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Spatial and Temporal Responses of Animals to Landscape Heterogeneity, Predation Risk, and Human Activity

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By

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Abstract

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Professor Justin S. Brashares, Chair

The global expansion of human activity has had profound consequences for wildlife. Research has documented the effects of widespread habitat destruction and defaunation on species and ecosystems, but the more subtle pathways through which humans alter the natural world have largely escaped quantification. Much like apex predators, humans can instill strong fear in wild animals, which may adjust their activity to avoid contact with humans. In this dissertation, my collaborators and I examine pathways through which human disturbance, predation risk, and environmental heterogeneity influence animal behavior and distribution. We review the literature and synthesize theory to develop a novel framework for studying landscapes of fear, and we apply this framework in a global meta-analysis and field studies from California and Mozambique to understand how large mammals perceive and respond to spatial and temporal patterns of risk from humans and carnivores. We consider links between risk and response in complex systems with multiple predators or multiple prey species, and we explore ecology of fear dynamics in the context of seasonality, human disturbance, and restoration. Together, this work integrates disciplines of behavioral ecology, community ecology, and landscape ecology, applying predator-prey theory to understand the role of humans in ecological communities. By elucidating behavioral pathways linking human disturbance to wildlife community dynamics, this research contributes to our understanding of wildlife ecology in human-dominated landscapes and highlights mechanisms for human-wildlife coexistence.

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GORONGOSA NATIONAL PARK, MOZAMBIQUE

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HOPLAND RESEARCH AND EXTENSION CENTER, CALIFORNIA

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Chapter 1. Introduction

COMMUNITY ECOLOGY IN THE ANTHROPOCENE

In an era of rapid global change, it is critical to understand the ways in which human disturbance is reshaping ecosystems so that we may effectively mitigate the negative impacts of our activities. Over the last several decades, conservation biologists and ecologists have highlighted the devastating consequences of habitat loss, overharvest, pollution, and invasive species, which have led to global species declines and extinctions (Dirzo et al. 2014, Ripple et al. 2015). But in many places around the world, biodiversity is making a comeback, as people have recognized and reversed environmental destruction through habitat restoration, species reintroductions, and policies that promote conservation (Chapron et al. 2014, Pringle 2017). As we continue to design conservation and restoration efforts, we must understand the dynamics of these recovering, and often novel, ecosystems.

Recovering animal populations are often returning to landscapes that bear little resemblance to those that they previously inhabited. The human footprint has expanded across the planet, and human populations and associated infrastructure continue to grow (Venter et al. 2016). Given that people and wildlife are increasingly sharing space, promoting human-wildlife coexistence has emerged as one of the critical challenges to conservation in the Anthropocene (Dickman 2010). As ecologists explore how these novel ecosystems function, we must consider humans not as external to these systems, but embedded within them (Miller and Hobbs 2002).

Theory from behavioral and community ecology can inform our understanding of interactions between humans and the other species with which we share the planet (Chapron and López-Bao 2016, Wilkinson et al. in press). In our role as both lethal and non-lethal apex super-predators (Darimont et al. 2015, Clinchy et al. 2016), humans may drive patterns of wildlife behavior and distribution through their interactions with prey species in a manner predicted by predator-prey theory and the ecology of fear (Lima and Dill 1990, Brown et al. 1999). For example, recent studies have documented shifts in animal movement (Tucker et al. 2018), foraging patterns (Smith et al. 2015), and habitat selection (Eldegard et al. 2012, Cristescu et al. 2013) in response to human activity. The fine-scale, behaviorally-mediated effects of humans on wildlife may initiate trophic cascades that greatly alter community dynamics.

In the body of work included in this dissertation, my collaborators and I draw on concepts from predator-prey and landscape ecology to explore the effects of landscape heterogeneity, predation risk, and human disturbance on species activity patterns and the dynamics of ecological communities. We present a novel framework for studying landscapes of fear, and apply this framework in several field studies and a global meta-analysis to understand how large mammals perceive and respond to spatial and temporal patterns of risk from humans and carnivores. We consider links between risk and response in complex systems with multiple predators or multiple prey species, and explore ecology of fear dynamics in the context of seasonality, human disturbance, and restoration.

TWO RECOVERING SAVANNA SYSTEMS

I conducted fieldwork for my dissertation in two study systems halfway around the world from one another: the University of California Hopland Research and Extension Center in California's Mendocino County, USA, and Gorongosa National Park, in central Mozambique. Both are spatially heterogeneous and highly seasonal savanna systems, with associated spatiotemporal variation in patterns of risk from predators and human activity. Notably, both Hopland and Gorongosa are experiencing a recovery of large mammal species amidst rapid human population growth and land conversion. Both systems host diverse large mammal communities with complex multi-species predator-prey dynamics: Hopland is home to several large predator species, including hunters, while Gorongosa's ungulate assemblage is exceptionally rich. Finally, both Hopland and Gorongosa are sites of ongoing restoration where research, management, and outreach are tightly linked, providing valuable opportunities to explore the ecological dynamics of human-wildlife coexistence.

Hopland Research and Extension Center, California

In California, large carnivores were nearly extirpated following decades of targeted persecution. As public attitudes have shifted and new policies have promoted tolerance and conservation, carnivores including wolves, mountain lions, and black bears are now returning to northern California's landscapes (Musiani and Paquet 2004, Kovacs et al. 2016). Meanwhile, human populations are also on the rise in the region. Land is increasingly being converted from rangeland to agriculture, with particularly large growth in the viticulture sector (Merenlender 2000). With these conversions comes a greater tolerance of carnivores, but a higher degree of landscape modification in the form of habitat loss, fencing, and intensive human activity (Hilty and Merenlender 2004).

Our Hopland field site exemplifies many of these dynamics, with greater detections of large carnivores at the site in recent years, and conversion of land to vineyards on neighboring properties. The site borders undeveloped Bureau of Land Management property to the north, and dense settlement and vineyards along highway 101 to the south, and is thus situated at an urban-wildland interface. The site itself is comprised of a mosaic of open grassland, oak woodland, and dense chaparral, and hosts a range of human activities, including a small sheep operation, multiple research projects, and seasonal hunting. This spatial heterogeneity, both in terms of habitat and human infrastructure, thus sets the stage for spatial variation in predator and human activity and associated patterns of risk for prey like black-tailed deer.

Gorongosa National Park, Mozambique

After losing 90% of its large mammal populations during Mozambique's civil war (1977-1992), Gorongosa National Park today serves as an emblem of ecological rebirth. This area traditionally supported some of the world's highest concentrations of large mammals, which were nearly extirpated due to high bushmeat demand during the war (Stalmans et al. 2019), with significant consequences for ecological dynamics (Daskin et al. 2016). Renewed investment in park management and select wildlife reintroductions have changed the park's trajectory, and many large mammal populations are now thriving thanks to a concerted restoration effort (Pringle 2017).

However, this wildlife restoration is not without its challenges: Gorongosa is surrounded by a multi-use landscape (Easter et al. 2019) and is currently experiencing rapid human development as tourism and research infrastructure grows and settlements expand along park borders. Carnivores have made a slower recovery than many of the herbivore species, with only lions persisting through the war at low densities (Bouley et al. 2018, Atkins et al. 2019).

Understanding the interactions between growing human and wildlife populations is critical for maintaining Gorongosa's ecological restoration while planning for the future of this dynamic system.

OVERVIEW OF DISSERTATION

My dissertation research is comprised of five chapters. Chapter 2 of my dissertation, "Landscapes of fear: spatial patterns of risk perception and response," provides a theoretical framework for the remaining chapters, integrating concepts from behavioral ecology, community ecology, and landscape ecology to explore spatial dynamics of predator-prey interactions. My co-authors and I synthesize research and theory on landscapes of fear, developing a framework for linking spatial heterogeneity in the physical landscape to patterns of predation and prey response, mediated by the landscape of fear. Using this framework, we generate hypotheses about expected patterns of mismatch between risk and response and the relative importance of the landscape of fear in different systems. We also employ this framework to explore the various pathways through which human disturbance is 1) altering existing landscapes of fear through predator removal or restoration and habitat change, and 2) generating novel landscapes of fear by instilling fear in wild animals. The concept of the landscape of fear has been increasingly applied to anthropogenic contexts, and provides a valuable lens for understanding the ways in which sensory stimuli associated with human activity and infrastructure are perceived as risky by wild animals, and how this risk then affects their spatiotemporal distribution and behavior.

While most research on landscapes of fear quantifies static risk from a single predator or type of human disturbance, many prey animals are exposed to risk from multiple predators—including humans—which varies over both space and time. In Chapter 3, "Black-tailed deer navigate contrasting patterns of risk from hunters and mountain lions in space and time," we use empirical data to explore multi-predator landscape of fear dynamics at Hopland. We compile information on kill sites and predator activity to quantify patterns of spatiotemporal risk from both hunters and mountain lions, and use camera traps to examine deer responses to these patterns of risk. We assess the role of human infrastructure and landscape heterogeneity in generating spatial patterns of predation risk, examine the consequences of contrasting patterns of risk from humans and natural predators for prey species, and explore importance of temporal niche partitioning as a strategy for risk avoidance by prey when spatial partitioning is constrained.

Given that people are largely active during the day and have a far-reaching spatial footprint in many ecosystems around the world, my colleagues and I hypothesized that fear of humans may drive an increase in nocturnality among wild animals in many contexts, not only when animals face actual risk from hunters. We draw on the concept of temporal niche partitioning between people and wild animals in Chapter 4, "The influence of human disturbance on wildlife nocturnality." Using a meta-analytic approach, my co-authors and I compile the results of 141 case studies from around the world to quantify the global impact of human disturbance on diel activity patterns of mammals. We compare shifts in wildlife nocturnality across habitats, guilds, and types of human disturbance. We then discuss the potential implications of our findings for population persistence, species interactions, and human-wildlife coexistence.

Human disturbance is not always a deterrent for wild animals; in some cases, human infrastructure may attract animals, providing accessible food resources and facilitating movement. Building on the previous chapter, Chapter 5 explores the extent to which animals use different areas of their home range at different times of day to avoid people at fine spatiotemporal scales while still taking advantage of anthropogenic resources. This chapter, “Effects of human settlement and roads on diel activity patterns of elephants,” evaluates the extent to which African elephants in Gorongosa National Park adjust their spatiotemporal activity in response to diel patterns of human disturbance. My co-authors and I compile camera trap data from four sources to document the timing of elephant activity on and off roads, and inside and outside of the park boundaries. We discuss the consequences of spatiotemporal partitioning between elephants and people for human-wildlife conflict and ecotourism.

In Chapter 6, “Seasonal dynamics of an ungulate assemblage in a savanna floodplain landscape,” we explore the dynamics of the Gorongosa system at a broader scale. Using two years of camera trap monitoring data, we characterize the spatiotemporal patterns of the ungulate assemblage in this heterogeneous and dynamic system. We examine how species distributions and interactions change in response to the loss of habitat associated with seasonal flooding, and explore how environmental and anthropogenic factors facilitate or constrain spatiotemporal niche partitioning among species. We discuss our findings in the context of ongoing ecological restoration and consider how continued species recovery and anthropogenic disturbance may reshape the dynamics of Gorongosa’s wildlife.

In Chapter 7, I briefly review the main themes and findings that emerge from the body of work as a whole. In these concluding remarks, I reflect on the ways in which human activity is reshaping landscape of fear dynamics at multiple scales and highlight the importance of temporal partitioning as a mechanism for risk avoidance in wild animals when spatial responses are constrained. I also use these concluding remarks to emphasize that we have only scratched the surface in our understanding of fear effects in ecology. To effectively link landscapes of fear theory to ecosystem management, conservation, and restoration, we must deepen our understanding of the spatial and temporal dynamics of fear-mediated interactions between humans and wildlife, and between predators and prey. I hope that my research has identified routes towards this deeper understanding, and highlighted the importance of exploring less obvious, though powerful, pathways through which humans are shaping the natural world.

Chapter 2. Landscapes of fear: spatial patterns of risk perception and response

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ABSTRACT

Animals experience varying levels of predation risk as they navigate heterogeneous landscapes, and behavioral responses to perceived risk can structure ecosystems. The concept of the landscape of fear has recently become central to describing this spatial variation in risk, perception, and response. We present a framework linking the landscape of fear, defined as spatial variation in prey perception of risk, to the underlying physical landscape and predation risk, and to resulting patterns of prey distribution and anti-predator behavior. By disambiguating the mechanisms through which prey perceive risk and incorporate fear into decision-making, we can better quantify the nonlinear relationship between risk and response and evaluate the relative importance of the landscape of fear across taxa and ecosystems.

INTRODUCTION

The risk of predation plays a powerful role in shaping behavior of fearful prey, with consequences for individual physiology, population dynamics, and community interactions (Brown and Kotler 2004, LaManna and Martin 2016). Theoretical and experimental research has revealed the importance of heterogeneity within and among habitats as a driver of spatial patterning of predation and prey response (Box 1). Moreover, recent technological advances in the collection of geospatial and animal movement data have allowed more detailed empirical studies of the spatial dynamics of predation and anti-predator strategies (Jordan and Ryan 2015). Over the last two decades, ecologists have adopted the concept of the "landscape of fear" to describe the spatial variation in predation risk as perceived by prey across their foraging or home range (Laundré et al. 2001). This concept draws on the disciplines of behavioral, population, community, and spatial ecology to consider the role of spatially heterogenous predation risk in driving prey behavior and trophic cascades (Box 2). Research on landscapes of fear has become central to the study of predator-prey interactions and has enhanced our understanding of animal ecology on heterogeneous, dynamic landscapes.

As noted in the past for transformative concepts in ecology such as keystone species (Power et al. 1996) and trophic cascades (Polis et al. 2000), rapid and widespread adoption of the landscape of fear concept has led to inconsistent definitions and applications. Given the difficulties in measuring risk perception, researchers have adopted a broad range of operational definitions for the concept. Subsequently, "landscape of fear" has become a catch-all for many spatial phenomena relating to predation, and the term is increasingly applied to discussion of risk outside of a spatial context (Peers et al. 2018). This drift toward ambiguity has, in turn, fueled significant inconsistencies in how landscapes of fear are measured. While some studies have considered the landscape of fear to be an intrinsic attribute of a physical landscape, others have suggested it is a spatial pattern resulting from predation, a cognitive map of risk perceived by prey, or a measurable response of prey manifested through their spatial distribution or foraging behavior (Table 1). Reflecting this confusion, recent studies have dedicated entire paragraphs to clarify their interpretation of the term among the conflicting definitions in the literature (Kohl et al. 2018).

A common source of confusion among studies of the landscape of fear results from the conflation of spatial patterns of predation risk with prey perceptions of that risk, or with prey anti-predator behavior in response to risk perception. The most immediate consequence of this ambiguity in definition is the inappropriate choice of proxies for measuring the phenomenon of interest, which can lead to circular inferences. For example, prey behavior, such as alarm calling or vigilance, is often used as a proxy for predation risk, which is then used to predict other aspects of prey response, such as distribution on a landscape (Willems and Hill 2009). Notably, the conflation of both predation patterns and prey behavior with the landscape of fear has impeded important discussions about mechanisms that link, or fail to link, risk and response. Amidst this confusion, there has been debate over the ecological importance of fear for prey species and community interactions, with different parties using different definitions for landscapes of fear (cf. (Fortin et al. 2005, Kauffman et al. 2010, Beschta and Ripple 2013)).

Here, in an effort to clarify and refocus the theory and science on landscapes of fear, we advocate for a definition of the landscape of fear as *the spatial variation in prey perception of predation risk*. The landscape of fear allows prey to integrate spatial variation in threats from predators with other spatially variable opportunities and hazards (Masello et al. 2017). For animals with advanced cognition, the landscape of fear may exist as a "mental map" that an animal proactively responds to, but the landscape of fear can also occur in real time as an animal navigates and responds to a landscape of heterogeneous risk. We introduce a framework around this definition that should allow researchers to better articulate what phenomena they are actually studying and measuring, rather than falling back on the term "landscape of fear" (Figure 1). The framework aims to help researchers to generate hypotheses and understand underlying assumptions.

