THESIS

FOREST ELEPHANTS MODULATE THEIR BEHAVIOR TO ADAPT TO SOUNDS OF DANGER

Submitted by

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ABSTRACT

FOREST ELEPHANTS MODULATE THEIR BEHAVIOR

TO ADAPT TO SOUNDS OF DANGER

The African forest elephant (*Loxodonta cyclotis*) plays a critical role in upholding the structure and function of the Congo Basin, the world's second largest tropical forest which crucially contributes to global carbon sequestration. Research has demonstrated an 86% decline in forest elephant population numbers between 1990-2021, largely because of hunting for ivory. Due to the species' cryptic nature in their dense rainforest habitat, little is known on how they respond to human disturbances such as gun hunting. The studies that have been completed reveal that forest elephants may respond to disturbance by demonstrating changes in their abundance, distribution, and nocturnal activity. Changes in forest elephant distribution and activity not only have ramifications for the species' activity budgets, which when affected, may influence their foraging and reproductive behaviors and success, but may also impact the species' interspecific interactions with vegetation in certain areas, affecting forest growth and function. However, little is known on how a key population of this critically endangered species in the northern Republic of Congo is responding to disturbance such as hunting in the region. Using acoustic detection models in combination with a landscape-scale acoustic monitoring effort in and around Nouabalé-Ndoki National Park, Republic of Congo, I assess how forest elephant vocal activity is being influenced by gun hunting. Using these data, I examine (1) how forest elephant vocal activity changes across an eight-day period and (2) if forest elephants are shifting to more nighttime vocal activity following a gun hunting event. Results show that, on average, forest

elephants are present and vocal at sites without gun events 53% of the time, but at sites with gun events, this value drops to 43%. Results also indicate that this change in activity following a gun hunting event is sustained over the eight-day period examined and does not vary from day-to-day. Results from the analysis exploring how the proportion of nighttime calling activity changes in response to gun hunting show that number of gunshots is an important predictor of nighttime vocal activity. Specifically, as the number of gunshots increase, there is a dramatic increase in the proportion of nighttime calling activity. Understanding the degree at which forest elephants are affected by gun hunting provides a convincing argument to focus limited conservation resources on developing more effective strategies to reduce indirect impacts from hunting on this critically endangered and ecologically important species.

ACKNOWLEDGEMENTS

I am grateful for the support of my family, especially my sister, Roksana, over these last three years as this support has allowed me to grow into the conservation biologist that I am today. At CSU, the connections I have formed with people at various stages of their careers from both the Department of Fish, Wildlife, and Conservation Biology and the Graduate Degree Program in Ecology have culminated into a true feeling of community. I would like to thank my committee members, Dr. George Wittemyer and Dr. Nathaniel Blanchard, for their guidance of my research over the last three years and for supporting my development into a more impactful researcher. I would like to give special thanks to the Bombaci lab for providing a safe and fun space to learn, grow, engage in shenanigans (like discovering a taxidermied redhead duck above the lab ceiling), plan treasure hunts across Colorado, and get out into nature. Erin Weingarten, Tamara Layden, Edder Antunez, Jasmine Nelson-Olivieri, Hanna McCaslin, and Sharon Martinson – you all have been truly incredible labmates and friends and I am so grateful for our paths crossing over these last years. I would also like to thank Maddie Pielmeier, Sam Kreda, Jana Wiegand, Caitlin Miller, Abbey Feuka, Giovana Matos Franco, Maia Parthasarathy, and Mallory Davies for their support throughout my degree and for always keeping me grounded and optimistic, even in some of the toughest moments. And speaking of tough moments, I am indebted to Dr. Adrienne Showler, the Section Chief of Tropical Medicine at Georgetown University Hospital who has rid me of worms that view the eyeball as their Mecca three times now (while simultaneously indulging my bizarre fascination of their whole parasitic life cycle within me). I am also very thankful for Dr. Helen Bowden and Amanda Walts, LCSW, who have supported my personal growth, helped me deepen my understanding of myself, and provided

safe spaces for me to heal and evolve from some difficult challenges I've experienced both in and out of graduate school.

I am grateful for Liz Rowland, Dr. Peter Wrege, Dr. Daniela Hedwig, and Dr. Michelle Fournet, mentors I crossed paths with while working with bioacoustics at Cornell University and whose guidance and support have had lasting impacts on how I conduct research, understand the natural world, and collaborate with others. The Elephant Listening Project research group is unlike any other I've worked with before, united by a passion for forest elephant conservation using acoustics and who fosters a true feeling of community. This feeling is only possible because of the people who are a part of it - Liz, Peter, Daniela, Katy Payne, Bobbi Estabrook, Dr. Sophie Trowbridge, Dr. Colin Swider, Ivonne Kienast, Phael Malonga, Frelcia Bambi, and Onesi Samba - I have not just enjoyed working with and learning from you all, but I have especially enjoyed our moments outside of the lab from camping to music festivals to getting a little bit too rowdy at Peter's game nights. I'd also like to give a special thanks to Colin for his support in completing the occupancy analysis of this study and for providing the habitat classification data. I am extremely thankful for my advisor, Dr. Sara Bombaci, who has been a role-model demonstrating how conservation may be practiced in inclusive and just ways, and how academia may better support folks with marginalized identities. I was diagnosed with bipolar disorder and ADHD while being advised by Sara and her continuous support and understanding during this time was essential to my continued pursuit of my degree. Sara has truly fostered a community that I am sad to be leaving but I look forward to taking all that I have learned from her and applying it to how I engage with the world moving forward. The completion of my degree would also not have been possible without the support of my beloved dog, Oscar. Even on the worst days of graduate school, Oscar would lay his full 90 lbs. body across mine first thing in the

morning, eliciting first groans and then laughter as I was eventually convinced to get up and give having a good, productive day a shot. His optimism and love for life have been contagious and I am so grateful I have had him as a companion during this time. Lastly, I would like to thank the Congo division of the Wildlife Conservation Society, the government of the Republic of Congo, and the Graduate Degree Program in Ecology whose support and funding made this study possible.

PREFACE

My understanding of the centrality of nature and the criticality of its protection has evolved over the last 27 years from many different moments and experiences. While this understanding has indeed developed from my coursework and the hours I have spent reading articles and textbooks, it is grounded in more than just the academic narratives I have been exposed to.

This understanding is rooted in my spirituality which centers around the Zoroastrian Gathas, 17 sacred hymns in the Avestan language that were first spoken 1500 BCE and carried across oceans by my ancestors from ancient Persia to Gujarat, India and then to the diaspora of North America. These hymns speak of our individual responsibility to choose between good and evil, to respect and support the symbiotic relationship amongst the Seven Creations: Earth, Sky, Water, Plant, Animal, Human, and Fire, and to ultimately practice Humata (think good thoughts), Hūxta (speak good words), and Huvaršta (practice good deeds) throughout the lives that we are gifted from this mysterious and beautiful entity.

This understanding has been shaped from my experiences with our planet as someone who is neurodivergent and queer and who has found parallel patterns of these dynamics in other organisms. It has been molded from the moments I found healing amongst soundscapes dominated by the harmony of natural life, seemingly endless green forest, and communities of powerful women unified by connection with nature. It has been formed from the wisdom that I have been privileged enough to learn from other animals who share our same capacities for nurturing, love, and connection and from Indigenous communities who have sacred understandings of what it means to coexist with the natural world. It has been altered in moments

of humility where I have found myself outmatched by life as little as the subcutaneous *Loa loa* worm, not even 500 micrometers in width, and as large as a belligerent, 4-ton forest elephant bull in musth.

This understanding has been sustained and nurtured from connections, family, and community. It has been supported by the privileges I hold as a white-passing, cis-gendered woman from an upper-middle class family with a strong background in higher-education; from the privileges I hold as a citizen of a country in the Global North; from the privileges I hold as an academic working on the traditional, ancestral, and stolen lands of the Ute, Arapaho, and Cheyenne Nations and peoples in Colorado and the BaAka Bangombé and Bambezelé tribes and the Sangha-Sangha Indigenous peoples in the Republic of Congo. This understanding has culminated into a strong ambition to support the conservation of nature and in 2016, it led me to a small, windowless room at the Cornell Lab of Ornithology where something much larger, and louder, than a bird was being studied.

When I first entered that room, I had no idea that forest elephants existed nor that I would be lucky enough to study them for the next seven years. The opportunity to study them using sound was even more appealing due to my background in music. Tagging and coding hours of sound could sometimes be tedious, but if I paused for a moment and listened, I could recognize kindred harmonies and rhythms from the forest and would feel reengaged. My captivation of these natural sounds grew even further when I *felt* my first forest elephant rumble. I stood in awe as I watched tiny cascades of dirt fall from the wrinkly forehead of an adult female forest elephant and felt my chest vibrate while goosebumps formed across my skin.

As I write this, I am unsure on where life will take me after my time at CSU comes to an end, and whether the future will offer me another chance to feel a forest elephant rumble. The

opportunity to learn more about this species from their compelling social lives to how their dung decays has been an absolute privilege. With this thesis, I hope to share insight into their complex lives, the dynamic ways in which they interact with their environment, the significance they hold for both humans and ecosystems, and ultimately, support their conservation.

DEDICATION

This thesis is dedicated to Katy Payne, a pioneer in the field of bioacoustics whose discoveries of humpback whale-song and elephant-infrasound changed the trajectory of our understanding of animal communication. Katy is a renaissance woman, combining her experience with music, motherhood, storytelling, and science with her immense insight into the natural world to deepen our understanding of some of the most cognitively complex creatures on our planet.

