessary. We therefore report on model selection and results using the more parsimonious models that included a non-spatial random effect for site. For the detection model component, which we investigated using the global models, the most parsimonious structure included only the random effect of primary sampling period. Gun events within 2 days of surveys were not frequent enough to estimate a parameter coefficient and justify inclusion. Including mean daily rainfall for detection probability also made models less parsimonious. We therefore specified the detection model components as a random effect for primary period and used this detection structure throughout model selection.

Of the three global models, the version with the strata covariate specified with 3 levels outperformed the other two versions according to WAIC and 4-fold CV deviance (Table 4.2). Other than the specification of the strata covariate, all other model components were identical across the 3 global models (Table 4.2). We proceeded with model selection using the 3-level strata specification for the simpler models, excluding one covariate at a time. Removal of most covariates from the global model revealed their importance through either (1) increases in both WAIC and deviance of the reduced model, or (2) substantial increases in WAIC but decreases in deviance (Table 4.3). These covariates explained some variation in the data and/or had predictive (out-of-sample) power. Only two covariates— gun events per month and cumulative gun events— were deemed uninfluential. When excluded from the global model, WAIC remained relatively static while deviance decreased, indicating better performance in their absence; these two covariates were removed from the final model (Table 4.3).

Final model and covariate effects

For the final model, Bayesian *p*-values calculated from posterior predictive checks revealed adequate model fit ($p = 0.54$), and *R-hat* values close to 1.0 (and < 1.1) indicated convergence of all parameter estimates. Overall detection probability of forest elephant rumbles was ~0.28. While all occurrence covariates in the final model were deemed important during the model selection process, they varied in effect sizes and whether their 95% credible intervals overlapped with zero (Table 4.4; Fig. 4.4). Overall probability of forest elephant occurrence showed a decreasing trend with primary period throughout the study (Fig. 4.5) and was higher in wet than in dry months (Figs. 4.4 & 4.5). Both trends were important, as indicated by CIs non-overlapping with zero (Table 4.4; Fig. 4.4). Forest elephant site usage decreased with increasing distance from rivers, while usage increased with increasing distance from clearings (Table 4.4; Fig. 4.4). Ongoing logging activity had the important effect of decreasing forest elephant occurrence (CIs non-overlapping with zero; Fig. 4.4). Increasing proportions of mixed forest increased the probability of forest elephant site usage (Table 4.4; Fig. 4.4), although this effect was constrained to the dry seasons; the important interaction of proportion mixed forest and primary period seasonality (wet vs. dry) nullified this effect in the wet season (Figs. 4.4 & 4.6). Probability of site usage was lowest in the national park, intermediate in the operational concession, and highest in the old logging concession (Fig. 4.7), although CIs for these parameter estimates overlapped with zero (Table 4.4; Fig. 4.4). Increasing occurrence probabilities accompanying the shift from the dry to the wet season were strongest for the operational concession and weaker for the old concession and national park sites (Fig. 4.7), although CIs for these interaction parameter estimates similarly overlapped with zero (Table 4.4; Fig. 4.4).

Discussion

In this study, we improved our understanding of African forest elephant landscape and habitat use by using a PAM approach to increase the spatiotemporal extent and resolution of data collection, and by simultaneously evaluating both anthropogenic disturbance pressures and habitat resources. Our results illuminate the important habitat characteristics and landscape features that shape the distribution of forest elephants in time and space, and how that distribution changes under the influence of certain anthropogenic pressures. These findings also have potential to aid conservation efforts by revealing the habitats, sites, and time periods most important for protection in NNNP and the adjacent logging concessions— for example, by increasing anti-poaching patrol effort in important areas (e.g., old logging concessions) and at times when elephant occurrence probabilities are high (e.g., rainy seasons).

Some of our results confirmed our expectations for how certain environmental covariates would influence forest elephant use of the landscape. Ongoing logging activity— clearing temporary roads, felling trees, dragging trees to the nearest logging road, and transporting trees out of the operational concession— clearly reduced forest elephants' use of nearby sites, as expected. The anticipated effect of distance to river was also confirmed— sites closer to major river mainstems were characterized by higher occurrence probabilities, indicating permanent water sources as important features of the landscape. This result is consistent with prior research suggesting that forest elephants are frequently constrained by water availability, despite inhabiting tropical rainforests (Blake, 2002; Buij et al., 2007; Mills et al., 2018).

Our results regarding the main effect of primary period seasonality are also relevant to the seasonal importance of water sources for forest elephants. Analyses of movement data suggest that forest elephants travel farther and engage in more directed movements during periods of higher rainfall. They more readily take extended excursions away from permanent water sources during the wet season when ephemeral sources of rainwater are abundant, but they may be reluctant to use habitat far from reliable water sources in the drier months (Blake, 2002; Buij et al., 2007; Mills et al., 2018). If forest elephant movement in our study area is higher in the wet season as these studies suggest, these increased movements could be responsible for the increased occurrence probabilities that characterize the wet months ($\beta_{\mathrm{PrimaryPeriodSeasonality(Wet)}} > 0$ and CIs not overlapping zero; Fig. 4.4). These higher wet season occurrence probabilities result in part from rumble detections at more sites in the wet months— oscillating seasonal trends are evident in the plotted monthly proportions of sites where elephants were detected, uncorrected for imperfect detection (Fig. 4.2). Occurrence probability may be higher in the wet season because the frequency with which forest elephants move between sites (site turnover) could be higher due to increased travel distances. An alternate possibility is that elephants immigrate into the acoustic grid study area during the rainy season but move to other parts of the national park (e.g., to the north) in the drier months (e.g., Blake, 2002). While our current PAM sampling and analysis framework does not allow us to arbitrate between these potential hypotheses, the latter explanation seems likely. Our results complement those of Blake (2002), who provided evidence of such movement patterns occurring in the same study area, including seasonal movements between the southern and northern regions of the park. Blake (2002) suggested that forest elephants leave the study area in the dry season and travel north to take advantage of *bais* clustered in a more northern sector of the park. Our results, which tentatively support this hypothesis, contribute to our awareness of forest elephant landscape use and movement patterns, and are also potentially informative for conservation efforts charged with protecting elephants in and around NNNP. Anti-poaching patrol effort, for example, could be increased in the study area during the wetter months of higher elephant occurrence, when the population may be at a higher density and more susceptible to poaching. However, the spatiotemporal scale at which patrol effort most effectively controls poaching activity in the study area remains unclear (Chapter 3), and further research is needed in order to optimize the allocation of these conservation resources.

Our impression based on preliminary data exploration (Fig. 4.2) that overall usage of the study area by forest elephants was decreasing over the 3.25 years of the study was confirmed by the negative effect (trend) of primary period on occurrence (Fig. 4.5). Whether this decline in elephant occurrence reflects diminishing populations (e.g., because of poaching or habitat changes) is an important consideration for further research. However, it is possible that patterns in elephant landscape use occur over long periods (e.g., years), and that our detected trend reflects the NNNP population shifting among different regions of the park, rather than a population decline. For example, while we revealed patterns in forest elephant use of the study area on a seasonal time scale (Figs. 4.4-4.7), site usage patterns characterized by several years and larger areas (e.g., park sectors) are also possible. To differentiate between a potential population decline versus distributional shifts, population size estimation methods could be used to complement a PAM approach (e.g., Brand et al., 2020; Laguardia, Bourgeois, et al., 2021; Laguardia, Gobush, et al., 2021).

Other results were more surprising and contradicted our initial hypotheses. Increasing proportions of mixed forest resulted in higher site usage in drier months, but this effect disappeared in the wet season (Fig. 4.6), opposite to our predictions. We had expected the attractive effect of mixed forest to operate more strongly in the wet season, when fruit availability in mixed forests is highest (Blake, 2002). Our use of proportion of mixed forest area and its interaction with seasonality to reflect fruit availability almost certainly failed to capture nuances in the timing and location of important fruit resources. While fruiting generally tracks precipitation for a diversity of species found in mixed forest, there are also less predictable but highly prolific fruiting events that happen, for example, in mast fruiting years in *Gilbertiodendron* monodominant forests. *Gilbertiodendron* mast fruiting events are asynchronous between stands and occur on average only once every 4 years (Blake & Fay, 1997; Hart, 1995), making them a less predictable and less reliable resource compared to the seasonal fruiting cycles in mixed forest. Nonetheless, stands of mast fruiting *Gilbertiodendron* can yield several tons of fruit per hectare (Blake & Fay, 1997) and forest elephants opportunistically take advantage of these abundant resources (Blake & Fay, 1997; Short, 1981, 1983). Our inability to identify where and when any such events may have occurred during our study period may be a limitation of our habitat type by season analysis. However, because these mast events are short-lived and patchily and sparsely distributed in time and space, it is unlikely that these events are responsible for our unexpected results regarding the effect of mixed forest. Even so, identifying and integrating mast fruiting events into analyses would improve our understanding of forest elephant resource use. A potentially informative next step would be to analyze sequences of satellite imagery taken over relatively short intervals (e.g., monthly), attempt to distinguish any spectral signatures of mast fruiting events, map their occurrence in time and space, and integrate this information as a covariate in occupancy analyses.

It is possible that the unanticipated mixed forest effect resulted in part from our inclusion of “shoulder season” primary periods (months), which may have hindered our ability to capture clear seasonal trends. While we categorized each month as either wet or dry according to amount of rainfall, some of these months likely occurred in the transition period between dry and rainy seasons. If forest elephants shift their use of resources seasonally, these “shoulder” months would likely encompass such transitions. One way to confirm or refute our current results would be to perform a multi-season occupancy analysis with fewer primary periods, with the “shoulder” seasons excluded, for example. A related option would be to employ several single-season occupancy models, each one comprised of detection data from only the core periods of the rainy and dry seasons as to avoid transitional months.