Below, we apply our framework to discuss how predation risk and behavioral responses map imperfectly onto one another. We contend that understanding these mismatches between risk, perception, and response will not only clarify definitions, but open doors to an array of important questions in predator-prey ecology and evolution and enable an understanding of the relative importance of the landscape of fear across systems.

MISMATCHES IN PREDATION RISK AND PREY RESPONSE

Our framework (Figure 1) envisions the landscape of fear at the center of distinct, measurable landscapes corresponding to the physical environment, predation risk, and prey response. By conflating these distinct spatial maps and referring to each of these elements as the "landscape of fear," as many studies have done (Figure 2, Table 1), scientists risk ignoring the important distinctions between them. Furthermore, many studies of the landscape of fear assume a linear relationship between these spatial patterns, but risk and response often fail to map closely onto one another due to non-linear relationships between, for example, predator activity and predation risk, predator cues and prey perception, or fear and anti-predator behavior. An understanding of the pathways linking habitat heterogeneity to anti-predator behavior via a landscape of fear, as outlined in Figure 1, enables predictions about when mismatches will occur between the magnitude and spatial heterogeneity of actual predation risk and prey response to that risk (Figure 3).

First, the landscape of fear will map more or less precisely onto the landscape of predation risk based on the strength and reliability of cues and the sensory and cognitive ability of prey to associate those cues with predation (Luttbeg and Trussell 2013). Given that prey should experience strong selection to be able to detect and respond to predators, mismatches between actual and perceived risk should be common in response to rare or novel habitats or predators (Abom and Schwarzkopf 2016). Invasive predators or human-induced habitat changes may create ecological traps, in which prey fail to optimize behavior due to anachronistic landscapes of fear (Schlaepfer et al. 2005). Such mismatches in actual versus perceived risks may be a hallmark of some captive animals, limiting inferences based on laboratory studies of the landscape of fear (Troxell-Smith et al. 2016). Detection of cues will still be imperfect among prey species that have co-evolved with their predators, as predators have evolved crypsis and hunting strategies to avoid detection (Abrams 2000). When studying landscapes of fear, it is therefore important to understand the cues that are most salient to prey, and the spatial and temporal scales of cue perception (Jordan and Ryan 2015). Studies of the chemosensory mechanisms underlying prey risk perception, for example, may provide insight into taxonomic differences in risk perception for many groups of species (Katz and Dill 1998, Jurcak and Moore 2018).

Given the large fitness cost of predation, some prey animals may have evolved a tendency to perceive a higher probability of predation than is actually present, and to “play it safe” (Bouskila and Blumstein 1992), particularly when the cost of responding is low (Abrams 1994). By perceiving high risk as a default, prey may exhibit more homogenous anti-predator behavioral responses when compared to the heterogeneous landscape of predation risk. The landscape of fear can also amplify underlying variation in predation risk, if cues associated with risk drive exaggerated risk perception. Furthermore, many prey species now live in predator-free environments but still associate landscape cues with predation risk (Bonnot et al. 2016). Such inaccuracies in risk perception suggest that behavior may not always be an appropriate proxy for the actual risk of predation.

Even when prey perceive risk with high accuracy, spatial patterns of prey distribution and anti-predator behavior rarely correlate perfectly with the landscape of fear due to cost-benefit trade-offs, including those associated with foraging (Figure 1). Prey must balance predator avoidance with other critical life functions such as acquiring food, and nearly all anti-predator strategies entail energetic or opportunity costs. Simply put, predation risk is not the only concern of most prey animals. Physiological, phylogenetic, or ecological constraints may limit a prey animal’s ability to respond to perceived predation risk (Creel 2011). If required resources like food and water are limited and concentrated, prey may have no choice but to use inherently risky areas (Valeix et al. 2009a, Schmidt and Kuijper 2015). Prey territoriality may also limit prey ability to adjust spatial distributions to avoid predation (Ford and Goheen 2015). Given these constraints, an animal may fail to exhibit anti-predator behavior, even when its landscape of fear accurately maps onto landscapes of risk.

If the relative costs or benefits of anti-predator responses vary spatially, prey may exhibit spatial variation in anti-predator behavior that does not reflect the landscape of fear. In high-quality forage patches, for example, the costs of anti-predator behavior may outweigh benefits of increased foraging, and in very risky areas, anti-predator behavior may not substantively reduce probability of detection or escape. For example, arboreal grey squirrels (*Sciurus carolensis*) in open areas are *less* vigilant than squirrels near trees, fitting the prediction that the benefits of vigilance will be greater when there is an easy escape route (Brown 1999). To more fully understand how risk translates (or fails to translate) into behavior, we must examine how other fitness-enhancing opportunities and behavioral trade-offs vary in space and time.

Trade-offs associated with foraging and the landscape of fear will also vary greatly with an individual prey animal's state and marginal valuation of food. According to the asset protection principle, an animal in better physical condition has more to lose from being killed than one in poorer condition (Clark 1994). Thus, a hungry animal will assess a lower foraging cost at the same level of risk than one that is well-fed, and animals with different resource needs will manifest more or less rugose spatial landscapes of behavioral response (Catano et al. 2015). In the extreme, an animal on the verge of starvation should cease to show any spatial variation in fear responses if food is present throughout the landscape, even when predation risk varies strongly in space (Brown et al. 1997).

PREDICTING LANDSCAPE OF FEAR EFFECTS

As the concept of the landscape of fear has gained prominence, researchers increasingly attribute a range of ecological outcomes to predation risk effects (Teckentrup et al. 2018), and the role of fear in driving trophic cascades has even become a common media narrative (Mech 2012). While fear can play a critical role in determining individual fitness, population dynamics, and community interactions, its relative importance will vary across systems with different predator and prey species and landscape features (Schmitz 2005, Heithaus et al. 2009, Creel 2011). By understanding the ecological processes that give rise to, and arise from, the landscape of fear, we can predict where the landscape of fear will have meaningful consequences for prey population dynamics and community structure (Table 2).

Landscape of fear effects on populations and communities should be most pronounced in landscapes that are highly heterogeneous, since the physical landscape sets the stage for spatial variation in predation risk and associated behavioral trade-offs (Atuo and O'Connell 2017). For example, in African and North American savannas, structural diversity in the form of open grassland and shrub or wooded patches provides diverse opportunities for escape, hiding, detection, ambush and capture for prey and predators alike (Eccard and Liesenjohann 2014). Prey may not experience or respond to predictably variable predation risk in more homogenous systems like mature European forests (Schmidt and Kuijper 2015) and the open ocean (Hammerschlag et al. 2015). Even in systems with heterogeneous risk, clumped resources may limit foraging opportunities and therefore constrain the ability of prey to incorporate fear into their behavioral decisions (Schmidt and Kuijper 2015).

For landscapes of fear to exist, predation risk must not only vary in space but must vary predictably, and must be associated with cues that create generally reliable signals for prey (Weissburg et al. 2014). Prey may perceive greater risk from cues associated with ambush predators, which require certain forms of habitat structure for cover, than from cues associated with active or coursing predators (Schmitz et al. 2004), a pattern supported by mesocosm studies (Schmitz 2008). Prey must also have the ability to associate cues with risk. In the absence of strong selective pressure on predation risk perception and response over evolutionary history, prey species may fail to perceive a landscape of fear from rare or novel predators (Soluk and Collins 1988). If prey do not perceive and respond to predation risk, landscapes of fear will not play a major role in determining fitness and population dynamics.

Differences in predator and prey densities can lead to widespread variation in predation rates across systems, with implications for landscape of fear dynamics (Middleton et al. 2013). Landscapes of fear are more likely to influence prey behavior where encountering a predator brings a high risk of attack, but encounters are infrequent. Conversely, as summarized by the risk allocation hypothesis, prey experiencing frequent encounters with predators may live in a state of constant fear and exhibit less spatial structure in their anti-predator responses (Lima and Bednekoff 1999). Furthermore, for a given prey species, the population effects of landscapes of fear should be strongest when there are similar spatial patterns of predation risk for all of their predators. In contrast, when prey must trade off contrasting landscapes of risk among multiple predators, the landscape of fear may be relatively homogenous, particularly under predator facilitation where each predator is more dangerous in a different habitat (Kotler et al. 1992, Murray et al. 1995, Cresswell and Quinn 2013).

Finally, even when predictable landscapes of fear exist and generate prey responses, these responses may not meaningfully impact prey population dynamics. While classical models of the landscape of fear assume there to be a strong cost to anti-predator behavior due to trade-offs between risk avoidance and foraging or other activities, such trade-offs may not always occur, particularly when prey rely more strongly on physical defenses than behavioral defenses (Creel 2011). Also, prey with dietary breadth or plasticity, or abundant food resources, may be able to choose among equivalent foraging areas to reduce predation risk (Valeix et al. 2009a), particularly when predators have a narrow habitat domain (Schmitz 2005). Sometimes, the riskiest habitat is also the habitat with the lowest-quality forage (Pierce et al. 2004), and prey may be able to avoid risk while tracking food (Bakker et al. 2005). In these cases, landscapes of fear will play a negligible role in prey population-level outcomes, although they may still alter community structure at lower trophic levels. Furthermore, risk mitigation strategies like vigilance may not be mutually exclusive with other fitness-enhancing behaviors like foraging, depending on an animal's physiology. Even where trade-offs do exist, and predation risk generates costly responses in prey, such costs may be insufficient to determine reproductive (fitness) outcomes or drive population dynamics and trophic cascades (Middleton et al. 2013).

STUDYING LANDSCAPES OF RISK AND RESPONSE

As scientists utilize remote sensing, GIS, and GPS technology, there is growing interest in moving beyond simple designations of safe and risky habitats to quantify spatially-explicit landscapes of risk and prey response. Much of our understanding of non-lethal predator effects comes from laboratory or mesocosm experiments, and there is a need to examine the determinants and consequences of landscapes of fear in natural systems (Peers et al. 2018). Opportunities exist to evaluate the hypotheses that emerge from our framework regarding the causes and consequences of mismatch between predation risk and prey response, and the relative strength of landscape of fear effects on population dynamics and species interactions.

Thus far, ecologists have used a wide range of observational and experimental methods to measure and map what they have defined as a landscape of fear (Figure 2), and these different approaches have hindered comparisons across systems (Moll et al. 2017). For example, distribution of kill sites by a predator is often used to infer landscapes of fear (Moll et al. 2017), but predation patterns can be skewed by variation in density and activity of prey across the landscape. Vigilance by prey is another commonly used proxy for measuring risk, but, as discussed above, vigilance may actually be lower in the riskiest habitats, and "safe" places may be made so by heightened vigilance (Brown 1999). Mapping activity patterns of prey across space is also commonly related to predation risk (Cresswell and Quinn 2013), but these patterns are often linked to other features of the landscape such as patterns of resource productivity or distribution of potential competitors (intra- or interspecific) or mates. Spatial variation in giving-up densities (GUDs) in natural or experimental food patches across a landscape may indicate differences in the perceived foraging cost of predation, proportional to predation risk (Brown and Kotler 2004), although GUDs pose methodological challenges (see (Bedoya-Perez et al. 2013, McMahon et al. 2018)).

This diversity of imperfect approaches for measuring landscapes of fear is understandable, given the challenges associated with quantifying perception. While there have been recent advances in our understanding of the cognitive basis of risk perception (Staples et al. 2009, Marzluff et al. 2012), studying cognition in wild animals presents significant challenges. Perceived risk may be associated with quantifiable physiological parameters such as glucocorticoid stress hormones and heart rate (Clinchy et al. 2013, Støen et al. 2015), but these physiological responses do not always align well with cognitive processes given their energetic costs and associated trade-offs (Clinchy et al. 2013). Furthermore, lag times in physiological responses can complicate studies of spatiotemporal variability.

Given the difficulties associated with measuring the cognitive or emotional state of an animal, research on the landscape of fear may be better served by explicitly measuring predation risk and behavioral responses and exploring congruence or mismatch between them, rather than further attempts to map the landscape of fear itself. Progress in the study of landscapes of fear will depend on researchers becoming more deliberate in selecting relevant variables to quantify (i.e., predation events, predation risk, prey distribution, prey behavior), choosing suitable methods, and clearly defining concepts and the relationships among variables of interest. In Table 3, we compile a list of measurable proxies for both spatial variation in predation risk and behavioral responses of prey and describe how each of these proxies relates mechanistically to the landscape of fear.

Ideally, by clarifying the elements that comprise a landscape of fear (Figure 1) we aim to reduce some of the difficulties outlined above by guiding study designs that account for the factors influencing the spatial and temporal scales of landscape of fear dynamics. In addition to reflecting the home range sizes and body sizes of both predator and prey, ecologically relevant scales will depend on the hunting behavior of predators, flight and escape behavior of prey, and detection abilities of predators and prey (Padié et al. 2015). Individual animals experience and respond to landscapes of fear at multiple scales, incorporating risk into selection of both broad habitat and microhabitat (Kuijper et al. 2015, Stears and Shrader 2015). Furthermore, while terrestrial landscapes of fear are often conceptualized and mapped as two-dimensional, many volant, arboreal, subterranean, or aquatic animals experience three-dimensional landscapes of fear (Emerson et al. 2011, Makin et al. 2012).

Regular changes at any given site in habitat structure, resource distribution, and productivity over time further complicate efforts to depict a single landscape of fear. Studies often present the landscape of fear as temporally static, but prey experience temporal variation in the magnitude of predation risk and in resource trade-offs, often on multiple time scales. Understanding the temporal dynamics of predator and prey ecology and behavior is as important as defining appropriate geographic scales in studies of the landscape of fear. Landscapes of fear vary predictably with daily (Tolon et al. 2009, Kohl et al. 2018), monthly (lunar) (Bouskila 1995, Palmer et al. 2017), or seasonal cycles (Druce et al. 2009, Hopcraft et al. 2014). Studies should account for this temporal variation by framing the question of interest. The measurement of a landscape of fear may be a single snapshot in time if the question concerns how the temporary presence of a predator influences the animal's fear responses. But this scale may not be useful when integrating across time scales where prey modulate their activity to take advantage of safe times and places to obtain food, and consequently influence the distribution and abundance of their food.

Finally, our framework emphasizes that the landscape of fear also varies among individual animals living on the same physical landscape and at the same time. Factors like sex, age, reproductive status and body condition can affect an individual's vulnerability to predators, its perception of risk at a given time and place, and the trade-offs involved in its response (McArthur et al. 2014, Lagos and Herberstein 2017). Recent studies have linked anti-predator behavior to personality or behavioral syndromes, with some individuals inherently more fearful than conspecifics (Quinn et al. 2012, Bonnot et al. 2015, Spiegel et al. 2016). Thus, population-level results should be interpreted with the understanding that they may describe an averaging of individual prey responses.

CONCLUDING REMARKS

The landscape of fear is an important concept in ecology, integrating behavioral, population, and community responses to predation and providing a central organizing principle for the study of predator-prey dynamics on heterogeneous landscapes. Despite broad acceptance and growth in the application of the landscape of fear concept, inconsistencies in its definition and application have clouded synthesis and advancement of theory. The landscape of fear has been repeatedly conflated with the physical landscape, spatial patterns of predation and predation risk, and heterogeneity in prey distribution and behavior. We suggest the use of a narrower definition of the landscape of fear as spatial variation in risk perception, and advocate for the use of more precise and appropriate terminology to describe the patterns of risk and prey behavior that are actually being studied (Figure 1).

By clarifying non-linear relationships between the physical landscape, predation risk, risk perception, and prey response, we highlight the complexity of animal fear while clarifying concepts to guide future research. While our landscape of fear framework is grounded in predator-prey interactions, it provides a useful lens to conceptualize the way that animals perceive and respond to various risks as they navigate complex environments, including competition (Swanson et al. 2016), and parasite or disease risk (Buck et al. 2018), for example. A synthetic understanding of the landscape of fear will enable comparisons of its role across taxa and ecosystems and improve predictions and studies of the effects of the landscape of fear on individual fitness, population dynamics, and community interactions. Such research is especially critical as humans reshape landscapes of fear through predator removal and reintroduction, habitat modification, and intensification of activities such as hunting and recreation (Box 4).

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BOX 1. PRE-CURSORS TO THE LANDSCAPE OF FEAR CONCEPT

Behavioral and population ecology

Behavioral ecologists have long recognized the importance of spatially variable predation risk and prey responses in stabilizing predator-prey population dynamics (Huffaker 1958, Sih 1987, Gilliam and Fraser 1987). Charnov introduced the concept of "behavioral resource depression" to describe changes in prey microhabitat selection in response to predation risk, which made prey less accessible to predators (Charnov et al. 1976). Early studies of the "ecology of fear" (Brown et al. 1999) combined mass action models (in which the lethal effects of predators drive numeric responses in prey populations), with optimal foraging theory (Sih 1980). These conceptual models provided the theoretical framework for empirical studies of free-ranging predators and prey on complex landscapes.

Subsequent studies linked anti-predator strategies to physiological outcomes, including stress and reproduction (Creel et al. 2007, Zanette et al. 2011). Mesocosm experiments have demonstrated that in some contexts, these **risk effects** of predation have a greater influence on prey population dynamics than the consumptive effects (Preisser et al. 2005). While the study of risk effects has proven challenging in heterogeneous natural landscapes, patterns of spatial variation in predation risk and response likely have important consequences for spatial demographic patterns (Hopcraft et al. 2005, Matassa and Trussell 2011).

Community ecology

Meanwhile, community ecologists observed that foraging behavior of fearful grazers structured the distribution of primary producers. Spatial variation in predation risk was hypothesized as a mechanism behind the formation of "grazing halos," denuded areas at the edge of coral reefs where urchins sought refuge from predatory fish (Ogden et al. 1973). Similar patterns were observed in terrestrial systems; for example, the effects of pika (*Ochotona princeps*) on vegetation were strongest near rocks that provided refuge (Huntly 1987). Through experiments, ecologists linked the structural complexity of the habitat back to predator efficiency, with refuges from predators reducing prey mortality rates and transforming prey communities (Crowder and Cooper 1982). Spatial variation in predation risk and accompanying patterns of prey foraging activity have been found to shape lower trophic levels via "predator-induced resource avoidance" (Power 1984).

The indirect effects of predators on lower trophic levels, mediated by fear in prey, have come to be known as trait-mediated indirect interactions, or behaviorally-mediated trophic cascades (Schmitz et al. 1997, Bolker et al. 2003, Werner and Peacor 2006). Many experiments have since found that trait-mediated interactions can be stronger drivers of food web dynamics than density-mediated effects (Preisser et al. 2005). These fear-driven interactions play out over landscapes where prey perception of risk is heterogeneous, and in turn, prey behaviors drive patterns of spatial heterogeneity in species distributions across trophic levels.

BOX 2: EMERGENCE AND LIMITATIONS OF THE LANDSCAPE OF FEAR CONCEPT

The "landscape of fear" term was coined by Laundré and colleagues in 2001 in their paper on elk and bison vigilance and foraging behavior in response to wolf reintroduction in Yellowstone

(Laundré et al. 2001). The core idea existed within earlier concepts (Box 1), like prey depression (Charnov et al. 1976) or predator-induced resource avoidance (Power 1984). However, the term "landscape of fear" was widely adopted, as it evoked an individual animal navigating a spatially explicit environment of variable predation risk. The "landscape of fear" captures the human imagination, and is intuitive, evocative, and relatable—in fact, the term originated in the fields of anthropology and human geography, where it is still used to describe spaces that induce dread and terror in people (Tuan 1979). While the accessibility of the term has made it appealing to researchers and the general public, it has also led to concerns about anthropomorphism and the attribution of conscious emotion to non-human animals (Adolphs 2013). Outside of the landscape of fear literature, there remains considerable debate among psychologists and animal behavior scientists about the definition and measurement of fear in both humans and non-human animals (Adolphs 2013, LeDoux 2014).

Despite the shortcomings of the term "fear," it has caught on widely, and is generally considered by ecologists to be equivalent to conscious or unconscious risk perception. Fear as an adaptation allows the animal or organism to assign an activity cost to the risk of injury or death (Kotler and Brown 2017). Initially, there was a taxonomic bias towards large terrestrial mammals in the landscape of fear literature. However, within the last several years, the term has been applied to a wide range of taxa, including birds (Atuo and O'Connell 2017, Masello et al. 2017), fish (Gil et al. 2017), and invertebrates (Hermann and Landis 2017, Hintz and Relyea 2017). Amidst this trend, it has becoming increasingly common to attribute observed ecological phenomena to landscapes of fear. However, given that at least 15 different processes and states have been called a "landscape of fear" (Table 1), it is no surprise that some so-called landscape of fear is implicated in so many studies. As the landscape of fear research continues to gain popularity, it is critical to examine its definition, application, and context in predator-prey theory so that we can refine its use and better design studies to evaluate its role in ecosystems.

BOX 3: A COMMUNITY-LEVEL PERSPECTIVE

The simplest models of the landscape of fear assume a single predator and prey, but the consequences of landscapes of fear often involve multiple trophic levels. Acknowledging the complexity of landscapes of fear within a community ecology framework is essential for realistically quantifying their role in shaping ecosystem dynamics (Teckentrup et al. 2018). While we present the landscape of fear as an experience of an individual prey animal navigating risk trade-offs, it corresponds to related patterns at other trophic levels. The landscape of fear for a prey species is simultaneously a landscape of opportunity for predators, and a landscape of refuge for the species consumed by prey (Laundré et al. 2010).

There are dynamic feedbacks across trophic levels, as predators perceive and respond to the prey species' response (Lima 2002). Ultimately, underlying habitat heterogeneity can be shaped by fear responses of foraging prey through behaviorally-mediated trophic cascades, feeding back (e.g. through vegetation height or density) to alter spatial patterns of predation risk. Often the standing crop of resources will be the inverse of the landscape of fear as animals deplete food availability where they feel safe and leave more food behind where risky (Gil et al. 2017). Prey can also intentionally engineer the physical landscape to reduce predation risk in a given area (Caro 2005).

Efforts to quantify cascading consequences of fear provide compelling new insights on the ecosystem impacts of individual responses to fear. For example, an apex predator can alter the landscape of fear of an herbivore through fear-induced behavioral changes in an intervening mesopredator (Frid et al. 2008). Lower-trophic level prey may even deliberately select for areas with apex predators, using them as cover from mesopredators that present more risk to the prey in question (Gordon et al. 2015).

Multi-predator systems require that prey respond to multiple sources of risk, which can be additive or orthogonal depending on predator distributions and hunting modes (Cresswell and Quinn 2013). To explore this complexity, some studies have overlain multiple maps of predation risk arising from different types of predators in an attempt to quantify their relative effects on prey behavior (Willems and Hill 2009). Furthermore, the availability of alternative prey species can affect predation risk, dependent on prey switching and predator preferences. In multi-prey systems, competition and apparent competition can influence landscapes of predation risk and response (Laundré et al. 2014). For example, caribou perceive heightened predation risk in areas of high moose density, presumably because moose are a primary prey species for wolves (Avgar et al. 2015).

BOX 4: LANDSCAPES OF FEAR IN THE ANTHROPOCENE

Our framework highlights pathways through which disturbance alters and creates landscapes of fear. Land use changes through agriculture (Hof et al. 2012) and deforestation (Sahlén et al. 2016) as well as pollution (Kerby et al. 2012) shape habitat structure, quality, and heterogeneity. Human activity thus alters the playing field for predator-prey dynamics, changing the effectiveness of predator and prey strategies and prey trade-offs, constraining the spatial scale of prey responses, and sometimes even altering sensory cues (Hintz and Relyea 2017). Climate change has also been implicated in reshaping landscapes of fear by changing habitat structure and habitat domain of predators and prey (Schmitz and Barton 2013, Riginos 2014).

Human activity has also fundamentally changed the nature of predation risk. The decline of large terrestrial carnivores through persecution and habitat loss has had clear consequences through the creation of landscapes of fearlessness, and many studies have documented fearless prey transforming ecosystems in the absence of predators (Creel et al. 2005, Bonnot et al. 2016). Consequently, some conservation biologists have advocated for the restoration of landscapes of fear through carnivore reintroductions (Manning et al. 2009), although some studies suggest prey exhibit atypical fear responses to reintroduced predators (Nicholson et al. 2014). In other cases, the provision of anthropogenic subsidies to predators or the introduction of invasive predators has increased populations or changed hunting patterns, with consequences for landscapes of fear in native prey (Gompper and Vanak 2008).

In addition to disrupting predation risk, humans also represent a new apex "super-predator" (Darimont et al. 2015, Clinchy et al. 2016). In places with hunting, lethal human activity creates potentially novel landscapes of fear for targeted species (Norum et al. 2015), with potential consequences for physiology, prey demographics, and the structure of human-natural communities. However, animals perceive risk from humans even in the absence of lethal reinforcement (Frid and Dill 2002), and anthropogenic landscapes of fear have been linked to demographic consequences (Sawyer et al. 2017). Human activity can also initiate behaviorally-mediated trophic cascades: "human shields" can arise when a predator avoids human, leading prey to preferentially seek refuge in those areas (Leighton et al. 2010, Kuijper et al. 2015). Ultimately, the landscape of fear associated with humans selects for species with plastic responses to threatening stimuli, resulting in habituation to non-lethal human activity over time (Sih 2013).

The landscape of fear framework can inform the design of strategies to reduce human-wildlife conflict, including threats to people, livestock, agriculture, and property. Many conflict mitigation techniques, like novel sensory stimuli or targeted lethal control, for example, are aimed at imposing landscapes of fear on target species so that animals avoid areas of potential conflict (Cromsigt et al. 2013, Van Eeden et al. 2018). By understanding the sensory cues that generate fear in animals, and the behavioral responses and trade-offs associated with them, managers can better design mitigation strategies to effectively change wildlife behavior (Atkins et al. 2017).

FIGURE 1. A FRAMEWORK FOR UNDERSTANDING THE ECOLOGICAL CONTEXT OF THE LANDSCAPE OF FEAR.

The (i) underlying physical landscape shapes visibility, detection, and movement before and during a predator-prey encounter. The structure of the landscape interacts with (ii) aspects of predator and prey biology to determine patterns of predator and prey distribution and risk. The physical landscape thus sets the stage for (iii) spatial variation in predation risk, or the likelihood of a predation event. This risk is then (iv) imperfectly perceived by prey, based on the reliability of cues, the sensory and cognitive capacities of the prey, and past experiences with predation in the individual's lifetime or in the species' evolutionary history. Cues of predation risk may be indirect (associated with the physical landscape) or direct (associated with predators themselves). The (v) landscape of fear is manifested in measurable behavioral outcomes, as prey (vi) incorporate information about predation risk into decisions about where to go and how to behave. The landscape of fear thus generates two behavioral strategies to proactively minimize risk: (vii) avoidance of high-risk areas, and (viii) modulation of behavior to reduce the probability of suffering predation while at a given location.

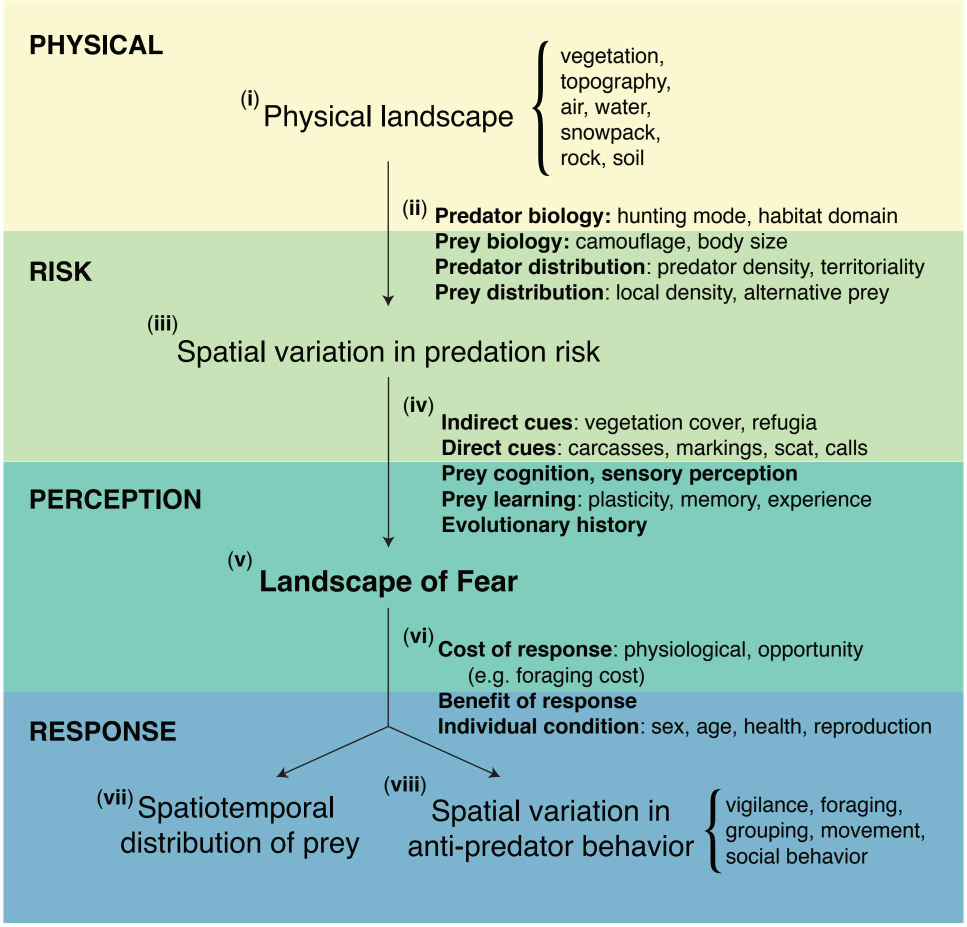

FIGURE 2. VISUALIZED LANDSCAPES OF FEAR FROM THE LITERATURE

Conflicting definitions of the landscape of fear have generated a contrasting range of methods to quantify and visualize these landscapes, most often by measuring either the physical landscape, predation, predator presence, or prey response (see also Table 3). Our framework provides a useful way to compare approaches across studies by articulating the differences between predation, risk, fear, and prey response. Representations of the so-called "landscape of fear" in the literature include spatial variation in: (A) *Predation risk*: modeled risk of wolf (*Canis lupus*) predation on elk (*Cervus elaphus*), based on known kill locations, habitat features, and elk density (squares and triangles represent study plots) (Kauffman et al. 2010); (B) *Reactive anti-predator responses*: density of observed leopard (*Panthera pardus*) alarm call vocalizations by vervet monkeys (*Cercopithecus aethiops*) (Willems and Hill 2009); (C) *Proactive anti-predator behavior*: contour lines of experimentally-determined giving-up densities for Nubian ibex (*Capra nubiana*) (Iribarren and Kotler 2012); (D) *Effects of prey responses on vegetation:* satellite imagery of grazing halos around reefs, resulting from foraging of fearful prey (Madin et al. 2011); (E) *Perceived risk, (true landscape of fear)*: conceptual representation of fear in the mind of a theoretical prey animal (Jordan and Ryan 2015)

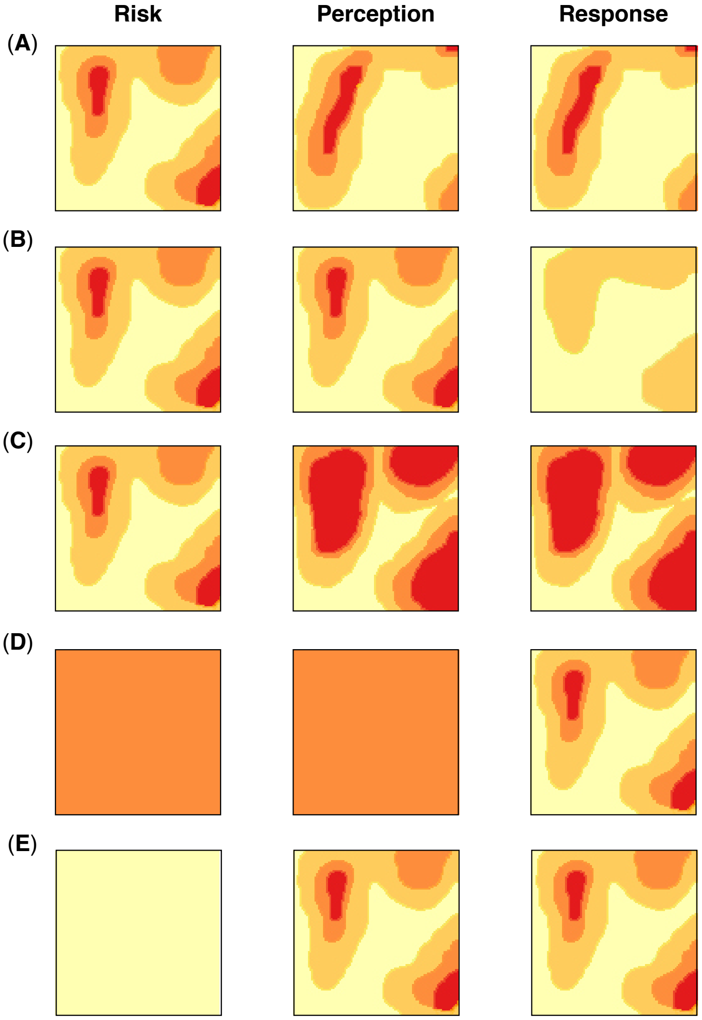

FIGURE 3. MISMATCH BETWEEN PREDATION RISK, THE LANDSCAPE OF FEAR, AND PREY ANTI-PREDATOR BEHAVIOR

The landscape of fear mediates the relationship between spatial variation in risk and prey response. Prey response includes both spatiotemporal distribution (as prey avoid areas of high risk) and spatial variation anti-predator strategies at a given place (including vigilance and grouping). There is often a mismatch in risk and response, due to limitations in prey perception and the trade-offs associated with decision-making. A) Prey may have imperfect information about predation risk, resulting in slight mismatches in their risk perception and response; B) Constraints on prey behavior, and steep costs associated with response, may lead to a reduced, more homogenous behavioral response to risk despite accurate perception of risk; C) Risk-averse prey may err on the side of caution, exhibiting more amplified anti-predator responses than the underlying risk surface (conversely, bold prey may exhibit muted anti-predator responses); D) Intrinsic risk and risk perception may be homogenous across a landscape, but spatial heterogeneity in forage quality, and therefore in behavioral trade-offs, may result in heterogeneity in prey distribution or anti-predator behavior; E) Predators may be extirpated in a system, resulting in no risk across the landscape, but evolved responses to cues can persist and influence prey behavior despite no actual risk.

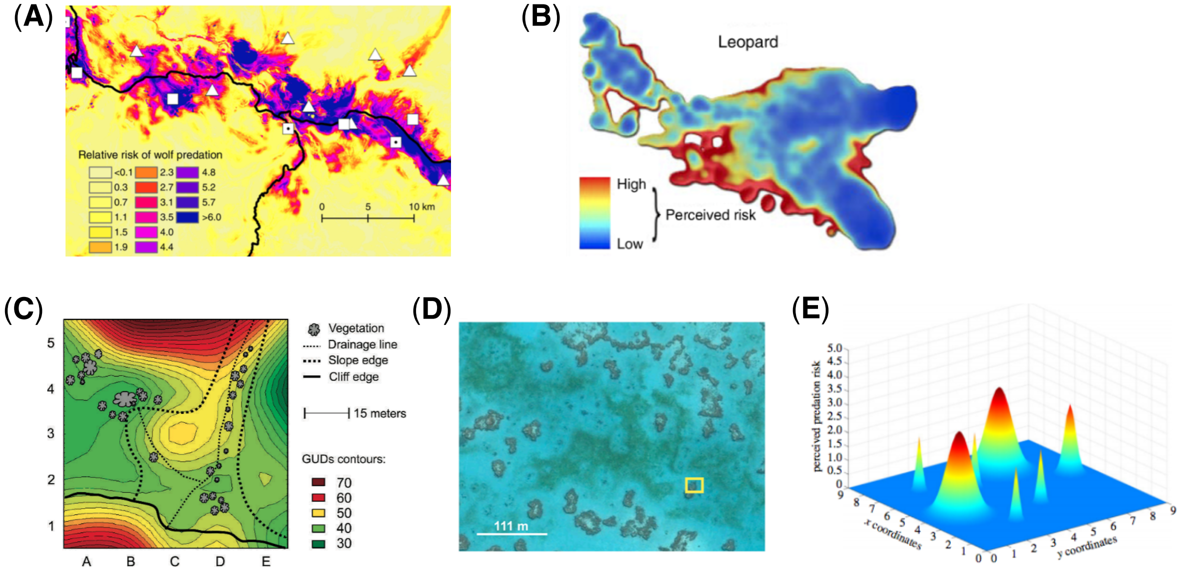

TABLE 1. DEFINITIONS OF THE LANDSCAPE OF FEAR AS APPLIED OR DESCRIBED IN THE LITERATURE, AND THEIR RELATIONSHIP TO OUR FRAMEWORK

Definitions of landscape of fear from the literature	References	Relationship to landscape of fear in our framework
Spatial variation of prey perception of predation risk	[1-3]	Landscape of fear (Figure 1v)
A complex ecological system involving a predator-prey response race	[4-5]	Entire framework (Figure 1)
Spatial variation in predation risk	[6-12]	Spatial variation in predation risk (Figure 1iii)
Spatial variation in predation	[13]	A product of both spatial variation in predation risk (Figure 1iii), prey response (Figure 1vii, viii), and predator response
Conceptual topographic map of predation risk	[14-16]	Optimal or idealized model of spatial variation in predation risk or landscape of fear (Figure 1iii, v)
The distribution of habitat types (with different intrinsic risk)	[17-18]	Physical landscape (Figure 1i)
An area in which prey perceive risk	[19-21]	Arguably any location within landscape of fear (Figure 1v), excluding extremes with near-zero risk perception
Distribution and intensity of sensory cues associated with predators	[22]	Factor mediating the relationship between landscape of predation risk and landscape of fear (Figure 1iv)
Spatial utilization of an area by risk-averse prey	[3, 23-27]	Spatial distribution of prey (Figure 1vii)
Area that excludes fearful prey animals	[28]	Part of spatial distribution of prey (area of complete avoidance; Figure 1vii)
Spatial variation in foraging costs of predation (result of foraging and risk trade-offs)	[4, 29-32]	Component of spatial variation in anti-predator behavior (Figure 1viii)
Spatial variation in interference competition	[33-34]	Analog of the landscape of predation risk (involving competitors, rather than predators and prey)
Output of experimental studies of prey behavior	[35-36]	Quantification of spatial variation in anti-predator behavior (Figure 1viii)
Response of lower trophic levels (e.g. plants) to foraging by prey	[37]	Trophic cascade caused by landscape of fear (consequence of Figure 1vii,viii)
A tool for measuring foraging trade-offs	[30]	Landscape-scale giving-up density experiments (Measure of Figure 1viii)

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TABLE 2. FACTORS THAT DETERMINE THE STRENGTH OF LANDSCAPE OF FEAR (LOF) EFFECTS FOR PREY POPULATION DYNAMICS AND TROPHIC INTERACTIONS

Factor determining strength of LOF effects	***Weak LOF effects***	***Strong LOF effects***
Physical habitat (Figure 1i)	Homogenous physical landscape	Heterogeneous physical landscape
Factors mediating relationship between physical habitat and risk (Figure 1 vi)		
Predator biology	Coursing predator, broad habitat domain	Ambush predator, narrow habitat domain
Prey biology	Strong reliance on morphological (rather than behavioral) defenses, large body size	No morphological defenses, small body size
Predator distribution	Widespread OR rare	Abundant but predictably distributed
Community dynamics	No overlap among predator distributions and hunting strategies	High degree of overlap among predator distributions and hunting strategies
Factors mediating relationship between risk and perception (Figure 1 vii)		
Predation cues	Absent, limited, unreliable	Apparent, reliable, widespread
Prey cognition and sensory perception	Very limited	Advanced abilities
Prey memory learning ability, and experience	Very limited, no prior experience	Advanced learning ability, prior experience with predator
Evolutionary history	Novel predator, OR predator has co-evolved strategies that limit prey perception of risk	Long history of coexistence with predator, with minimal predator co-evolution (perhaps due to many alternative prey species)
Factors mediating relationship between perception and response (Figure 1 viii)		
Cost of response	No foraging trade-offs with anti-predator response (e.g. risky habitat is also poor quality)	Very high fitness cost of anti-predator response
Benefit of response	Limited effectiveness of response	Clear benefit of anti-predator response
Individual condition	Weak or ill individuals respond strongly (compensatory effects)	Individuals at peak fitness respond strongly (additive effects)
Physiological constraints	Many physiological constraints	Few constraints, highly plastic behavior

TABLE 3. METHODS OF MEASURING PREDATION RISK AND PREY RESPONSE ASSOCIATED WITH LANDSCAPES OF FEAR

Phenomenon of Interest	**Measurable components or proxies**	**Methods or data sources**	**Relationship to landscape of fear**
Spatial variation in predation risk	Density and distribution of kill sites (actual predation)	Carcass surveys Inference from GPS telemetry	Predation patterns relate to actual predation risk, and may inform the landscape of fear via direct and indirect cues. However, predation patterns can also be *influenced by* the landscape of fear via fear-induced changes in prey behavior
	Density and distribution of predators (or predator:prey ratio)	GPS telemetry Camera traps Scat, track, or visual surveys Expert knowledge	The density and distribution of predators is associated with direct risk cues, which may influence the landscape of fear. Predation risk arises not only from predator presence but also characteristics of the physical landscape
	Physical landscape correlates of predation risk (habitat type, topography, density/distribution of refugia, human activity)	Remotely sensed imagery (satellite, drone) Field observations (vegetation surveys, mapping of refugia)	The physical landscape sets the stage for predation risk, and may be associated with indirect cues that signal chronic, intrinsic risk and thus inform the landscape of fear. Researchers should have an understanding of how the physical landscape is correlated with risk
	Simulated predation risk	Playback experiments Chemical or visual cues	Simulations allow researchers to manipulate the landscape of fear; however, simulated risk cues may not be perceived in the same way as actual predation risk

Phenomenon of Interest	**Measurable components or proxies**	**Methods or data sources**	**Relationship to landscape of fear**
Behavioral response of prey	Spatiotemporal distribution of prey	GPS telemetry Camera traps Scat, track, or visual surveys	Prey distribution is influenced by the landscape of fear, as animals avoid areas of perceived high risk. Distribution is also influenced by many other spatially variable factors (forage quality, conspecifics, etc.) that should also be studied if possible
	Vigilance	Visual observation (focal samples) Camera trap observations (video)	The landscape of fear influences prey decisions about vigilance, which can increase probability of predator detection. While vigilance generally increases with risk perception, the benefits and costs of vigilance may vary spatially given the physical environment (obstacles, distance to refuge, forage quality, etc.)
	Group size	Visual observation (surveys) Camera traps	In areas of high risk, prey may aggregate to increase probability of predator detection and to dilute risk. Group size is also a function of other factors relating to competition and sociality
	Movement (speed, distance, other metrics)	GPS telemetry	The landscape of fear may shape prey movement, as prey seek to avoid encounters with predators or avoid detection by predators. However, movement ecology is related to many other spatiotemporal factors that should be controlled for if possible
	Foraging (duration, rate, food choice, giving-up density)	Visual observation (focal samples) Giving-up density experiments Effects on vegetation	The landscape of fear can influence spatial patterns of foraging as prey seek to minimize the probability of lethal predator encounters. Giving-up density experiments with a more controlled foraging arena provide one of the most promising avenues to estimate perception of risk by quantifying the foraging cost of predation

Chapter 3. Black-tailed deer navigate contrasting patterns of risk from hunters and mountain lions in space and time

ABSTRACT

Prey animals navigate landscapes of fear, and these landscapes are often conceptualized as static, spatial patterns of risk resulting from a single predator. However, in most cases, prey face risk from several predator species, and this risk varies not only spatially but also across multiple time scales. To understand prey responses to risk from multiple predators, we examined how black-tailed deer (*Odocoileus hemionus*) navigated layered landscapes of fear imposed by hunters and mountain lions (*Puma concolor*). First, to model spatiotemporal variability in risk of harvest by humans, we compiled 20 years of data on harvest locations at the Hopland Research and Extension Center in Mendocino County, California and deployed fine-scale GPS trackers on >300 hunters over three years. To quantify predation risk from wild carnivores, we built models of mountain lion spatiotemporal activity using data from 52 camera traps deployed in the study area. Finally, we used data from a subset of 36 of these camera traps in a systematic grid deployed from 2015 to 2017 to assess the spatiotemporal responses of deer to patterns of risk from both hunters and mountain lions.

We found that humans and mountain lions exhibited distinct, contrasting patterns of spatiotemporal activity: risk from hunters was confined to the daytime and was highest near roads and in open grasslands, while risk from mountain lions was highest during the night and crepuscular periods, and highest in dense chaparral habitat in the northern part of the property, which has greater connectivity with undeveloped wilderness areas. While deer did not avoid areas of greatest risk from humans and mountain lion, they adjusted the timing of their diel activity to reduce the risk of encounters with both types of predators, with stronger responses in areas of higher risk. During the hunting season, deer exhibited greater temporal avoidance of humans than mountain lions, thereby potentially increasing their vulnerability to mountain lions. Our study demonstrates that interactions between predator hunting mode, habitat cover, and anthropogenic disturbance can result in distinct patterns of predation risk from multiple predators that lead to trade-offs for prey species. Furthermore, our study highlights the importance of temporal partitioning as a mechanism of predation risk avoidance when spatial responses are constrained.

INTRODUCTION

Predation risk plays an important role in ecological communities, driving patterns of prey behavior that ultimately shape population dynamics and species interactions (LaManna and Martin 2016). In heterogeneous landscapes, spatial variation in predation risk generates landscapes of fear for prey species, as prey perceive some areas as safer or riskier than others (Laundré et al. 2001, Gaynor et al. 2019). Prey may avoid areas of high risk (Broekhuis et al. 2013), thereby reducing the risks of detection and capture by predators (Lima and Dill 1990). Landscapes of fear can influence the spatial distribution of prey animals (Willems and Hill 2009) and alter spatiotemporal patterns of prey activity and behavior (Valeix et al. 2009b) in diverse systems. Despite recent attention on landscapes of fear (Teckentrup et al. 2018, Peers et al. 2018, Gaynor et al. 2019), important questions remain about how risk-response dynamics influence prey behavior in complex natural systems (Prugh et al. 2019). The landscape of fear framework is useful for conceptualizing links between the physical habitat, predation, and prey behavior, but depictions of static, simplified landscapes do not capture the underlying complexity of dynamic, interactions of many species (Moll et al. 2017).

Prey in most systems do not experience fixed patterns of predation risk from a single predator. Rather, prey must balance complementary and contrasting patterns of risk from diverse predators over multiple spatial scales. At coarse scales, variation in the presence or relative densities of different predator species will shape encounter probabilities, making prey more or less vulnerable in different portions of the landscape (Creel et al. 2007). On finer scales, hunting modes or habitat preferences of different predators interact with the physical environment and prey anti-predator responses to generate spatial heterogeneity in predation risk (Preisser et al. 2007, Atwood et al. 2007, Miller et al. 2013). For example, sit-and-wait or ambush predators rely on cover for surprise attacks and thus closed habitats may be associated with higher risk of encountering these species relative to active or coursing predators (Hopcraft et al. 2005, Schmitz 2005). Physiological constraints also influence how predators are distributed (i.e., the predator's habitat domain;(Preisser et al. 2007). In particular, predators with narrow habitat domains may be restricted to certain areas of a physical landscape, thereby concentrating predation risk in these areas. Vulnerability of prey in a given habitat type is also a function of the prey's anti-predator defenses; the success of strategies like vigilance, crypsis, flight, body size, and aggregation varies with habitat structure (Lima and Dill 1990, Makin et al. 2017).

While landscapes of fear are often presented as static spatial patterns, predation risk at a site may vary across multiple temporal cycles, in ways that differ among predator species. For example, risk of a predator encounter may vary seasonally with changes in predator and prey densities, food requirements, and reproductive status of either species (Druce et al. 2009, Hopcraft et al. 2014). Risk may also vary on shorter time scales as predators shift their home ranges (Valeix et al. 2009a). The relative vulnerability of prey and the efficiency of predators vary with light availability across lunar cycles (Bouskila 1995, Palmer et al. 2017) and diel periods (Tolon et al. 2009, Kohl et al. 2018). In particular, landscapes of fear change dramatically and predictably every day, as darkness reshapes the playing field for interactions between predators and prey with different circadian cycles and sensory modalities (Kohl et al. 2018). Many predators are active only at certain times of the day, perhaps to avoid competitors or their own predators, and therefore restricted to a narrower temporal habitat domain (Smith et al. 2019). These restrictions create dramatically different landscapes of fear at different times of the 24-hour cycle. To minimize predation risk while continuing to meet foraging and other demands, prey may use high-risk places at low-risk times of day (Fischhoff et al. 2007, Kohl et al. 2018, Courbin et al. 2019, Smith et al. 2019).

The dynamic risk landscape created for prey by the accumulated effects of several predators can take many forms. In some cases, predation risk from multiple predators may be additive, with similar spatial and temporal patterns for each predator. Such overlap would intensify the spatiotemporal peaks and troughs of risk for prey (Sih et al. 1998). More often, however, prey must trade off risk from multiple predators that hunt in different habitats or at different times of day (Willems and Hill 2009, Atwood et al. 2009, Morosinotto et al. 2010, Cresswell and Quinn 2013). Minimizing exposure to risk in these scenarios may involve constant adjustments in the habitat selection and behavior of prey. In systems in which risk from multiple predators varies over both space and time, temporal refugia may allow prey to balance risk from multiple predators. For example, roe deer (*Capreolus capreolus*) face distinct patterns of spatial risk from lynx (*Lynx lynx*) and human hunters (Lone et al. 2014): lynx hunt at night and humans by day. Roe deer select different habitats during the day versus at night, presumably to minimize risk from both predators (Lone et al. 2017). However, avoidance of temporally-variable risk is less of an option for prey when that risk overlaps spatially and surrounds a critical resource. For example, to access dry season water holes in Zimbabwe, ungulates must face either daytime risk from human hunters or nighttime risk from lions (*Panthera leo*) (Crosmary et al. 2012a, 2012b). Alternatively, multiple predators may have a risk averaging effect and create a somewhat homogenous landscape of fear. In these cases, it could be adaptive for prey to largely ignore predation risk and prioritize other factors such as food, conspecifics or thermal refugia (Gaynor et al. 2019). The potential for disparate outcomes associated with prey response to multiple predators motivates expanding our studies of carnivore-ungulate systems beyond their current focus on a single predator and prey species (Montgomery et al. 2019).

Study objectives

Fully quantifying the vast complexity of interactions in multi-predator, multi-predator systems over space and time is unrealistic for most wildlife communities. However, ecologists can greatly advance our understanding of landscapes of fear by considering more than one predator or prey in their studies and accepting that risk will vary in both space and time. Here, we set out to provide an example of such an approach with research on the following questions:

1) How do landscape heterogeneity and predator hunting mode interact to generate complementary or contrasting patterns of spatiotemporal risk from multiple predators?
2) How do patterns of prey activity in both space and time map onto patterns of risk generated by multiple predators?

To answer these questions, we examined the spatial and temporal patterns of risk associated with two major predators of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in northern California: mountain lions (*Puma concolor*) and human hunters. Deer are an abundant species in California and are a major prey item for multiple predator species (Allen et al. 2015) and an important game species for hunters (Conover 1997). Given their mixed feeding strategy (Baker and Hansen 1985), deer are able to use a variety of habitats. The absence of strong habitat constraints may facilitate avoidance of risk, allowing deer to incorporate risk into habitat selection as they navigate landscapes of fear.

While coyotes (*Canis latrans*) and American black bears (*Ursus americanus*) also prey on deer at Hopland, they predominantly kill fawns. Furthermore, coyote and bear activity is widespread throughout the study area and not associated with any particular habitat type. Preliminary analyses suggest homogenous patterns of risk from coyotes and bears throughout the property. Any behavioral responses of adults to these predators are likely minimal, and we therefore excluded them from this study and focused instead on the two primary predators of adult deer: hunters and mountain lions.

For both mountain lions and hunters, we examined the natural and anthropogenic landscape features associated with the risk they posed to deer in and characterized the temporal periods during which they impact deer. We then assessed overlap of risk from the two predators in both space and time and examined the relative influence of risk from mountain lions and hunters on the spatiotemporal activity patterns of deer inside and outside of the hunting season. Human hunting is generally constrained to particular seasons, areas, and times of day, and so provides a unique opportunity to evaluate and isolate the effects of risk on a prey species (Proffitt et al. 2009). Furthermore, hunters play an important role as top predators in ecosystems throughout North America, but their effects on the behavior of game species remain understudied. Mountain lions also serve as a useful focal predator species for exploring spatial patterns of risk, given that they are ambush predators with a restricted habitat domain in both space and time (Smith et al. 2019).

We predicted that the spatial and temporal patterns of risk from mountain lions and hunters would contrast with one another, given differences in diel activity patterns and hunting modes. Hunting risk is entirely confined to the daylight hours, whereas mountain lions are generally most active at night. We predicted that hunters would be most active near roads, given that they typically travel in vehicles and use roads as access points, and that mountain lions would be most active in the northern portion of the study area bordering undeveloped land, which facilitates habitat connectivity. We predicted that deer would be most vulnerable to humans in flat, open areas where hunters had longer lines of sight and could more easily detect deer. In contrast, deer should be most vulnerable to mountain lions in rugged, closed areas, where lions are better able to ambush and trap deer.

Given these predicted contrasting patterns of risk, we expected deer to be more nocturnally active in areas of high hunter risk and more diurnally active in areas of high mountain lion risk. Where deer face trade-offs between risks from hunters and mountain lions, we expected stronger avoidance of hunters, due to the predictability of hunting risk and the strong sensory cues associated with the presence of hunters. We expected to observe stronger risk avoidance by deer in time than in space, given that the deer in our study area occur at high densities and exhibit strong side fidelity and may therefore be constrained in their spatial responses. We also expected deer to show seasonal responses to hunting risk, with decreased activity in areas of high hunting risk during the hunting season as compared to outside of the hunting season.

METHODS

Study area

We conducted our research at the Hopland Research and Extension Center (henceforth, Hopland) in southern Mendocino County, California (Latitude: 39.002, Longitude: -123.084; Figure 1). Hopland is a 2,168 hectare research facility operated by the University of California. Located in the Mayacamas Mountains, Hopland is dominated by oak savanna, with a mosaic of habitats including grassland, woodland, and chaparral. Hopland hosts a diversity of large mammal species, including Columbian black-tailed deer, mountain lions (at least three distinct animals), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray foxes (*Urocyon cinereoargenteus*). Of these carnivores, mountain lions, bears, and coyotes are known to prey on deer in the study area, with adult deer most vulnerable to mountain lions, and fawns most vulnerable to bears and coyotes.

There is a network of well-maintained dirt roads throughout Hopland. To the north, Hopland is bordered by a rugged, 25,000 hectare Bureau of Land Management-owned recreation area, providing connectivity to the rest of the Mayacamas Range and expansive remote Mendocino National Forest lands to the north. To the south, Hopland is bordered by settlement and agriculture along highway 101. Hopland maintains a flock of around 600 sheep and there is a history of lethal predator control onsite directed almost exclusively at coyotes.

A public deer hunt occurs at Hopland during the first three weekends (Saturday and Sunday) of the annual California Zone 1 hunting season; the first Saturdays of the public hunts that occurred during this study were August 8, 2015, August 13, 2016, and August 12, 2017. No more than 20 hunters per day were permitted on the site during the days when hunting was allowed, resulting in a maximum of 120 hunters per year. Only bucks with forked antlers (henceforth "legal bucks") were allowed to be harvested. Hunting was permitted throughout the site, with the exception of a 200 ha area near headquarters, staff residences, and other infrastructure.

Determining spatial patterns of risk

Spatial data

We compiled spatial data for the study area, including raster layers that we hypothesized to be related to spatial patterns of predation risk from hunters and mountain lions and to deer activity (Table 1). Any rasters not originally created at a 10m x 10m resolution were resampled to this resolution and clipped to the Hopland property boundaries. Prior to all modeling, we standardized each of the raster layers by setting the mean value of the raster pixels to 0 and the standard deviation to 1 using the normImage function in the RStoolbox package in R (Leutner et al. 2018).

We created a fine-scale habitat map of Hopland by manually digitizing remotely-sensed satellite imagery. We ground-truthed this map in 2015 by navigating to 50 random points and cross-validating their on-the-ground classification with the remotely sensed classification (49 of the 50 classifications matched, for an accuracy of 98%). For our analyses, we condensed habitat into three categories: grassland (20% of study area), woodland (41%), and chaparral (38%).

We used data on slope and elevation from the 10-meter USGS National Elevation Dataset, and imagery from the National Agriculture Imagery Program (NAIP) for 2016 NDVI. We also calculated ruggedness, which considers variability in both slope and aspect within a neighborhood using the Vector Ruggedness Measure tool for ArcGIS, which was adapted from Hobson 1972. We calculated this metric over a series of neighborhood sizes, from 900m^2 to 12,100m^2, to test whether the scale of terrain variation was influential.

In ArcGIS, we created raster layers corresponding to the distance (in meters) to the nearest road, the nearest fence, the nearest water source, the nearest habitat edge (defined as the boundary between two habitat polygons of different types), the boundary with BLM land, the Hopland headquarters, and the Hopland property boundary.

To account for hunter visibility from roads, we established points spaced one meter apart on all roads as potential observation points. Effectively, by establishing points every meter, we created a continuous map of visibility from the road network; using a smaller interval would have been too computationally intensive and ultimately unnecessary, given that all rasters were resampled to a 10x10 m grid size. We divided the road network on the site into segments between road junctions or pull-off locations, and for each segment we masked elevation within a 400m buffer, as this is the maximum distance at which a hunter is likely to locate a deer (Higley 2002). For each segment, we then ran the Viewshed 2 tool in ArcGIS within the surrounding masked elevation, with each of the road points (at one-meter intervals) as an observer point. Each resulting cell value represented the number of points in the road segment from which it was visible. We combined these viewshed rasters to make a visibility surface for the entire site, and we also reclassified them into visible/not visible areas.

Risk of harvest by hunters

A unique historical dataset, combined with recent GPS tracking, allowed us to explore patterns of hunting on fine spatial scales. We quantified the spatial distribution of risk of harvest by hunters by creating a spatial model based on known locations of deer harvests on the study site. We compiled data on the locations of all deer killed during the Hopland public hunt from 1994-2017 (with the exception of 1995, 1996, 1999, and 2001). For the years for which hunting data were available, a total of 465 deer were harvested. The GPS coordinates of each harvest location were determined from pins that hunters placed on a large printed satellite image of the property immediately after returning to headquarters following a kill. For 2015-2017, we validated these points by comparing the hunter-reported locations to the clusters from the hunter GPS tracks described below; the difference between measures was typically <50 meters.

To understand spatial patterns of deer harvest, we compared the spatial characteristics of the 465 harvest locations to those of a set of 2000 random points within the Hopland boundaries (excluding areas where hunting was prohibited). We used the spsample function in the sp package in R to generate the random points (Pebesma & Bivand 2005). We extracted the raster values of each covariate at all harvest sites and all random points using the extract function in the raster package in R (Hijmans 2017).

We used a logistic regression model to determine which spatial covariates influenced harvest risk. We considered all covariates that we expected to have an effect on spatial patterns of harvest, including vegetation type, slope, distance to road, distance to fence, distance to headquarters, ruggedness in a 900 m^2 neighborhood, ruggedness in a 2500 m^2 neighborhood, viewshed, and distance to edge of chaparral habitat. All covariates were continuous variables, with the exception of vegetation, which was categorical. We used the glmulti function in the glmulti package in R (Calcagno 2013) to test all possible combinations of covariates and determined the best fit model based on AICc (corrected for small sample size). To make inferences based on all top models (<2 AICc of the best model), we averaged the coefficients of variables in these models using the coef function. To ensure that correlated covariates were not confounding the results of our analyses, we tested all covariates in the top models for collinearity and confirmed that variance inflation factors (VIF) < 4.

Hunter activity

In addition to modeling risk based on harvest, we also quantified the spatial distribution of hunter activity using GPS loggers. From 2015-2017, we provided each hunter at Hopland (N = 306) with an iGotU GT-600 GPS unit to be carried throughout the day. Participation was voluntary, but the participation rate was 100%. The iGotU units recorded a GPS location every 5 seconds; we down-sampled the locations to every 10 minutes to increase independence of data points and resolve computer processing constraints.

We combined all GPS locations recorded during 2015-2017, excluding points that fell within the zones where hunting was prohibited. Given the extent of this data set, we chose to map hunter activity based on the locations of all points rather than estimating activity based on spatial covariates. To generate a raster layer of hunter activity, we calculated an unweighted Gaussian kernel density estimate based on the locations of all of the points using the sp.kde function in the spatialEco package in R (Evans 2018). We set the distance bandwidth of the Gaussian kernel to 400m.

Mountain lion activity

We modeled the spatial distribution of mountain lion activity in the study area based on camera trap records. We used data from 52 Reconyx HyperFire camera traps set up from 2015-2018: 16 camera traps were placed opportunistically throughout the property (operating for a range of 59 to 1,566 trap-nights, mean 651, SD 569), and 36 were placed systematically in a grid (operating for a range of 388 to 939 trap-nights, mean 569, SD 82). We deployed cameras at the center points of hexagonal grid cells, with each camera located 750 meters away from its six nearest neighbors. After navigating to the pre-determined GPS location in each grid cell, we identified a suitable camera location within 50 meters of that location. When possible, we pointed cameras towards animal trails to maximize detections. All cameras were placed in security boxes attached to trees. Cameras were motion-activated, and took three consecutive photographs per detection event, with a 30-second refractory interval between detection events.

We calculated the number of independent detections of mountain lions by each camera trap. For spatial analysis we defined a record as independent if it occurred at least 15 minutes after the previous record of a mountain lion at the same camera. For temporal analysis, we removed records occurring within 15 minutes of another record at any camera in the same grid cell (resulting in the removal of 8 records). For each camera, we then calculated a mountain lion Relative Activity Index (RAI), corresponding to the number of mountain lion detections per trap-night (RAI = total detections / total trap-nights). We pooled data from 2015-2018, given the relatively low number of mountain lion detections.

We used a generalized linear model to determine the spatial covariates that influenced the mountain lion RAI. Covariates that we expected to affect mountain lion activity included vegetation type, distance to BLM land, distance to headquarters, ruggedness within a 900m^2 neighborhood, ruggedness within a 2500m^2 neighborhood. All covariates were continuous variables, with the exception of vegetation type, which was categorical. We used the glmulti function in the glmulti package in R to test all possible combinations of covariates and selected the model with the lowest AIC. We tested all covariates in the final model for collinearity (ensuring that VIF < 4).

We then predicted and mapped RAI for the entire study area. We used the predict function in the raster package, based on the best model and the raster layers for the corresponding covariates.

Determining temporal patterns of risk

In addition to quantifying and mapping spatial patterns of activity by and associated risk from hunters and mountain lions, we also examined diel (24-hour) activity patterns of these predators. We determined the timing of hunter activity from GPS tracking data; for each subsampled fix (interval of 10 minutes) in which hunters were within legal hunting zone, we considered the hunter to be “active.” We determined the times of hunter risk based on the known times at which deer were harvested from 2015-2017; hunters reported the time of each kill, which we validated using the iGotU GPS data. We determined the timing of mountain lion activity from camera traps, using only images recorded >15 minutes from the previous detection at a given location.

To account for the circularity of 24-hour temporal data and for seasonal differences in sunset and sunrise time, we scaled all times to radians so that $\pi/2$ corresponded to sunrise and $3\pi/2$ to sunset. We used kernel density estimation to model diel activity patterns for mountain lions and hunters, as described by Ridout and Linkie (Ridout and Linkie 2009). We conducted separate analyses for hunter activity and harvest times.

Comparing patterns of risk

To compare spatial patterns of risk from mountain lions and hunters, we first recategorized the model-predicted rasters for hunter harvest and mountain lion activity (based on the model with the lowest AIC, as described above) into "low" and "high" categories. Both rasters had strong bimodal distributions, and we split the low and high categories according to the clear break in the data (Supplementary Figure 1). We then identified each cell in the study area as "Both Low" (low risk from both hunters and mountain lions), "Hunter High" (high risk from hunters, low risk from mountain lions), "Mountain Lion High" (high risk from mountain lions, low risk from hunters), or "Both High" (high risk from both mountain lions and hunters).

To compare temporal patterns of risk from hunters and mountain lions, we calculated a coefficient of temporal overlap, d-hat, using the overlap package in R (Ridout and Linkie 2009). The value d-hat represents the area under the curve formed by taking the minimum of two activity density distributions (0 represents no temporal overlap, and 1 complete overlap). We used the dhat4 formula, as recommended by (Ridout and Linkie 2009) for sample sizes >50, and calculated 95% bootstrap confidence intervals. We conducted these analyses for both hunter activity and harvest times.

Quantifying deer response to risk

We used the grid of 36 camera traps described above (Figure 1) to quantify spatial and temporal patterns of deer activity. We calculated a Relative Activity Index (RAI) for deer at each camera trap and calculated diel activity patterns using kernel density estimation, following the protocols described above for mountain lions. We calculated RAI for all deer combined, and separately for does and legal bucks.

When comparing the spatiotemporal distribution of deer in relation to hunting, we calculated RAI (RAI = total detections / total trap-nights) for the period before the hunt (the one month prior to the public hunt), during the hunt (from the first to the last day of the public hunt; a 16-day period), and after the hunt (the one month after the public hunt). We chose a one month period before and after the hunting period to ensure a large enough sample size while minimizing seasonal confounds resulting from changes in reproductive status.

We determined the level of hunter activity, mountain lion activity, hunter risk, and mountain lion risk at each of the grid camera locations, extracting the raster values from each of the modeled spatial layers. We also binned cameras into "low" and "high" activity and "low" and "high" risk as described above, to create categorical variables associated with each of these layers. We then compared deer RAI in areas of low and high risk and activity, examining interactions with hunting season and habitat type.

We quantified the amount of temporal overlap between deer and hunters in areas of low and high risk, calculating the overlap coefficients as described above. The same procedure was used to quantify temporal overlap between deer and mountain lions. Similarly, we compared diel activity distributions of deer in areas of low and high risk, and inside and outside of the hunting season, to determine whether deer shifted the timing of their activity in response to spatially and seasonally-variable risk.

RESULTS

Patterns of risk from hunters

For black-tailed deer in our study area, risk of predation from human hunters was strongly correlated with vegetation type and distance to road (Table 2; Figure 2). These two predictors were present in all top models of spatial risk. Harvest risk increased closer to roads, and was highest in grassland, intermediate in woodland, and lowest in chaparral. Several other predictors of harvest risk emerged in some (but not all) of the top models: harvest risk increased with ruggedness in a 2,500m^2 window, visibility from road (viewshed), proximity to chaparral edge, headquarters, and fences but decreased with slope and with ruggedness in a 900m^2 window. After distance to road and vegetation type, the most important predictors of harvest risk were ruggedness in a 2,500m^2 window and distance to chaparral edge (Table 2).

Hunters were exclusively diurnal, given that hunting at night is illegal. Hunters were active at all hours of the day with a slight but consistent decline in activity from sunrise to sunset. Harvest times had a large peak at dawn, a smaller peak at midday, and tapered off after sunset. The overlap coefficient between hunter activity and harvest time was 0.887; there was no statistically significant difference in when hunters were active and when they harvested deer (bootstrapped 95% CI: 0.842 – 1.038; overlap with 1.000 indicates a non-significant difference).

GPS tracking of hunters from 2015-2017 revealed that patterns of hunter activity were spatially similar to the modeled patterns of risk based on the locations of harvest locations (Supplementary Figure 2). We used the model of harvest locations for all subsequent analyses because we considered harvest location to be a more direct proxy for the actual risk of being killed by a hunter (Moll et al. 2017).

Patterns of risk from mountain lions

There was a total of 120 mountain lion camera trap detections (29 records from the grid cameras, 91 records from the opportunistically-placed cameras). The relative activity of mountain lions varied with vegetation type (present in both of the top two models) and distance to the BLM boundary (present in only the top model; Table 3; Figure 3). Mountain lion activity was highest in chaparral, intermediate in woodland, and lowest in grassland. Mountain lion activity increased with proximity to the BLM boundary to the north of the property. Mountain lions were generally nocturnal with increased activity in crepuscular hours, showing a strong peak in activity just after sunset and a smaller peak in activity around sunrise.

Comparing patterns of risk

Spatial patterns of risk from hunters and mountain lions were strongly contrasting (Figure 4). After classifying spatial risk associated with each predator species into low and high categories, 24% of the study area was associated with low risk for both hunters and mountain lions, 56% of the area was associated with high risk from hunters only, 20% of the area was associated with high risk from mountain lions only, and <0.01% of the area was associated with high risk from both hunters and mountain lions.

Similarly, temporal patterns of risk differed between mountain lions and hunters (Figure 5; Supplementary Figure 3). The coefficient of temporal overlap between mountain lion activity and hunter activity was 0.379 (95% CI: 0.262 – 0.426); the coefficient between mountain lion activity and hunter harvest times was 0.386 (95% CI: 0.204 – 0.459). In both cases, these outcomes indicate statistically significant differences between diel activity patterns for mountain lions and hunters (bootstrapped confidence intervals do not overlap 1.00).

Deer response to hunting risk

Activity of bucks was lower in areas of higher modeled risk and during the hunting season. RAI values for legal bucks were lower during the hunting season compared to periods before and after the hunt; the decrease in activity during the hunt was more apparent in areas of high hunting risk (Figure 6). None of the differences in RAI values for bucks across seasons or risk levels were statistically significant, perhaps due to the high number of cameras with a buck RAI of 0 (n = 49 (26%) of the 191 camera-seasons included in the analysis). There was no significant difference in RAI values for bucks across seasons (before, during, after) in either low risk (F(2, 82) = 1.04, p = 0.36) or high risk areas (F (2, 103) = 1.18, p = 0.31). There was no significant difference in RAI values for bucks in areas of low and high hunting risk in any time period (before, during, or after hunt; p > 0.05 for all t-tests). RAI values for does revealed no spatial or temporal effects of hunting on their activity (Supplementary Figure 4).

Throughout the study area, the diel activity patterns of bucks and does differed during the public hunting period compared to the period before the hunt (Figure 7A). Before the hunt, legal bucks were somewhat active throughout the day, with a peak of activity around sunset. During the hunt, bucks decreased their daytime activity and shifted their activity peak from sunset to just after sunset (overlap coefficient dhat = 0.745, 95% CI: 0.599 – 0.824). Before the hunt, does exhibited two peaks in their activity: one in the morning between sunrise and sunset, and one just after sunset. During the hunt, does reduced their activity during the morning and increased activity just before sunrise and at sunrise (overlap coefficient dhat = 0.838, 95% CI: 0.779 – 0.884).

These shifts in diel activity patterns during the hunting season resulted in an increase in temporal overlap with mountain lions for does, but not for bucks (Figure 7A). The degree of overlap between does and mountain lions increased from 0.790 before the hunt (95% CI: 0.703-0.859) to 0.843 during the hunt (95% CI: 0.783-0.922), although the 95% confidence intervals overlap, indicating that the difference between overlap coefficients is small. The overlap between bucks and mountain lions was similar before and during the hunt (Before: overlap coefficient = 0.833, 95% CI: 0.789-0.941; During: overlap coefficient = 0.820, 95% CI: 0.741-0.953)

During the hunt, bucks and does adjusted their diel activity patterns in response to spatial patterns of hunting risk (Figure 7B). While bucks in areas of both high and low hunting risk were mostly active at night, those in high-risk areas were relatively less active at sunrise and throughout daylight hours when compared to bucks in low-risk areas. Further, while bucks in high risk areas waited until after sunset to resume activity levels, those in low risk areas were more active around sunset. There was significantly greater temporal overlap of bucks and hunters in areas of low risk (overlap coefficient dhat = 0.396, 95% CI: 0.214 – 0.508) compared to areas of high risk (dhat = 0.117, 95% CI: -0.066, 0.190). Similarly, there was greater temporal overlap between bucks and harvest times in areas of low risk (overlap coefficient dhat = 0.397 (95% CI: 0.183– 0.533) compared to areas of high risk (dhat = 0.120 (95% CI: -0.098 – 0.187), although this difference was not significant.

Similar to bucks, does were less active during the day in areas of high risk compared to areas of low risk. There was significantly greater temporal overlap between doe and hunter activity in areas of low risk (overlap coefficient dhat = 0.508 95% CI: 0.412 – 0.549) than in areas of high risk (dhat = 0.347, 95% CI: 0.245, 0.387). As with bucks, there was greater overlap between doe activity and harvest times in areas of low risk (overlap coefficient dhat = 0.555 (95% CI: 0.355– 0.580) than in areas of high risk (dhat = 0.349 (95% CI: 0.169 – 0.398), although this difference was not significant.

Deer response to mountain lion risk

The mean RAI of deer at cameras in areas of high mountain lion risk (0.61 ± SD 0.32, n = 7) was higher than at cameras in areas of low mountain lion risk (0.44 ± SD 0.39, n = 29), although the difference was not significant (t = -1.15, df = 10.69, p = 0.28; Supplementary Figure 5).

Both deer and mountain lions exhibited crepuscular activity, with detections at camera traps peaking around dawn and dusk. Year-round temporal overlap between deer and mountain lions was high (overlap coefficient = 0.798, 95% CI: 0.713 – 0.876). Mountain lions had a small activity peak at dawn, and a much larger peak at dusk. Deer in areas of lower mountain lion activity (based on modeled RAI) exhibited slightly more activity at dusk than dawn, while deer in areas of higher mountain lion activity exhibited slightly more activity at dawn than dusk (Figure 8). Although temporal overlap between mountain lions and deer was lower in areas of high mountain lion activity (overlap coefficient dhat = 0.737, 95% CI: 0.664 – 0.814) compared to areas of low mountain lion activity (overlap coefficient dhat = 0.816, 95% CI: 0.735 – 0.897), the difference was not statistically significant.

DISCUSSION

Black-tailed deer experience contrasting patterns of spatiotemporal risk from their two primary predators, mountain lions and humans. Natural features like vegetation type and topography interact with the hunting modes of each predator to generate variation in intrinsic risk, while anthropogenic features like roads and development further shape general patterns of hunter and mountain lion activity. Temporal patterns of risk are also markedly different: hunters are exclusively diurnal and mountain lions are crepuscular and nocturnal. These contrasting patterns of risk may create spatiotemporal refuges for deer, which can use high-lion-risk areas during the day and high-hunter-risk areas at night, thus minimizing risk from both predators (Lone et al. 2017, Gehr et al. 2018). While we did not observe any spatial avoidance of predation risk by deer, we detected changes in daily activity patterns of deer in response to seasonal and spatial variation in hunting risk and, to a lesser extent, to spatial patterns of mountain lion risk.

Contrasting patterns of risk from multiple predators

Human infrastructure substantially shaped the distributions of both mountain lions and hunters. Hunters spent much of their time driving on roads in search of bucks, resulting in higher hunter activity and therefore greater risk from hunters near roads. Hunter risk was also somewhat higher near Hopland headquarters, which serves as the activity center for hunting parties. Mountain lion activity was higher in the north near the border with BLM land, which is undeveloped and provides connectivity to the rest of the Mayacamas Mountains. In contrast, the southern portion of the property has a higher level of human activity, and borders vineyards and houses, with highway 101 and the town of Hopland further to the south. It is likely that mountain lions perceive risk from, and therefore avoid, human activity (Smith et al. 2017), especially given the history of lethal predator control in the study area.

About a quarter of the study area was associated with low risk from both hunters and lions, providing a refuge from predation for deer. Much of this low risk zone was located in the south-central portion of the property, which encompasses several residences, office buildings, and a sheep operation and where human activity is particularly concentrated. Hunting is prohibited and mountain lion activity is low. Human infrastructure thus creates a shield for deer, which experience lower risk from both mountain lions and hunters in areas of higher anthropogenic disturbance (Berger 2007). Such human shields may provide a refuge for deer in other portions of California—while deer are thought to be declining in rural areas of the state (CDFW Website), they typically thrive in urban and suburban areas (DeStefano and DeGraaf 2003) and a anthropogenic shield from natural predators and hunters may contribute to this phenomenon (Harden et al. 2005).

With regard to habitat type, the observed contrasting spatiotemporal patterns of risk associated with hunters and mountain lions are consistent with their hunting modes. Given that mountain lions are ambush predators, they tend to attack deer in areas of denser vegetation and more rugged topography (Laundré 2010, Smith et al. 2019) (Wilmers et al. 2013, Benson et al. 2016). Hunters who use rifles often behave similarly to ambush predators, relying on stealth and surprise rather than on chase and strength to take down prey. However, the use of rifles means that hunters can ambush prey from a distance, thus relying more on clear sightlines than on dense cover. Accordingly, we found that hunters are more likely to harvest deer in open grassland areas than in more closed woodland or chaparral habitats, where visibility is limited. It is possible that in other systems where hunters rely more on sit-and-wait tactics and therefore harvest more deer in areas with greater cover, spatial patterns of risk between hunters and mountain lions would be additive rather than contrasting (Norum et al. 2015).

Constraints on the diel patterns of hunting for each predator also generate distinct and predictable temporal habitat domains (Smith et al. 2019). As ambush predators, mountain lions are adapted to hunt under the cover of darkness (Harmsen et al. 2011, Soria-Díaz et al. 2016), while humans are legally restricted to hunting only during the day. Diel patterns of hunting from both predators are therefore predictable. Our findings echo those of earlier studies that documented contrasting patterns of spatial and temporal risk from lynx (also an ambush predator) and hunters for roe deer in forests in Norway (Lone et al. 2017) and Switzerland (Gehr et al. 2018), suggesting that hunted ungulates in diverse systems worldwide may experience contrasting risk from humans and felid predators.

Weak spatial responses to risk by deer

Despite strong spatial patterns of risk associated with each predator species, we found little evidence that deer adjust their spatial activity in response to spatial variation in predation risk. There was no relationship between mountain lion risk and overall deer activity. During the hunting season, there was a slightly greater reduction in legal buck activity at cameras in areas of high hunting risk compared to cameras in areas of low risk; this difference was not significant and was not evident among does, consistent with other studies that have documented greater response by males in populations in which only males were hunted (Paton et al. 2017).

Several factors may contribute to the failure of deer to respond spatially to predation risk. First, mule deer are generally less plastic in their movement paths and home ranges as compared to other ungulate species (Sawyer et al. 2018). In our study system, GPS collar data suggest that these animals exhibit a high degree of site fidelity (even following a catastrophic wildfire in 2018), occur at high densities, and occupy small home ranges to which they confine their activity. Deer at Hopland are therefore unlikely to adjust their home ranges in response to perceived predation risk. Second, the hunting season and preceding months coincide with late summer drought, the period of greatest resource scarcity during the year, and animals tend to exhibit weaker responses to predation risk when food is scarce (Sinclair and Arcese 1995, Oates et al. 2019). Third, even if prey attempt to avoid predators in space, predators seek out areas of high prey density (Sih 1984, Laundré 2010). Prey avoidance may therefore be counteracted by predator attraction, resulting in the absence of a relationship between prey activity and predation risk or predator activity. Finally, given contrasting spatial patterns of risk from hunters and mountain lions, it is not possible for deer to simultaneously avoid both predators in space, although this trade-off only exists during the hunting season.

It is possible that we were not able to capture responses of deer at the appropriate spatial scale; in particular, our ability to evaluate fine-scale spatial responses to predation risk was limited by our reliance on camera trap data. Deer may be selecting habitat to avoid risk within their home ranges, seeking out low-risk habitats at times of day or in areas where risk from a given predator is highest (Moll et al. 2017). For example, a study of African ungulates found that the risk-based selection or avoidance of particular habitats was more important than avoidance of broader areas of carnivore activity (Thaker et al. 2011). Similarly, roe deer in France responded to risk within their home ranges by changing their habitat selection or distance to cover, but did not respond not at broader spatial scales, for example by shifting their home range to areas of lower risk (Padié et al. 2015). In future studies, we plan to deploy GPS collars on deer to understand how risk influences movement decisions and activity patterns within individual home ranges. By quantifying predation risk and prey behavior at multiple scales, we can better evaluate the influence of landscapes of fear on prey behavior (Prugh et al. 2019).

Plasticity in diel activity patterns in response to risk

Although we did not find evidence that deer change their overall use of space in response to predation risk, they exhibited spatial variation in the timing of their diel activity in response to seasonal and spatial patterns of risk. Our results indicate that deer can shift diel activity patterns to minimize encounters with predators. Our finding that deer become more active at night after the onset of the hunting season echoes those of other studies that have documented an increase in nocturnal activity in prey species in response to daytime hunting (Kilgo et al. 1998, Sunde et al.

2009, Thurfjell et al. 2013, Marchand et al. 2014, Hertel et al. 2016, Espinosa and Salvador 2017). Notably, the change in the timing of activity by both bucks and does was stronger in areas of higher hunting risk, suggesting that deer perceive spatial variation in risk and respond by adjusting temporal activity.

Similarly, we found that deer reduced their temporal overlap with mountain lions when in areas of higher mountain lion activity by switching their peak activity from dusk to dawn, when lions are less active. Over evolutionary time scales, carnivores and ungulates have engaged in an arms race and plasticity in ungulate diel activity patterns likely evolved as an anti-predator strategy (Wu et al. 2018). Generally, however, both mountain lions and deer are crepuscular with a high degree of overlap in diel activity. Many ungulates, including deer, remain morphologically and physiologically adapted to crepuscular activity, when they can effectively forage under low light conditions and avoid temperature extremes that occur during the day and at night (Bennie et al. 2014). Carnivores, including mountain lions, have co-evolved to track their prey over diel cycles and other studies of diel patterns of mountain lions and their most common prey have also found a high degree of synchrony (Harmsen et al. 2011).

We found some evidence that deer temporal shifts are stronger in response to risk from hunters than to risk from mountain lions and, when faced with trade-offs, deer may minimize temporal overlap with hunters rather than with mountain lions. Hunting risk is highly predictable at both seasonal and daily scales and hunters are conspicuous on the landscape, and prey generally respond to risk from predators associated with more reliable cues (Makin et al. 2017). Previous studies of hunted elk populations documented greater changes in elk grouping patterns and movement rates (Proffitt et al. 2009) and vigilance (Ciuti et al. 2012) in response to risk from hunters than to risk from wolves. Our study suggests that hunting risk similarly generates a greater response in deer than risk associated with mountain lions, an ambush predator, which are typically thought to have more predictable spatial patterns of risk than coursing predators like wolves.

Consequences for deer populations

Although does did not exhibit a spatial response to hunting, and the response of bucks was weak, both does and bucks exhibited changes in their diel activity patterns in response to both hunting season and spatial patterns of hunting risk. Notably, the shift in diel activity patterns of does after the onset of the hunting season led to a decrease in their temporal overlap with hunters, but also increased their temporal overlap with mountain lions. Given that only bucks are hunted, hunting may therefore present an ecological trap to does, in which does seek to minimize predation risk by avoiding hunters but actually increase predation risk by coming into greater contact with mountain lions (Kilgo et al. 1998, Robertson and Hutto 2006).

Contrasting patterns of risk from multiple predators may lead to predator facilitation, in which the combined effects of multiple predators on prey are synergistic rather than additive. At Hopland, contrasting risk may thus increase overall predation rates if bucks are unable to avoid both hunters and mountain lions simultaneously (Soluk 1993, Atwood et al. 2009) or if does increase their vulnerability to mountain lions. A study of roe deer in Switzerland documented super-additive mortality of roe deer from hunting as a result of predator facilitation, finding that avoidance of hunters by deer led to increased predation by lynx (Gehr et al. 2017). While contrasting patterns of risk may result in an increase in lethal effects of predation, we would also expect a decrease in the non-lethal effects of predation. These non-lethal (risk) effects of predation arise as a result of costly behavioral responses to risk, but prey may exhibit weak anti-predator responses in the face of trade-offs between risk from multiple predators (Creel and Christianson 2008, Cresswell and Quinn 2013). Contrasting risk from multiple predators may therefore reduce the importance of the landscape of fear for individual fitness and population dynamics.

CONCLUSION

Studies of the landscape of fear often characterize static patterns of risk from a single predator, but our understanding of complex predator-prey dynamics in natural landscapes requires a more nuanced examination of predator and prey activity over space and time. Here, we demonstrated that black-tailed deer face contrasting spatial and temporal patterns of risk from mountain lions and hunters. While deer do not avoid areas of high risk, likely due to constraints on space use and strong site fidelity, they adjust the timing of their activity in response to spatial patterns of risk to minimize encounters with predators. As large carnivore populations in North America continue to expand, prey species will increasingly face risk from multiple predators, including hunters, which play an outsized but understudied role in many systems. It is increasingly important to understand the role of risk from multiple species in driving prey behavior and population dynamics, particularly in areas of human disturbance.

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FIGURE 1. STUDY SITE

A) The study was conducted at the Hopland Research and Extension Center in Mendocino County, California (indicated with the blue star). B) Detail of study site, showing vegetation cover, locations of gridded camera traps, buildings and parking, and areas where hunting is prohibited (diagonal lines).

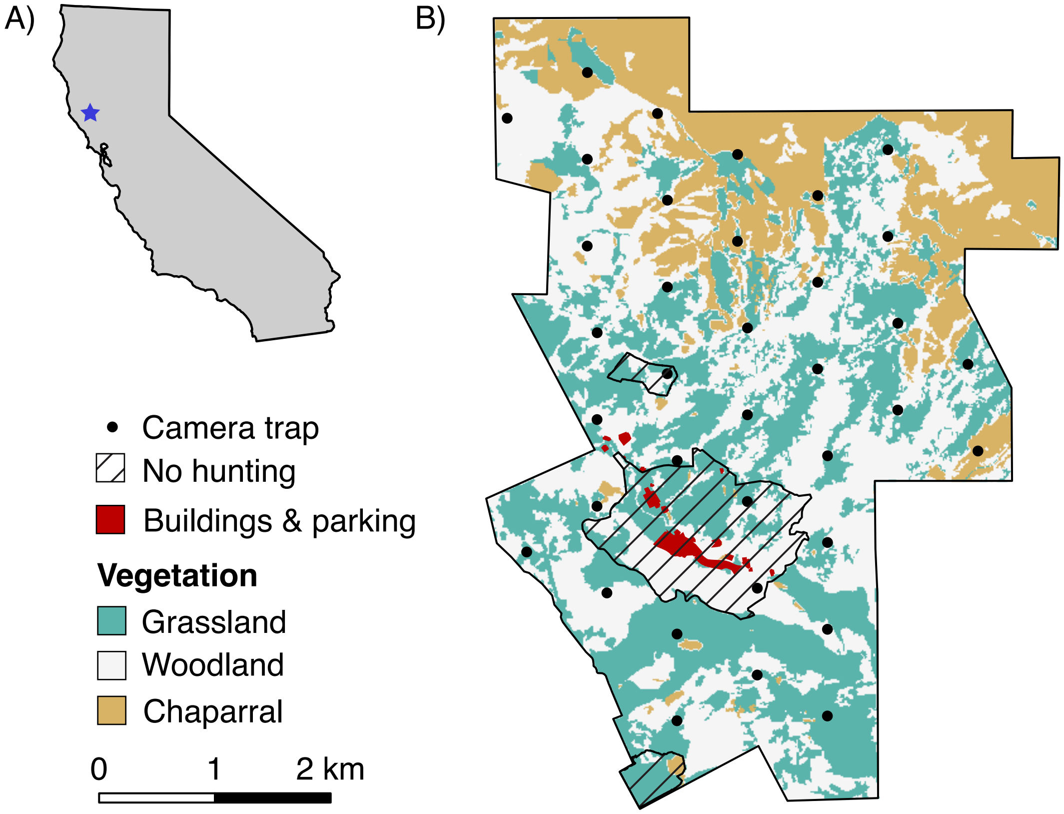


FIGURE 2. SPATIAL PATTERNS OF RISK FROM HUNTERS

Predicted risk of hunter harvest (successful kills) on black-tailed deer, modeled based on historical harvest locations. Roads are indicated on the map, and areas where hunting is prohibited are shown in white.

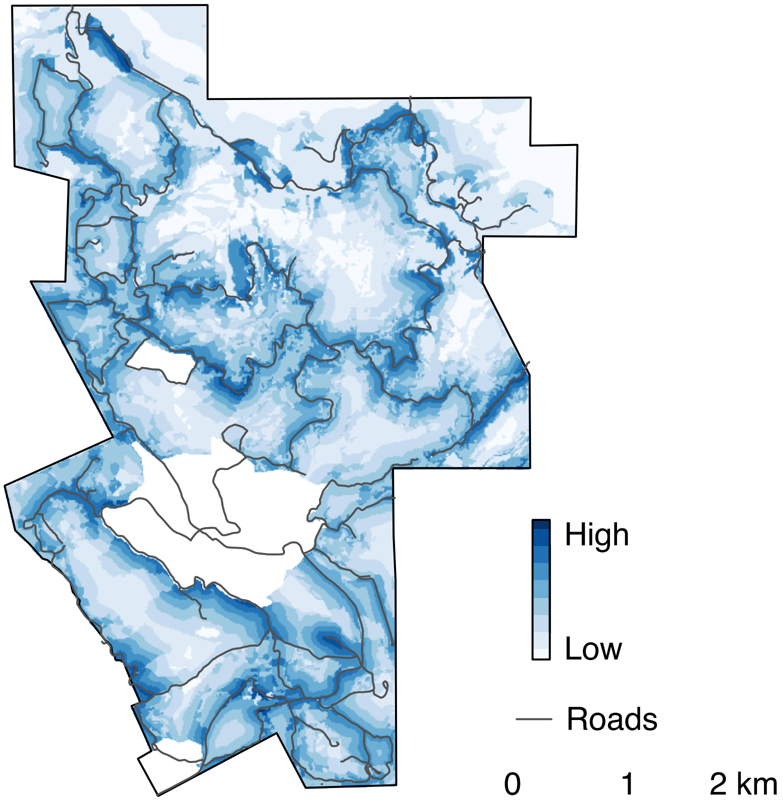


FIGURE 3. SPATIAL PATTERNS OF RISK FROM MOUNTAIN LIONS

Predicted mountain lion activity in the study area, modeled from camera trap data (Relative Activity Index = detections / trap-night).

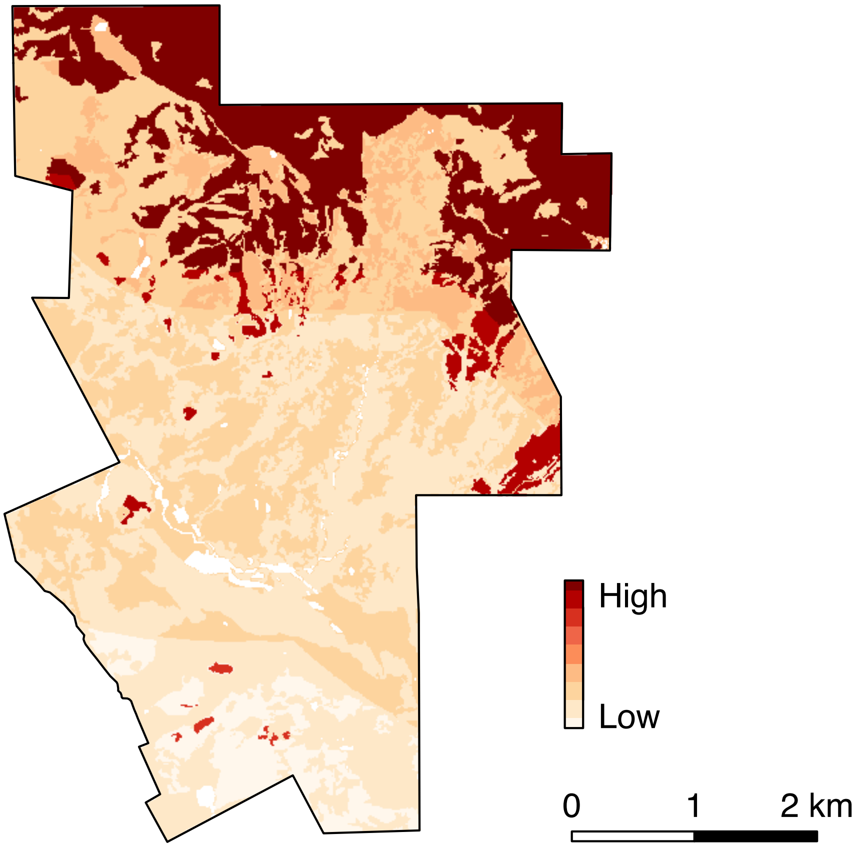


FIGURE 4. CONTRASTING PATTERNS OF RISK FROM MULTIPLE PREDATORS

There are distinct spatial patterns of risk from the two predators of black-tailed deer at Hopland. We identified areas of low and high risk from hunters and mountain lions by reclassifying the hunter harvest model raster and the mountain lion relative activity index model raster according to clear breaks in each dataset (both were bimodal; see Supplementary Figure 1). Areas where both mountain lion risk and hunter risk are high are virtually non-existent and account for <0.001% of the study area.

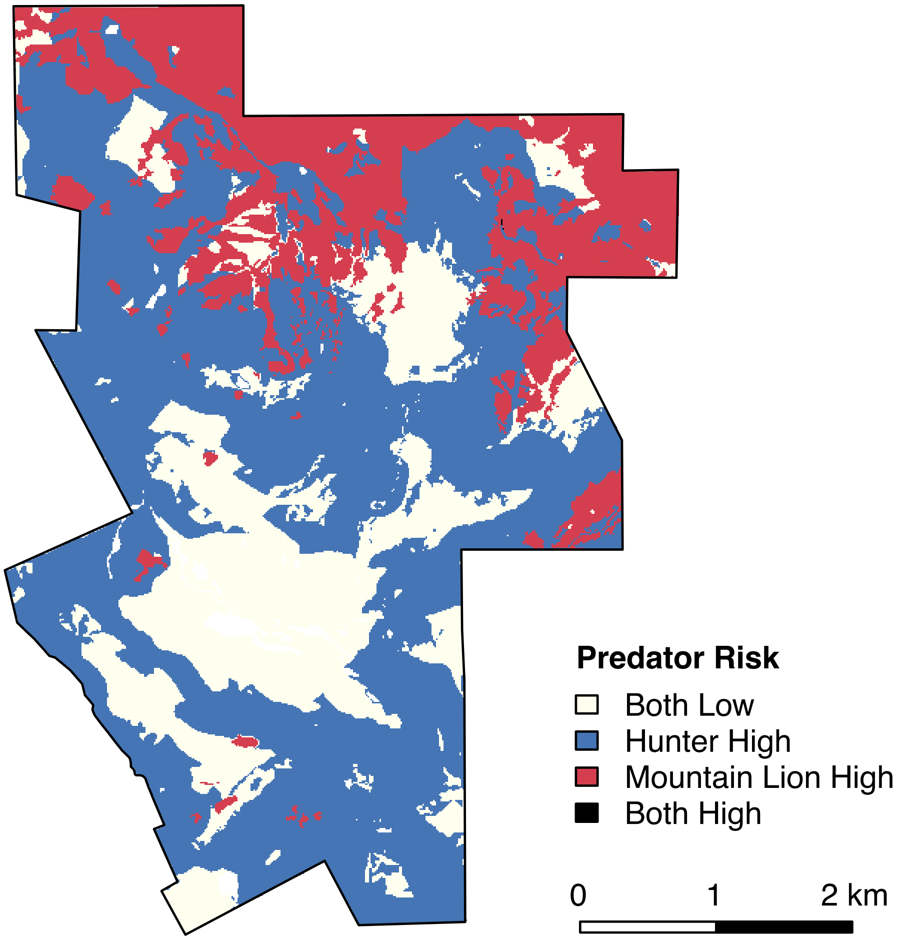


FIGURE 5. TEMPORAL PATTERNS OF RISK FROM MULTIPLE PREDATORS

Kernel density distributions representing the timing of mountain lion and lion detections, where the area under the curve is equal to 1. There are distinct temporal patterns of risk from the two predators of black-tailed deer at Hopland. Mountain lions are mostly active at night, with a peak of activity around sunset and small peak around sunrise. Hunters are exclusively active during the daytime.

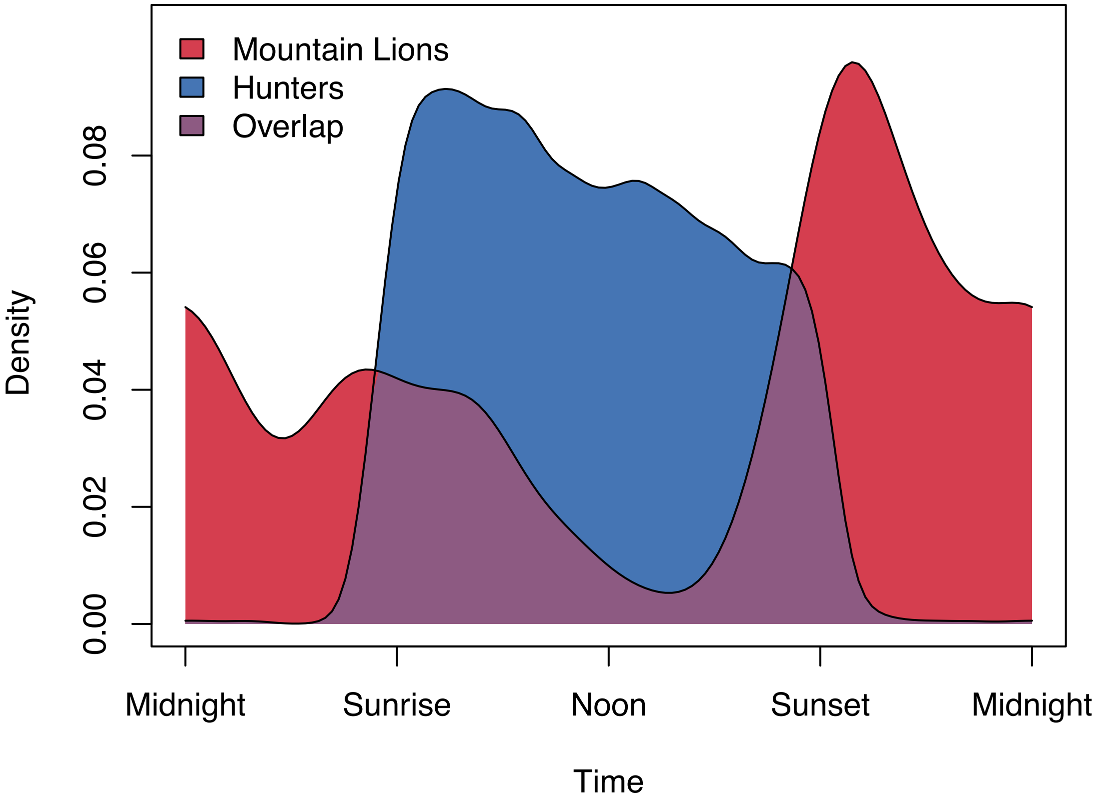


FIGURE 6. BUCK ACTIVITY IN RELATION TO HUNTING RISK IN SPACE AND TIME

The Relative Activity Index (RAI) of legal bucks was generally low, but decreased slightly during the hunting season. This decrease was more apparent at cameras in areas of high hunting risk (n=21) than those of low risk (n=15). None of the differences in buck RAI across seasons or risk were statistically significant. The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points).

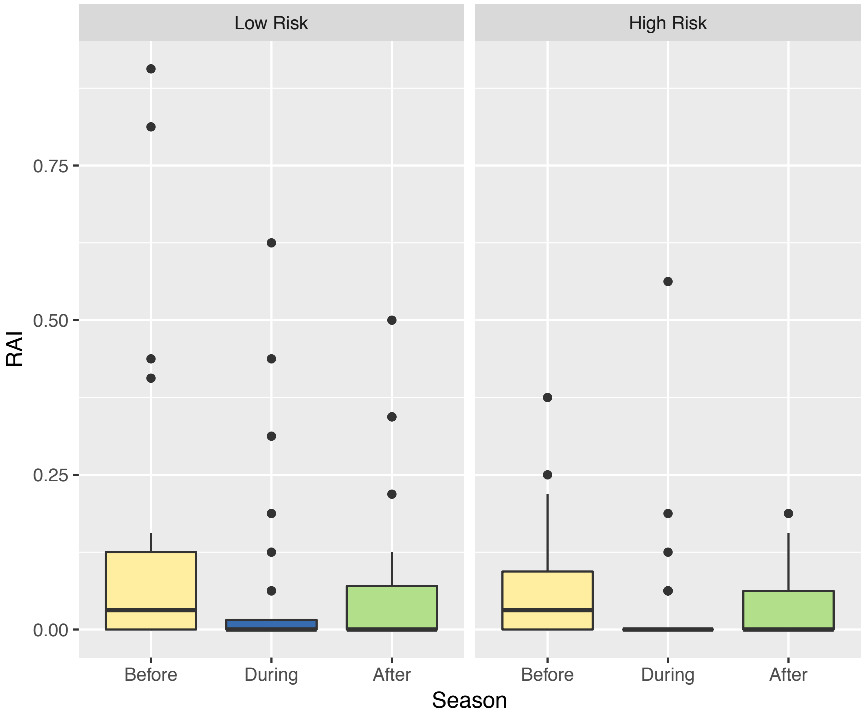


FIGURE 7. DEER DIEL ACTIVITY PATTERNS IN RELATION TO HUNTING RISK

Kernel density distributions representing the timing of buck and doe detections in response to hunting season and spatial risk. The activity patterns of both does and bucks shifted to be more nocturnal in response to the hunting season to reduce temporal overlap with hunters, particularly in areas of higher hunting risk. A) Diel activity patterns of deer in the entire study area, before and during the hunting period. During the hunt, the overlap between does and mountain lion activity patterns increased. B) Diel activity patterns for deer during the hunting period, in areas of low hunting risk (n = 15 cameras) and high hunting risk (n = 21 cameras), with hunter activity shown as a dotted line.

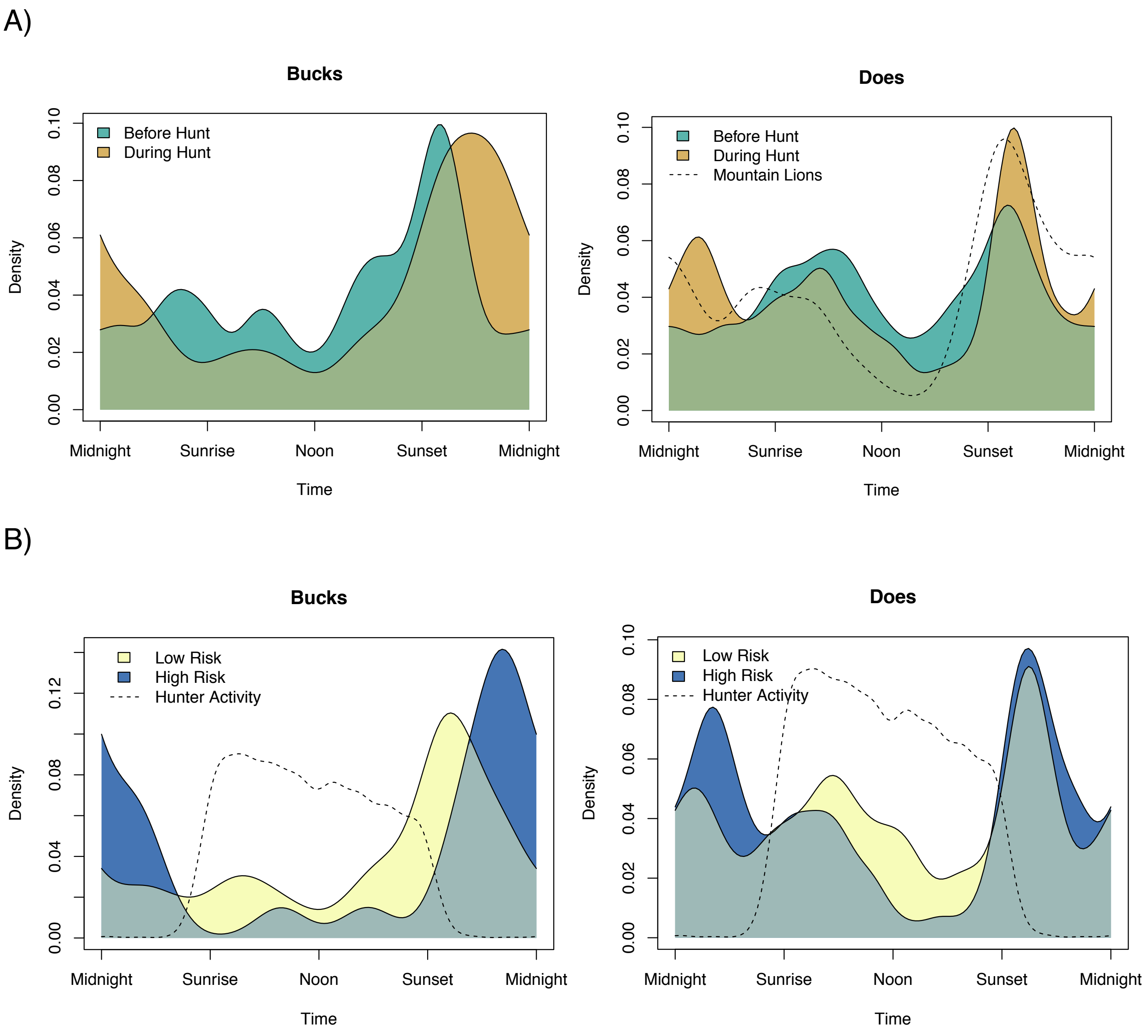


FIGURE 8. DEER AND MOUNTAIN LION TEMPORAL ACTIVITY

Kernel density distributions representing the timing of mountain lion detections, and deer detections in response to spatial patterns of mountain lion risk. Deer and mountain lions exhibited crepuscular activity patterns year-round. Mountain lions were most active at dusk, and deer exhibited slight adjustments in the timing of their activity in response to spatial patterns of mountain lion activity. While deer in areas of low mountain lion activity were slightly more active at dusk than at dawn (n = 29 cameras), deer in high risk areas were more active at dawn than dusk (n = 7 cameras), possibly to avoid encounters with mountain lions.

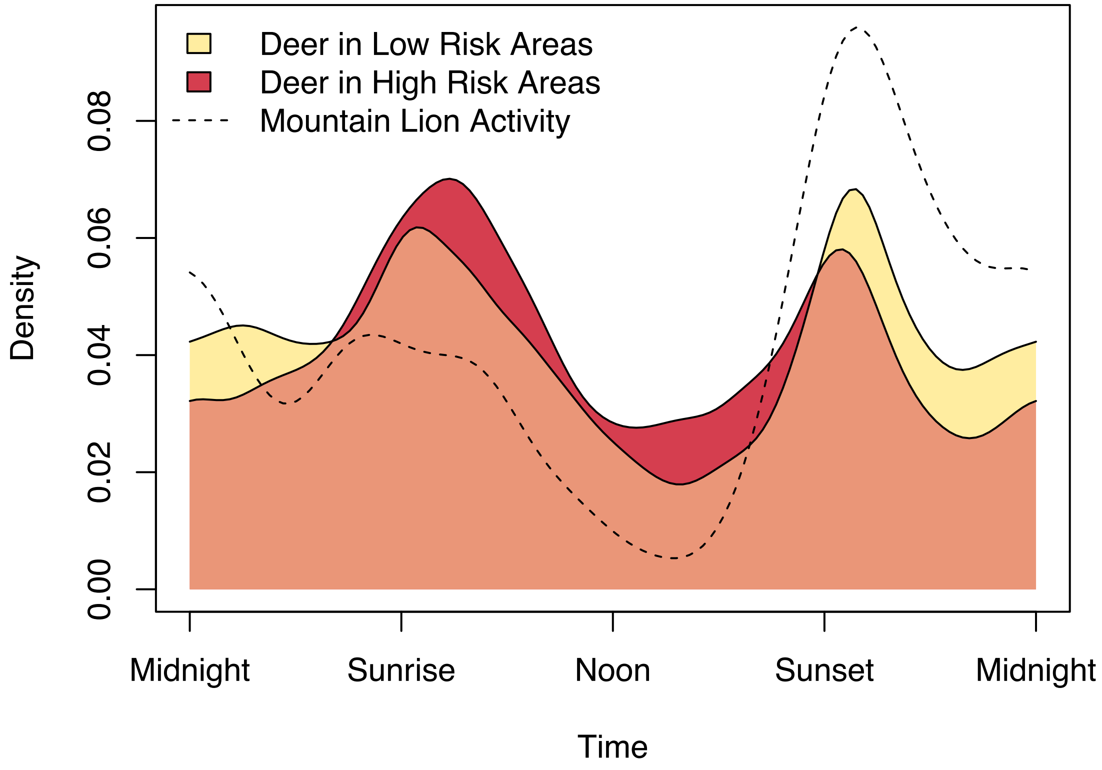


TABLE 1. SPATIAL VARIABLES INCORPORATED INTO RISK MODELS

We predicted that the following natural and anthropogenic variables would influence spatial patterns of risk for black-tailed deer at Hopland. We generated raster layers corresponding to each variable, which we incorporated into models of spatial risk from hunters and mountain lions. We were conservative in our selection of predictor variables for the mountain lion models, given a low sample size of camera traps.

	Variable	**Predicted relationship with hunting risk**	**Predicted relationship with mountain lion risk**
Natural	Vegetation (grassland, woodland, and chaparral)	Higher risk in more open habitat (grassland), and lower risk in more closed habitat (chaparral)	Higher risk in more closed habitat (chaparral), and lower risk in more open habitat (grassland)
	Ruggedness (in $900m^2$ and $2,500m^2$ windows)	Higher risk in less rugged areas	Higher risk in more rugged areas
	Distance to chaparral edge	Higher risk near chaparral edge	Higher risk near chaparral edge
	Slope	Higher risk in flatter areas	NA
	Viewshed	Higher risk in areas with greater viewshed (more visibility from point)	NA
Anthropogenic	Distance to BLM land	NA	Higher risk in proximity to BLM land (smaller distance)
	Distance to road	Higher risk in proximity to roads (smaller distance)	NA
	Distance to headquarters	Higher risk in proximity to headquarters (smaller distance)	NA
	Distance to fence	Higher risk in proximity to fences (smaller distance)	NA

TABLE 2. FACTORS ASSOCIATED WITH SPATIAL RISK FROM HUNTERS

Spatial features associated with the probability of deer harvest by hunters, as determined from a logistic regression comparing characteristics of harvest and random locations. Model-averaged estimates and confidence intervals are reported. All covariates were standardized prior to modeling. For covariates corresponding to the distance to a feature, a negative estimate means that hunter harvest risk increased closer to that feature. The reference value for the vegetation layer is chaparral, so positive estimates mean that hunting risk was higher in woodland and grassland as compared to chaparral.

Covariate	**Estimate (with 95% Confidence Interval)**	**Number of Top Models (<2 ∆AICc) Present**	**Relative Importance**
Intercept	-2.991 (-3.408 – -2.574)	8	1.000
Vegetation = Woodland	1.331 (0.884 – 1.778)	8	1.000
Vegetation = