

ABSTRACT

STARR, STEVEN DEWAYNE. Anthropause Impacts and Fosa Abundance in Madagascar (Under the direction of Dr. Lisa Paciulli and Dr. Roland Kays).

Madagascar is a biodiverse island with estimated endemism rates between 75% and 100%.

Located off the southeast coast of Africa, it is consistently one of the poorest countries in the world, and the unique wildlife here face intense pressures commonly associated with developing nations. These include destruction of key habitats for farmland and bushmeat hunting as a means of survival. At the same time, Madagascar's extraordinary floral and faunal diversity makes it a major destination for ecotourism, which provides important economic support but also places additional pressure on the wildlife that tourists come to see. The onset of COVID-19 caused a rapid 93% reduction in tourists—from 387,000 at its peak in 2019 down to 32,000 in 2021—creating an “anthropause.” Once restrictions were lifted, visitation quickly rebounded toward pre-pandemic levels, an “anthropulse.” This sharp decline followed by a rapid influx of visitors allowed us to investigate how these shifts in human pressure affect wildlife in Andasibe by combining camera-trap data from pre-COVID surveys (2017, 2019), anthropause surveys (2020, 2021), and an anthropulse survey (2023). Using generalized linear mixed models to estimate changes in detection rates and multi-season occupancy models to evaluate shifts in site use, we found substantial increases in animal activity during the anthropause followed by declines as tourism increased again. Although occupancy estimates were highly uncertain, these results show that reductions in human presence can rapidly alter wildlife behavior and highlight the potential value of managing tourism to avoid peak wildlife activity periods.

Madagascar is also home to an endemic family of carnivores (Eupleridae), with the fosa (*Cryptoprocta ferox*) being the largest and most wide-ranging. Despite the fosa's critical role as an apex predator, it remains one of the most understudied carnivores globally. Our goal was to

identify the drivers of fosa abundance at an island-wide scale. We combined 16 years of camera-trap data from 12 protected areas across Madagascar and modeled fosa detections using generalized linear mixed-effects models. Our findings highlight the importance of forest cover as a mitigating factor against increasing anthropogenic pressures and the complex nature of fosa-dog interactions. Human population density emerged as the strongest negative predictor of fosa detections, while fosa detections showed context-dependent patterns across dog-habitat gradients. Overall, the combined presence of dogs and humans created the most substantial pressure on fosa across the landscape. This study represents the first broad-scale analysis of fosa ecology and provides a foundation for targeted conservation efforts.

© Copyright 2025 by Steven Starr

All Rights Reserved

Investigating the Impacts of The Anthropause and Understanding Island-Wide Drivers of Fosa
Abundance in Madagascar

by
Steven Dewayne Starr

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of Master of Science

Fish, Wildlife, and Conservation Biology

Raleigh, North Carolina
2025

APPROVED BY:

Dr. Lisa Paciulli
Committee Co-Chair

Dr. Roland Kays
Committee Co-Chair

Dr. Jeffrey Doser

Dr. Zach Farris

DEDICATION

To my grandmother, grandfather, and mother. I wish you were here to see what I've accomplished, thank you for the confidence and perseverance you've instilled in me. I love you. Until we meet again.

To my sister, thank you for all the love and support, I wouldn't be here and I couldn't have done this without you!

To my cat, thanks Kleo for helping to keep me sane, for being the best travel buddy, and for being the best companion I could ask for.

BIOGRAPHY

In 2019 Steven graduated from Oklahoma State University with a Bachelor of Science in Zoology having gained undergraduate research experience focusing on dolphins and frogs. After graduating he went on to work for research labs at The University of Oklahoma Health and Sciences Center as well as for a private lab in Colorado. He knew his true calling was in the wildlife field and decided to pursue graduate school to ultimately establish a career in conservation. In 2023 he landed at North Carolina State University to begin his graduate studies under the mentorship of Dr. Roland Kays, Dr. Lisa Paciulli, Dr. Jeffrey Doser and Dr. Zach Farris. He was able to capitalize on an opportunity to travel to Madagascar for 2.5 months before beginning the graduate program. Here he gathered field data that would be compiled with collaborator data and serve as the foundation for his graduate studies investigating the impacts of COVID driven shift in tourism on animal activity in Madagascar and understanding island-wide drivers of Madagascar's largest carnivore, the fosa.

ACKNOWLEDGMENTS

I would like to thank Dr. Zach Farris for the continued mentorship over these years and being the catalyst that got me to North Carolina and to Madagascar. I would like to thank Dr. Roland Kays and Dr. Lisa Paciulli for their continued guidance and support throughout this graduate program.

I would like to thank Dr. Jeff Doser for the statistical guidance. Thank you to The Mad Dog Initiative, Association Mitsinjo, Madagascar National Parks, Ranomafana National Park Team, and The University of Antananarivo for their collaboration and data. A very big thank you to the guides who made my fieldwork possible and to the people of Madagascar for being so kind and welcoming. My experience there was truly a life-changing experience, I can't wait to visit again.

Sorry if I forgot anyone, your contributions are greatly appreciated!

AUTHORSHIP STATEMENT

Chapter 1: Anthropauses and Anthropulses: Investigating the Impacts of COVID on Animal Activity and Occupancy in Andasibe Madagascar

Conceptualization: Steven Starr, Roland Kays, Zach Farris

Methodology: Steven Starr, Roland Kays, Zach Farris

Investigation: Steven Starr

Data curation: Zach Farris, Steven Starr

Formal analysis: Steven Starr, Roland Kays, Zach Farris

Software: Steven Starr

Validation: Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

Visualization: Steven Starr

Project administration: Steven Starr

Supervision: Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

Writing (original draft): Steven Starr

Writing (review and editing): Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

Chapter 2: Island-Wide Patterns of Fosa Abundance in Madagascar's Protected Areas

Conceptualization: Zach Farris, Roland Kays, Zach Farris

Methodology: Steven Starr, Roland Kays, Zach Farris

Investigation: Steven Starr

Data curation: Zach Farris, Steven Starr

Formal analysis: Steven Starr, Roland Kays, Zach Farris

Software: Steven Starr

Validation: Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

Visualization: Steven Starr

Project administration: Steven Starr

Supervision: Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

Writing (original draft): Steven Starr

Writing (review and editing): Lisa Paciulli, Roland Kays, Jeffrey Doser, Zach Farris

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii-ix
Chapter 1: Anthropauses and Anthropulses: Investigating the Impacts of COVID on Animal Activity and Occupancy in Andasibe Madagascar	
Abstract	1
Introduction.....	1-4
Methods.....	4-13
Results.....	12-15
Discussion	15-20
Literature Cited	21-27
Chapter 2: Island-Wide Patterns of Fosa Abundance in Madagascar’s Protected Areas	
Abstract	26
Introduction.....	26-29
Methods.....	29-33
Results.....	33-37
Discussion.....	37-42
Literature Cited	43-47

LIST OF TABLES

CHAPTER 1

Table 1	Sampling effort and detection counts from camera-trap surveys in Andasibe, Madagascar (2017–2023). For each survey period we list the date range, number of active camera stations, successful trap-nights (one functioning camera for one 24hr period.), and the number of detection events for fosa, dogs, birds, small mammals, tourists, and lemurs. Periods are classified as pre-COVID, anthropause (COVID-era), and anthropulse (post-COVID rebound).	7
Table 2	Generalized Linear Mixed Model structures and significant covariates for four detection count models using data collected from Andasibe, Madagascar (2017-2023). Fcount (fosa), Bcount (birds), Lcount (lemurs), and Mcount (small mammals). Covariates considered were Edge (distance to forest edge (m), Settlement (distance to nearest human settlement (m), Elevation (m), Dog (dog detection rate), Tourist (tourist detection rate), Trail size (small/medium/wide), Forest type (secondary/degraded/open matrix), Canopy (percent sky covered at the camera station), Duration (successful trap nights), and Site (camera station). The table lists only covariates retained as significant in the top model. A (+) sign indicates a positive relationship, a (-) sign indicates a negative relationship, and no sign is present when the covariate is a categorical variable with variable effects.	10
Table 3	Multi-season Occupancy Model structure. P indicates the detection portion of the model; Psi indicates the occupancy portion of the model. Covariates considered were Edge (distance to forest edge (m), Settlement (distance to nearest human settlement (m), Dog (dog detection rate), Tourist (tourist detection rate), Trail size (small/medium/wide), Canopy (percent sky covered at the camera station), Effort (successful trap nights), and Station (camera station). Station1 and occasion1 represent the station and occasion covariates but in a grid layout as is required by the occupancy portion of the model. The table lists only covariates retained as significant. A (+) sign indicates a positive relationship, a (-) sign indicates a negative relationship.	11
Table 4	Naïve and model-based fosa occupancy and survey period for camera-trap surveys in Andasibe, Madagascar (2017–2023). Survey 1 (June 2017), survey 2 October – December 2021, survey 3 (June – July 2019), survey 4 (November 2020 – January 2021), survey 5 (September – October 2021) survey 6 (June – August 2023)	15

CHAPTER 2

Table 1	Fixed and interaction effects from the generalized linear mixed model predicting fosa detections. “Positive” and “Negative” indicate the direction of statistically significant effects.	37
---------	---	----

LIST OF FIGURES

CHAPTER 1

- Figure 1 Left- A green dot representing the region of Madagascar where the repeated camera trap surveys took place. Right - Layout of the camera grids in Andasibe, Madagascar. Each orange dot represents one camera station located in the Mitsinjo Reserve. Each green dot represents one camera station located in the V.O.I. Community Reserve. Each blue dot represents one camera station located in Analamazaotra Rainforest. Repeated surveys used these same locations across years. 5
- Figure 2 Camera-trap detection rates (detections/day; mean \pm error bars) across six sampling periods in Andasibe, Madagascar. Highlights mark “anthropause” periods (4: November 2020–January 2021; 5: September–October 2021). Periods 1–3 are pre-COVID (1: June 2017; 2: October - December 2017; 3: June–July 2019), and period 6 represents the post-COVID “anthropulse” (June–August 2023). Panels: top left = tourists; top right = non-tourists; middle left = dogs; middle right = small mammals; bottom left = fosa; bottom right = birds; center bottom = lemurs. 13-14

CHAPTER 2

- Figure 1 Locations of the 12 protected areas in Madagascar where camera-trap surveys were conducted from 2007–2023. Points a single camera location within each protected area. Basemap imagery from OpenStreetMap 2025 30
- Figure 2 Spatial context and camera-trap sampling design across three protected areas in Madagascar representing contrasting levels of habitat degradation. Pink points indicate individual camera-trap stations. Colored points on the inset map show the locations of the focal protected areas: Ankarafantsika National Park (green), Andasibe–Mantadia National Park (red), and Masoala National Park (blue). Satellite imagery panels illustrate the surrounding landscape context and camera-trap arrays within each park, highlighting differences in forest cover, fragmentation, and anthropogenic modification across sites: Ankarafantsika (top; more fragmented and degraded), Andasibe–Mantadia (middle; intermediate degradation), and Masoala (bottom; largely intact forest). All satellite images are shown at the same spatial scale. 31
- Figure 3 Hourly distribution of fosa detections across a 24-hour period. Orange bars represent diurnal hours, magenta bars represent sunrise and sunset (crepuscular periods), and blue bars represent nocturnal hours. Data were collected from 12 protected areas across Madagascar between 2007 and 2023. Numbers above each bar indicate the total number of detections. 34
- Figure 4 Interaction effects of human activity, dog activity, and forest cover on predicted fosa detections (per 100 trap-nights). Left: Interaction between human detection rate and dog detection rate. Human detection rate is measured in detections per trap-night;

dog detection rate is measured in standard deviations from the mean. Middle: Interaction between dog detection rate and percent forest cover. Dog detection rate is measured in standard deviations from the mean. Right: Interaction between human detection rate and percent forest cover. Percent forest cover is measured in standard deviations from the mean. Data were collected from 2007–2023 across 12 protected areas in Madagascar. 36

CHAPTER 1

Anthropauses and Anthropulses: Investigating the Impacts of COVID-19 on Animal Activity and Occupancy in Andasibe Madagascar

ABSTRACT:

As the human population continues to grow, anthropogenic pressures increasingly permeate natural ecosystems, making it difficult to disentangle human influence from natural processes. The COVID-19 pandemic created a rare natural experiment: a global anthropause during which human travel declined by an estimated 73% worldwide and by 98% in Madagascar. This was followed by a rapid anthropulse as tourism rebounded to, and in some cases exceeded, pre-pandemic levels. We investigated how these shifts affected wildlife in Andasibe, Madagascar by combining camera-trap data from pre-COVID surveys (2017, 2019), anthropause surveys (2020, 2021), and an anthropulse survey (2023). Using generalized linear mixed models to estimate changes in detection rates and multi-season occupancy models to evaluate shifts in site use, we found substantial increases in animal activity during the anthropause—often two- to four-fold higher than pre-COVID levels—followed by a decline as tourism increased again. However, our occupancy models yielded highly uncertain estimates, leaving little room for inference. These results demonstrate that reductions in human presence can rapidly alter wildlife behavior, and they highlight the potential value of managing tourism to avoid peak wildlife activity periods.

Introduction

The global biodiversity crisis continues to unfold as humans expand the extent and intensity of our activities on the planet (Dirzo *et al.* 2014). This negative influence on other species is a result not only in the direct action of humans (e.g. disturbance, hunting, introduction of exotic species), but also in the infrastructure associated with human development (e.g. roads, buildings). Research has focused on aspects of these pressures including how noise pollution (Shannon *et al.* 2016), light pollution (Longcore and Rich 2004), human presence (Nickel *et al.* 2020), and the global introduction of dogs (Doherty *et al.* 2017), impact wildlife. However, the expansion of humans and their infrastructure across the planet has resulted in anthropogenic pressures that are so pervasive that it is difficult to study wildlife in the absence of human influence, and it is now

difficult to disentangle the effects of human presence vs human footprint. A unique opportunity to study disentangled systems came through changes in human activity, but not infrastructure, associated with the COVID-19 pandemic.

In response to the emergence of the COVID-19 virus and the global pandemic that followed, many countries implemented lockdown measures that led to greatly reduced travel, both domestically (Hotle and Mumbower 2021) and internationally (UNWTO World Tourism Barometer and Statistical Annex, May 2021 2021). The reduction in human activity during this period has been referred to as the “anthropause” (Rutz *et al.* 2020) and created a natural experiment to separate the effects on wildlife of humans from their infrastructure. Some areas experienced a 10-fold decrease in human activity (Burton *et al.* 2024). Globally, tourism and travel experienced an unprecedented reduction. 2020 went down as the worst year on record for international tourism, dropping by a staggering 73%. There were about 1 billion fewer travelers in 2020 as compared to 2019 (World Tourism Organization (UNWTO) 2021). Surprisingly, tourism seems to have returned to normal as quickly as it fell. In the first 9 months of 2024, 1.1 billion international tourist arrivals were recorded, some locations reported returning to or exceeding pre-pandemic numbers as early as 2023. These 1.1 billion travelers serve as a benchmark that represents 98% of the pre-pandemic levels (World Tourism Organization (UNWTO) 2024). This rapid return to normality or exceeding previous numbers represents another new phenomenon termed “anthropulse,” describing the sudden influx of anthropogenic presence in areas that had previously experienced extended anthropause (Rutz 2022). This period of drastically low human presence (anthropause), followed by a sudden rush of human activity (anthropulse) has created a set of conditions ideal for studying the short-term effects of people on wildlife.

The anthropause created novel research opportunities by providing a rare setting to study ecosystems under abruptly altered anthropogenic pressures (Rutz 2022). Resulting studies have shown that wildlife responses to the anthropause varied greatly. In places where human activity decreased, studies documented increased wildlife breeding success (Manenti *et al.* 2020), reduction in roadkill (Shilling *et al.* 2021), and decreases in song intensity in White-Crowned Sparrows (*Zonotrichia leucophrys*) in response to lower ambient noise levels (Derryberry *et al.* 2020). One study analyzing tracking data from 43 species reported that during lockdowns

animals traveled longer distances and in highly populated areas, animals moved less frequently and ventured closer to roads (Tucker *et al.* 2023). Another large scale comparison analyzed camera trapping data from 163 species across 21 countries and reported that when human activity was high, mammals in undeveloped areas moved less, but in more developed areas, mammals moved much more frequently (Burton *et al.* 2024). These studies have helped begin to untangle the mystery of the impacts of human presence vs human activity. However, most of these findings are geographically skewed towards the ‘Global North’, highlighting a need for studies in rural communities of the ‘Global South’.

Human development of natural habitat, especially for rural communities across the Global South, are a complex ongoing issue, and this is particularly true for Madagascar. This island is a recognized biodiversity hotspot with extraordinarily high terrestrial endemism, 92-100% (Goodman and Benstead 2005), but these species are threatened by the typical conservation challenges of a developing country with large human populations and associated habitat loss and disturbance from development. Madagascar lost 44% of its forest cover between 1953 and 2014 to various factors including, development of land for agriculture, and slash and burn practices (Vieilledent *et al.* 2018). Malagasy carnivores are particularly vulnerable and have found themselves threatened by habitat degradation, introduction of invasive species, disease, and direct conflicts with humans (Wampole, Farris and Gerber 2021). Lemurs, the flagship taxa of the island, also face mounting pressures via habitat degradation, forest fragmentation, and poaching (Schwitzer *et al.* 2014). Both native carnivores and lemurs are increasingly affected by feral and free-roaming dogs (Valenta *et al.* 2025) whose presence is closely tied to human activity. While local anthropogenic pressures (e.g., deforestation, poaching, dogs) have rightly received attention, the effects of external pressures, namely ecotourism, on wildlife remain poorly understood. This is an especially important topic for Madagascar, whose economy depends heavily on tourism.

Madagascar was hit particularly hard by the global reduction in tourism during anthropause. In 2019, Madagascar experienced its all-time peak number of visitors welcoming 384,000 tourists. In the following year the number of tourists dropped to 68,000 and first quarter reports of 2021 reported a 93% reduction in tourist arrivals as compared to 2019 (UNTWO 2021). Secondary

reports further suggest that Madagascar received approximately 8,000 visitors in 2021, representing only 1.6% of the 2019 peak. This suggests Madagascar may be among the countries most severely impacted by the anthropause and presents an opportunity to untangle the effects of humans vs human infrastructure on its wildlife. First, due to the large volume of tourists that were present pre-COVID followed by the large reduction in tourism, we can investigate the effects of tourist presence as an anthropogenic effect separate from local sources of pressure such as hunting and habitat destruction. Second, the reduction of human presence in an area allows us to isolate the effects of human presence vs human footprint (i.e., infrastructure). Third, as tourism rapidly rebounded, we are able to study the effects of a rapid influx of human presence after an extended quiet period, anthropulse after the anthropause. These findings will allow us to better understand the impacts of human presence, footprint, and activity on native wildlife. Further, this understanding will inform NGOs and Madagascar National Parks on human-wildlife relationships while continuing to support tourism that is critical to the economy of the island.

The purpose of our study is to assess the impacts of anthropogenic presence on the wildlife of Andasibe, Madagascar, a popular eco-tourism destination, before (hereafter pre-COVID), during COVID (hereafter anthropause), and after (hereafter anthropulse). To achieve this goal, we used data from camera traps to 1) compare activity levels of wildlife, 2) investigate shifts in occupancy levels across the three periods while considering concurrent changes in human and dog activity and 3) investigate how anthropogenic and habitat factors affected these shifts. Our results show how shifts in human and dog activity shape wildlife activity and patterns, informing strategies to balance ecotourism with conservation.

Methods

Study Site

From 2017 to 2023, we used camera traps to sample three protected areas located around Andasibe, Madagascar (Figure 1). Surrounding this village are three rainforest protected areas, V.O.I.M.M.A Community Reserve (hereafter VOI) is a smaller area managed by the local Andasibe community (400 ha). Analamazaotra Rainforest (876 ha), is a national park managed by the government agency ‘Madagascar National Parks’, and Mitsinjo Reserve (710 ha), is an area managed by the non-profit organization “ Association Mitsinjo” (Goodman 2022). Given its

high levels of diversity and its proximity to the capital city (Antananarivo), Andasibe represents Madagascar's most heavily visited tourist site (Goodman 2022). Analamazaotra Rainforest is contiguous with VOI. These two forests are separated from Mitsinjo rainforest by a paved road that runs the length of the boundary between these two contiguous forests and Mitsinjo. Together, these three forests serve as home to a diverse range of endemic wildlife, including several critically endangered lemur species, such as the indri (*Indri indri*) and diademed sifaka (*Propithecus diadema*).

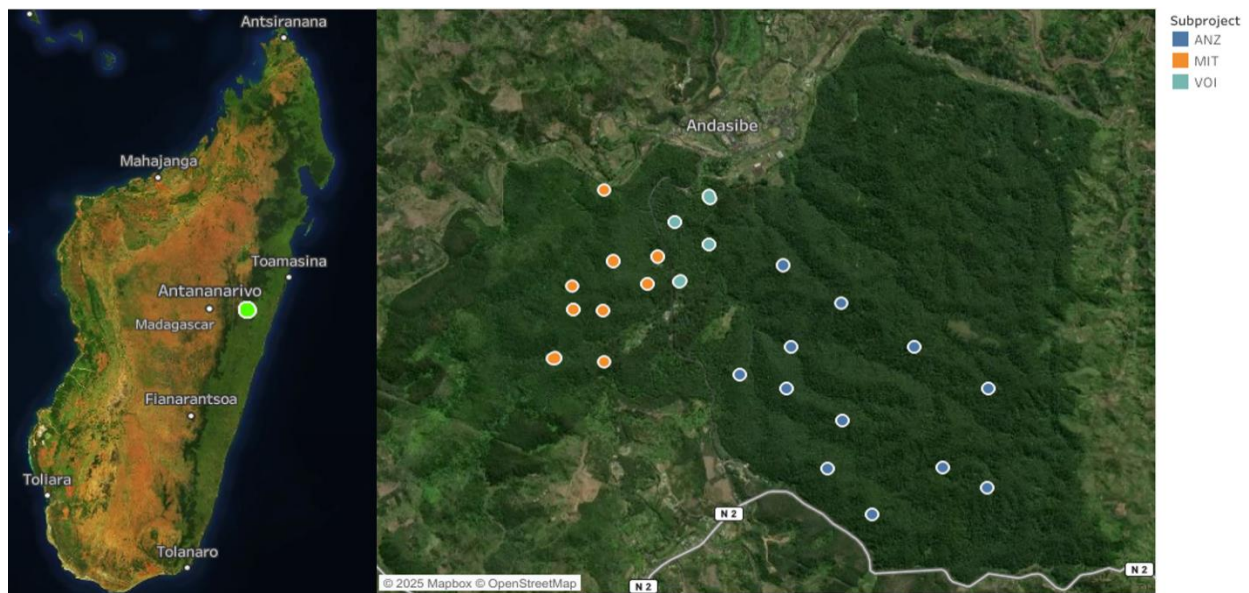


Figure 1: Left- A green dot representing the region of Madagascar where the repeated camera trap surveys took place. Right - Layout of the camera grids in Andasibe, Madagascar. Each orange dot represents one camera station located in the Mitsinjo Reserve. Each green dot represents one camera station located in the V.O.I. Community Reserve. Each blue dot represents one camera station located in Analamazaotra Rainforest. Repeated surveys used these same locations across years.

Camera Trap Surveys

Madagascar first implemented lockdowns on March 20th, 2020, the last of the travel restrictions were lifted in November of 2021. With these dates in mind, the surveys conducted in 2017 and 2019 will be considered pre-COVID, those conducted in 2020 and 2021 will be considered anthropause, and the 2023 survey will be considered anthropulse. For pre-COVID, we used two surveys conducted in 2017 (June and October - December) and one conducted in 2019 (June - July), henceforth survey 1,2,3 respectively. Two surveys were used to represent anthropause (November 2020 - January 2021 and September - October 2021), henceforth survey 4,5 respectively. One 2023 survey was used to represent anthropulse (June - August of 2023),

henceforth survey 6. Due to issues obtaining permits, the final survey did not include cameras inside Analamazaotra Rainforest.

Within these forests, we set up ~25 camera stations per session, with the exception of the final survey which only consisted of 13 camera stations (Table 1). A camera station consists of one unbaited camera trap placed on a tree adjacent to a wildlife or human trail. We placed stations approximately 300 meters apart with cameras placed ~25 cm off the ground and running for 24 hours a day. We checked cameras every 5-7 days to ensure no malfunctions, and to change the memory cards. We used a combination of Browning Strike Force FHDR, Moultrie M- and D55-series, and Reconyx Hyperfire (HC500) to conduct these surveys, which are similar in having a <0.5s trigger time. We identified photo data for the 2017 surveys and the survey conducted in 2019 using a multiple observer method with ID recorded directly into excel by identifying each image with a subject and then recording relevant data such as time, date, species, and human type. We processed the 2021 and 2023 surveys using the Wildlife Insights platform (Ahumada *et al.* 2019). For all surveys, any images taken less than 1 minute apart from each other were grouped together as a sequence and classified as a single photo event. All humans in these data sets were classified as tourist, non-tourist, or researcher. These classifications were made based on appearance and group size. We identified local guides (classified as non - tourist) due to our familiarity through frequent personal interactions. Non-tourists and tourists were identified based on differences in clothing and footwear. Researchers were individuals identified as part of our research team. Classifying these human types was a critical step in quantifying the impacts of COVID tourism. In doing so, we isolated tourism as an anthropogenic source separate from a much broader category where we combine all human types (researcher, tourist, non-tourist). We obtained enough data to model fosa, birds, small mammals, and lemurs. We grouped all birds together and grouped rodents with tenrecs as “small mammals” because we had many detections and limited time for species-level IDs. We grouped all lemur species together in our analyses to maximize the use of available data. However, it should be noted that ~80% of the lemur detections were of one species-the common brown lemur (*Eulemur fulvus*).

Table 1: Sampling effort and detection counts from camera-trap surveys in Andasibe, Madagascar (2017–2023). For each survey period we list the date range, number of active camera stations, successful trap-nights (one functioning camera for one 24hr period.), and the number of detection events for fosa, dogs, birds, small mammals, tourists, and lemurs. Periods are classified as pre-COVID, anthropause (COVID-era), and anthropulse (post-COVID rebound)

Start/End Date		Camera Stations	Successful Trap Nights	Fosa Detections	Dog Detections	Bird Detections	Small Mammal Detections	Tourist Detections	Lemur Detections	COVID Period
6/7/2017	6/25/2017	24	385	7	46	41	56	420	25	Pre-COVID
10/12/2017	12/9/2017	24	1253	27	56	222	148	1183	34	Pre-COVID
6/25/2019	7/27/2019	22	513	11	13	112	71	263	7	Pre-COVID
11/20/2020	1/10/2021	24	1050	12	130	468	620	124	47	Anthropause
9/10/2021	10/28/2021	24	866	67	39	151	54	83	27	Anthropause
6/8/2023	8/2/2023	13	705	46	116	13	1	1571	10	Anthropulse

Covariate Information

To evaluate the anthropogenic, habitat, and landscape variables affecting wildlife activity we used a total of ten covariates: trail width, tourist detection rate, dog detection rate, distance to human settlement, distance to town, distance to forest edge, forest type, canopy cover, elevation, sampling occasion. We measured trails with a tape measure in the field and categorized them as narrow (<0.5 m), medium (0.5-1 m), and wide (>1 m). We calculated tourist and dog detection rate as the number of detections at a particular station divided by the number of successful trap nights at that same station. We calculated distance to nearest human structure as the distance from a camera station to any form of human establishment such as a house, a security watch station, or a storage structure. We calculated distance to town as the distance from a camera station to a large human settlement consisting of 10 or more dwellings grouped together in a cluster. Distance to forest edge was measured as the distance from a camera station to the forest boundary observed on Google Earth (Google Earth Pro 2025). These google satellite images were taken between 1/29/2022 and 7/5/2024. We defined the edge of the forest as the boundary of the forest where closed canopy of at least 5m or more no longer exists. This boundary would generally be a road or agricultural land. We assigned each station a forest type of 1, 2 or 3 categorizing the type of forest at that location. Type 1 is secondary forest, type 2 is degraded, mixed, low canopy forest, and type 3 is open matrix, non-forest area. We defined canopy coverage as the amount of sky covered by the canopy at the camera site. This was measured at each station by multiple observer methods and averaged across three observers. Elevation was measured using a Garmin GPS handheld unit. Sampling occasion indicates which survey period (month/ month-month, year, e.g. June 2017, Sept - October 2017) the capture occurred in. We scaled and centered all numerical covariates for use in the models. We calculated pairwise collinearity values, all pairwise values fell below our threshold for concern of 0.8. We had one high value of .75 between distance to the edge of the forest and distance to nearest human structure. We then used the “car” package in R, to calculate the variance inflation factor for each covariate and found that there were no conflicts between covariates.

Detection Count Generalized Linear Mixed Models

Using the R package LME4 (Bates *et al.* 2015), we constructed Generalized Linear Mixed Models to compare animal activity across three time periods while also considering spatial factors. We first selected all relevant covariates using an *a priori* approach and formulated a hypothesis as to why each covariate may be relevant in the model. We then constructed a global model including the response variable and all relevant covariates. After constructing this global model, we used the MumIn package in R (Bartoń 2025) to perform a dredge, which creates a list of all possible response and covariate combinations. This list was ordered by AIC value. We looked at each model within a delta AIC of 2 of the top models and selected the model with the lowest number of covariates.

Table 2: Generalized Linear Mixed Model structures and significant covariates for four detection count models using data collected from Andasibe, Madagascar (2017-2023). Fcount (fosa), Bcount (birds), Lcount (lemurs), and Mcount (small mammals). Covariates considered were Edge (distance to forest edge (m)), Settlement (distance to nearest human settlement (m)), Elevation (m), Dog (dog detection rate), Tourist (tourist detection rate), Trail size (small/medium/wide), Forest type (secondary/degraded/open matrix), Canopy (percent sky covered at the camera station), Duration (successful trap nights), and Site (camera station). The table lists only covariates retained as significant in the top model. A (+) sign indicates a positive relationship, a (-) sign indicates a negative relationship, and no sign is present when the covariate is a categorical variable with variable effects.

Group	Model Set up	Significant Covariates
Fosa	glmer(Fcount ~ edge + occasion + dog + offset(log(duration)) + (1 site))	-Edge, + Dog, Occasion
Bird	glmer(Bcount ~ canopy + edge + occasion + forest + settlement + trail + offset(log(duration)) + (1 site))	+Canopy, -Edge, Forest type, Trail size, Occasions.
Lemur	glmer(Lcount ~ occasion + dog + tourist + canopy + offset(log(duration)) + (1 site))	-Dog, +Canopy, +Tourist, Occasion
Small Mammal	glmer(Mcount ~ edge + occasion + dog + tourist + settlement + trail + canopy + elevation + offset(log(duration)) + (1 site))	-Edge, +Dog, +Tourist, +Settlement, Trail, +Canopy, -Elevation, Occasion

Multi-season Occupancy Models

Using Unmarked (Fiske and Chandler 2011), we fit a multi-season occupancy model to compare animal activity across three time periods while also considering spatial factors. To achieve this, all data was compiled into a “stacked” format and sampling occasion was used as a covariate. We used the MumIn (Bartoń 2025) package in R to perform a dredge to determine the best combination of covariates for detection with the fewest covariates and within a delta of 2 from the lowest AIC value. After selecting the optimal combination of detection covariates, we used a forward selection process to build the occupancy model. The detection covariates remained constant, and covariates were added to the occupancy portion of the model. We constructed individual models with detection covariates plus each psi covariate (e.g., detection ~ covariate 1, detection ~ covariate 2, detection ~ covariate 3). For each model, we compared AIC values to guide selection. Models with higher AIC were excluded, and those with lower AIC were carried forward. At each step, the model with the lowest AIC became the new base (e.g., detection ~ covariate 1 + covariate 2, detection ~ covariate 1 + covariate 3). This process continued until adding predictors no longer reduced AIC, at which point the model was selected as the final occupancy model for that group. Since we used a stacked occupancy approach, each model included a random site level effect in the occupancy portion to account for pseudo-replication across multiple sampling occasions at each station.

Table 3: Multi-season Occupancy Model structure. *P* indicates the detection portion of the model; *Psi* indicates the occupancy portion of the model. Covariates considered were *Edge* (distance to forest edge (m)), *Settlement* (distance to nearest human settlement (m)), *Dog* (dog detection rate), *Tourist* (tourist detection rate), *Trail size* (small/medium/wide), *Canopy* (percent sky covered at the camera station), *Effort* (successful trap nights), and *Station* (camera station). *Station1* and *occasion1* represent the station and occasion covariates but in a grid layout as is required by the occupancy portion of the model. The table lists only covariates retained as significant. A (+) sign indicates a positive relationship, a (-) sign indicates a negative relationship.

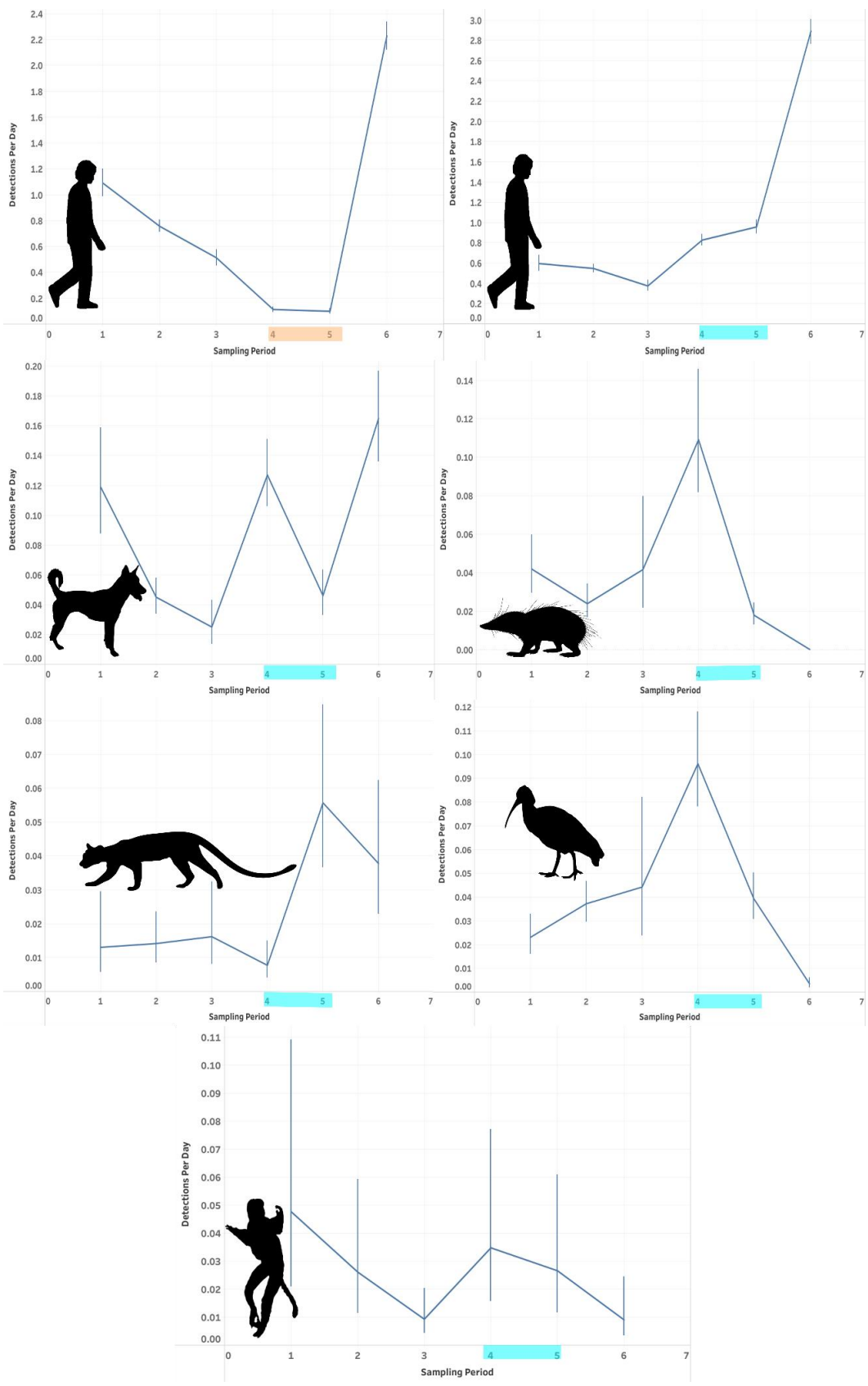
Group	Model Set up	Significant Psi Covariates
Fosa	P (dog + edge + effort + Occasion + settlement), Psi (1 station1) + dog + tourist + edge + occasion1)	- Dog, + Tourist

Results

We had a total of 4716 successful trap nights with the minimum being 385 in survey 1 (2017) and the highest being 1253 in survey 2 (2017 #2). The lowest number of successful trap nights for a single station was 11 and the highest was 59. Survey 5 (2021) had the lowest total subject captures at 421 captures. Survey 6 (2023) had the highest total subject captures at 1757 captures. There were a total of 2742 pre-COVID captures (2017-19), 1822 anthropause captures, and 1757 anthropulse captures. Across all surveys, we had a total of 170 fosa captures, 400 dog captures, 1007 bird captures, 950 small mammal captures, and 3401 tourist captures. Fosa showed peak activity times between 0:00 and 5:00, while dogs showed peak activity times between 4:00 and 10:00. (Supplemental figure 1).

Human tourists showed steady decline with a strong increase occurring during the anthropulse period while non-tourist humans showed steady activity with increases during anthropause and -pulse periods (Figure 2). Dogs showed highly variable activity across all three periods. Fosa, birds, and small mammals all showed peak capture rate during anthropause. Lemurs showed very little change across all periods (Figure 2). Significant covariates of note for the fosa were distance to edge of the forest (-0.42 ± 0.20 SE, $p = 0.03$), and dog detection rate (0.16 ± 0.08 SE, $p = 0.04$). Lemur detection rate had a significant, positive relationship with the detection rate of tourists (0.31 ± 0.11 SE, $p = 0.00$), and a negative relationship with dog detection rate (-0.26 ± 0.11 SE, $p = 0.02$). Sampling occasion was a significant covariate for every model and every group (table 2).

Figure 2. Camera-trap detection rates (detections/day; mean \pm error bars) across six sampling periods in Andasibe, Madagascar. Highlights mark “anthropause” periods (4: November 2020–January 2021; 5: September–October 2021). Periods 1–3 are pre-COVID (1: June 2017; 2: October - December 2017; 3: June–July 2019), and period 6 represents the post-COVID “anthropulse” (June–August 2023). Panels: top left = tourists; top right = non-tourists; middle left = dogs; middle right = small mammals; bottom left = fosa; bottom right = birds; center bottom = lemu



For the multi-season occupancy model, there was no change in fosa occupancy. Overall, the model structure we used for the fosa was not a good fit for the birds, lemurs and small mammal groupings which led to results with extremely high standard errors. We structured our models in a way to return a survey-wide occupancy estimate per sampling occasion. This method failed to converge for the previously mentioned groups, but when survey occasion was left out then the models were able to converge. We reported the Sampling occasion was not a significant covariate in any of the models and reported model estimates were extremely high.

Table 4: Naïve and model-based fosa occupancy and survey period for camera-trap surveys in Andasibe, Madagascar (2017–2023). Survey 1 (June 2017), survey 2 October – December 2021, survey 3 (June – July 2019), survey 4 (November 2020 – January 2021), survey 5 (September – October 2021) survey 6 (June – August 2023)

Survey	Naïve Occupancy	Model Occupancy	SE
1	0.21	0.96	0.69
2	0.54	0.96	0.73
3	0.36	0.95	0.93
4	0.38	0.95	1.04
5	0.71	0.97	2.31
6	0.62	0.95	0.75

Discussion

Human activity is a major force shaping wildlife with more than half of vertebrate species experiencing intense human pressure in over half of their home range (O’Bryan *et al.* 2020; Munstermann *et al.* 2022). The impacts of this widespread human activity are complex and context dependent, such that results from one country may not predict the effect in another. The impacts of COVID led to a massive reduction in global tourism. In Madagascar specifically, tourism declined by approximately 98% due to international safety measures, temporarily reducing pressure on its fragile ecosystems. Our camera trap surveys documented strong decreases in human activity during the anthropause and corresponding increases in fosa, bird, small mammal, and dog activity across the same period. Subsequently, during anthropulse, human activity rapidly increased and we saw decreases in those same groups. These shifts

highlight how anthropogenic pressures shape wildlife behavior showing that humans using the forest, even in ecotourism, decreases local wildlife activity. Our camera-trap results from Andasibe extend anthropause research to the global south and a biodiversity hotspot.

Changing animal activity in the anthropause and anthropulse:

Our camera-trap surveys revealed clear temporal patterns in wildlife activity that closely tracked fluctuations in human presence across the anthropause–anthropulse sequence. During the period of reduced tourism associated with the COVID-19 lockdowns (2019–2021), detections of small mammals, birds, and fosa increased by two- to four-fold relative to pre-COVID levels. These gains in activity coincided with a sharp reduction in tourist and local human detections, indicating that wildlife responded rapidly to the decrease in anthropogenic disturbance.

As human activity rebounded during the anthropulse (2021–2023), the reverse pattern emerged. Detections of birds and small mammals declined to pre-pandemic levels, and fosa activity also decreased, though it remained slightly above pre-COVID values. These synchronized shifts among multiple taxa suggest a broad community-level response to changing human activity, with wildlife generally more active when human presence was low and less active as human pressure returned.

Although occupancy models did not detect significant differences in space use across time periods, naïve occupancy patterns increased during the anthropause, mirroring the rise in detection rates. Together, these findings highlight the behavioral flexibility of Andasibe’s wildlife and demonstrate that even short-term reductions in human activity can substantially alter observed patterns of animal activity and detectability.

Mechanisms shaping wildlife responses:

The covariates identified in our models help explain the mechanisms underlying the observed shifts in wildlife activity. Among these, dogs and tourists emerged as key anthropogenic drivers influencing multiple taxa, while habitat features such as forest edge and canopy cover also played important roles.

Dog detection rate was a significant covariate in three of the four detection count models, showing positive associations with fosa and small mammal detections but a negative relationship with lemur detections. The remains of rodents and tenrecs, which were grouped as small mammals in this study, have been documented in the scats of free-ranging dogs (Valenta *et al.* 2025), suggesting that this positive relationship may reflect dogs tracking these species as prey. Lemurs are also frequently harassed or preyed upon by free-ranging dogs (Farris *et al.* 2019; Valenta *et al.* 2025). Resident diurnal lemurs of the area share overlapping activity times with dogs (Overdorff 1996; Powzyk and Mowry 2003, 2006), though their arboreality likely reduces direct encounters.

Fosa detections also increased with dog activity, yet the occupancy model revealed a negative relationship between the two species—consistent with earlier studies reporting spatial overlap but competitive exclusion between them (Farris *et al.* 2017). To further explore this relationship we conducted a post-hoc analysis and found that fosa activity peaked between midnight and 05:00, dogs were most active between 04:00 and 10:00. Such patterns support the hypothesis that fosa avoid dogs temporally, adjusting their activity to minimize direct encounters (Farris *et al.* 2015; Merson *et al.* 2018)

Tourist detection rate was a significant positive covariate in the models for lemurs, small mammals, and fosa occupancy. This result contrasts with the broader temporal trend of wildlife activity peaking during periods of reduced tourism, suggesting that while animals are more active overall in the absence of people, they tend to be associated with people, probably because the tourists are looking for the animals. Lemurs, particularly the common brown lemur (*Eulemur fulvus*), showed the strongest positive relationship with tourist activity. This population in Andasibe protected areas is known to be habituated to humans. Furthermore, local guides with tourists actively track lemurs to enhance viewing opportunities, meaning that camera traps located along trails are more likely to record both tourists and lemurs in the same locations. Because many tourist trails lead directly to sleeping or feeding trees, these areas represent key resource sites used by lemurs regardless of human presence. Consequently, reductions in tourism may not strongly affect their space use, explaining the relatively stable detection rates across periods.

The close tracking of lemurs by guides and tourists may also influence predator behavior. Fosa are lemur hunters—one study found lemur remains in over 50% ($n = 376$) of fosa scat samples (Hawkins and Racey 2008)—and so fosa, along with tourists, are likely attracted to sites with lemurs. Similarly, small mammals showed higher detections in association with tourist activity, potentially due to food subsidies. Tourists frequently bring food on excursions, and unintentional food drops or litter may serve as attractants, particularly for invasive *Rattus* spp., which are highly opportunistic.

Edge effects were also evident across taxa. Three of the four detection models (fosa, birds, and small mammals) showed a negative relationship between distance to the forest edge and detection rate, indicating that these species were more frequently detected near forest boundaries. This relationship may reflect the combined influence of resource concentration, increased prey availability, or greater ease of movement along trail systems that often parallel forest margins. Additionally, this may serve as further indication of the high amount of fragmentation within the area and within Madagascar as a whole with 46% of Madagascar's remaining forest lying within 100m of the forest edge (Vieilledent *et al.* 2018).

Stability in space use despite behavioral shifts:

Although clear shifts in activity were evident across years, occupancy patterns remained relatively stable throughout the study period. The multi-season occupancy model for fosa indicated little change in estimated occupancy between pre-COVID, anthropause, and anthropulse periods (Table 4). This suggests that while fosa modified their behavior in response to changes in human activity, they did not substantially alter their spatial distribution. In other words, the same individuals or populations likely continued to occupy the same regions but decreased their amount of activity to avoid people.

The distinction between occupancy and detection, as measured in our GLMM, is particularly relevant in this context. Occupancy reflects the probability that a site is used, whereas detection reflects how often a species passes by when it is present. Our findings—constant occupancy but variable detection—indicate that behavioral flexibility, rather than large-scale spatial redistribution, was the dominant response to changes in human presence. Given time, the

increased activity might lead to increased population sizes for animals in the absence of people, but in this case, people returned to the forest, and animals, once again, reduced activity levels and/or space use.

Uncertainty in the occupancy model was relatively high, as reflected by wide standard errors, and models for birds, lemurs, and small mammals failed to converge. These difficulties likely stem from combining multiple species into broad taxonomic groups, which can mask heterogeneity in both occupancy (ψ) and detection (p) among species. Seasonal differences in activity and uneven sampling effort across years may also have contributed to poor model fit. However naïve occupancy estimates increased during the anthropause mirroring the trends observed in detection data, reinforcing the interpretation that wildlife use of existing areas intensified when human activity decreased.

Together, these results suggest that short-term reductions in human activity led to behavioral rather than spatial responses among Andasibe's wildlife. Such flexibility may allow species to persist in human-dominated landscapes, at least temporarily, though long-term consequences for population viability remain uncertain. These finding also gives some insight on how fosa, and other wildlife, likely adapt their behavior to coexist with humans and dogs on human-dominated landscapes.

Implications for conservation and management:

Our findings highlight the complex relationship between human activity, tourism, and wildlife in Madagascar's protected areas. The survey period covariate was significant across all detection models, reaffirming that tourism and associated human presence exert measurable influences on wildlife behavior. This aligns with global evidence showing that human disturbance—whether through recreation, ecotourism, or settlement—can suppress wildlife activity even in otherwise intact habitats (Higginbottom and Scott 2016; Gaynor *et al.* 2018).

However, because there was no control for this study, we cannot rule out the possibility that unmeasured environmental or anthropogenic factors contributed to this result.

Balancing tourism and conservation is especially critical in regions such as Andasibe, where local economies and conservation initiatives are intertwined. Tourism revenues support livelihoods and fund protection for many of the same species most sensitive to human activity. Consequently, strategies to mitigate disturbance must focus on management rather than restriction—reducing ecological impacts without undermining the economic and social benefits of ecotourism.

Several practical recommendations emerge from our results. First, tourism activities could be regulated spatially and temporally, concentrating visitor movement along designated trails and restricting use during periods of peak wildlife activity (e.g., early morning or nighttime hours). Second, managing free-ranging dogs is imperative. Our models show that dogs interact with both native predators and prey, amplifying disturbance through direct predation, competition, and potentially disease transmission (Young *et al.* 2011; Hughes and Macdonald 2013). Measures such as vaccination campaigns and buffer zones around protected areas could reduce these risks. Third, management should consider synergistic effects—for example, human activity near forest edges may compound with infrastructure impacts, or dogs may be particularly problematic near disturbed boundaries. Integrating these interactions into conservation planning will improve outcomes for multiple species simultaneously.

Ultimately, the anthropause–anthropulse sequence illustrates both the vulnerability and resilience of wildlife living alongside people. Short-term reductions in human presence yielded immediate increases in animal activity, demonstrating that behavioral recovery is possible when disturbance subsides. Long-term coexistence, however, will depend on maintaining these conditions through proactive, adaptive management that allows tourism and biodiversity to persist together.

Literature Cited

- Ahumada J, Fegraus E, Birch T, Flores N, Kays R, O'Brien T, Palmer J, Schuttler S, Zhao J, Jetz W *et al.* 2019. Wildlife Insights: A Platform to Maximize the Potential of Camera Trap and Other Passive Sensor Wildlife Data for the Planet. *Environmental Conservation* 47:1–6. <https://doi.org/10.1017/S0376892919000298>
- Bartoń K. 2025. MuMIn: Multi-Model Inference.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software* 67(1). <https://doi.org/10.18637/jss.v067.i01>
- Burton AC, Beirne C, Gaynor KM, Sun C, Granados A, Allen ML, Alston JM, Alvarenga GC, Calderón FSÁ, Amir Z *et al.* 2024. Mammal responses to global changes in human activity vary by trophic group and landscape. *Nature Ecology & Evolution* 8(5):924–935. <https://doi.org/10.1038/s41559-024-02363-2>
- Derryberry EP, Phillips JN, Derryberry GE, Blum MJ, Luther D. 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science* 370(6516):575–579. <https://doi.org/10.1126/science.abd5777>
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014. Defaunation in the Anthropocene. *Science* 345(6195):401–406. <https://doi.org/10.1126/science.1251817>
- Doherty TS, Dickman CR, Glen AS, Newsome TM, Nimmo DG, Ritchie EG, Vanak AT, Wirsing AJ. 2017. The global impacts of domestic dogs on threatened vertebrates. *Biological Conservation* 210:56–59. <https://doi.org/10.1016/j.biocon.2017.04.007>
- Farris ZJ, Chan S, Rafaliarison R, Valenta K. 2019. Occupancy Modeling Reveals Interspecific Variation in Habitat Use and Negative Effects of Dogs on Lemur Populations. *International Journal of Primatology* 40(6):706–720. <https://doi.org/10.1007/s10764-019-00120-y>

Farris ZJ, Gerber BD, Karpanty S, Murphy A, Andrianjakarivelo V, Ratelolahy F, Kelly MJ. 2015. When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores. *Journal of Zoology* 296(1):45–57. <https://doi.org/10.1111/jzo.12216>

Farris ZJ, Gerber BD, Valenta K, Rafaliarison R, Razafimahaimodison JC, Larney E, Rajaonarivelo T, Randriana Z, Wright PC, Chapman CA. 2017. Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation* 210:116–124. <https://doi.org/10.1016/j.biocon.2017.04.010>

Fiske I, Chandler R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software* 43:1–23. <https://doi.org/10.18637/jss.v043.i10>

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360(6394):1232–1235. <https://doi.org/10.1126/science.aar7121>

Goodman SM. 2022. *The New Natural History of Madagascar*. Princeton: Princeton University Press.

Goodman SM, Benstead JP. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39(1):73–77. <https://doi.org/10.1017/S0030605305000128>

Google Earth Pro. 2025.

Hawkins CE, Racey PA. 2008. Food Habits of an Endangered Carnivore, *Cryptoprocta Ferox*, in the Dry Deciduous Forests of Western Madagascar. *Journal of Mammalogy* 89(1):64–74. <https://doi.org/10.1644/06-MAMM-A-366.1>

Higginbottom K, Scott N. 2016. *Wildlife Tourism: a strategic destination analysis*.

Hotle S, Mumbower S. 2021. The impact of COVID-19 on domestic U.S. air travel operations and commercial airport service. *Transportation Research Interdisciplinary Perspectives* 9:100277. <https://doi.org/10.1016/j.trip.2020.100277>

- Hughes J, Macdonald DW. 2013. A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation* 157:341–351. <https://doi.org/10.1016/j.biocon.2012.07.005>
- Longcore T, Rich C. 2004. Ecological light pollution. *Frontiers in Ecology and the Environment* 2(4):191–198. [https://doi.org/10.1890/1540-9295\(2004\)002%255B0191:ELP%255D2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002%255B0191:ELP%255D2.0.CO;2)
- Manenti R, Mori E, Di Canio V, Mercurio S, Picone M, Caffi M, Brambilla M, Ficetola GF, Rubolini D. 2020. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. *Biological Conservation* 249:108728. <https://doi.org/10.1016/j.biocon.2020.108728>
- Merson S, Dollar L, Tan C, Macdonald D. 2018. Activity patterns of sympatric living exotic and endemic carnivores (the fosa) in Western Madagascar’s deciduous forests. *Journal of Zoology* 307. <https://doi.org/10.1111/jzo.12630>
- Munstermann MJ, Heim NA, McCauley DJ, Payne JL, Upham NS, Wang SC, Knope ML. 2022. A global ecological signal of extinction risk in terrestrial vertebrates. *Conservation Biology* 36(3):e13852. <https://doi.org/10.1111/cobi.13852>
- Nickel BA, Suraci JP, Allen ML, Wilmers CC. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation* 241:108383. <https://doi.org/10.1016/j.biocon.2019.108383>
- O’Bryan CJ, Allan JR, Holden M, Sanderson C, Venter O, Di Marco M, McDonald-Madden E, Watson JEM. 2020. Intense human pressure is widespread across terrestrial vertebrate ranges. *Global Ecology and Conservation* 21:e00882. <https://doi.org/10.1016/j.gecco.2019.e00882>
- Overdorff DJ. 1996. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology* 40(4):327–342. [https://doi.org/10.1002/\(SICI\)1098-2345\(1996\)40:4%253C327::AID-AJP3%253E3.0.CO;2-%2523](https://doi.org/10.1002/(SICI)1098-2345(1996)40:4%253C327::AID-AJP3%253E3.0.CO;2-%2523)

Powzyk JA, Mowry CB. 2003. Dietary and Feeding Differences Between Sympatric Propithecus diadema diadema and Indri indri. *International Journal of Primatology* 24(6):1143–1162.

<https://doi.org/10.1023/B:IJOP.0000005984.36518.94>

Powzyk JA, Mowry CB. 2006. The Feeding Ecology and Related Adaptations of Indri indri. In: Gould L, Sauther ML, editors. *Lemurs. Developments in Primatology: Progress and Prospect*. Boston, MA: Springer US; p. 353–368. https://doi.org/10.1007/978-0-387-34586-4_16

Rutz C. 2022. Studying pauses and pulses in human mobility and their environmental impacts. *Nature Reviews Earth & Environment* 3(3):157–159. <https://doi.org/10.1038/s43017-022-00276-x>

Rutz C, Loretto M-C, Bates AE, Davidson SC, Duarte CM, Jetz W, Johnson M, Kato A, Kays R, Mueller T *et al.* 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology & Evolution* 4(9):1156–1159.

<https://doi.org/10.1038/s41559-020-1237-z>

Schwitzer C, Mittermeier R, Johnson S, Donati G, Irwin M, Peacock H, Ratsimbazafy J, Razafindramanana J, Louis E, Chikhi L *et al.* 2014. Averting Lemur Extinctions Amid Madagascar's Political Crisis. *Science* 343:842–843. <https://doi.org/10.1126/science.1245783>

Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, Brown E, Warner KA, Nelson MD, White C, Briggs J *et al.* 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews* 91(4):982–1005.

<https://doi.org/10.1111/brv.12207>

Shilling F, Nguyen T, Saleh M, Kyaw MK, Tapia K, Trujillo G, Bejarano M, Waetjen D, Peterson J, Kalisz G *et al.* 2021. A Reprieve from US wildlife mortality on roads during the COVID-19 pandemic. *Biological Conservation* 256:109013.

<https://doi.org/10.1016/j.biocon.2021.109013>

Tucker MA, Schipper AM, Adams TSF, Attias N, Avgar T, Babic NL, Barker KJ, Bastille-Rousseau G, Behr DM, Belant JL *et al.* 2023. Behavioral responses of terrestrial mammals to COVID-19 lockdowns. *Science* 380(6649):1059–1064. <https://doi.org/10.1126/science.abo6499>

UNTWO 2021.

UNWTO World Tourism Barometer and Statistical Annex, May 2021. 2021. World Tourism Barometer (English version) 19(3):1–42. <https://doi.org/10.18111/wtobarometereng.2021.19.1.3>

Valenta K, Rajaonarivelo T, Ferreira A, Raharinirina A, Rafaliarison RR, Farris A, Watson JM, deFrance S, Mayo D, Filla C *et al.* 2025. The impact of free-roaming dogs on lemurs in Madagascar: a decade of research and intervention. *Folia Primatologica* 1–18. <https://doi.org/10.1163/14219980-bja10047>

Vieilledent G, Grinand C, Rakotomalala FA, Ranaivosoa R, Rakotoarijaona J-R, Allnutt TF, Achard F. 2018. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation* 222:189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>

Wampole EM, Farris ZJ, Gerber BD. 2021. A synthesis of life-history traits, functional traits, and consequences of anthropogenic pressures on Madagascar’s threatened carnivorans, Eupleridae. *Mammal Review* 51(3):402–419. <https://doi.org/10.1111/mam.12234>

World Tourism Organization (UNWTO) editor. 2021. The Economic Contribution of Tourism and the Impact of COVID-19. World Tourism Organization (UNWTO). <https://doi.org/10.18111/9789284423200>

World Tourism Organization (UNWTO). 2024. Global tourism set for full recovery by end of the year with spending growing faster than arrivals. [accessed 3 June 2025] <http://www.unwto.org/news/global-tourism-set-for-full-recovery-by-end-of-the-year-with-spending-growing-faster-than-arrivals>

Young JK, Olson KA, Reading RP, Amgalanbaatar S, Berger J. 2011. Is Wildlife Going to the Dogs? Impacts of Feral and Free-roaming Dogs on Wildlife Populations. *BioScience* 61(2):125–132. <https://doi.org/10.1525/bio.2011.61.2.7>

CHAPTER 2

Island-Wide Patterns of Fosa Abundance in Madagascar's Protected Areas

ABSTRACT:

The fosa is Madagascar's largest and most widespread native predator. Despite its ecological importance, it remains one of the world's most understudied carnivores, and the drivers of its abundance are still poorly understood. Our goal was to identify these drivers at an island-wide scale. We combined 16 years of camera-trap data from 12 protected areas spanning a gradient of habitats—from highly degraded forest fragments to large, contiguous forests—and modeled fosa detections using generalized linear mixed-effects models. Our findings highlight the importance of forest cover as a mitigating factor against increasing anthropogenic pressures. Human population density emerged as the strongest negative predictor of fosa detections, and dog–forest interactions revealed sharp declines in fosa detections in forested areas with high dog activity. In contrast, dog presence in degraded habitats coincided with increased fosa detections, reflecting context-dependent relationships observed in previous single-site studies. Overall, the combined presence of dogs and humans created the most substantial pressure on fosa across the landscape. This study represents the first broadscale analysis of fosa ecology and provides a foundation for targeted conservation efforts. Conservation programs should prioritize expanding protected areas and restoring forest habitats, followed by managing free-ranging and feral dogs, which pose serious threats not only to fosa but to other native species. As an umbrella species, conservation actions directed at the fosa will yield broad benefits for Madagascar's forest ecosystems.

Introduction

The island of Madagascar is one of 36 global biodiversity hotspots. It has an estimated 98-100% endemism rate (Goodman 2022), but this unique biodiversity is currently facing mounting, multi-faceted, pressures that threaten their long term viability. These pressures include introduction of exotic species, expansion and growth of the human population and, perhaps currently the most critical, rapid deforestation. Between 1953 and 2014 Madagascar lost approximately 44% of its remaining forest cover, leaving the residual forest highly fragmented with 46% of the remaining forests now occurring less than 100m from the forest edge (Vieilledent *et al.* 2018). This

extensive deforestation and fragmentation has created a dire situation for forest-dependent species such as the fosa (*Cryptoprocta ferox*).

The fosa is the largest native predator in Madagascar and, following the extinction of the giant fosa (*Cryptoprocta spelea*) in the last 2000 years, the only extant member of its genus (Goodman 2022). They can be found throughout the island in deciduous dry forest, rainforest, and spiny forest habitats, making them the most widely distributed of the Malagasy carnivores (Goodman 2022). Originally listed as Data Deficient on the IUCN Red List, their conservation status was changed to Vulnerable in 1996, later ranked as Endangered due to low population estimates of as few as 2500 individuals (Hawkins and Racey 2005), and then reclassified again as Vulnerable in 2008 (Hawkins and Racey 2008), where it remains today with an estimated 2,635–8,626 mature individuals (Gerber, Karpanty and Randrianantenaina 2012a). Density estimates are higher in deciduous forests (0.26 individuals/km²; (Hawkins and Racey 2005) compared to eastern rainforests (0.15–0.20 individuals/km²; (Gerber *et al.* 2010; Murphy *et al.* 2018). Amidst rapid forest loss, conservationists have focused research efforts on this species, yielding insights into their ecology. *Cryptoprocta ferox* has a broad diet including birds, lizards, snakes, small mammals, and lemurs (Dollar, Ganzhorn and Goodman 2007; Hawkins and Racey 2008). It also exhibits polyandrous mating practices (Hawkins and Racey 2009) and maintains large home ranges (Wyza *et al.* 2020). Although research on the fosa has increased over the years, the species remains among the most understudied carnivores (Brooke *et al.* 2014), and more data are needed to enact effective conservation strategies. Major threats include habitat loss from agricultural expansion and timber extraction, hunting, competition with non-native species, and disease transmission from introduced animals (IUCN 2015). Fosa densities are higher in contiguous forests and the species is absent from fragmented forests located more than 15 km from primary forest (Gerber, Karpanty and Randrianantenaina 2012a), further highlighting their forest dependency. However, some studies indicate no negative influence of habitat degradation on fosa occupancy, suggesting short-term resilience to moderate disturbance (Gerber, Karpanty and Randrianantenaina 2012a); (Merson *et al.* 2020). Furthermore, surveys conducted in Makira National Park—Madagascar’s largest protected area—found that fosa showed no preference between degraded and non-degraded forest (Farris *et al.* 2015b). Additional work has shown that fosa strongly prefer forested habitats and avoid human-modified landscapes such as agricultural

lands and villages, yet they regularly use forest corridors and patches to traverse degraded areas (Wyza *et al.* 2020). Collectively, these findings suggest that while fosa exhibit some behavioral and ecological flexibility, their long-term persistence likely depends on maintaining large, connected forest tracts. However, these same forests are increasingly shared with exotic predators, most notably domestic dogs, creating additional pressures on native carnivores.

Studies suggest that domestic dogs (*Canis domesticus*) are a major threat to native carnivores in Madagascar through harassment, predation, direct competition, and their role as hosts and vectors of parasites and diseases (Farris *et al.* 2017; Rasambainarivo *et al.* 2018; Valenta *et al.* 2025). However, the relationship between dogs and fosa remains poorly understood. For example, (Farris *et al.* 2016) found no significant effect of dogs on fosa occupancy, whereas a subsequent study reported spatial overlap between fosa and dogs at Ranomafana National Park (Farris *et al.* 2017). Dogs exhibit higher occupancy rates than fosa in degraded landscapes, indicating that they have potentially become the dominant carnivore in these increasingly prevalent habitats (Farris *et al.* 2017). While generally cathemeral (Gerber, Karpanty and Randrianantenaina 2012b), fosa display behavioral avoidance of dogs and humans with evidence that this avoidance occurs across all seasonal periods (Farris *et al.* 2015a; Merson *et al.* 2018). Together, these findings indicate that the impacts of dogs on fosa are complex and may be context dependent, warranting further investigation. Overall, existing studies suggest that dogs can alter fosa activity patterns but have mixed or neutral effects on occupancy, and that while fosa appear capable of tolerating moderate habitat degradation in the short term, continued disturbance and competition with exotic carnivores may undermine their long-term population viability.

While the fosa has shown some resilience to intensifying anthropogenic pressures, previous studies suggest that the current extent of protected forest may not be sufficient to ensure the species' long-term survival, given its low population density and continued forest loss across Madagascar (Hawkins and Racey 2005). This challenge has been compounded by the spread of exotic carnivores and increasing human disturbance. To date, most ecological studies of the fosa have been single-site investigations within protected areas, leaving broad-scale patterns in abundance and responses to environmental gradients largely unexplored. However, sustained

camera-trapping efforts across Madagascar over the last two decades now provide an unprecedented opportunity to investigate these dynamics at the island scale (Wampole *et al.* 2022).

In this study, we address this knowledge gap by modeling the island-wide relative abundance of fosa using camera-trap data collected between 2007 and 2023, encompassing 43 surveys and over 1,300 camera-trap deployments across 12 protected areas. We test how forest cover, human activity, and dog presence influence fosa abundance and temporal activity, including key interaction effects that evaluate whether forested habitats buffer the impacts of human and dog disturbance. By identifying the ecological and anthropogenic factors shaping fosa distribution across diverse habitats, this work provides the first quantitative, landscape-scale assessment of fosa ecology and offers critical insight into the conservation of Madagascar's largest carnivore within its rapidly changing environment.

Methods

We used recently compiled camera trap data from 12 protected areas across Madagascar to model the relative abundance of fosa related to forest cover, human disturbances, and exotic carnivore presence (domestic dogs). The protected areas with camera data include: Andasibe–Mantadia National Park (154.8 km²), Ankarafantsika National Park (1,365 km²), Andranomena Special Reserve (64.2 km²), Anjanaharibe-Sud Special Reserve (29.7 km²; source), Betampona Strict Nature Reserve (22.2 km²), Ialatsara Private Nature Reserve (10 km²), Loky–Manambato Protected Landscape (2,500 km²), Makira Natural Park (3,725 km²), Mantadia National Park (100 km²), Ranomafana National Park (435.5 km²), Tsitongambarika–Ampasy Natural Resource Reserve (600 km²), and Masoala National Park (2,300 km²). Figure 1.

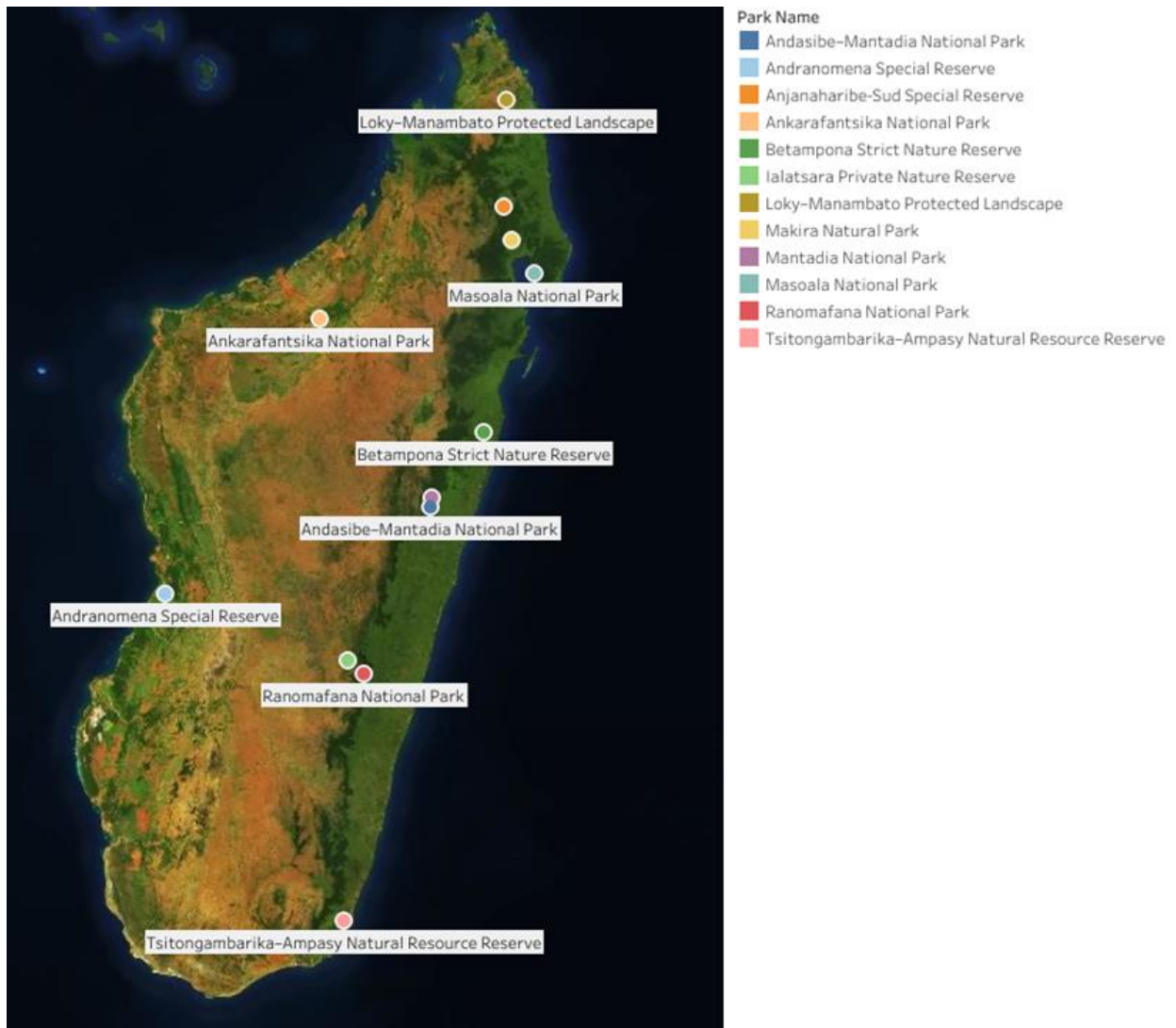


Figure 1: Locations of the 12 protected areas in Madagascar where camera-trap surveys were conducted from 2007–2023. Points a single camera location within each protected area. Basemap imagery from OpenStreetMap 2025.

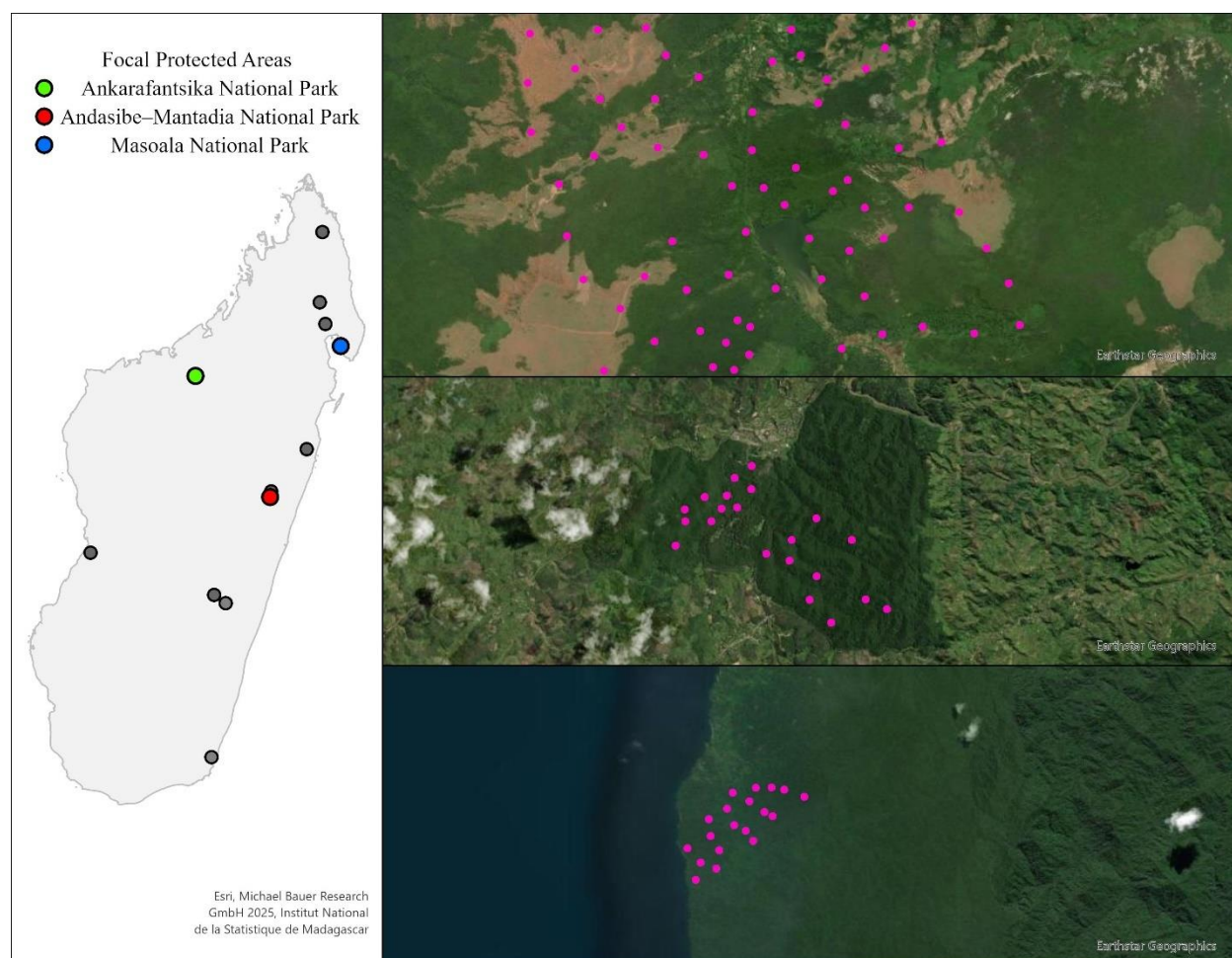


Figure 2: Spatial context and camera-trap sampling design across three protected areas in Madagascar representing contrasting levels of habitat degradation. Pink points indicate individual camera-trap stations. Colored points on the inset map show the locations of the focal protected areas: Ankarafantsika National Park (green), Andasibe–Mantadia National Park (red), and Masoala National Park (blue). Satellite imagery panels illustrate the surrounding landscape context and camera-trap arrays within each park, highlighting differences in forest cover, fragmentation, and anthropogenic modification across sites: Ankarafantsika (top; more fragmented and degraded), Andasibe–Mantadia (middle; intermediate degradation), and Masoala (bottom; largely intact forest). All satellite images are shown at the same spatial scale.

Camera Trap Protocol

We used camera trap data recently compiled from 43 camera trap surveys in 12 different protected areas across Madagascar conducted between the years of 2007 and 2023, totaling 1306 camera station deployments. A camera trap survey consists of an array of camera stations. A camera station consists of one or more camera traps placed 20–30cm above the ground on a tree adjacent to a wildlife or human trail. For any stations where 2 or more cameras were present, all captures of a given species were collapsed into a single capture event. Stations were spaced

>250m apart to ensure detection independence. Surveys in Ranomafana National Park from 2007 and 2008 utilized bait (raw chicken) at camera stations; all surveys after 2008 did not utilize bait. Some areas were surveyed multiple times. For all surveys, any images taken less than 1 minute apart from each other were grouped together as a sequence and classified as a single independent detection event (Kays and Waldstein Parsons 2014).

Successful trap nights per camera array ranged from 84 being the lowest to 7072 as the max. The number of fosa detections for one survey ranges from 0 to 223. The number of camera stations per survey ranges from 7 to 79, the number of human detections for a single survey ranges from 0 to 8564, and the number of dog detections ranges from 0 to 857 (Wampole *et al.* 2022).

Covariate Information

We selected covariates to evaluate the relative influence of habitat characteristics and human disturbance on fosa distribution and abundance. Data were compiled for seven covariates: Elevation(m), defined as the elevation measured in meters at a specific camera station, and was derived from the “NASA 30m Digital Elevation Model” dataset (Earth Science Data Systems 2025a), Percent forest cover, defined as the percent of total forest cover of a 250 meter pixel where the camera station falls within, was derived from “MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250m SIN Grid V006” (Earth Science Data Systems 2025b). Human disturbance covariates included population density at 1km (Earth Science Data Systems 2025c) and human detection rate, defined as the number of human detections at a camera station divided by the total effort at that station and dog detection rate calculated similarly. Study design covariates included camera array, representing the specific sampling array, and a categorical lure variable, indicating whether a station was “baited” or “unbaited.” Because camera arrays were deployed across multiple years, we matched each covariate to data from the corresponding year of sampling when available, or from the nearest available subsequent year. All continuous covariates were scaled and centered prior to analysis. All covariates were collected at the camera station level.

Generalized Linear Mixed Model

To understand drivers of relative fosa abundance we built a Generalized Linear Mixed Model using the lme4 package (Bates *et al.* 2015) in R (R Core Team 2025). We used deployment level

fosa counts as the response variable, and effort (successful trap nights) were used as an offset to account for variation in sampling effort across deployments. This totaled 1306 camera trap deployments. We included all covariates described above along with four interaction terms designed to test specific hypotheses about how forest cover and human disturbance jointly influence fosa abundance. The dog detection rate \times percent forest cover interaction tested whether greater forest cover reduces the negative influence of dogs. The dog detection rate \times human detection rate interaction evaluated whether these two sources of disturbance have compounding effects on fosa occurrence. The percent forest cover \times human detection rate interaction assessed whether increased forest cover mitigates the effects of human disturbance, and the human detection rate \times population density (1 km) interaction examined whether the influence of human activity varies across gradients of local population density. These terms were included based on previous findings that greater forest cover benefits fosa, dogs have varying effects on them, and human activity has context-dependent effects. Finally, we included an array level random effect to account for non-independence among deployments within the same array. We then performed a dredge using the MUMIn (Bartoń 2025) package. This function tests all combinations of covariates and returns an AIC associated with each combination. We chose the model with the lowest number of covariates with an AIC within delta 2 of the top model. We ran models with all data as well as models with the 2 baited camera surveys excluded. Results were similar so we chose to present the expanded dataset. Our final model included fixed effects for baiting status (lure), elevation, and human population density at 1 km, as well as interaction terms between dog detection rate and forest cover, dog detection rate and human detection rate, and human detection rate and forest cover.

Results

We had a total of 65,424 successful trap nights across 43 surveys between 2007 and 2023 across 12 protected areas. Four of 12 protected areas had multiple surveys and the remaining 7 only had a single survey conducted. Two surveys were conducted in Tsitongambarika-Ampasy Natural Resource Reserve, six surveys were conducted in Andasibe -Mantadia National Park, 14 surveys were conducted in Makira Natural Park, and 15 surveys were conducted in Ranomafana National Park. Successful trap nights per survey ranged from 84 (Loky-Manambato Protected Landscape) to 7072 (Mantadia National Park). Average forest cover for a protected area ranged from 38.4%

(Ankarafantsika National Park) to 80.5% (Masoala National Park). Elevation ranged from 15 meters (Andronomena Special Reserve) up to 1654 meters (Ranomafana National Park). The number of camera stations per survey ranged from 7 (Makira Natural Park) to 79 (Ankarafantsika National Park).

We had a total of 1,577 fosa detections ranging from 0 (Loky-Manambato Protected Landscape) to 223 (Ankarafantsika National Park) for a single survey. Human detections for a single survey ranged from 0 (Anjanaharibe-Sud Special Reserve, Betampona Strict Nature Reserve, Loky-Manambato Protected Landscape) to 8564 (Ankarafantsika National Park). Dog detections ranged from 0 (Loky-Manambato Protected Landscape, Ranomafana National Park, Tsitongambarika-Ampasy Natural Resource Reserve) to 857 (Ankarafantsika National Park). Fosa were primarily nocturnal, although had some early morning activity (Figure 2).

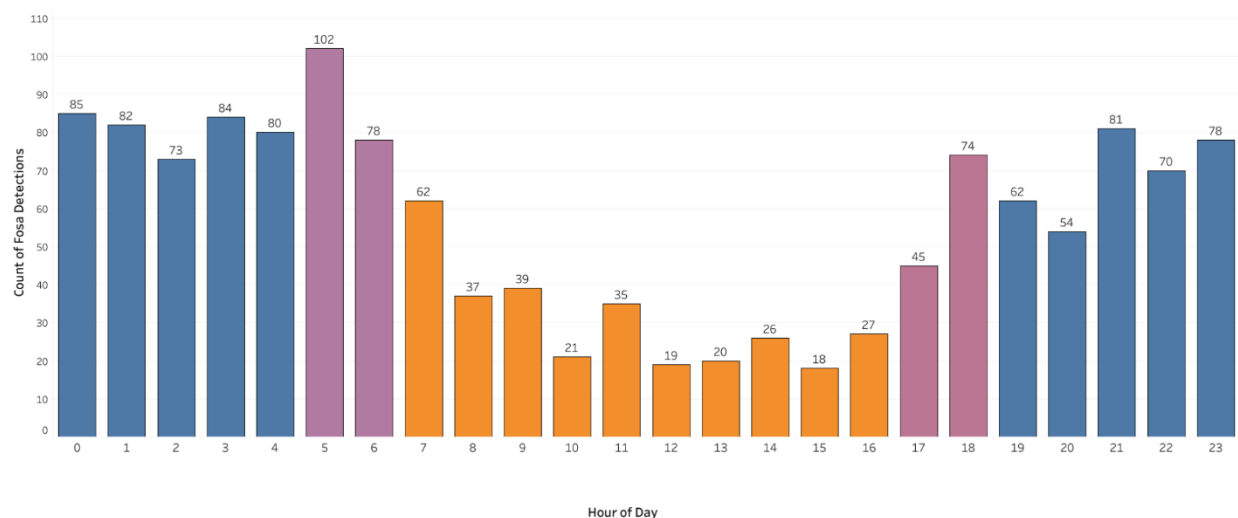


Figure 3: Hourly distribution of fosa detections across a 24-hour period. Orange bars represent diurnal hours, magenta bars represent sunrise and sunset (crepuscular periods), and blue bars represent nocturnal hours. Data were collected from 12 protected areas across Madagascar between 2007 and 2023. Numbers above each bar

Significant covariates (estimate \pm standard error) of the model include unbaited camera traps (-1.25 ± 0.38), 1km population density (-0.43 ± 0.11), human detection rate (0.29 ± 0.03), elevation (-0.30 ± 0.09), and percent forest cover (0.10 ± 0.04). Interaction effects (estimate \pm standard error) revealed that fosa had high detection rates at sites where humans were present,

but significantly lower detection in the presence of both high human and dog presence (-0.05 ± 0.01 ; Fig. 3). The effect of dogs was habitat dependent: in highly forested areas, increasing dog activity reduced fosa detections, whereas in degraded or open habitats, fosa detections increased with dog activity ($-.13 \pm 0.03$; Fig. 3). Finally, forest cover and human activity interacted positively—fosa detections rose with increasing forest cover, and this effect was amplified in areas of high human activity (0.09 ± 0.03 ; Fig. 3). (Table 1.)

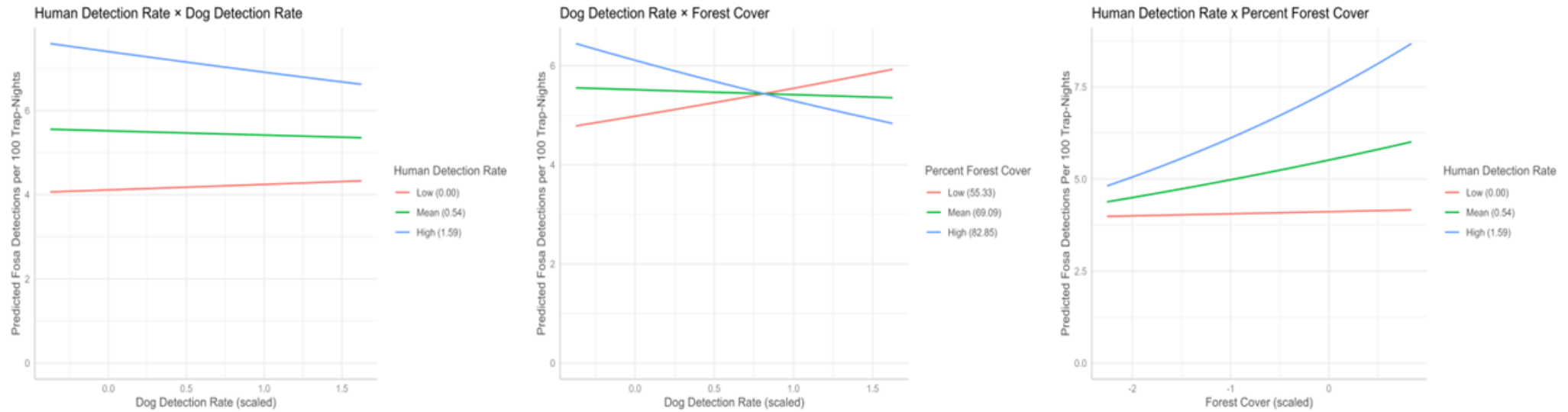


Figure 4: Interaction effects of human activity, dog activity, and forest cover on predicted fosa detections (per 100 trap-nights).

Left: Interaction between human detection rate and dog detection rate. Human detection rate is measured in detections per trap-night; dog detection rate is measured in standard deviations from the mean.

Middle: Interaction between dog detection rate and percent forest cover. Dog detection rate is measured in standard deviations from the mean.

Right: Interaction between human detection rate and percent forest cover. Percent forest cover is measured in standard deviations from the mean.

Data were collected from 2007–2023 across 12 protected areas in Madagascar.

Table 1: Fixed and interaction effects from the generalized linear mixed model predicting fosa detections. “Positive” and “Negative” indicate the direction of statistically significant effects.

Response	Effect Type	Term	Direction of Effect
Fosa Detections	Fixed	lure (Unbaited)	Negative
	Fixed	Elevation	Negative
	Fixed	Population Density 1 km	Negative
	Fixed	Percent Forest Cover	Positive
	Fixed	Human Detection Rate	Positive
	Interaction	Dog Detection Rate × Forest	Negative
	Interaction	Dog Detection Rate × Human Detection Rate	Negative
	Interaction	Human Detection Rate × Forest	Positive

Discussion

We conducted the first island-wide study of fosa ecology, combining data from 12 protected areas across Madagascar. Our dataset spans a gradient of disturbance, from protected areas with low human presence and large, contiguous forests to highly degraded landscapes with elevated human and dog activity. Across this gradient, we found that fosa abundance is shaped by interactions between forest cover and disturbances from humans and dogs. Human population density emerged as the most influential driver of fosa abundance, having a universal negative influence. Protected areas such as Masoala National Park and Makira Natural Park likely represent the highest-quality habitats in our analysis due to their extensive intact forest and lower levels of human and dog disturbance. Our models highlighted the complex nature of the dog-fosa relationship showing that in highly forested areas, increasing dog presences corresponds to fewer fosa detections, whereas in degraded forests, increasing dog detections coincide with increased fosa detections. Together, these findings underscore that conserving fosa across Madagascar will require strategies that integrate habitat protection with targeted management of human- and dog-related disturbance.

A study conducted in Mantadia National Park investigated plant-based habitat metrics such as distance to forest edge, shrub height, percent high canopy, and percent open canopy (Wampole *et al.* 2024). Building on that work, our results highlight percent forest cover as a particularly important metric. Forest cover was significant both as a fixed effect and in all interaction terms. We found that forest cover is generally beneficial for fosa, even when human activity is high. This confirms the well-established idea that fosa are forest-dependent carnivores, and their persistence as a species relies on large, contiguous forest patches (Hawkins and Racey 2005). However, it seems counterintuitive that their abundance is higher in forests with high levels of human activity. We suspect this is not a direct effect, but shared resource attraction, since both humans and fosa may focus on areas with high lemur densities, especially in tourist-heavy protected areas (e.g., Andasibe-Mantadia National Park). Similarly, in large multi-use forests such as Makira and Masoala, non-tourist forest users travel deep into the forest for resource collection and hunting, overlapping with fosa foraging zones and prey availability, resulting in co-occurrence through shared resource attraction. These trends may be further strengthened by replicated surveys in tourist-heavy areas (six surveys conducted in Andasibe-Mantadia National Park), and large forest areas used for resource gathering (14 surveys conducted in Makira National Park).

Domestic dogs have been identified as a significant threat to Malagasy carnivores through resource competition, disease transmission and direct interference (Farris *et al.* 2017; Rasambainarivo *et al.* 2018; Valenta *et al.* 2025). Previous single-site studies have shown that the relationship between dogs and fosa is variable and thus might be context-dependent, underscoring the need for broader-scale evaluation. In both the southeastern rainforest of Ranomafana and the northeastern forests of the Masoala–Makira complex, fosa have been shown to shift their activity patterns in response to dog activity. In Ranomafana, fosa exhibited greater spatial overlap with dogs, yet were absent from sites with very high dog abundance. (Gerber, Karpanty and Randrianantenaina 2012b; Farris *et al.* 2015a, 2017).

In the western deciduous forests of Ankarafantsika National Park, invasive feral and stray dogs have been shown to limit the population of fosa (Barcala 2009). In our analysis, dog detections alone did not have a significant direct effect on fosa detections; however, all interactions involving dogs were significant, indicating that the influence of dogs on fosa is strongly context-

dependent and emerges only under specific combinations of habitat condition and human presence. This aligns with results from (Wampole *et al.* 2024), which showed that exotic carnivores alone do not necessarily alter the space use of native carnivores; rather, it is their interaction with environmental context that shapes the relationship.

Fosa are capable of tolerating degraded habitats, with studies showing that fosa have no preference between degraded and non-degraded forests (Farris *et al.* 2015b). However, it has been shown that degraded forests do not support large populations of fosa and protected areas of at least 555 km² are recommended to maintain viable populations of fosa - minimum 100 individuals (Hawkins and Racey 2005). The interaction between dog detections and forest cover revealed that the fosa-dog relationship is strongly habitat dependent. In areas of high forest cover, increasing dog detections corresponded to declines in fosa detections, likely reflecting competition for resources and spatial or temporal avoidance. This aligns with previous findings showing that fosa exhibit behavioral plasticity and can shift their activity patterns in response to anthropogenic pressures (Farris *et al.* 2015a; Rivera *et al.* 2022). In contrast, in more degraded landscapes with low forest cover, increases in dog detections actually coincided with increases in fosa detections. This surprising result is likely influenced by the composition of our dataset, where many surveyed sites consisted of small, highly degraded, or fragmented forest patches. For example, Andasibe includes areas with frequent human traffic, regular dog presence, selective logging, close proximity to homes and farmland, and forest fragments separated by roads. In contrast, protected areas such as Masoala contain large, contiguous tracts of forest with relatively limited disturbance. Our dataset contained far more sites resembling Andasibe than sites resembling Masoala. Dogs also tend to reach higher occupancy in degraded habitats (Farris *et al.* 2017), where they can function as primary predators. In small or degraded protected areas, fosa are likely forced into areas of limited space and resources which may intensify competition and lead to greater spatial overlap rather than avoidance—a pattern consistent with studies investigating the effects of habitat fragmentation, degradation, and human encroachment on native Malagasy carnivores (Farris *et al.* 2016). As Madagascar continues to lose its forest at an alarming rate (Vieilledent *et al.* 2018), these fragmented, degraded landscapes are rapidly becoming the norm rather than the exception. Although the dog × forest interaction was statistically significant, the effect was estimated with wide confidence intervals, leaving the

magnitude of the interaction uncertain. This pattern warrants further investigation to clarify the processes driving the association and to strengthen our understanding of these effects.

While forest cover modified the effects of dogs on fosa, the statistical interactions between dogs and people amplify the problems for fosa. The combined effects of humans and dogs showed that fosa can tolerate either pressure independently, but when both are present together, fosa abundance declines sharply. This likely reflects variation in protected area management. Some protected areas such as Makira Natural Park (3,725 km²) have limited enforcement on human and dog entry, increasing the likelihood of human–dog co-occurrence within forests. In contrast, heavily regulated sites such as Andasibe-Mantadia National Park and Ranomafana National Park restrict both non-tourist access and dog movement, subsequently reducing overall pressure on fosa. However, data and local reports indicate that both humans and dogs do enter these areas. Malagasy people often have close bonds with their dogs, and dogs commonly accompany them into protected areas. One study found that 41.2% (N = 211) of dog owners in Ranomafana National Park reported witnessing their dog kill wildlife; a subsequent survey recorded 57% (N = 206) reporting wildlife kills there, and 58% (N = 329) of dog owners in Andasibe-Mantadia reported the same (Valenta *et al.* 2025). These surveys highlight that even in highly regulated protected areas, pressures from both humans and dogs remain substantial.

Finally, increasing human population density had the largest overall effect on fosa detections indicating that high human population density is significantly detrimental to the abundance of the species. Population density is typically also associated with land modification and forest loss, suggesting that beyond a certain threshold, habitat degradation overwhelms fosa tolerance. Elevation also had a negative effect on detections, consistent with previous reports that fosa densities decline at higher elevations (Goodman 2022). The negative effect of unbaited stations is expected, as bait is designed to attract target species, but this result is likely biased by survey design because only the first two surveys used baited stations, resulting in uneven representation.

Recommendations for Conservation

Our findings show that both humans and dogs, particularly their combined effects, exert substantial pressure on fosa populations. While the relationship between fosa and dogs remains

complex, existing studies have shown that the presence of dogs introduces multiple negative impacts on native wildlife. Our study adds to existing literature highlighting the widespread and significant pressure imposed by feral and free-roaming dogs. The interaction effects we identify here provide a clearer framework for prioritizing and structuring targeted conservation actions. Furthermore, unlike previous studies, our dataset reflects patterns across the island, allowing for broader inference and management relevance. In light of this, we recommend reinforced management of dog activity within protected areas. Programs such as The Mad Dog Initiative (The Mad Dog Initiative) which work to control dog and cat populations through spay-neuter and vaccination campaigns have been well received and have positively influenced the management of feral and free-ranging dogs, yet additional efforts are needed to mitigate the wide-ranging impacts of dogs on all native wildlife species. Regulation of dog movement and activity inside protected areas would also help reduce direct and indirect pressures on fosa. Even in parks where regulations technically prohibit dogs, reports and field observations (Valenta *et al.* 2025) indicate that dogs continue to accompany people within these zones, creating a persistent disturbance. Local NGOs such as The Mad Dog Initiative could collaborate with local and national governments to create structured, targeted plans of actions to aid in reduction of dog activity within protected areas. Strengthening enforcement, improving monitoring of human entry points, and expanding community-based dog management programs will be critical steps toward reducing these impacts.

Our results show that fosa detections increase alongside human detections but decline sharply when both humans and dogs are present. These trends may arise for several reasons: First, tourists and guides seek wildlife-rich areas, overlapping with fosa foraging zones. Second, non-tourists, including local residents, enter forests for resource gathering and hunting, leading to spatial overlap with fosa. Finally, when non-tourists are accompanied by dogs, fosa may experience harassment or direct hunting pressure, driving avoidance or local displacement.

To address the first scenario, tourism remains vital for both local and national economies. Therefore, rather than restricting ecotourism, we recommend better management of visitor activities—for instance, concentrating tours outside of peak fosa activity times. Although fosa are nocturnal, they tend to be most active around dawn and dusk; limiting forest visitation during

these hours could reduce disturbance with fosa and other native wildlife. Furthermore, our results suggest that while human presence alone may not be detrimental, dogs should not accompany people into the forest, or at minimum should be restricted during times when fosa activity is highest.

Mitigating the impacts of scenarios two and three requires a holistic, targeted, robust, and wide-ranging approach that simultaneously addresses wildlife conservation and human livelihoods. Monitoring and regulating access to protected areas is important, but equally crucial is ensuring that communities dependent on forest resources have alternative means of meeting subsistence needs without relying on extraction from natural forests.

Finally, our findings and those of previous studies emphasize that forest cover is essential for fosa—both as core habitat and as a buffer against anthropogenic pressures. We recommend expanding the size of protected areas where possible and increasing available habitat through reforestation projects such as those led by the non-profit EcoVision organization operating near Andasibe-Mantadia protected area. This project focuses on restoring native tree species removed through agriculture and slash-and-burn practices and has prioritized establishing a forest corridor to reconnect the region with Andasibe-Mantadia National Park, providing an avenue for wildlife travel. EcoVision's reforestation program demonstrates how restoration initiatives that incorporate local leadership, native species plantings, and community benefits can promote forest recovery while aligning with long-term conservation goals for fosa and other forest-dependent wildlife. Because the fosa serves as an umbrella species for Madagascar's ecosystems, expanding and reconnecting forest habitat will yield multi-species benefits, supporting other forest-dwelling taxa such as lemurs, tenrecs, and birds. Reforestation projects prioritizing fosa should focus on establishing forest corridors, as fosa are known to use these pathways to traverse degraded landscapes.

Literature Cited

Barcala O. 2009. Invasive Stray and Feral Dogs Limit Fosa (*Cryptoprocta ferox*) Populations in Ankarafantsika National Park, Madagascar.

Bartoń K. 2025. MuMIn: Multi-Model Inference.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>

Brooke ZM, Bielby J, Nambiar K, Carbone C. 2014. Correlates of Research Effort in Carnivores: Body Size, Range Size and Diet Matter. *PLOS ONE* 9(4):e93195. <https://doi.org/10.1371/journal.pone.0093195>

Dollar L, Ganzhorn JU, Goodman SM. 2007. Primates and Other Prey in the Seasonally Variable Diet of *Cryptoprocta ferox* in the Dry Deciduous Forest of Western Madagascar. In: Gursky SL, Nekaris KAI, editors. *Primate Anti-Predator Strategies*. Boston, MA: Springer US; p. 63–76. https://doi.org/10.1007/978-0-387-34810-0_3

Earth Science Data Systems N. 2025a. NASA Shuttle Radar Topography Mission Global 1 arc second V003 | NASA Earthdata.

Earth Science Data Systems N. 2025b. MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250m SIN Grid V006 | NASA Earthdata.

Earth Science Data Systems N. 2025c. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11 | NASA Earthdata.

Farris ZJ, Gerber BD, Karpanty S, Murphy A, Andrianjakarivelo V, Ratelolahy F, Kelly MJ. 2015a. When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores. *Journal of Zoology* 296(1):45–57. <https://doi.org/10.1111/jzo.12216>

Farris ZJ, Gerber BD, Valenta K, Rafaliarison R, Razafimahaimodison JC, Larney E, Rajaonarivelo T, Randriana Z, Wright PC, Chapman CA. 2017. Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation* 210:116–124. <https://doi.org/10.1016/j.biocon.2017.04.010>

Farris ZJ, Golden CD, Karpanty S, Murphy A, Stauffer D, Ratelolahy F, Andrianjakarivelo V, Holmes CM, Kelly MJ. 2015b. Hunting, Exotic Carnivores, and Habitat Loss: Anthropogenic Effects on a Native Carnivore Community, Madagascar. *PLOS ONE* 10(9):e0136456. <https://doi.org/10.1371/journal.pone.0136456>

Farris ZJ, Kelly MJ, Karpanty S, Ratelolahy F. 2016. Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar: Spatial co-occurrence of native-exotic carnivores. *Animal Conservation* 19(2):189–198. <https://doi.org/10.1111/acv.12233>

Gerber B, Karpanty S, Crawford C, Kotschwar M, Randrianantenaina J. 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely-triggered camera traps. *Oryx* 44:219–222. <https://doi.org/10.1017/S0030605309991037>

Gerber BD, Karpanty SM, Randrianantenaina J. 2012a. The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx* 46(3):414–422. <https://doi.org/10.1017/S0030605311001116>

Gerber BD, Karpanty SM, Randrianantenaina J. 2012b. Activity patterns of carnivores in the rainforests of Madagascar: implications for species coexistence. *Journal of Mammalogy* 93(3):667–676. <https://doi.org/10.1644/11-MAMM-A-265.1>

Goodman SM. 2022. *The New Natural History of Madagascar*. Princeton: Princeton University Press.

Hawkins CE, Racey PA. 2005. Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: implications for protected area management. *Oryx* 39(1):35–43. <https://doi.org/10.1017/S0030605305000074>

Hawkins CE, Racey PA. 2008. Food Habits of an Endangered Carnivore, *Cryptoprocta Ferox*, in the Dry Deciduous Forests of Western Madagascar. *Journal of Mammalogy* 89(1):64–74.

<https://doi.org/10.1644/06-MAMM-A-366.1>

Hawkins CE, Racey PA. 2009. A novel mating system in a solitary carnivore: the fossa. *Journal of Zoology* 277(3):196–204. <https://doi.org/10.1111/j.1469-7998.2008.00517.x>

IUCN. 2015. *Cryptoprocta ferox*: Hawkins, F.: The IUCN Red List of Threatened Species 2016: e.T5760A45197189. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T5760A45197189.en>

Kays R, Waldstein Parsons A. 2014. Mammals in and around suburban yards, and the attraction of chicken coops. *Urban Ecosystems* 17. <https://doi.org/10.1007/s11252-014-0347-2>

Merson S, Dollar L, Tan C, Macdonald D. 2018. Activity patterns of sympatric living exotic and endemic carnivores (the fossa) in Western Madagascar's deciduous forests. *Journal of Zoology* 307. <https://doi.org/10.1111/jzo.12630>

Merson SD, Dollar LJ, Tan CKW, Macdonald DW. 2020. Effects of habitat alteration and disturbance by humans and exotic species on fossa *Cryptoprocta ferox* occupancy in Madagascar's deciduous forests. *Oryx* 54(6):828–836.

<https://doi.org/10.1017/S003060531800100X>

Murphy A, Gerber BD, Farris ZJ, Karpanty S, Ratelolahy F, Kelly MJ. 2018. Making the most of sparse data to estimate density of a rare and threatened species: a case study with the fossa, a little-studied Malagasy carnivore. *Animal Conservation* 21(6):496–504.

<https://doi.org/10.1111/acv.12420>

R Core Team. 2025. R: The R Project for Statistical Computing. [accessed 7 Dec 2025]

<https://www.r-project.org/>

Rasambainarivo F, Andriamihajarivo M, Dubovi E, Parker P. 2018. Patterns of Exposure of Carnivores to Selected Pathogens in the Betampona Natural Reserve Landscape, Madagascar. *Journal of Wildlife Diseases* 54. <https://doi.org/10.7589/2017-09-225>

Rivera K, Fidino M, Farris ZJ, Magle SB, Murphy A, Gerber BD. 2022. Rethinking Habitat Occupancy Modeling and the Role of Diel Activity in an Anthropogenic World. *The American Naturalist* 200(4):556–570. <https://doi.org/10.1086/720714>

The Mad Dog Initiative. The Mad Dog Initiative. [accessed 17 Nov 2025]

<https://www.maddoginitiative.com>

Valenta K, Rajaonarivelo T, Ferreira A, Raharinirina A, Rafaliarison RR, Farris A, Watson JM, deFrance S, Mayo D, Filla C *et al.* 2025. The impact of free-roaming dogs on lemurs in Madagascar: a decade of research and intervention. *Folia Primatologica* 1–18. <https://doi.org/10.1163/14219980-bja10047>

Vieilledent G, Grinand C, Rakotomalala FA, Ranaivosoa R, Rakotoarijaona J-R, Allnutt TF, Achard F. 2018. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation* 222:189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>

Wampole EM, Farris ZJ, Razafy P, Gerber BD. 2024. Forest carnivores living on the edge with invasive predators. *Animal Conservation* 27(4):492–506. <https://doi.org/10.1111/acv.12926>

Wampole EM, Gerber BD, Farris ZJ, Razafimahaimodison JC, Andrianarisoa MH, Ralazampirenena CJ, Wright PC, Rasamisoa CD, Gibson D, Tobler MW *et al.* 2022. Madagascar Terrestrial Camera Survey Database 2021: A collation of protected forest camera surveys from 2007-2021. *Ecology* 103(6):e3687. <https://doi.org/10.1002/ecy.3687>

Wyza E, Dollar L, Rahajanirina LP, Popescu V, Stevens NJ. 2020. Spatial dynamics and activity patterns of the fosa *Cryptoprocta ferox* in Ankarafantsika National Park, Madagascar: carnivores

navigating a human-influenced landscape. *Oryx* 54(6):837–846.

<https://doi.org/10.1017/S0030605319000498>