Katy, thank you for all our chats over tea over the years. Each moment with you has left me feeling courageous, inspired, and optimistic that we will safeguard the natural songs of our planet for generations to come.

TABLE OF CONTENTS

ABSTRACT ii
ACKNOWLEDGEMENTS iv
PREFACE vii
DEDICATION x
INTRODUCTION 1
METHODS 9
Study Area 9
Acoustic Sampling Study Design 11
Acoustic Data Processing 12
Exploring Hunting Activity Approach 14
Vocal Activity Analytical Approach 14
Nighttime Calling Activity Analytical Approach 16
RESULTS 19
Exploring Hunting Activity Results 20
Vocal Activity Analysis Results 22
Nighttime Calling Activity Analysis Results 24
DISCUSSION 27
STUDY LIMITATIONS 31
CONCLUSION 33
REFERENCES 34

FOREST ELEPHANTS MODULATE THEIR BEHAVIOR TO ADAPT TO SOUNDS OF DANGER

INTRODUCTION

Throughout the world, endangered species are declining at an alarming rate. A 2022 report by the World Wildlife Fund found that monitored populations of wildlife experienced an average decline in their abundance of 69% between 1970-2018 (WWF 2022). Declines in wildlife have catalyzed dramatic changes in trophic cascades, impacting our planet's dynamics of disease, invasive species, carbon sequestration, biogeochemical cycles, and ecosystem resilience (Estes et al. 2011). This trend also has ramifications for humans as many species act as sources of food (Golden et al. 2011), medicine (Mardiastuti et al. 2020), and other resources (Roth & Merz 1997). Wildlife declines can also increase zoonotic disease risk by either directly or indirectly releasing controls on the abundance of disease vectors such as rodents (Young et al. 2014). Declines in wildlife abundance have even been linked to oppressive and exploitative practices such as starvation, child labor, human trafficking, physical abuse, and murder (Brashares et al. 2014).

A prime example of a species whose decline will have drastic impacts on our world is the African forest elephant (*Loxodonta cyclotis*), a species which is experiencing rapid population decline due to factors such as habitat destruction, climate change, and poaching for ivory. In 2021, the species was listed as critically endangered by the IUCN, a decision based on evidence indicating that >80% of the population has been lost over the last 93 years (Gobush et al. 2021). Between 2002-2011, the species lost 30% of its geographical range and experienced a population

decline of 62% (Maisels et al. 2013). Strong predictors of this decline include proximity to expanding infrastructure (Maisels et al. 2013), poor governance (Bennett 2015; Maisels et al. 2013), and hunting intensity, with poaching for ivory most strongly driving the rapid weakening of population numbers (Bouché et al. 2011; Maisels et al. 2013; Wittemyer et al. 2014).

Declines in populations of this keystone species not only have ramifications for the species' existence, but for the structure and function of the Congo Basin, the world's second largest tropical forest which crucially contributes to global carbon sequestration (Molua 2019). Forest elephants play important roles in their dense forest environment as architects and mega-gardeners of the rainforest. As architects, they use their strong tusks and brute strength to create natural forest clearings, locally known as "bais", to access rich mineral water flowing underground. These bais not only provide elephants with nutrients and an engaging social arena but benefit numerous other species as well including western lowland gorillas (Metsio Sienne et al. 2014), sitatungas (Vanleeuwe et al. 1998), and bongos (Klaus-Hügi et al. 2000) who also use bais as sources of minerals and food. Forest elephant architecture expands beyond bais and well into the forest where elephant paths may be created in areas where they have repeatedly stomped down vegetation. In savanna-forest mosaic, these trails have been found to act as firebreaks where the paths prevent the spread of fire from the savanna to the fire-sensitive forest nearby (Cardoso et al. 2020). As mega-gardeners, they travel throughout the forest and spread their dung, crucially contributing to the growth of many tree species. A forest elephant can move over 2,800 km annually and has an average home range of about 700 km^2 (Mills et al. 2018); thus, this critical ecosystem service is provisioned at large scales. Elephants also increase carbon stocks by dispersing seeds of large trees with high wood density and by preferentially browsing on leaves from low wood density species, hence promoting the growth of high wood density species

(Berzaghi et al. 2023). The extinction of forest elephants would consequently result in a 7% decrease in carbon stocks, a statistic which equates to a loss in carbon storage services valued at $43 billion USD (Berzaghi et al. 2019) and which exposes the very critical roles that forest elephants play in maintaining diverse, high-carbon tropical forests.

Forest elephants are also known for their charisma and compelling social lives which in some respects parallel our own, drawing in many tourists each year who are eager to see these elusive giants, supporting local economies and communities. Forest elephants are also important cultural symbols to Indigenous communities who have been living in Central Africa for millennia, such as the Baka communities residing in Cameroon and Gabon. Ngouhouo Poufoun et al. 2016 found that forest elephants help maintain the cultural identity, spiritual enrichment, and knowledge of the forest for these communities. Other Indigenous communities such as the BaAka community in the Central African Republic also value forest elephants for their sentient nature, complex social lives, and ability to sustain communities through the use of their meat (Bahuchet 1985). Remis & Jost 2020 highlight the mutual ecologies of the BaAka and forest elephants by providing an overview of how transnational networks of elephant trails (locally referred to in Aka as bembo) support both people and elephants. Bembo not only provide routes for elephants to use to access sources of nutrition but allow BaAka community members to traverse the forest in search of food and medicine as well. Bembo also support sociality, allowing elephants to reunite with kin hundreds of kilometers away and BaAka community members to travel to neighboring communities for spiritual and traditional experiences.

While poaching may have dire effects on the ecosystem services that forest elephants provide both locally and globally, our understanding of how the species itself is being impacted remains limited, largely due to the species' dense rainforest habitat where consistent visual

observation is difficult, if not impossible. However, there is a substantial amount of research examining the long-term effects of poaching in African savanna elephants (*Loxodonta africana)*, providing useful insight for those who are conducting comparable research on forest elephants.

In areas where poaching occurs, elephants may hear gunshots, encounter poachers and carcasses, and witness the death of conspecifics and even family members. As a result, savanna elephants have responded by increasing their flight behavior and shifting their activity to nighttime hours (Graham et al. 2009). Elephants who have experienced poaching in some form may become more aggressive towards people and human infrastructure, heightening the risk of human-elephant conflict (Compaore et al. 2020). Poaching also alters elephant population dynamics by skewing sex ratios, reducing survivorship and life expectancy, increasing the number of orphans, and targeting older, more experienced individuals resulting in disruptions of social and ecological knowledge (Wittemyer et al. 2013; Foley et al. 2008).

Both savanna and Asian elephants have been found to experience increases in stress hormones including cortisol and glucocorticoids in response to human disturbances such as poaching and habitat destruction (Tang et al. 2020; Jachowski et al. 2012). Asian elephants additionally demonstrated decreased estradiol concentrations with increasing stress levels, indicating that chronic exposure to disturbance may have ramifications for elephant reproductive behavior and success (Tang et al. 2020). As a result, elephants may choose to remain in areas with relatively little human disturbance, but this strategy may result in their loss of access to widespread food sources and increased feeding competition. Consequently, populations could experience increases in aggressive social interactions, resulting in negative impacts to social cohesion and reproductive behavior, ultimately affecting population size (Wittemyer et al. 2007).

Populations may also become isolated from one another, reducing their overall genetic fitness and increasing the probability of extinction (Wilcox & Murphy 1985).

The impacts that poaching may have on elephants are varied, meaning that the species may employ diverse temporal, spatial, and behavioral strategies to minimize human-induced mortality risk. If we are to effectively conserve the species, we must learn more about these strategies to better understand how to protect them. One study conducted in the Ruaha-Rungwa ecosystem in Tanzania explored how savanna elephants' responses differed between 'high' and 'low' risk sites. The researchers found that the elephants were more active at night at high-risk sites relative to low-risk sites, and they more frequently performed behaviors such as foraging and use of water sources at night (Smit et al. 2023). This finding is further demonstrated by other studies which have found that elephants shift to nighttime activity outside of and near protected area boundaries (Gaynor et al. 2018; Graham et al. 2009; Sitati et al. 2003; Wittemyer et al. 2017). In northern Kenya, it was found that both male and female elephants moved more at night when poaching levels in the area were high (Ihwagi et al. 2018). Prior research also conducted in Kenya found that elephants moved faster along unprotected corridors than in protected areas, indicating that they might have awareness of nearby hunting pressure (Douglas-Hamilton et al. 2005).

The research that has investigated forest elephant response to human disturbance has found that forest elephants are responding to human activity in similar ways to savanna elephants. Some studies that have been completed such as occupancy analyses on a forest elephant population located in southwest Gabon found that elephants continuously avoided human settlements and roads, and these features directed their distribution more than ecological factors such as the presence of wetlands and fruit (Buij et al. 2007). Moreover, across Gabon, the

presence of roads seems to have large-scale, negative impacts on the abundance of forest elephants, with elephant densities increasing with distance from human activity (Barnes et al. 1991; Laurance et al. 2006). Forest elephants have also demonstrated pronounced shifts to increased nocturnal activity in response to oil exploration in Gabon (Wrege et al. 2010). In Nouabalé-Ndoki National Park in the Republic of Congo, where a relatively large forest elephant population remains (IUCN 2014) and where my study on forest elephant response was based, camera traps were set up around the site of a poached elephant carcass at the perimeter of a bai for 8 months and it was found that it took 8 days for elephants to return to the area where the incident had occurred (Stephan et al. 2020). Another study conducted in this same study area by Swider et al. 2022 found that following a gun hunting event, the population's vocal activity increased above the control state level for the first five hours following the event but then from hours six to twenty-four, calling activity dropped below the control state level. This study also examined the population's vocal activity for the six hours prior to the gun hunting event and found that vocal activity fell below the control state level during this time, indicating that forest elephants may have some awareness of the presence of hunters in the forest and may change their behavior as a result. Forest elephant abundance has also been negatively linked to human disturbances such as logging and hunting in southern Cameroon (Djoko et al. 2022). In areas with higher human disturbance, elephants were also found to move less, had smaller home ranges, were less active during the day, and exhibited fewer exploratory movements (Beirne et al. 2021).

While these studies demonstrate that forest elephants are shifting their behaviors and activity in response to human disturbance, most studies exploring forest elephant distribution have used dung sampling methods (Barnes et al. 1991; Yackulic et al. 2011; Buij et al. 2007;

Theuerkauf et al. 2001; Blake 2002; Laurance et al. 2006; Danquah 2016). While dung sampling studies have shown that forest elephants avoid areas with high human activity (Barnes et al. 1991; Yackulic et al. 2011; Buij et al. 2007; Blake 2002; Laurance et al. 2006; Danquah 2016), it is a spatially and temporally constrained sampling method, limiting the scales at which we can explore forest elephant response. Dung sampling is often only conducted across transects through the forest (Barnes et al. 1991), limiting the spatial area covered. Moreover, to produce an estimate of elephant density from dung-pile density, it is important to calculate dung decay rate (Barnes & Jensen 1987). However, dung decay is a complex process and can be affected by factors such as habitat type, decomposer abundance and diversity, fruit content, and microclimate (White 1995; Mubalama & Sikubwabo 2022; Masunga et al. 2006). These dynamics have implications for using decay rates obtained at one site to estimate elephant density at another (Nchanji & Plumptre 2001; Breuer & Hockemba 2007). Furthermore, given that it may take a long time for behavioral changes to manifest as changes in distribution, it is important to explore how human activity may cause short-term behavioral changes in elephant species, such as shifts in nocturnal activity. However, these shifts cannot always feasibly be monitored using dung sampling given the associated costs and human effort required.

To deepen our understanding of forest elephant behavioral responses to human activity, I examined forest elephant response to hunting across two different scales in and around Nouabalé-Ndoki National Park, Republic of Congo, where very little is known on how this specific population is being impacted by hunting in the area. Instead of using dung sampling methods, I utilized sound data collected in and around Nouabalé-Ndoki National Park and first explored hunting activity by examining the temporal distribution and intensity of gunshot events (gunshots that were recorded within one hour of each other at the same recording site were

grouped into “events”). Using this information, I hoped to gain insight into the hunting pressure that forest elephants are exposed to. For my first analysis, I aimed to use an occupancy framework to compare how forest elephant occupancy changes across the eight days following a gun hunting event, and if there is a response, whether it is sustained throughout this entire eight-day duration. For this framework, my primary sampling period was a 24-hour day and my secondary sampling periods were the four six-hour intervals in each primary sampling period. I predicted that there would be an effect of the interaction between gun event presence and primary sampling period (i.e., day) on occupancy, colonization, and extinction probability which would indicate that gun events are causing forest elephants to change their use of certain areas of the forest differently across days. However, it is important to note that observed changes in occupancy can also be interpreted as changes in vocal activity with no difference in forest elephant presence. Due to this limitation, this analysis more explicitly addresses questions related to the population’s calling activity rather than occupancy and will be referred to as the vocal activity analysis throughout the rest of this thesis. I next investigated whether the population’s proportion of nighttime calling activity changes in response to gun hunting on the day level. I additionally examined whether other variables such as habitat, season, protection status of the forest, and distance to nearest mainstem river influence the proportion of their nighttime calling behavior. I predicted that number of gunshots would positively relate to their proportion of nighttime calling behavior based on previous studies which have shown that elephants shift to nighttime activity in response to gun hunting (Graham et al. 2009; Ihwagi et al. 2018). Monodominant forest (*Gilbertiodendron dewevrei)* is dominated by open understory and increases in this habitat type have been previously linked to decreases in forest elephant abundance (Breuer et al. 2021). As monodominant forest is characterized by a more open

structure, consequently increasing the visibility of elephants to hunters, I predicted that as the proportion of monodominant forest increases, the proportion of nighttime calling activity would increase as well due to elephants being on higher guard. Gunshots have been found to occur more frequently close to rivers (unpublished data by the Elephant Listening Project), indicating that hunters may be using rivers as routes to enter the forest to hunt in the vicinity. As a result, for my study, I predicted that as distance to nearest mainstem river increases, the proportion of nighttime calling activity would decrease due to these areas having lower hunting pressure. I also predicted that unprotected areas would demonstrate a higher proportion of nighttime calling activity than protected areas based on previous research that has shown that forest elephants may have awareness of nearby hunting pressure and will adjust their behavior accordingly (Gaynor et al. 2018; Graham et al. 2009; Sitati et al. 2003; Wittemyer et al. 2017; Douglas-Hamilton et al. 2005). For the season covariate, I predicted that the proportion of nighttime calling activity would be higher in the wet season due to higher amounts of rainfall which will reduce forest elephant range of hearing and consequently, ability to detect nearby hunters.

METHODS

Study Area

Central Africa is home to the Congo Basin - the world's second largest tropical forest with a range of about 3.3 million km^2. The region is characterized as a mosaic of rivers, forests, savannas, swamps, and flooded forests and has high biodiversity. There are approximately 10,000 species of tropical plants, 400 species of mammals, 1,000 species of birds, and 700

species of fish found in the region. The main forest elephant stronghold is Gabon (Laguardia et al. 2021) but a relatively large population still remains in the Sangha Trinational Protected Area. This protected area is composed of four national parks across three Central African countries including the Dzanga-Sangha and Dzanga-Ndoki National Parks in the Central African Republic, Lobéké National Park in Cameroon, and Nouabalé-Ndoki National Park in the Republic of Congo. Nouabalé-Ndoki National Park sits at the core of the Ndoki Forest, which is found between 1.5° to 3°N, and 16° to 17°E. The Ndoki Forest transitions in the north to Guineo-Congolian lowland rainforest and in the south to swamp forests (White 1983). The forest is dominated by Sterculiaceae-Ulmaceae semi-deciduous forest (Rollet 1964; Letouzey 1968) with large patches of swamp forests and monodominant forest along upland plateau and watercourses (Blake & Fay 1997). The forest experiences a minimum mean monthly temperature of 21.1 °C and a maximum of 26.6 °C and an average annual rainfall of 1,694 mm (Breuer et al. 2021). Nouabalé-Ndoki National Park offers a unique opportunity to explore forest elephant activity due to the presence of a landscape-scale acoustic grid managed by the Elephant Listening Project and the Congo division of the Wildlife Conservation Society. The park is located in the Republic of Congo along the borders of the Central African Republic and Cameroon (Figure 1).

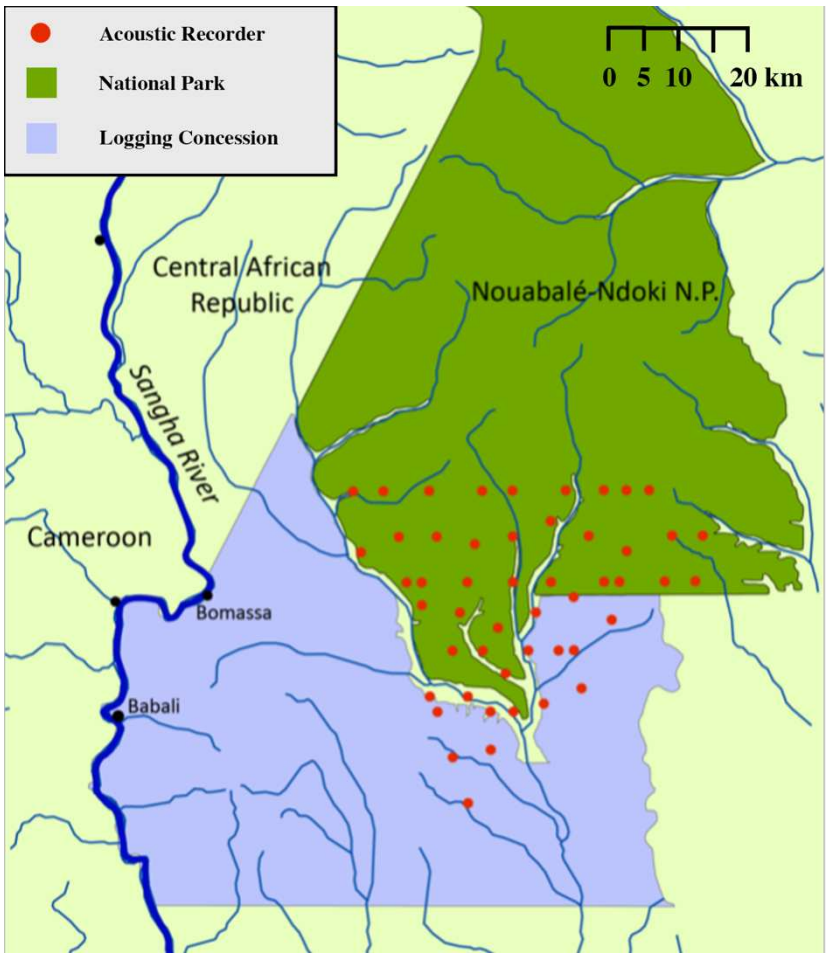


Figure 1. A map of the study site with red dots representing the acoustic recorders, the northern region (dark green) representing the national park, and southern region (purple) representing logging concessions.

Acoustic Sampling Study Design

Passive Acoustic Monitoring (PAM) has recently gained recognition as an effective method for wildlife monitoring across a range of temporal and spatial scales. Using sounds of interest such as elephant rumbles, their predominant type of vocalization, and gunshots from sound recordings taken from the landscape-scale acoustic grid, we can use PAM to study forest elephant populations and their response to human disturbances such as hunting. The acoustic grid is made up of 50 SWIFT acoustic recorders, designed and manufactured by the K. Lisa Yang

Center for Conservation Bioacoustics, and were deployed in a grid within and around the park in October 2017 (Figure 1). Each acoustic recorder was systematically and randomly placed within a 25 km^2 grid cell across the landscape of the study area, which ultimately covers an area of 1,250 km^2. Each unit was suspended approximately 7-10 meters high on an appropriate tree branch and was left to record continuously for 3-4 months. At the end of this period, the unit was revisited, the SD card and batteries were replaced for the next recording period, and the data were downloaded. The sound data collected from the recorders were stored on 256 GB SD cards as 16-bit WAV files using an 8 kHz sampling rate. The microphones for SWIFT recorders are omnidirectional and sample a forest area of about 0.8 km^2 on average (unpublished data from the Elephant Listening Project).

Acoustic Data Processing

More than 5 TB of sound data are collected from the acoustic grid every three months. While a major benefit of PAM is the ability to more feasibly collect large amounts of data, the raw audio files must be processed to transform the data into a format useful for investigating wildlife-related research questions. Automated detection algorithms are becoming increasingly more popular tools to process large acoustic datasets for those working with PAM, including those studying forest elephants.

A rumble detector, as outlined in Keen et al. 2017 and Wrege et al. 2017 (Appendix S3), was trained to execute a four-step process including pre-processing, feature extraction, classification, and clustering of frames. Sound files were converted into spectrograms using the short-time Fourier transform with a 1024-sample Hanning window, 200-point overlap, frequency resolution of 1.9531 Hz, and a time resolution of 100 ms. Spectrograms were then converted to

the logarithmic frequency scale and time frames of 100 ms were created for feature extraction. Both harmonic features and horizontal features were extracted. Harmonic features quantified the harmonic structure that often characterizes rumbles and horizontal features measured the power in the frequencies where most energy in forest elephant rumbles is concentrated (8-64 Hz; Figure 2). Classification of the frame was then completed using the Adaboost algorithm (Freund & Schapire 1996) which produces a value for the likelihood that the frame contains a rumble. Clustering was then completed by smoothing the likelihood scores of all time frames in the spectrogram using overlapping Gaussian windows. For the purposes of this study, detections that exceeded a likelihood threshold of 0.4 were tagged as rumbles and then manually reviewed using Raven Pro (K. Lisa Yang Center for Conservation Bioacoustics & Cornell Lab of Ornithology 2019) to confirm the classification. A gunshot detector, as outlined in Wrege et al. 2017 (Appendix S3), was created using a cross-correlation algorithm trained on example signal spectrograms to locate similar signals in novel sound recordings. Signals that had a correlation value of 0.53 were tagged as gunshots and then were manually reviewed in Raven Pro to confirm the classification.

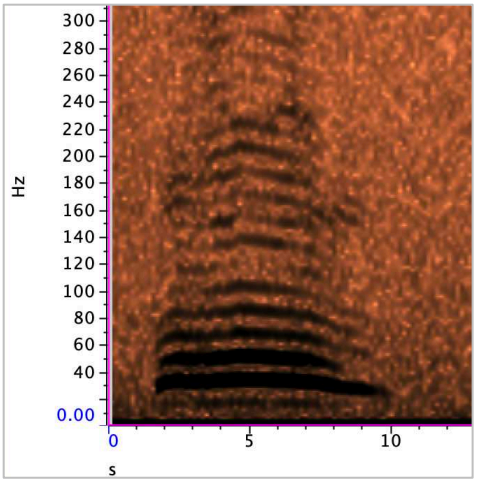


Figure 2. A spectrogram of a forest elephant rumble with time in seconds on the x-axis and frequency in Hz on the y-axis. Each curved line represents one harmonic within the rumble. Most of the rumble's energy is concentrated within the lower frequency range, as seen by the darker and more pronounced harmonics.

Exploring Hunting Activity Approach

All confirmed gunshots were grouped into gunshot events, with gunshots that occurred within one hour of each other at the same recording site being grouped into the same event. Events were categorized into classes of hunting pressure intensity by their number of gunshots. "Low" intensity events ranged from 1-5 gunshots, "Medium" intensity events ranged from 6-13 gunshots, and "High" intensity events ranged from 23-58 gunshots. Events were also classed by whether they occurred during the day or night. Hours 6-17 were classified as day and hours 0-5 and 18-23 were classified as night to follow the patterns of dawn and dusk in the equatorial forest.

Vocal Activity Analytical Approach

To examine how forest elephant vocal activity changes across the eight days following a gun hunting event, acoustic detection models developed by the Elephant Listening Project were used to find both rumbles and gunshots within the sound recordings taken between November 2017 and October 2018. Gunshots that occurred within one hour of each other and that were recorded at the same recording site were grouped into "events". Following these events, rumbles were compiled for each of the eight days and across all recording sites that are located within 10 km of the recording site the gunshot event was recorded on in order to increase the spatial scale at which I was exploring forest elephant response. Rumbles were also compiled using the same methods for the control event periods, which were set 3-5 weeks before the gunshot event and had the following eight days examined as well. These rumble counts were then converted into presence and absence data for the analysis, with rumble counts of one or greater being coded as present, or 1, and rumble counts of zero being coded as absent, or 0. To maintain independence,

rumbles were only used for one event and the eight-day periods following both the gunshot and control events did not have any gunshots within them, both at the recording site the event was recorded on and across all recording sites located within the 10 km radius. In total, eight-day periods following 42 gunshot events and 42 control events were used. As I wished to examine whether vocal activity changed from day to day throughout the eight-day period, or in an occupancy framework, from 'season' to 'season', a dynamic multi-season modeling approach (MacKenzie et al. 2003) was applied using the unmarked R package (Fiske & Chandler 2011). Definitions of analysis covariates and related predictions examined in the models are listed in Table 1. The most parsimonious model among candidate models was chosen based on Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2004) and using the AICcmodavg (Mazerolle 2023) package in RStudio Version 2023.03.0

Table 1. Variable key, definitions, predictions, and associated model statements for the vocal activity analysis.

Variable	Definition	Prediction	Model Statements
Gun	Whether a gun event was present prior to the start of the eight-day period.	Gun event presence will decrease occupancy (psi) and colonization (gamma) and increase extinction (epsilon) or may only affect one of these parameters. Gun event presence will also decrease forest elephant detection probability (p).	1. psi(gun), gamma(.), epsilon(.), p(.) 2. psi(gun), gamma(gun), epsilon(.), p(.) 3. psi(gun), gamma(.), epsilon(gun), p(.) 4. psi(gun), gamma(gun), epsilon(.), p(gun) 5. psi(gun), gamma(.), epsilon(gun), p(gun)
Day	The eight-day periods were broken up into eight individual days that were each used as primary sampling periods (i.e., seasons) within the analysis. Each primary sampling period (i.e., day) was broken up into four secondary sampling periods, each six hours in length.	Primary sampling period, or day, will cause occupancy (psi), colonization (gamma), extinction (epsilon), and detection probability (p) to vary across the eight-day period or may only affect one of these parameters.	1. psi(day), gamma(.), epsilon(.), p(.) 2. psi(day), gamma(day), epsilon(.), p(.) 3. psi(day), gamma(.), epsilon(day), p(.) 4. psi(day), gamma(day), epsilon(.), p(day) 5. psi(day), gamma(.), epsilon(day), p(day)
Null	N/A	None of the predictor variables evaluated explain variation in occupancy (psi), colonization (gamma), extinction (epsilon), and detection probability (p).	psi(.), gamma(.), epsilon(.), p(.)

Nighttime Calling Activity Analytical Approach

To examine how the population's proportion of nighttime calling activity changes on the day level in response to gun hunting, the proportion of nighttime calling activity was compared between 54 days with gunshots and 54 control days, with night calls being compiled over an

‘elephant day’. An elephant day, as outlined in Wrege et al. 2012, is the 24-hour period beginning at 06:00 on one day and ending at 05:59 the next consecutive day. Formatting the data into elephant days is useful for interpretation of forest elephant activity as previous research at bais has shown that forest elephants are the most active at night between 16:30-06:30, meaning that their ‘days’ end closer to 06:00 in the morning rather than at midnight (Fishlock 2010). An elephant day is then divided into a 12-hour day (06:00–17:59) and 12-hour night (18:00–05:59) (Wrege et al. 2012; Gessner et al. 2014) to follow the patterns of dawn and dusk in the equatorial forest. For each elephant day, the number of calls recorded at night was divided by the total number of calls recorded during the elephant day to calculate the proportion of nighttime calling activity. Sound recordings used for this analysis were collected between December 2017 and December 2020 which marks the last month gunshots were detected from the acoustic grid as of June 2023.

The total number of gunshots recorded for each day was also calculated and used as a predictor in the model. Additional covariates include protection status (whether the recording site was located in a protected area or a logging concession), season (defined below), proportion of monodominant forest located within 600 m of the recording site, distance between the recording site and the nearest mainstem river, and an interaction between protection status and the number of gunshots. The recording site was included as a random effect in the model. To determine season, long-term seasonal trends based on rainfall data collected by the Goualougo Triangle Ape Project in the Goualougo Triangle of the national park were used. The trends show that the months of January, February, and December are dry with the rest of the months being wet. Dry seasons are characterized by months that experience less than 60 mm of rainfall. The distance between each recording site and the nearest mainstem of the Ndoki or Goualougo river

(whichever was closest) was measured using GIS watercourse layers. Layers were created by manually tracing digital elevation models and were then confirmed with on-the-ground GPS mapping conducted during routine acoustic grid maintenance. A random forest classifier was created for habitat classification and had an overall accuracy of 0.91 and a Kappa coefficient of 0.86 (Swider et al. in prep). For the monodominant forest class, the model had a producer's accuracy and user's accuracy of 0.87. Using the classifier, the proportion of monodominant forest within 600 m of each recording site was then quantified.

A zero-inflated binomial regression model was used due to the high counts of zeros present in both the rumble and gunshot data, and it was fitted to a binomial family as the response variable is a proportion. Models were developed using the glmmTMB R package (Brooks et al. 2017) which allows for a zero-inflation parameter to be applied to all observations when fitting zero-inflated models. Definitions of analysis covariates and related predictions examined in the models are listed in Table 2. The most parsimonious model among candidate models was chosen based on AICc (Burnham & Anderson 2004) and using the AICcmodavg (Mazerolle 2023) package in RStudio Version 2023.03.0

Table 2. Variable key, definitions, and predictions for the proportion of nighttime calling activity analysis.

Variable	Definition	Prediction
NumShots	The number of gunshots detected within a 24-hour day.	Positively related to proportion of nighttime calling activity.
Protection	Whether the recording site is located in protected national park or in a logging concession.	Proportion of nighttime calling activity will be higher in unprotected areas.
Season	Pattern of rainfall (dry months < 60 mm).	Proportion of nighttime calling activity will be higher in the wet season.
PropMono	The proportion of monodominant forest located within 600 m of the recording site.	Positively related to proportion of nighttime calling activity.
RivDist	The distance between the recording site and the nearest mainstem river (either Ndoki or Goualougo).	Negatively related to proportion of nighttime calling activity.
Site	Recording site where the data was collected. Included as a random effect.	No change.

RESULTS

A total of 8,421 rumbles and 112 gunshots were found from the 5,018 unique site-date recordings used for the vocal activity analysis. A total of 298 rumbles and 175 gunshots were found from the 108 unique site-date recordings used for the proportion of nighttime calling activity analysis.

Exploring Hunting Activity Results

In total, 340 gunshots were detected across all dates spanning both analyses. These 340 gunshots were grouped into 87 gunshot events. The distribution of gun events across hour, grouped by day and night, for low, medium, and high hunting pressure are seen in Figures 3a, 3b, and 3c respectively.

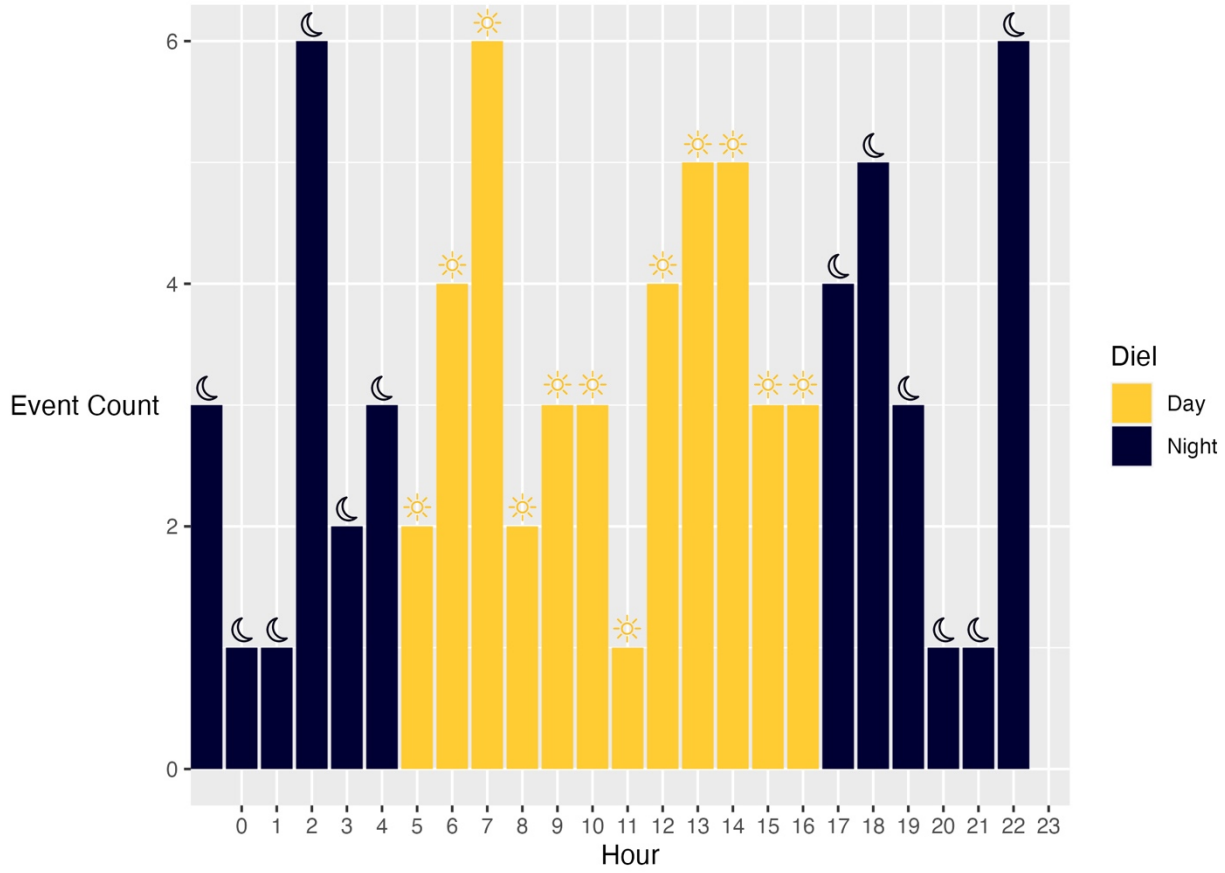


Figure 3a. Count of gun events (an "event" consists of gunshots that were recorded within one hour of each other on the same recording unit) by hour for low hunting pressure (1-5 gunshots within the event).

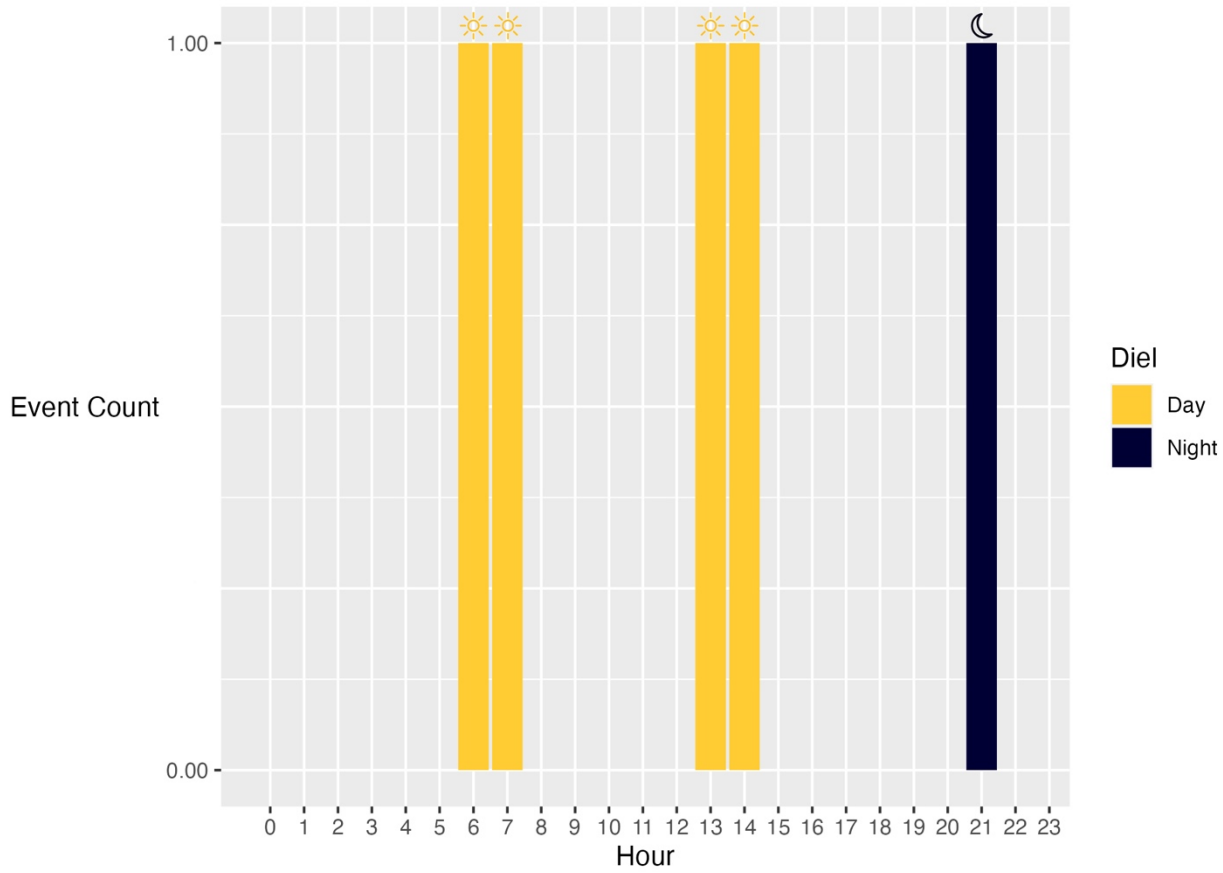


Figure 3b. Count of gun events by hour for medium hunting pressure (6-13 gunshots within the event).

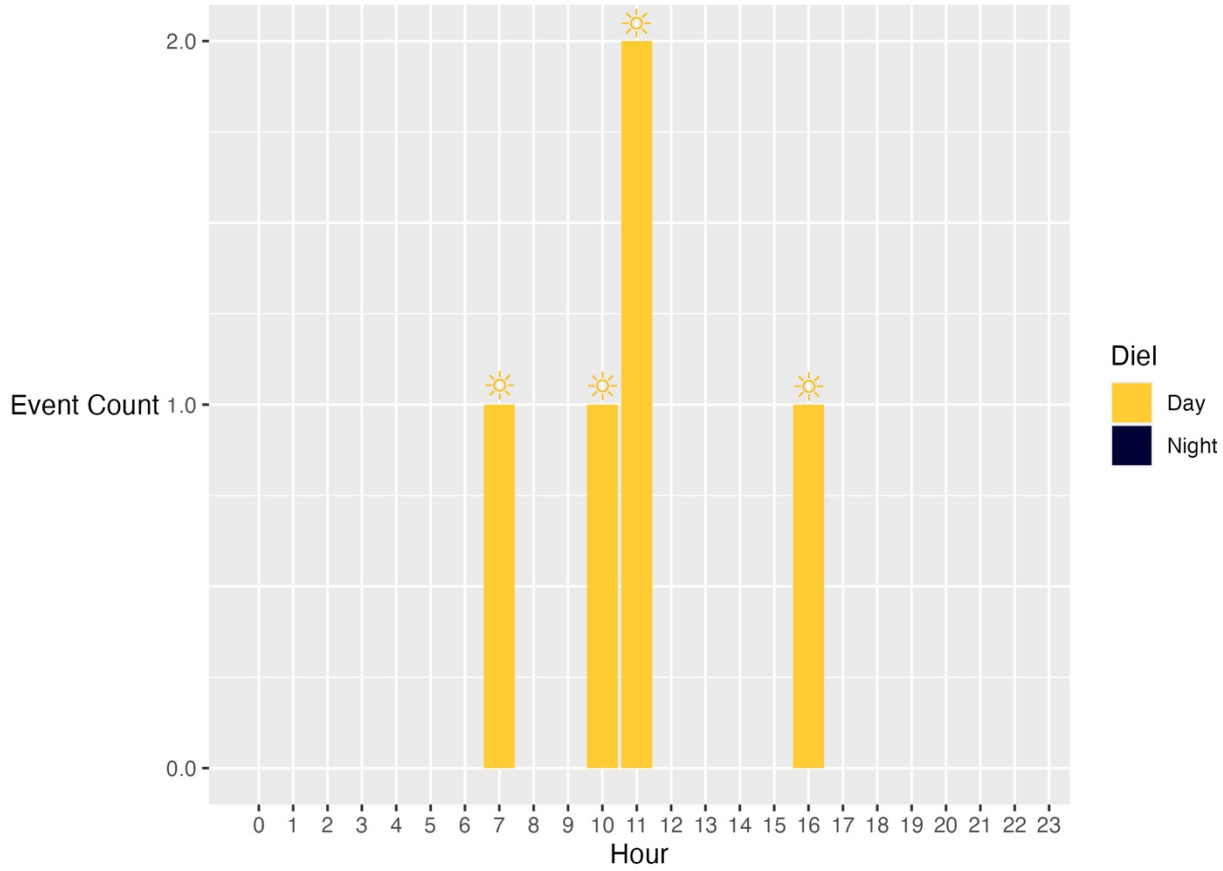


Figure 3c. Count of gun events by hour for high hunting pressure (23-58 gunshots within the event).

Vocal Activity Analysis Results

The top model only included an effect of the presence of a gun event on occupancy probability (β = -0.401, SE = 0.242, z = -1.658) but did not include effects of any predictors on colonization, extinction, and detection probabilities (Table 3). The second top-competing model was the null model, and the third top-competing model included an effect of gun event on occupancy and colonization probabilities but did not include effects of any predictors on extinction and detection probabilities (Table 3). Results show that, on average, forest elephants

are present and vocal at sites without gun events 53% of the time while at sites with gun events, this value drops to 43% (Figure 4).

Table 3. Output from the candidate models for the occupancy analysis.

Model	AICc	ΔAICc	AICc Weight	Log-Likelihood	K
$\psi(gun), \varepsilon(.), \gamma(.), p(.)$	9753.83	0.00	0.33	-4871.88	5
$\psi(.), \varepsilon(.), \gamma(.), p(.)$	9754.59	0.76	0.22	-4873.27	4
$\psi(gun), \varepsilon(.), \gamma(gun), p(.)$	9755.32	1.49	0.16	-4871.61	6
$\psi(gun), \varepsilon(gun), \gamma(.), p(.)$	9755.62	1.79	0.13	-4871.75	6
$\psi(gun), \varepsilon(.), \gamma(gun), p(gun)$	9756.45	2.62	0.09	-4871.15	7
$\psi(gun), \varepsilon(gun), \gamma(.), p(gun)$	9756.84	3.01	0.07	-4871.35	7
$\psi(day), \varepsilon(.), \gamma(.), p(.)$	9770.94	17.11	0.00	-4873.27	12
$\psi(day), \varepsilon(day), \gamma(.), p(.)$	9772.54	18.71	0.00	-4873.03	13
$\psi(day), \varepsilon(.), \gamma(day), p(.)$	9772.71	18.88	0.00	-4873.12	13
$\psi(day), \varepsilon(.), \gamma(day), p(day)$	9774.40	20.57	0.00	-4872.93	14
$\psi(day), \varepsilon(day), \gamma(.), p(day)$	9774.51	20.68	0.00	-4872.98	14
$\psi(gun * day), \varepsilon(.), \gamma(.), p(.)$	9786.96	33.13	0.00	-4871.88	21
$\psi(gun * day), \varepsilon(.), \gamma(gun * day), p(.)$	9790.26	36.43	0.00	-4870.35	24
$\psi(gun * day), \varepsilon(gun * day), \gamma(.), p(.)$	9790.83	37.00	0.00	-4870.63	24
$\psi(gun * day), \varepsilon(.), \gamma(gun * day), p(gun * day)$	9795.11	41.28	0.00	-4869.56	27
$\psi(gun * day), \varepsilon(gun * day), \gamma(.), p(gun * day)$	9795.51	41.68	0.00	-4869.76	27

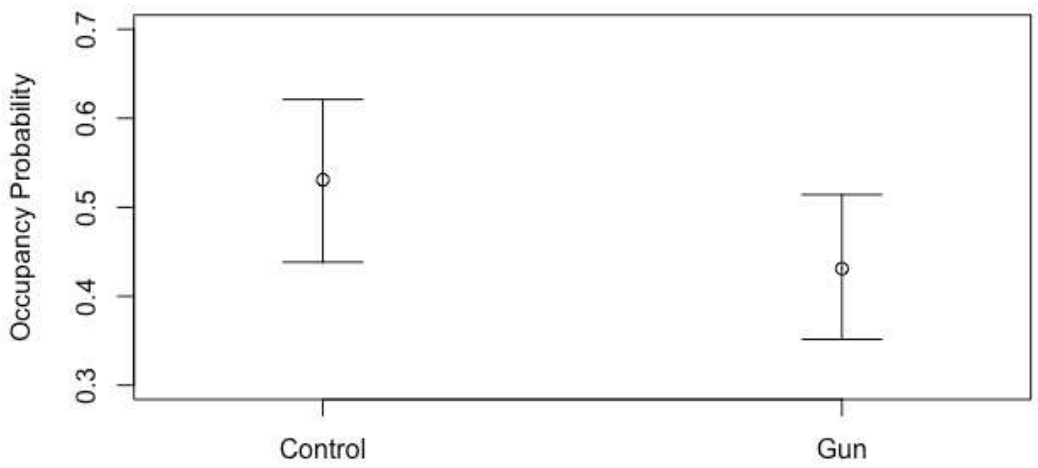


Figure 4. Probability of an elephant being present and vocal (i.e., vocal activity) at control sites without gun events (53%) and sites with gun (43%) events.

Nighttime Calling Activity Analysis Results

For the proportion of nighttime calling activity analysis, the top model included an effect of the number of gunshots, protection status, season, proportion of monodominant forest, distance to nearest mainstem river, an interaction between number of gunshots and protection, and site was included as a random effect. The second top-competing model was the same as the first excluding the effect of distance to nearest mainstem river. The third top-competing model was the same as the first excluding the effect of proportion of monodominant forest. However, the top model had strong support (AICc weight = 0.60; Table 4) and was used to interpret results from the data.

Proportion of nighttime calling activity was positively associated with the number of gunshots (β = 1.3063, SE = 0.2977, z = -2.425; Figure 5a), the proportion of monodominant forest (β = 9.5182, SE = 4.9580, z = 1.920; Figure 5d), and distance to nearest mainstem river (β = 0.3033, SE = 0.2262, z = 1.341; Figure 5c). The wet season was positively associated with the proportion of nighttime calling activity (β = 3.4291, SE = 1.8008, z = 1.904; Figure 5b).

There was a negative association between proportion of nighttime calling activity and the greater protection provided in the national park (β = -2.2405, SE = 1.7946, z = -1.248; Figure 6a) and the interaction effect between protection and number of gunshots demonstrated a similar trend for the national park as well (β = -1.0340, SE = 0.466, z = -2.219; Figure 6b).

Table 4. Output from the candidate models for the nighttime calling activity analysis. *Note that all models had "Site" included as a random effect [+ (1|Site)].

Model	**AICc**	**ΔAICc**	**AICc Weight**	**Log-Likelihood**	**K**
NumShots + Protection + Season + PropMono + NumShots*Protection + RivDist	147.36	0.00	0.60	-63.76	9
NumShots + Protection + Season + PropMono + NumShots*Protection	149.64	2.28	0.19	-66.09	8
NumShots + Protection + Season + NumShots*Protection + RivDist	151.26	3.91	0.09	-66.90	8
NumShots + Protection + PropMono + NumShots*Protection	151.27	3.92	0.09	-68.08	7
NumShots + Protection + PropMono + NumShots*Protection + RivDist	153.14	5.79	0.03	-67.84	8
Protection + Season + PropMono + RivDist	170.31	22.96	0.00	-77.60	7
Season + RivDist	171.92	24.57	0.00	-80.67	5
Season + PropMono + RivDist	172.65	25.29	0.00	-79.91	6
Protection + Season + RivDist	173.49	26.13	0.00	-80.33	6

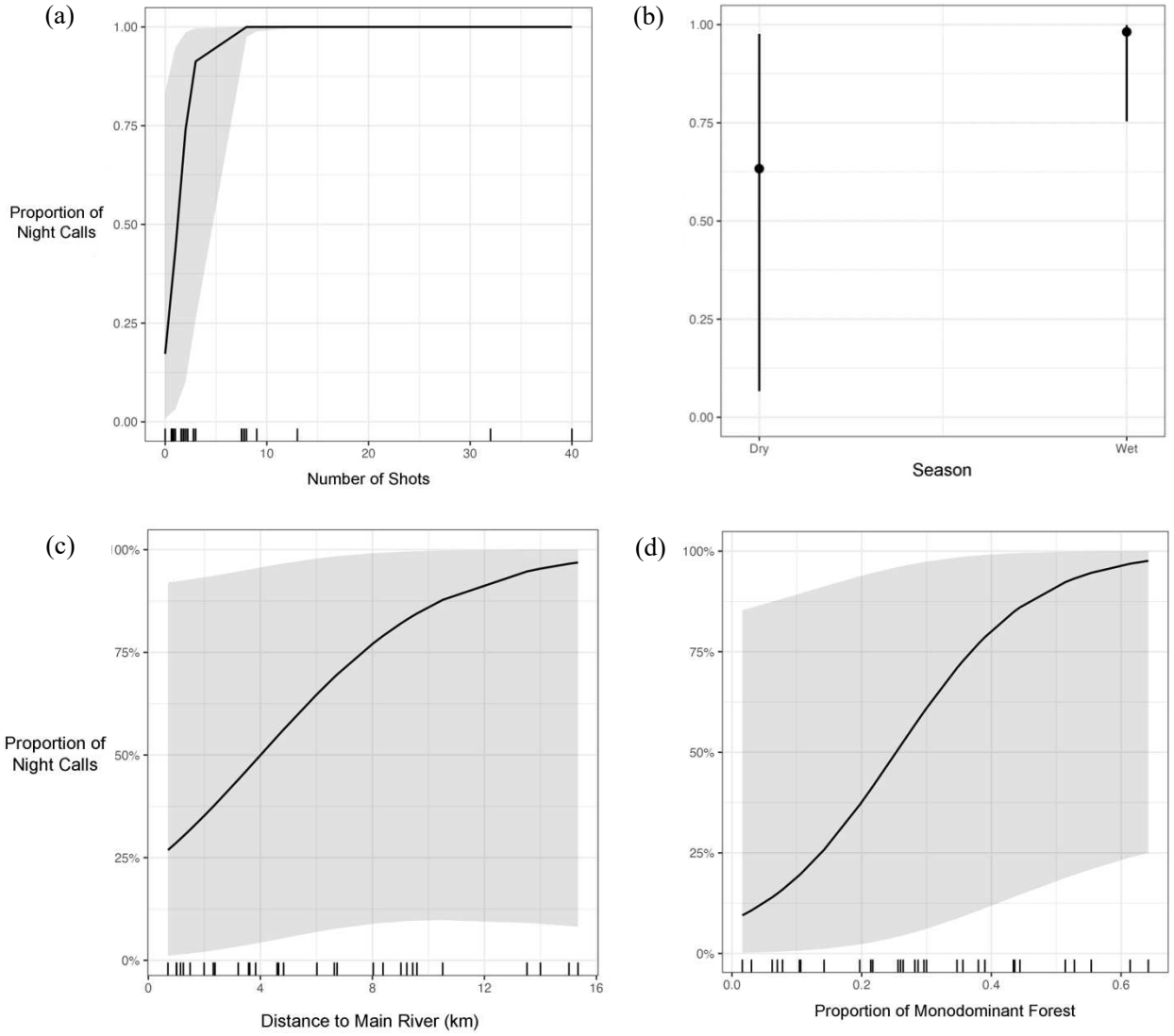


Figure 5. Panel of figures showing the positive association between proportion of night calls and number of shots (a), wet season (b), distance to main river in km (c), and proportion of monodominant forest (d).

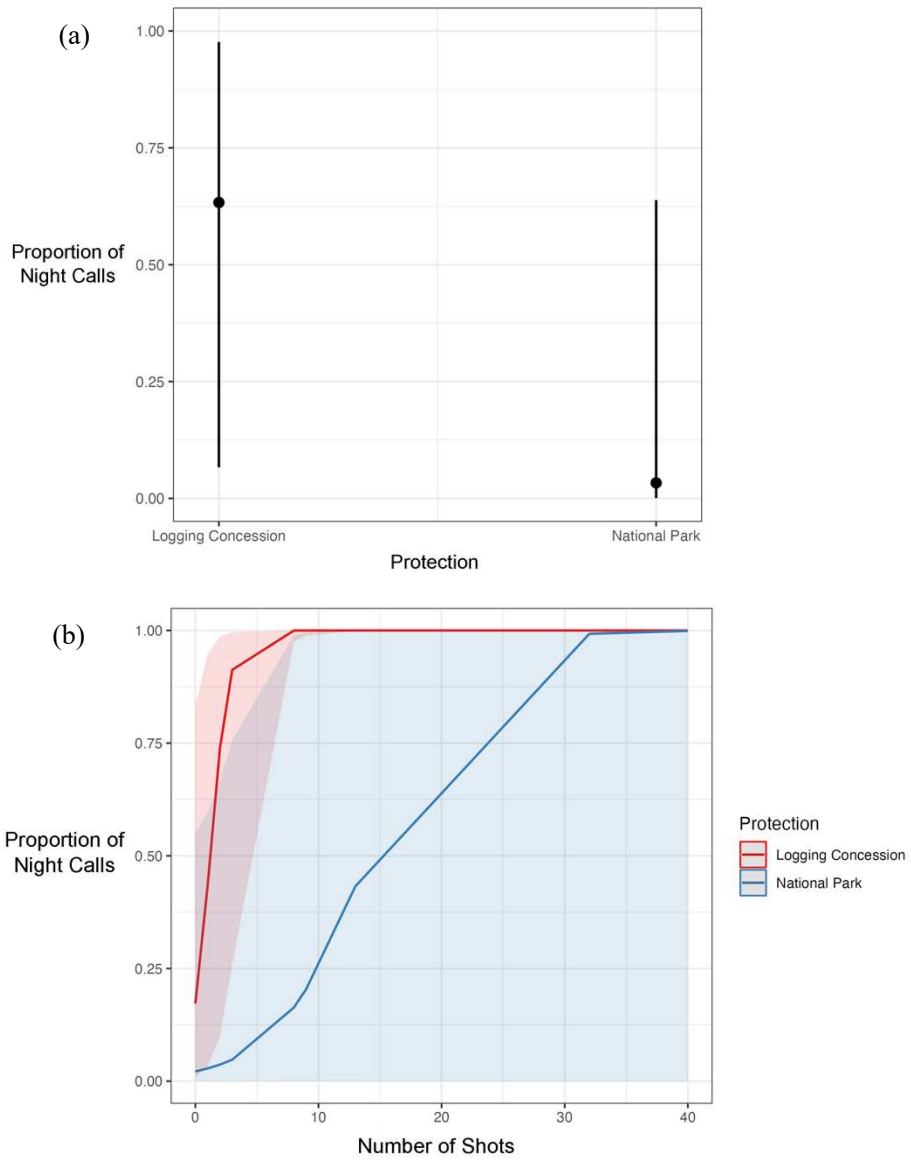


Figure 6. Panel of figures showing that recording sites located in the national park experience lower proportion of nighttime calling activity both for protection as its own predictor variable (a) and for the interaction effect between protection and number of gunshots (b).

DISCUSSION

Gun hunting patterns demonstrated trends based on the intensity of hunting, with low intensity hunting occurring during both the day and night. Medium hunting intensity occurred

more during the day, but also was observed to occur once at night. High hunting intensity occurred only during the day, indicating that this is the time of day where hunters performing more serious types of wildlife crime are active. This provides a convincing argument for conservation practitioners such as ecoguards to focus their limited resources on prioritizing the monitoring of high intensity hunting during their daily patrols.

Overall, the results of this study suggest that gun hunting is having a significant impact on forest elephant vocal activity. My main findings highlight that forest elephants are present and vocally active at sites without gun hunting events 53% of the time but when gun hunting occurs, this estimate drops to 43%. As the "day" covariate was not found to influence occupancy, colonization, and extinction probabilities, this indicates that this change in forest elephant vocal activity is sustained over the eight-day period examined and does not vary from day-to-day within this period. Results also show that the species is demonstrating shifts in their behavior to more nighttime calling activity as hunting pressure increases.

Previous research conducted in this same study area by Swider et al. 2022 focused on examining the same population's calling activity 24 hours after a gunshot event. Their results show that for the five hours following a gunshot event, forest elephant vocal activity increased above the control state level, but then from hours six to twenty-four, their calling activity dropped below the control state level. Their results in combination with the results from my vocal activity study indicate that this drop in calling activity begins six hours following a gun hunting event and is sustained throughout the eight days following this time, meaning that future research should focus on determining how long it takes for the population's vocal activity to return to the control state level following gun hunting. These changes in vocal activity may represent changes in occupancy, which may influence the important interspecific interactions

forest elephants are engaged in with forest vegetation, having implications for trophic dynamics (Patten et al. 2019) and forest growth and function in certain areas, ultimately eroding carbon storage services (Bello et al. 2015). Savanna elephants have been shown to minimize risk by compressing populations into more secure areas which has been shown to relate to population super abundance and associated vegetation damage (Barnes 1983; Lewis 1986). Forest elephants are attracted to mast fruiting events (White 1994; Blake & Fay 1997; Morgan & Lee 2007) but as demonstrated from this study, human activity such as hunting may influence forest elephant occupancy in certain areas, ultimately affecting elephant feeding behavior and ranging patterns. Reduced occupancy may lead to losses in foraging opportunities, influencing forest elephant body conditions and associated biological processes. Changes in forest elephant occupancy in certain areas of the forest may also increase human-elephant conflict in areas where the population feels more secure, negatively affecting the species' conservation (Breuer et al. 2016).

However, it is also possible that my findings are capturing changes to vocal activity instead of changes to site occupancy, e.g., elephants are remaining present at sites but are reducing their vocalizations after a gun event. Shifts in vocal activity may affect coordination within and between family groups over both short and long distances (Thompson 2009), meaning that family group cohesion and other social behaviors such as finding potential mates may be affected (Wittemyer et al. 2007). In savanna elephants, rumbles allow individuals to communicate information about their identity (McComb et al. 2000), their emotional state (Soltis et al. 2005; Soltis et al. 2009), and external threats that they may be aware of (Soltis et al. 2014). Reductions in vocal activity may consequently lead to reductions in these important intraspecific interactions that help maintain forest elephant populations by supporting their reproduction, sociality, cognition, and survival.

Results of the proportion of nighttime calling activity analysis indicate that on the day level, forest elephants are shifting to more nocturnal calling activity as the severity of gun hunting increases and especially in unprotected areas, which is in line with previous research examining diel activity in response to human activity for savanna elephants (Smit et al. 2023; Gaynor et al. 2018; Graham et al. 2009; Sitati et al. 2003; Wittemyer et al. 2017) and forest elephants (Wrege et al. 2012). It was also found that as the proportion of monodominant forest increases, so does the proportion of nighttime calling activity. Monodominant forest has a more open forest structure, meaning that forest elephants may be more on guard in these areas due to the higher chance of being visible to hunters. The wet season was associated with a higher proportion of nighttime calling activity which may be due to the soundscape being more saturated with rainfall, reducing the population's range of hearing and heightening their caution during the day when gun events are higher. Distance to nearest mainstem river had a positive association with proportion of nighttime calling activity which was counter to my prediction for this covariate. Breuer et al. 2021 have previously found that proximity to rivers was not an important predictor of forest elephant density, indicating that the benefits of being near a river may compensate for the costs associated with being in areas that experience higher levels of hunting activity. In addition, sound signals that occur near rivers may be amplified as the sound waves are channeled through the pathway clear of vegetation over the water, suggesting that in these areas, forest elephants may experience a better range of hearing and be less on guard and perform less nighttime calling as a result.

Vocalizations play a key role in maintaining cohesion of forest elephant groups in their dense environment, meaning that shifts in vocal activity to the nighttime hours may have ramifications for their social behaviors such as meeting with family members or finding potential

mates, ultimately affecting population size (Wittemyer et al. 2007). Previous research at bais has shown that after a poaching event, it may take years for forest elephants to return to diurnal activity and habituate to humans, which will affect the ecotourism industries that depend on the presence of these animals (Breuer et al. 2016). The potential cost associated with being in the vicinity of a hunter (i.e., death) outweighs the cost of continuously adopting avoidance strategies such as temporal niche partitioning. However, temporal shifts in vocal activity may change the frequency at which important vocal interactions occur in social settings such as bais. Aggregations of forest elephants at these bais provide them with social learning hubs where information on resources may be shared and social and ecological traditions may be established (Fishlock et al. 2016). Consequently, shifts in the frequency and timing of vocal interactions at bais may impact forest elephant biology, sociality, and cognition.

STUDY LIMITATIONS

This study provides novel insights into how gun hunting is impacting forest elephant behavior. However, there are several limitations which provide the foundation for future research. As mentioned previously, reductions in occupancy can also be interpreted as reductions in vocal activity but no change in the species presence. While the presence of a call means a caller is present, callers may choose to go quiet for any number of reasons, highlighting a major limitation of PAM in inferring species presence, especially as shifts in vocal behavior become more widespread. Moving forward, research can capitalize on the benefits of combining PAM and other sampling methods such as mark-recapture to confirm species presence, estimate population size, and calculate vocal activity rates, providing a more robust estimate of

occupancy. These estimates are critical metrics for effective monitoring of forest elephants as they can provide us with information on the species' spatial and temporal use of habitat, movement, and population trends, advancing our abilities to both make data-driven conservation decisions and understand the effects of these decisions in the future.

Both analyses had low sample sizes for both the rumble and gunshot datasets, limiting the number of predictors and interaction effects we could explore. As the Elephant Listening Project continues to collect more data, the sample size for these analyses may be expanded to broaden our understanding of how different variables are impacting the species behavior. For example, other habitat types in the area such as mixed forest, which is associated with higher fruit abundance (Blake 2002) and has been found to be a preferred habitat type over monodominant forest by forest elephants (Stokes et al. 2010), may have different effects on the proportion of nighttime calling activity than monodominant forest. In addition, the proportion of nighttime calling activity analysis in this study demonstrates that forest elephants were less vocally active at night near rivers, indicating that some feature or features of rivers may be supporting the population's comfort in being more vocally active during the daytime in these areas despite higher hunting activity. Future research can explore which river-related variables may impact forest elephant vocal activity including river size, vegetation types proximal to the rivers, and even how sounds attenuate differently in the airspace above rivers versus in their vicinity.

While this study provides us with a deeper understanding of the population's response to gun hunting across 1,250 km^2 of their range, the population has access to approximately 7,500 km^2 of contiguous forest across the Sangha Trinational Protected Area. This limits the scales at which we may understand fear-induced shifts in forest elephant behavior. As PAM becomes a more accessible and applicable tool, future research can expand the acoustic grid to cover a

larger portion of the population's range, deepening our understanding of their landscape behavior.

CONCLUSION

The results of this study have provided insight into how forest elephants are responding to gun hunting, having implications for their monitoring and conservation. The demonstrated shifts in their behavior provide evidence that nontarget elephants in the vicinity of gun hunting events are also intensely affected, dramatically shifting their 24-hour vocal activity to the night and sustaining changes in vocal activity for at least a week following gun hunting. Reductions in safe spatial and temporal niches may have ramifications for the species' population size, genetic fitness, group cohesion, and the social learning and relationships that are vital for their survival. These reductions may also influence forest structure and reduce our planet's ability to sequester carbon (Berzaghi et al. 2019) as the Congo Basin's mega-gardeners may choose to depart vital parts of the forest and compress into more secure areas. Understanding the degree at which forest elephants are affected by gun hunting provides a convincing argument to focus limited conservation resources on developing more effective strategies to reduce indirect impacts from hunting on this critically endangered and ecologically important species.

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