We compared multiple specifications of the levels of the stratum covariate (NP, old concession, operational concession) in an attempt to reveal whether forest elephant landscape use depended primarily on protected status, operational logging activity, or logging induced habitat resources (e.g., secondary regrowth). As previously described, comparing the global models with the alternative specifications of this stratum covariate could help arbitrate between hypotheses regarding the importance of these different factors. Our results indicate that this covariate is best modeled with all 3 strata specified independently (Global v1; Table 4.2). This suggests that protected status, operational logging activity, and logging related habitat characteristics all influence the distribution of forest elephants across the landscape to some degree. The global models with the strata combined into 2 levels (Global v2 and Global v3; Table 4.2) performed less well in explaining variation in the data (WAIC) and in prediction (k-fold CV deviance). We were therefore not able to arbitrate or rule out the importance of any of these 3 potential influences by comparing alternate specifications of the stratum covariate.

Comparing the parameter estimates of the 3 strata, on the other hand, can indicate which of these 3 factors— protected status, operational logging activity, or logging related habitat resources— are most influential. The relative importance and effects of the 3 strata were unanticipated. For example, overall occurrence was lower in the national park than in the logging concessions (Fig. 4.7). This suggests that whatever advantages are afforded by nominal protected status are outweighed by the value of resources in the concessions. We did expect logging concessions to offer important resources for forest elephants in the form of increased browse abundance due to secondary regrowth of sites disturbed by selective logging (Blake, 2002;

White, 1992). However, we anticipated these browse resources to be more important in the dry season, when fruit availability is limited. For this reason, the direction of the interaction of stratum with primary period seasonality came as a surprise. The increase in site usage in the wet season was stronger in the logging concessions than in the national park (Fig. 4.7)— the opposite of what we had predicted (although the CIs of parameter estimates overlapped with zero). It may be that the resources affiliated with logging concessions (e.g., secondary browse) are attractive and consistent enough that use of the habitat is high regardless of potential fruit availability in other areas. Furthermore, the logging concessions also contain mixed species forest, so potential effects of secondary regrowth in disturbed logging sites and fruiting in mixed forest are not entirely separable in our analysis. Accordingly, the expectation of overall higher occurrence probability in the national park was based on the hypothesized negative effects of the logging concession strata (e.g., logging activity/disturbance) and on differences in protection, not on differences in the amount of mixed forest and fruit availability between strata. While we revealed an important deterrent effect of ongoing logging activity (Table 4.4; Fig. 4.4), such activities occurred only in the operational concession during the first 2/3 of the study period—many concession sites and primary periods were not characterized by any ongoing logging activity. This allowed the overall positive effect of logging stratum habitat resources to overcome the poignant negative (but spatiotemporally limited) effect of ongoing logging activity (Fig. 4.4).

It is also useful to consider patterns in logging pressure at the longer scale of a forest elephant lifetime, which can exceed 70 years (Turkalo et al., 2018). Adult elephants that experienced historical logging activity in the old concession may associate that area with human disturbance more strongly than they do the operational concession, in which logging began more recently. Despite resource extraction activities having transitioned to the operational concession, elephants may still remember it as characterized by less human disturbance than the old concession. It is possible that this historical context has contributed to the pattern of occurrence probabilities that we detected (i.e., highest in the operational concession).

Regardless of the degree to which historical context influences elephant site usage in addition to the more immediate response to disturbance that we have revealed, our results indicate that the value of logging concession habitat for forest elephants is dynamic and dependent on both season and the timing of resource extraction activities. Management of logging activity for forest elephant conservation should take these results into consideration and plan the timing of logging activity to result in minimal interruptions to the natural patterns of elephant landscape use. At present, providing recommendations is difficult because the importance of the stratum effects and their interactions with season remains uncertain (50% and/or 95% CIs overlap with zero; Fig. 4.4). As more data from the acoustic grid become available for integration into this modeling framework, we hope to solidify our understanding of these interactions and provide concrete recommendations for the management of logging activities and the allocation of conservation law enforcement resources (e.g., patrol effort).

While ongoing logging activity was a distinct deterrent to elephant site usage, we detected no effect of poaching/gunfire events, the other major anthropogenic disturbance under investigation in this study. Neither the number of gunfire events per month nor the cumulative number of gunfire events since study onset were influential enough to be included in the final model (Table 4.3). This was surprising, given that recent research has indicated that gunfire events influence either forest elephant vocal behavior, use of nearby sites, or both (Swider et al., 2022; Chapter 2). However, these previous findings focused on forest elephant response to gunfire events at a much more immediate and high-resolution time scale (Swider et al., 2022).

The temporal resolution of the current analysis may not have been sufficient to capture any variability in elephant landscape use resulting from recent or cumulative gunfire events. Similarly, gunfire-induced changes in elephant habitat use behavior may be ephemeral, and site use and distribution may return to baseline status in a relatively short elapse of time (Swider et al., 2022; Chapter 2). This is especially likely if the gunfire events have occurred in high quality habitat where the value of resources outweighs the level of risk perceived by the elephants. Ongoing research is expanding upon the recent response to gunfire research (e.g., Swider et al., 2022) to determine the time scale at which gunfire events affect forest elephant behavior, the time required for behavior to return to normal/baseline activity, and the degree to which this depends on metrics of habitat quality (Verahrami, Swider, personal communication). Results of this upcoming work will be of interest to foraging theory— specifically, foraging under predation risk— and will improve our understanding of how forest elephants respond to anthropogenic disturbance and balance the needs of safety versus food acquisition.

This study has revealed some of the anthropogenic disturbance- and habitat resource-related variables that influence the use of the NNNP landscape by African forest elephants. Particularly important patterns included an overall declining trend in forest elephant occurrence over the 3.25 years of the study; higher occurrence probability in the wet seasons; higher occurrence probabilities closer to major rivers; a deterrent effect of ongoing logging activity that decreased elephant site usage; and the changing importance of mixed species forest between seasons. Poaching activity did not impact forest elephant use of the landscape at the temporal scale and resolution of our analysis. Forest elephants' use of the landscape in and around NNNP is influenced by a combination of both anthropogenic disturbances and habitat resources. These results shed light on our understanding of forest elephant ecology and can be used for planning and managing conservation initiatives (e.g., patrol effort) and anthropogenic activity (e.g., logging) to protect the species and minimize disturbance to their landscape use patterns.

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Figures and tables

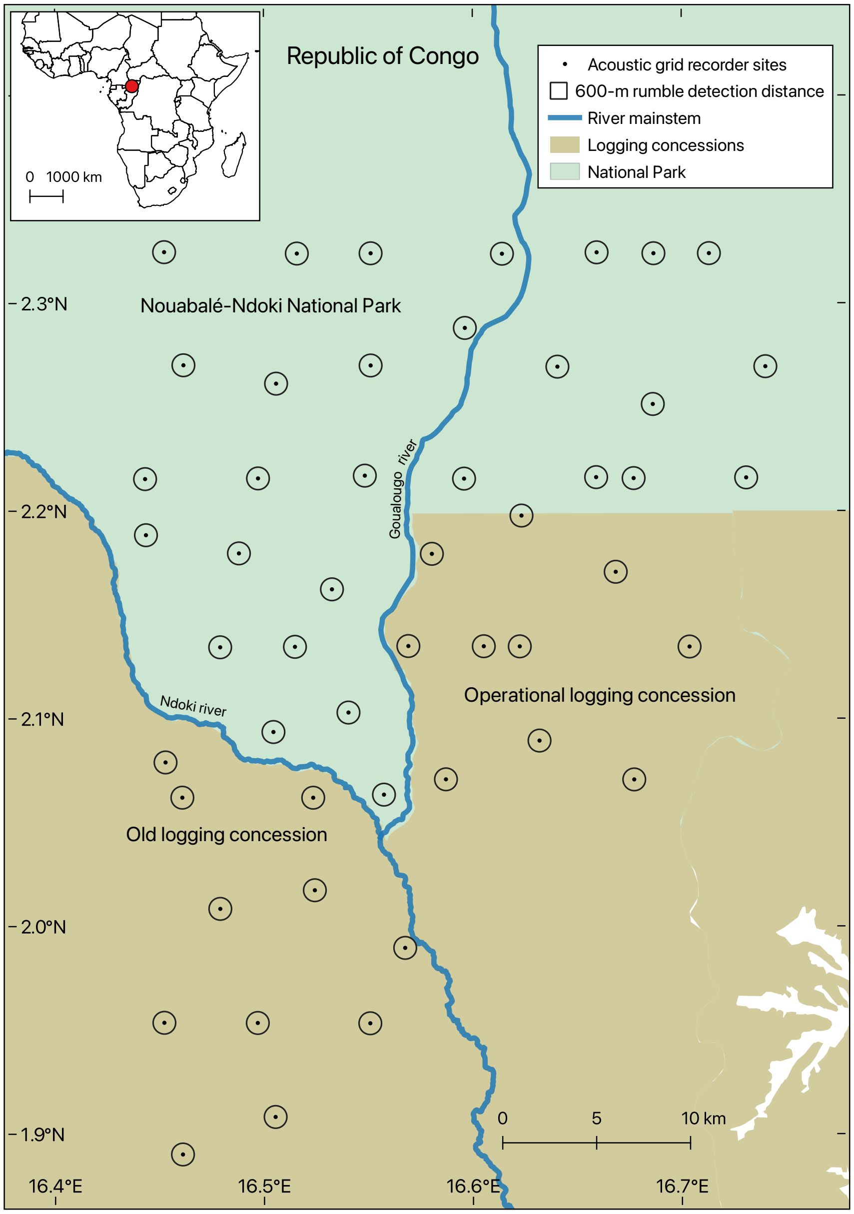

Figure 4.1 The grid of 50 acoustic recorders, covering portions of NNNP and adjacent logging concessions. The "old" concession, west of the Ndoki river, was selectively logged prior to 2010. The "operational" concession, east of the Ndoki and Goualougo rivers, was selectively logged during the initial years of the study, from 2017 to 2019. The 600-m approximate detection distance for forest elephant rumbles is displayed as a circle around each recorder. The red circle in the inset map shows the approximate location of the study area in northern Republic of Congo in central Africa.

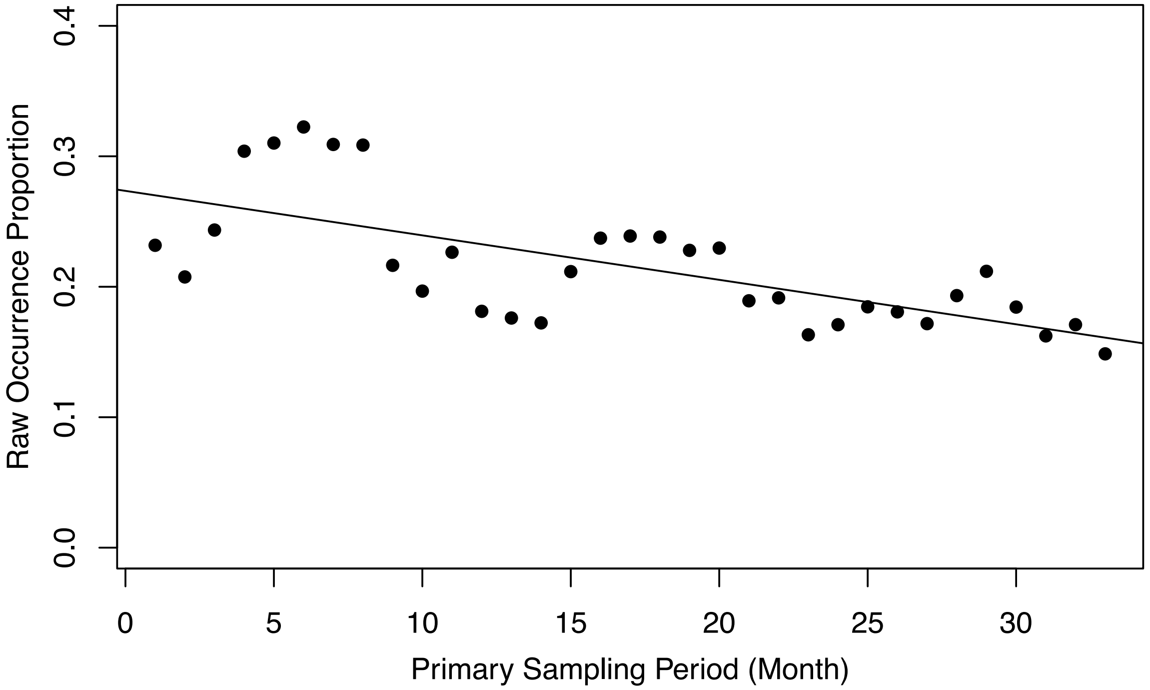

Figure 4.2 Raw proportions of sites at which forest elephants were detected, uncorrected for detection probability, as a function of months since January 2018. A linear model fit to the data suggests a trend of decreasing site usage by forest elephants (Adjusted R-sq. = 0.45, $p < 0.0001$). This preliminary trend supported the decision to include primary sampling period as an occupancy model covariate.

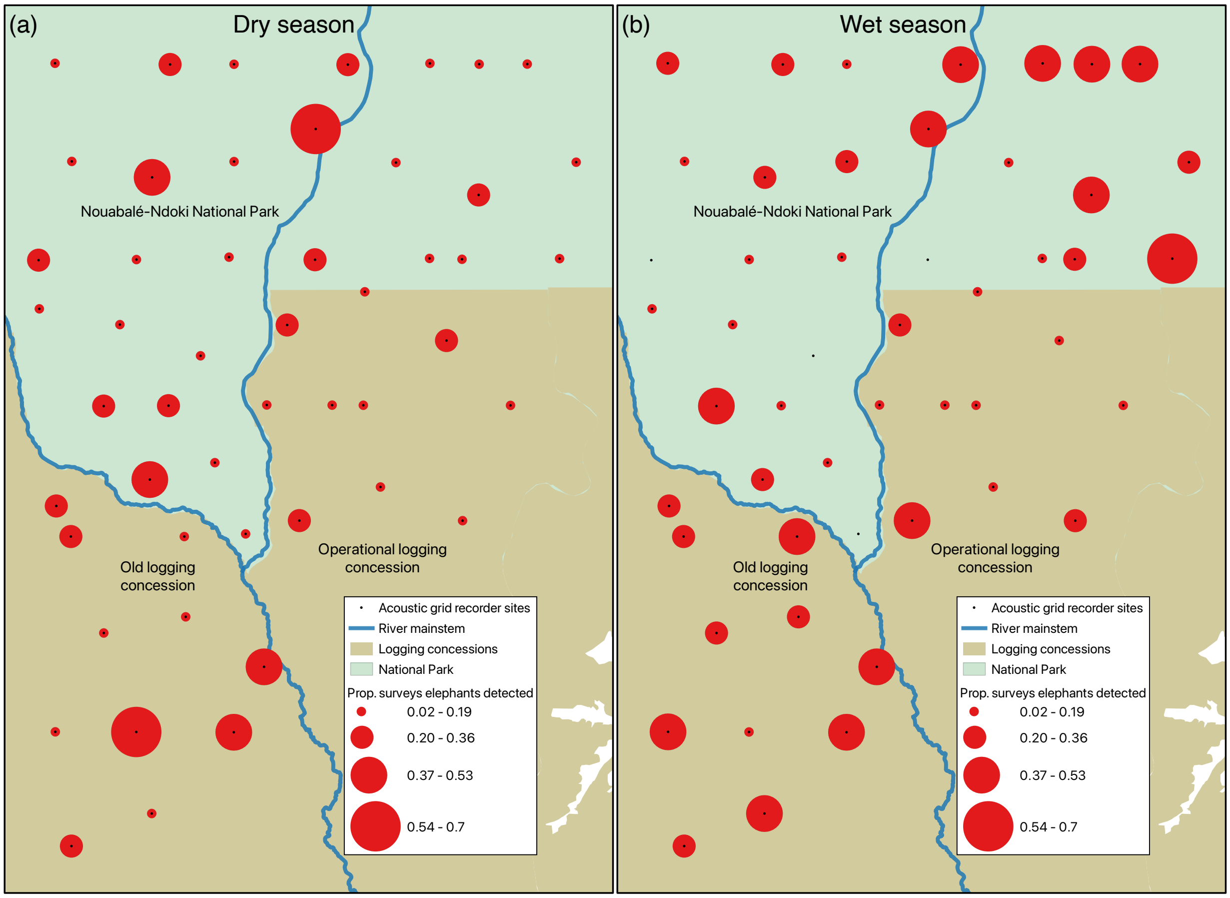

Figure 4.3 Forest elephant rumble detection data suggested a shifting distribution between (a) dry and (b) wet seasons. The proportions of surveys with rumble detections displayed here used data from 8 of the primary periods— December and January (dry season) and July and August (wet season) from 2018 and 2019. Data from 2020 was excluded from this figure because recording in the focal months was interrupted due to the Covid-19 pandemic.

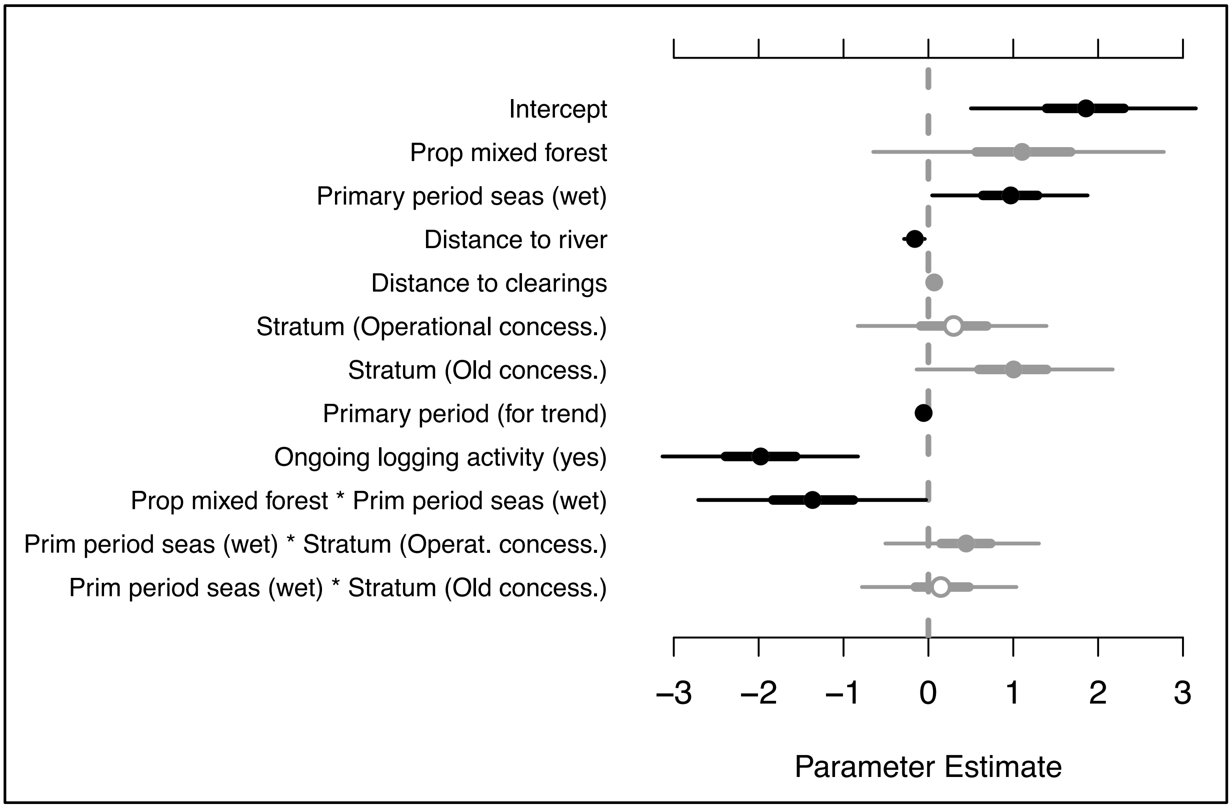

Figure 4.4 Final model parameter estimates on the logit scale; positive or negative values can be interpreted as having a positive or negative effect on forest elephant occurrence, respectively. Circles indicate the median parameter value from the posterior distribution. Thick and thin line segments indicate the 50% and 95% credible intervals (CIs), respectively. Parameter estimates whose 95% CIs did not overlap with zero are displayed as black circles and lines. Grey filled circles and lines indicate the 95% CI overlapped with zero; grey unfilled circles indicate the 50% CI overlapped with zero. The intercept (reference level) is where Stratum = National Park, Primary period seasonality = Dry, and Ongoing logging activity = No.

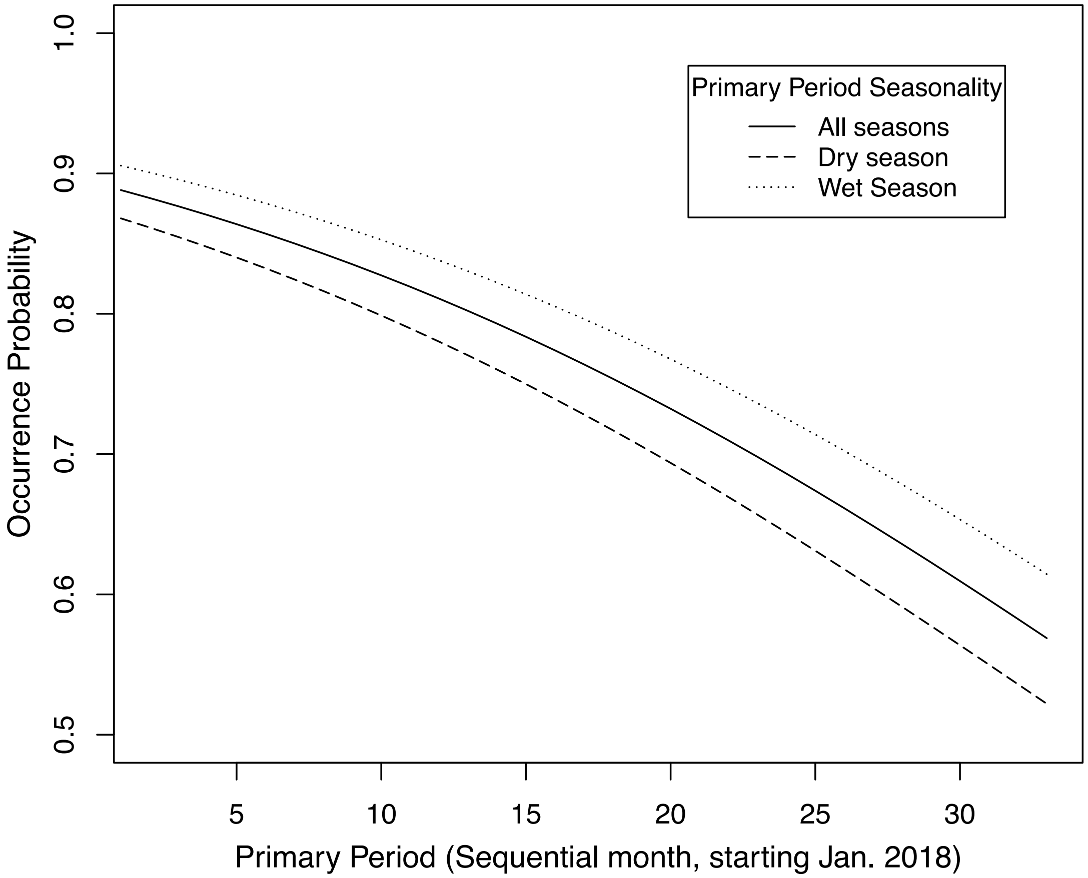

Figure 4.5 Overall probability of forest elephant occurrence showed a decreasing trend over the course of the study and was higher in the rainy months than in the dry months.

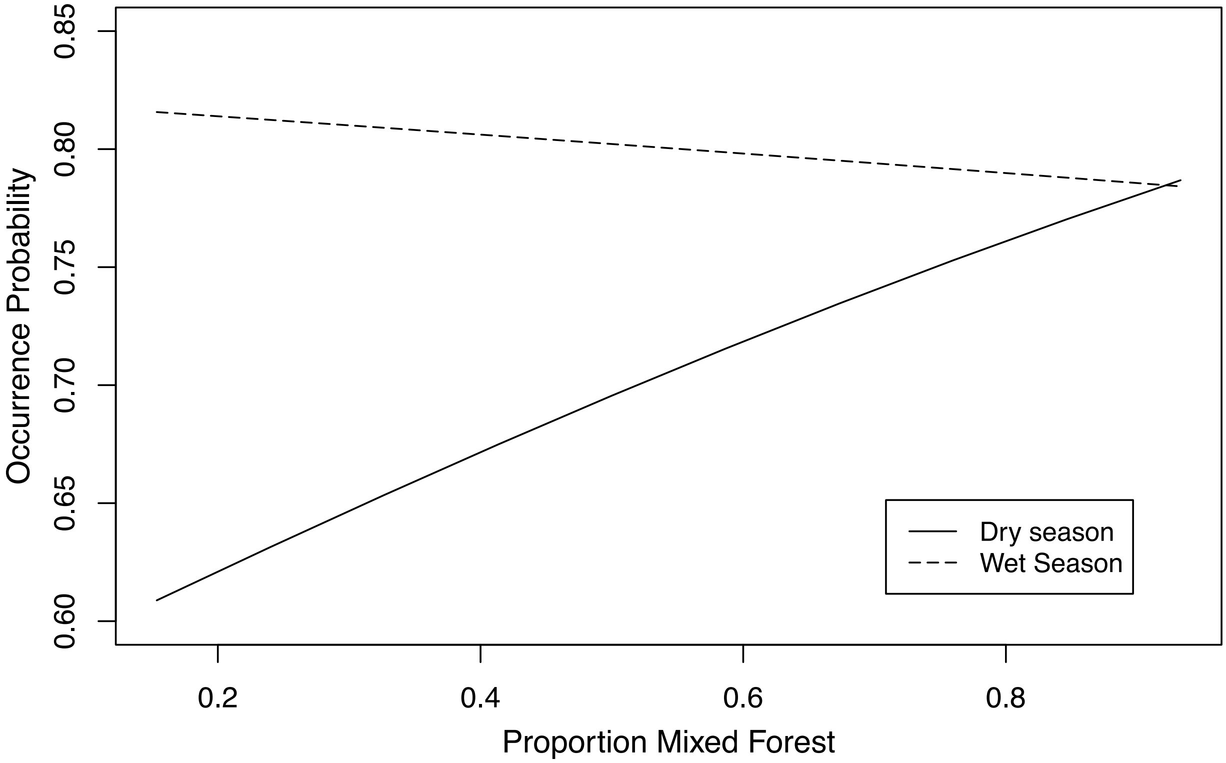

Figure 4.6 In the dry season, forest elephant site usage increased with increasing proportion of mixed species forest characterizing sites. The important interaction with primary period seasonality (CIs non-overlapping zero; Fig. 4.4) nullified the effect of mixed forest during the rainy season.

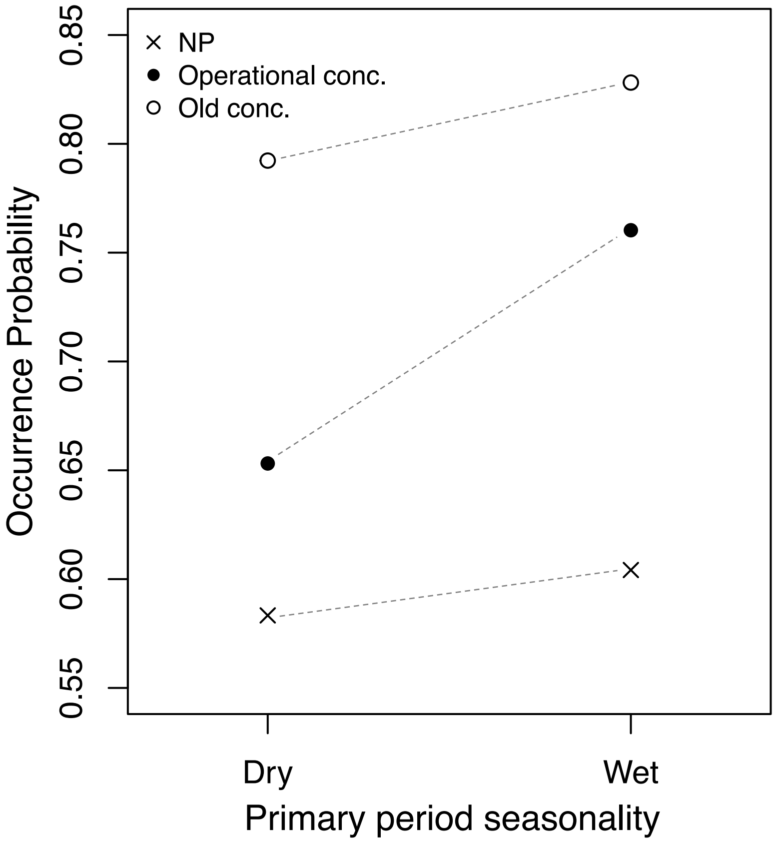

Figure 4.7 Forest elephant site usage was highest in the old logging concession, intermediate in the operational concession, and lowest in the national park, although parameter estimate CIs overlapped zero (Fig. 4.4). The increase in occurrence probability between the dry and wet seasons was strongest for the operational concession and weaker for the old concession and national park, although CIs for these interaction parameter estimates similarly overlapped zero (Fig. 4.4).

Table 4.1 Covariates included in the multi-season occupancy models included occurrence variables related to anthropogenic disturbance (poaching/hunting and logging), habitat resources, and time since study onset. Variables pertinent to detection probability were included to account for imperfect detection of forest elephants. Predicted effects of each covariate on either occurrence or detection are displayed in the last column.

Hypothesis			Covariate	Predicted effect
Occurrence	Anthropogenic disturbance		Number of gunfire events per primary period (i.e., month)	-
			Cumulative number of gunfire events since study onset	-
			Ongoing logging activity within 600 m, by primary period (yes/no)	-
			Operational logging strata, 2 levels (NP and old concession vs. operational concession)*	+/-
		Habitat resources	Protection strata, 2 levels (NP vs. either concession)*[a]	+/- (season dependent)
			Protection/Logging strata, 3 levels (NP vs. operational vs. old concession)*[a]	+/-/- (season dependent)
			Proportion mixed forest[a]	+ (wet season)
			Distance to nearest river mainstem (Ndoki and/or Guoalougo rivers)	-
			Distance to nearest bai/eyanga	-
			Seasonality of primary sampling period (wet vs. dry months)	+ or -
	Time		Primary sampling period (i.e., season, month) (main effect indicating trend)	-
			Primary sampling period (i.e., season, month) (random effect)	NA
Detection Probability			Gunfire event within 2 days of survey	+ or -
			Mean daily rainfall, weekly intervals (indicating rain/thunder)	-
			Primary sampling period (i.e., season, month) (random effect)	NA

* = spatial categorical covariates that are variations of a common strata system

[a] = also included as an interaction with seasonality of primary period (wet vs. dry months)

Table 4.2 Of the three global models, the version with the strata covariate specified with 3 levels outperformed the other two versions according to WAIC and 4-fold CV deviance. Other than the specification of the strata covariate, all other model components were identical across the 3 global models.

Rank	Name	Strata covariate specification	Occurrence fixed covariates	Detection covariates	WAIC	Deviance (4-fold CV)
1	Global v1	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events, (1|site)	(1|Prim period)	17312.549	18437.64
2	Global v2	Operational logging strata, 2 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary eriod, Ongoing logging, Gun events/mo, Cumul gun events, (1|site)	(1|Prim period)	17313.285	18454.67
3	Global v3	Protection strata, 2 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events, (1|site)	(1|Prim period)	17315.137	18457.12

Table 4.3 Candidate models ranked by WAIC and 4-fold CV deviance. The global model was compared to models in which each covariate was excluded at a time. Sometimes the excluded main effect was part of an interaction term, in which case the interaction was also excluded. Comparing the WAIC and 4-fold CV deviance between the global model and models with each covariate excluded allowed us to assess the importance of each variable. Covariates that we deemed uninfluential were removed from the final model. Covariates remaining in the final model (bottom row of table) have explanatory and predictive power. All candidate models shared the same structure for the detection component (random effect of primary period) and for the spatial autocorrelation component (non-spatial random effect of site).

WAIC rank	**Name**	**Strata covariate specification**	**Occurrence fixed covariates**	**Excluded occurrence covariates**	**WAIC**	**Deviance (4-fold CV)**	**Dev. rank**	**Remove cov. from final mod?**
1	Global	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	None	17312.549	18437.64	7	NA
2	Global minus Gunevents/mo	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Cumul gun events	Gun events/mo	17312.855	18424.63	4	Yes
3	Global minus Cumul gun events	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo	Cumul gun events	17312.974	18422.4	3	Yes
4	Global minus Dist to clearing	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Dist to clearing	17313.52	18450.18	10	No
5	Global minus Stratum* PPwet/dry	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Stratum* PPwet/dry	17314.501	18427.49	5	No
6	Global minus Dist to river	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Dist to river	17314.62	18536.97	12	No
7	Global minus Stratum (and interaction)	NA	Prim period wet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Stratum, Stratum*PPwet/dry	17316.04	18439.24	8	No
8	Global minus Prop mix forest* PPwet/dry	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Prop mix*PPwet/dry	17318.574	18411.46	1	No
9	Global minus Prop mix forest (and interaction)	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging, Gun events/mo, Cumul gun events	Prop mix forest, Prop mix*PPwet/dry	17318.909	18420.51	2	No
10	Global minus Prim period wet/dry (and interactions)	Protection/logging strata, 3 levels	Stratum, Prop mix forest, Dist river, Dist clearing, Primary Period, Ongoing logging, Gun events/mo, Cumul gun events	Prim period wet/dry, Stratum*PPwet/dry, Prop mix*PPwet/dry	17319.11	18430.87	6	No
11	Global minus Ongoing logging	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Gun events/mo, Cumul gun events	Ongoing logging	17325.689	18461.59	11	No
12	Global minus Primary period	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Ongoing logging, Gun events/mo, Cumul gun events	Primary period	17349.429	18441.95	9	No
13	Null	NA	None	All	17381.179	18579.97	13	No
Top	Final model	Protection/logging strata, 3 levels	Prim period wet/dry, Stratum, Stratum*PPwet/dry, Prop mix forest, Prop mix*PPwet/dry, Dist river, Dist clearing, Primary period, Ongoing logging	Gun events/mo, Cumul gun events	17312.044	18426.65	-	-

Table 4.4 Mean parameter estimates (logit scale) and quantile values from their posterior distributions, estimated using the final model.

Occurrence fixed effects (logit scale)	**Mean**	**SD**	**Posterior quantiles**		
			2.50%	**50%**	**97.50%**
Intercept (Stratum=Nat'l Park; Ongoing logging activity=No; Prim period seas=Dry)	1.8383	0.6675	0.501	1.8569	3.152
Proportion mixed forest	1.1077	0.8591	-0.6499	1.1042	2.7747
Primary period seasonality (wet)	0.9628	0.4706	0.0445	0.97	1.8757
Distance to river	-0.161	0.0611	-0.2868	-0.1594	-0.0428
Distance to clearing	0.0696	0.0386	-0.0032	0.0686	0.1443
Stratum (Operational concession)	0.2964	0.564	-0.8324	0.2973	1.3922
Stratum (old concession)	1.0024	0.5915	-0.1387	1.0043	2.1718
Primary period (for trend)	-0.0561	0.0088	-0.0726	-0.056	-0.0391
Ongoing logging activity (yes)	-1.9741	0.597	-3.1333	-1.9772	-0.8296
Prop mixed forest* PPseasonality (wet)	-1.3605	0.6855	-2.7119	-1.3649	-0.0266
PPseasonality (wet)*Stratum (operational concession)	0.435	0.4496	-0.5068	0.4456	1.3026
PPseasonality (wet)*Stratum (old concession)	0.1472	0.4676	-0.7832	0.1462	1.0373
Occurrence random effect variance (logit scale)					
Site	1.5289	0.4984	0.7954	1.4569	2.6616
Detection fixed effects (logit scale)					
Intercept	-0.964	0.0591	-1.0544	-0.9643	-0.8703
Detection random effect variance (logit scale)					
Primary period	0.0549	0.0175	0.0297	0.0521	0.0971

APPENDIX

Supervised classification of satellite imagery to quantify habitat types across the Nouabalé-Ndoki National Park acoustic grid study area

Rationale

Identifying and quantifying the habitat type(s) around each of the 50 recorders of the Nouabalé-Ndoki National Park (NNNP) acoustic grid is an integral part of Chapters 3 and 4, as habitat is a potentially important predictor variable for the distributions of both gunfire event (Ch. 3) and forest elephant (Ch. 4) detections across the landscape. Assessing habitat is especially important for Chapter 4, as the main objective of the chapter is to understand forest elephant habitat and landscape use, and how this is influenced by both resources and anthropogenic disturbance.

I required a metric that would reflect the variability in the amount of mixed forest (forest composed of mixed tree species) around each of the 50 recorder sites of the acoustic grid. In NNNP, fruit tree density is highest in *terra firma* mixed forest compared to other habitat types such as *Gilbertiodendron* monodominant forest (Blake, 2002). The proportion of mixed species forest around each site is therefore an indicator of the availability of fruit, an indispensable food source for forest elephants. This is especially relevant in the rainy season because fruiting generally tracks precipitation; the most tree species and the highest proportion of individual trees fruit during the months of highest rainfall (Blake, 2002).

Methods

Imagery (provided courtesy of the US Geological Survey)

To find appropriate satellite imagery, I searched the USGS database (USGS, 2016) for satellite data of the NNNP study area taken since recording started in late 2017. Frequent cloud cover over the Congo Basin rainforest limits the utility of much of the satellite imagery taken of this part of the world (Friedl et al., 2006), so finding cloud-free imagery was a top priority. I filtered the database to include only imagery with less than 5% cloud cover. This drastically reduced the set of candidate imagery, of which I found two Landsat 8 (30-m resolution) scenes that together covered the full extent of the acoustic grid area. No single Landsat 8 scene provided full coverage of the study area. One scene covered the northern and one the southern extent of the study area, although the scenes overlapped in the mid-latitudes. The acquisition dates for the two sets of imagery were April 24, 2019, and March 28, 2021. I do not consider the approximately two-year interval between acquisition dates to be an issue because the distribution of forest types in the study area should not have changed over this time scale. Importantly, the two scenes were taken at approximately the same time of year (March/April). This helps control for factors that could otherwise introduce variation in reflectance measurements, such as seasonal differences in atmospheric conditions, sun angles, extents of open water (e.g., rivers, swamps), and conditions of foliage (Lillesand et al., 2015). The imagery that I selected was available as fully pre-processed Level 2 Science Products (L2SP), and therefore required no additional correctional processing or calibration (e.g., atmospheric, radiometric, geometric) prior to use. To remove extraneous land area distant to the acoustic grid, I clipped the raster areas of each Landsat scene to a convex hull area surrounding the grid sites, using a 10-km buffer around the outer sites.

Training and testing the classifier

While several habitat sub-types can be considered, I categorized the acoustic grid study area into three main classes. I classified the two major forest types of the study area as either mixed forest composed of many tree species, or monodominant forest composed of trees in the genus *Gilbertiodendron*; this is a common stratification system used for this area (e.g., Blake, 2002). My third category, which I refer to as "open", included habitats associated with water that all exhibited similar spectral signatures— river floodplain with sparser (or no) canopy, open-canopy swamps, open water (rivers), aquatic vegetation and grasses, and small clearings known as *bais* and *eyangas*. By representing different combinations of Landsat spectral bands 1-7 as false color images, I was able to visually discriminate between pixels of the three land cover types of interest. Translating the near infrared (NIR) band into the visible spectrum (e.g., into the red band) was particularly useful, as a high percentage of NIR light is reflected by plant leaves. Habitats composed of different tree and plant species reflect NIR light to varying extents, depending on the amount and composition of chlorophyll in the leaves of the species that constitute the habitat (Lillesand et al., 2015; Wegman et al., 2016). In this way, visualizing NIR as red in the false color images allowed me to visually identify changes in habitat types over space.

Ground truth habitat data was obtained during surveys conducted on foot by the Wildlife Conservation Society (WCS) in 2016-2019. Several hundred habitat-labeled points were available for each of the habitat classes of interest, from within and around the acoustic grid study area. I used these points to verify the habitat types that were discriminable in the false color representations of the satellite imagery (Fig. A.1). For each of the two Landsat scenes covering the study area, I created approximately 300 polygons ("regions of interest") of known (ground truth) habitat type, using QGIS software (*QGIS 3.22*, 2022). I allocated a habitat-stratified random selection of 2/3 of the polygons to provide pixels for training the classifier. The pixels of the remaining 1/3 of the polygons were used to test the classifier's accuracy.

Prior to performing the supervised classification, I manually masked all cloud and cloud shadow pixels from the raster of both scenes. This was possible because the area of cloud cover was less than 1% in each of the now spatially reduced scenes (clipped to the study area), allowing me to identify and mask these pixels by hand. I also manually masked a section of permanent road that ran through the corner of the clipped study area. Manually masking the cloud and road pixels reduced the number of required classes in the supervised classification and avoided having to train the model with these “nuisance” classes. This simplified the model and likely improved the accuracy of predictions. The supervised classification therefore included only the three habitat classes of interest— mixed forest, monodominant (*Gilbertiodendron* sp.) forest, and open (river floodplain, swamp, clearings, etc.).

The atmospheric conditions and therefore the spectral characteristics differed slightly between the two sets of imagery (northern and southern scenes) due to their different acquisition dates. Such differences could potentially introduce errors if a single classification were implemented on a mosaic of the two scenes combined. I therefore performed a classification on each of the two scenes separately. Using spectral bands 1-7, I implemented the classifier as a random forest algorithm using the ‘RStoolbox’ package (Leutner et al., 2022) in R (R Core Team, 2022). To train the classifier, 1000 pixels for each of the three habitat classes were randomly selected from the set of training polygons for each scene. To serve as reference data for evaluating the accuracy of each classification, another 1000 pixels per class were randomly selected from the set of polygons reserved for testing. For each scene, I calculated several accuracy metrics from the confusion matrices resulting from each classification.

Results

Accuracy assessment

Accuracies derived from confusion matrices revealed that the two classifications (one for each scene) performed well and had very similar accuracies (Table A.1). Overall accuracy is the total number of correctly classified pixels divided by the total number of reference pixels. Producer's accuracy (i.e., sensitivity, or recall) is the proportion of correctly classified pixels per class (the number of correctly classified pixels in a class divided by the number of test pixels used for that class). This metric reflects how well the model recognizes a given class (Lillesand et al., 2015; Wegman et al., 2016). User's accuracy, or precision, is the number of correct predictions relative to the total number of times a class was predicted (the number of correctly classified pixels in a class divided by the number of pixels classified as that class). This metric represents the probability that a given pixel is predicted to the correct class. The Kappa value indicates the extent to which the correct predictions are due to "true" agreement versus "chance" agreement (Lillesand et al., 2015; Wegman et al., 2016). The Kappa values in Table A.1 suggest the classifications are approximately 87% better than a classification resulting from chance.

Output and calculation of covariates

Given that neither classification outperformed the other— both had relatively high accuracy metrics (Table A.1)— I quantified habitat type from each one separately. Because the two classified scenes overlapped substantially in the mid latitudes of the acoustic grid area, there were two possible versions of the final mosaicked output raster and classified habitat maps. Each version is a mosaic of the classified northern and southern scenes, but they differ in which one overlays and therefore masks the other in the overlapping region (Fig. A.2).

Using the output raster files of habitat-classified pixels, I was able to quantify the proportion of area of each habitat type in any arbitrary portion of the study area. I calculated these proportions for areas with radii of 600 m and 2 km, centered on each of the 50 recorder locations. These distances correspond to the approximate acoustic detection distances for elephant rumbles and gunshots, respectively. Around each site, the proportion of area composed of a given habitat type is the number of pixels classified to that type divided by the total number of pixels in the defined area.

For the northern- and southernmost recorder sites (outside the region of overlap between the two scenes), I calculated these proportion metrics from the corresponding classified output raster. Most sites, however, were located within the region of overlap in the mid latitudes of the grid. For these sites, I averaged the proportion estimates calculated from each of the two classified output rasters. These metrics serve as potentially important spatial covariates that may explain the distribution of poaching event (Ch. 3) and forest elephant (Ch. 4) detections across the acoustic grid study area (Fig. A.3).

Figures and tables

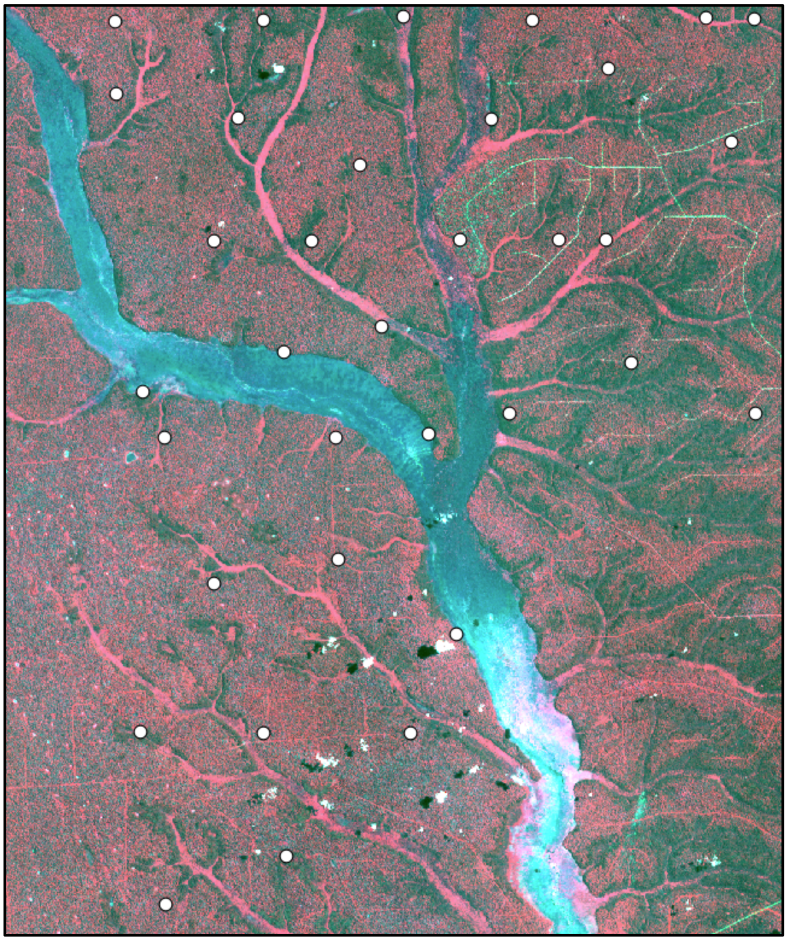

Figure A.1 A false color rendition of the Landsat 8 satellite imagery over the southern extent of the acoustic grid. The NIR band is shifted into the visible red band to aid in discriminating different vegetation/habitat types. River floodplain/swamp pixels appear turquoise, pink, or occasionally purple, likely depending on differences in composite vegetation and water levels in the mainstem floodplain (blue) versus the tributaries (pink). The *Gilbertiodendron* monodominant forests, often found adjacent to the river floodplain/swamp, appear as dark green pixels. Mixed species forest, which makes up almost all the area that is not open/floodplain or monodominant forest, has an overall reddish appearance. Recorder sites are displayed as white dots.

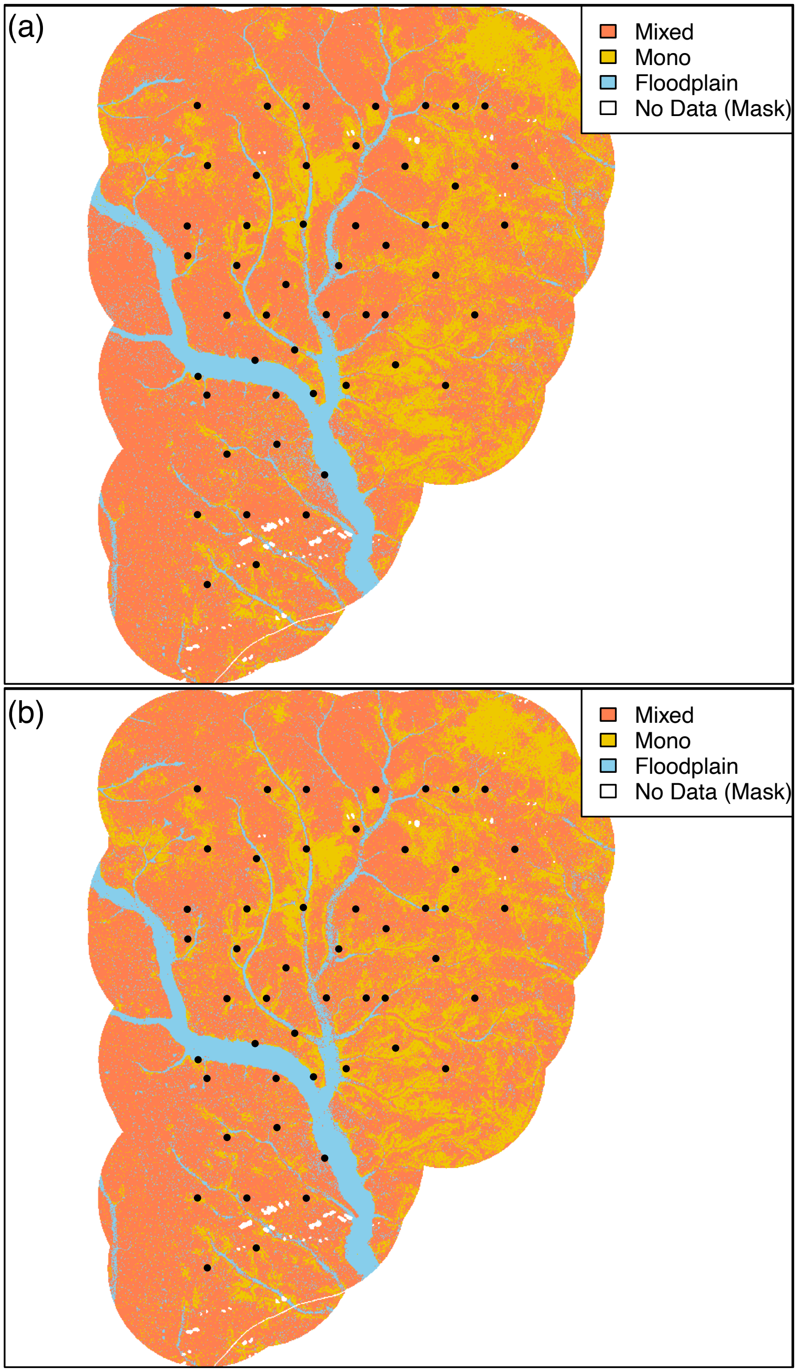

Figure A.2 Classified habitat maps created from model predictions. The classified northern and southern scenes were mosaicked to produce maps encompassing the entire extent of the acoustic grid study area. The two map versions differ by which classified scene overlays (and masks) the other in the region of overlap at mid latitudes. In version (a), the northern scene overlays the southern scene in the middle region of the grid. In version (b) the southern scene masks the northern. The similarity between the two map versions indicates high agreement between the predictions of the two classifications.

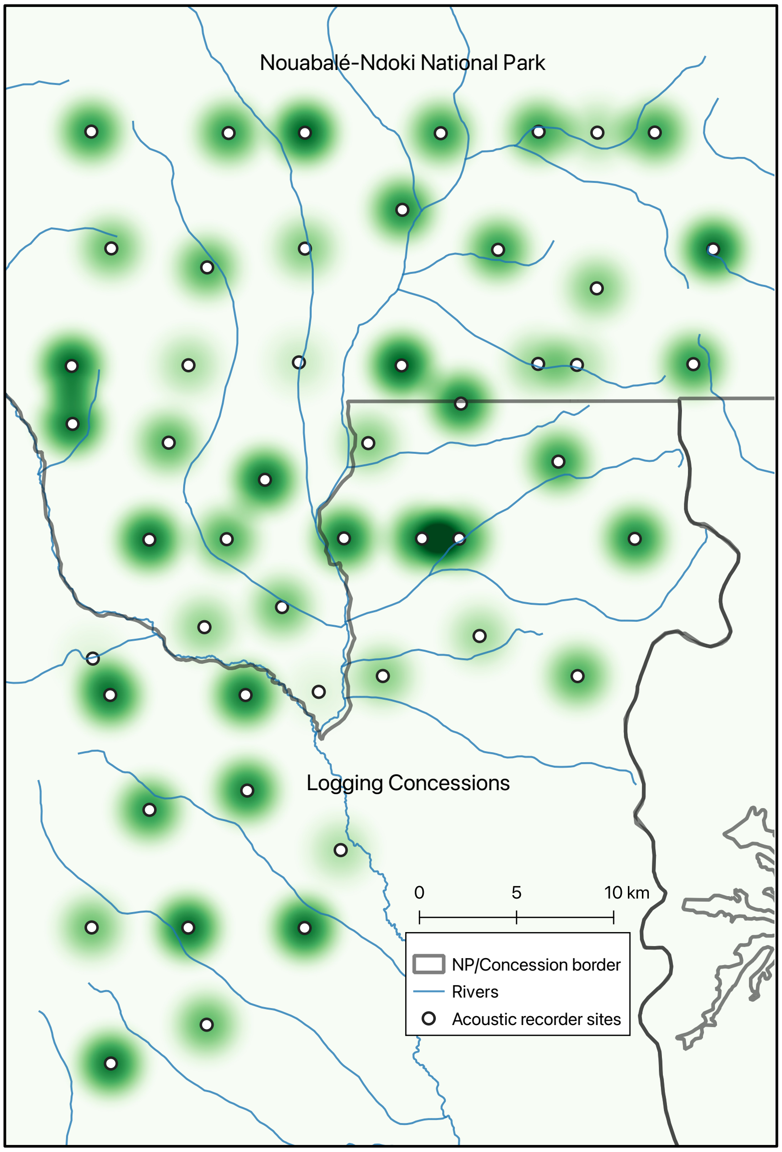

Figure A.3 Variation in the proportion of mixed forest area within 600 m of acoustic recorder sites, displayed as varying intensities of green. Values ranged from 0.15 (lightest green) to 0.93 (darkest green). Proportions were calculated from rasters of habitat-classified pixels produced by the supervised classification. Note: radius of green areas is arbitrary (not equal to 600 m).

Table A.1 Summary of accuracies for the two classifications (northern and southern portions of the acoustic grid area). Both classifications had high overall and per-class accuracies. Accuracies were similar between the two scenes. Kappa values suggest that the classifications are ~87% better than what would be expected by chance.

Classification	Overall	Producers Accuracy (Sensitivity)			Users Accuracy (Precision)			Kappa
	Accuracy	Mixed	Mono	Floodplain	Mixed	Mono	Floodplain	
Northern Landsat 8 scene	0.915	0.9209	0.8583	0.9503	0.8922	0.9036	0.9555	0.8683
Southern Landsat 8 scene	0.9184	0.9054	0.861	0.9554	0.9089	0.8404	0.9617	0.8702

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Yackulic, C. B., Strindberg, S., Maisels, F., & Blake, S. (2011). The spatial structure of hunter access determines the local abundance of forest elephants (Loxodonta africana cyclotis). *Ecological Applications*, *21*(4), 1296–1307.

Zafra-Calvo, N., Lobo, J. M., Prada, C., Nielsen, M. R., & Burgess, N. D. (2018). Predictors of elephant poaching in a wildlife crime hotspot: The Ruvuma landscape of southern Tanzania and northern Mozambique. *Journal for Nature Conservation*, *41*, 79–87.

VITA

Colin R. Swider

EDUCATION

Syracuse University, Syracuse, NY
PhD Candidate, Biology (in progress, May 2023 planned graduation)
Dissertation: *Acoustic behavior, poaching risk, and habitat use in African forest elephants (Loxodonta cyclotis): Insights from passive acoustic monitoring*
Bioacoustics and Behavioral Ecology Lab (PI: Dr. Susan Parks)
National Defense Science and Engineering Graduate Fellow; Syracuse University Fellow
GPA: 4.0/4.0

State University of New York, College of Environmental Science and Forestry, Syracuse, NY
Bachelor of Science, Environmental Biology (2012)
GPA: 4.0/4.0; Summa cum laude (highest honors); Ranked 1st of 332 students; President's List every semester

Finger Lakes Community College, Canandaigua, NY
Associate in Science, Liberal Arts and Sciences (2010)
GPA: 4.0/4.0; High Honors; Dean's List every semester
Associate in Science, Music Recording Technology (2008)
GPA: 4.0/4.0; High Honors; Dean's List every semester

RESEARCH AND WORK EXPERIENCE

Collaborative Researcher (May 2017-present)
Elephant Listening Project, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, New York

Teaching Assistant (August 2022-present)
Biology Department, Syracuse University, Syracuse, New York

Bioacoustics Technician and Project Co-manager (January 2013-January 2015)
Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

Research assistant (May-August 2012)
Sacramento River riparian forest dynamics study, SUNY Research Foundation, Central Valley, California

Research assistant and Spanish interpreter (March 2012)
Costa Rica fungal diversity study, SUNY ESF, Costa Rica

Teaching Assistant (January-May 2012)
Diversity of Plants course, SUNY ESF, Syracuse, NY

Researcher (May-June 2011)
Cranberry Lake Biological Station, SUNY ESF, Adirondack Park, NY

Research assistant (April-November 2011)
Adirondack avian diversity study, SUNY ESF, Adirondack Park, NY

Independent Researcher (March 2011)
Service-Learning project, SUNY ESF, Dominica, West Indies

Producer/audio technician (2008)
Finger Lakes Community College, Canandaigua, NY

PUBLICATIONS

Swider, C.R., Gemelli, C.F., Wrege, P.H., and S.E. Parks. (2022). Passive acoustic monitoring reveals behavioural response of African forest elephants to gunfire events. *African Journal of Ecology*, 60, 882-894. https://doi.org/10.1111/aje.13070

Rosa, P., Swider, C.R., Leston, L. and N. Koper. (2015). Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. *Wildlife Society Bulletin*, 39: 364–372. doi:10.1002/wsb.546

WORKSHOPS AND PROFESSIONAL DEVELOPMENT COURSES

Syracuse University Teaching Assistant Orientation (August 17-19, 2022)
Syracuse University, Syracuse, NY

Northeast Regional Environmental Acoustics Symposium (May 2-3, 2022)
Center for Acoustics Research and Education, University of New Hampshire, Durham, NH

Excellence in Communicating Science Series: Scientific Writing (January 9, 2018)
Syracuse University, Syracuse, NY

Modeling patterns and dynamics of species occurrence workshop (March 13-17, 2017)
Cornell University, Ithaca, NY

SEABASS 2016 and 2018: Bioacoustics Summer School (June 5-10, 2016 & July 8-13, 2018)
Syracuse University, Syracuse, NY (2016) & University of New Hampshire, Durham, NH (2018)

Study design and quantitative methods for resource and environmental management (January-April 2014)
Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

Acoustic Communication in Animals (January-April 2014)
Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

Academic Writing Workshops (January 2014)
Natural Resources Institute, University of Manitoba, Winnipeg, MB, Canada

CERTIFICATIONS

Standard First Aid and CPR Levels A-C certification
Workplace Hazardous Materials Information System (WHMIS) certification
Chemical Hygiene Plan and Hazardous Waste Management training
H_2S Alive certification
Transportation of Dangerous Goods (TDG) certification
Animal User Training Course (Wildlife and Behavioral Sciences) certification from University of Manitoba
Institutional Animal Care and Use Committee (IACUC) course through Collaborative Institutional Training Initiative (CITI) Program
Identifying and Overcoming Bias Training through Syracuse University
PADI Advanced Open Water Diver SCUBA certification
PADI Open Water Diver SCUBA certification

AWARDS AND RECOGNITIONS

Syracuse University Biology Department Travel Grant for bioacoustics career symposium (May 2022)
2nd Place Best Standard Talk Award at the African Bioacoustics Community Conference (2020)
Most Popular Movie Submission Award at the African Bioacoustics Community Conference (2020)
Syracuse University Graduate Student Organization Travel Grant for fieldwork training (November 2018)
Syracuse University Biology Department Travel Grant for conference presentation (June 2017)
Syracuse University Graduate Student Organization Travel Grant for attending workshop (March 2017)
National Defense Science and Engineering Graduate Fellowship (2016-2019)
Syracuse University Graduate Fellowship (awarded 2016, instated 2019-2021)
Best Poster Presentation at the North America Congress for Conservation Biology (2014)
Departmental Scholar for ESF Dept. of Environmental and Forest Biology for class of 2012
Distinguished Biology Scholar Award for the ESF Dept. of Environmental and Forest Biology for class of 2012
Distinguished Biology Scholar Award (All Majors) for ESF class of 2012
ESF Alumni Scholar of class of 2012
Graduated from SUNY ESF Summa cum laude (highest honors) (2012)
President's List every semester at SUNY ESF (2010-2012)
Presidential Scholarship for SUNY ESF (2010)
Graduation from FLCC with High Honors (2008 and 2010)
Dean's List every semester at FLCC (2006-2010)
National Award of Accomplishment from National Society of Leadership and Success (2008)
FLCC Foundation John M. Meuser Memorial Scholarship (2007)
NYS Education Department Award for Academic Excellence (2006)
NYS Education Department Robert C. Byrd Honors Scholarship (2006)
Public Employees Federation Joseph Scacalossi Scholarship (2006)
Finger Lakes Region Top 10% Scholarship (2006)
Frederick Douglass and Susan B. Anthony Award in Humanities and Social Sciences from University of Rochester (2005)
Designated a Finger Lakes Scholar by Hobart and William Smith College (2005)
Chemistry Achievement Award from American Chemical Society (2004)

CONFERENCE PRESENTATIONS AND INVITED PRESENTATIONS

Presented in person

Hedwig, D., Swider, C.R., Estabrook, B., and I. Kienast. 2021. Meet the Elephant Listening Project: Saving African Forest Elephants Using Sound. Cornell Lab of Ornithology Seminar, Nov. 17, 2021, Cornell University, Ithaca, NY (virtual event). https://academy.allaboutbirds.org/live-event/meet-the-elephant-listening-project-saving-african-forest-elephants-using-sound/

Swider, C.R., Gemelli, C.F., Parks, S.E., and P.H. Wrege. 2020. Landscape use response to gunshot events in African Forest Elephants (*Loxodonta cyclotis*). African Bioacoustics Community Conference, Nov. 2-5, 2020, Muizenberg, South Africa (online in 2020).

- Won 2nd Place Best Standard Talk Award at the *African Bioacoustics Community*

Conference (2020)

Swider, C.R. 2019. Bioacoustics for conservation: Forest elephants and poaching pressure in the Congo Basin. Biology Department seminar series, May 1, 2019, State University of New York Potsdam, Potsdam, NY, USA.

Swider, C.R. 2018. Insights into animal ecology using passive acoustics. Biology Department annual seminar series, April 3, 2018, Syracuse University, Syracuse, NY, USA.

Swider, C.R., Parks, S.E., and M.V. Lomolino. 2017. Variation in dawn chorus acoustic complexity across a global latitudinal gradient. Acoustical Society of America: Joint Meeting of the Acoustical Society of America and the European Acoustics Association, June 25-29, 2017**,** Boston, Massachusetts, USA.

Swider, C.R. 2017. Global soundscape ecology. Biology Department annual seminar series, March 28, 2017, Syracuse University, Syracuse, NY, USA.

Rosa, P., Swider, C.R., and N. Koper. 2014. Isolating effects of anthropogenic noise on wildlife: design for high-fidelity playback experiments. Society for Conservation Biology: North America Congress for Conservation Biology, July 13-16, 2014, Missoula, Montana, USA.

- Won award for Best Poster Presentation at the *North America Congress for Conservation Biology* (2014).

Rosa, P., Swider, C.R., and N. Koper. 2014. Current research on grassland songbirds in Brooks and surrounding areas. Annual Cenovus Energy Langevin Safety Meeting, June 11, 2014, Heritage Inn, Brooks, Alberta, Canada.

Coauthored but not presented in person

Logan, A.T., Swider, C.R., Root-Gutteridge, H., and S.E. Parks. 2019. Vocal development and individuality in the Humboldt penguin (*Spheniscus humboldti*). 27th International Bioacoustics Congress, August 31-September 5, 2019, University of Sussex, Brighton, England.

Ewing, S.J., Swider, C.R., Sullivan, M.E., and J. VanNeil. 2019. Chemical communication in gray squirrels: Using camera traps to uncover patterns in scent marking behavior. Animal Behavior Society Annual Conference and 36th International Ethological Conference, July 23-27, 2019, University of Illinois, Chicago, USA.

Koper, N., Bernath-Plaisted, J., Curry, C., Antze, B., Warrington, M., Nenninger, H., Swider, C., and P. Rosa. 2015. Effects of oil and gas infrastructure and operating noise on grassland songbirds in Alberta. The Wildlife Society Annual Meeting, October 21, 2015, Winnipeg, Manitoba, Canada.

Koper, N., Rosa, P., Lockhart, J., Lwiwski, T., Rodgers, J., Molloy, K., Curry, C., Fischer, S., Swider, C.R., and J. Yoo. 2015. From mensurative to manipulative: diverse study designs to understand effects of anthropogenic disturbance and habitat fragmentation on grassland birds. Ontario Grassland Guild, March 24, 2015, MacDonald Stewart Art Centre, Guelph, Ontario, Canada.

Koper, N., Rodgers, J., Yoo, J., Molloy, K., Bernath-Plaisted, J., Curry, C., Antze, B., Warrington, M., Nenninger, H., Swider, C.R., and P. Rosa. 2015. Effects of shallow gas and oil infrastructure and operating noise on grassland songbirds. Canadian Wildlife Service, March 23, 2015, Edmonton, Alberta, Canada.

Koper, N., Bernath-Plaisted, J., Curry, C., Nenninger, H., Rosa, P., and C.R. Swider. 2015.

Effects of energy infrastructure and operating noise on grassland songbirds. Alberta Chapter of the Wildlife Society, March 22, 2015, Delta Edmonton Centre, Edmonton, Alberta, Canada.

Antze, B., Swider, C.R., and N. Koper. 2014. The effects of industrial noise on anti-predator communication in Savannah sparrows. Parks and Protected Areas Research Forum of Manitoba, November 21-22, 2014, Winnipeg, Manitoba, Canada.

- Won 1st place, Natural Sciences presentations.

Rosa, P., Swider, C.R., and N. Koper. 2014. Design for high-fidelity playback experiments: isolating effects of anthropogenic noise on grassland birds. Quebec Society for the Biological Study of Behaviour, 39th AGM, November 8, 2014, Montreal, Quebec, Canada.

Koper, N., Rosa, P., Swider, C.R., Bernath-Plaisted, J., Nenninger, H., and B. Antze. 2014. Effects of oil infrastructure and operating noise on grassland songbirds. American Ornithologists Union Annual Meeting, September 6, 2014, YMCA of the Rockies, Estes Park, Colorado, USA.

Koper, N., Rosa, P., Swider, C.R., Antze, B., Bernath-Plaisted, J., Nenninger, H., Rodgers, J., Yoo, J., and K. Molloy. 2014. Effects of oil and gas development on grassland birds. Cenovus Energy, May 30, 2014, Calgary, Alberta, Canada.

Koper, N., Rosa, P., Antze, B., Bernaith-Plaisted, J., Nenninger, H., Leston, L., and C.R. Swider. 2014. Effects of oil wells and noise on grassland songbirds in Alberta. St. George's University, April 2014, Grenada, West Indies.

Rosa, P., Swider, C.R., Leston, L., and N. Koper. 2014. A novel approach to playback experiments in the study of anthropogenic noise produced by oil infrastructure. The Wildlife Society, Manitoba Chapter: Bi-annual Conference and Annual General Meeting, March 14, 2014, Oak Hammock Marsh, Manitoba, Canada.

POPULAR SCIENCE AND PRESS ATTENTION

Griffin, S.H. "Listening to Elephants". Syracuse University. Syracuse, New York, USA. July 28, 2020. https://www.syracuse.edu/stories/phd-student-colin-swider-elephant-communication/

Ryan, T. "Endangered elephants 'eavesdrop' on poachers in Republic of Congo". *Radio France Internationale*. Paris, France. October 30, 2020. https://www.rfi.fr/en/africa/20221030-critically-endangered-forest-elephants-eavesdrop-on-poachers-in-drc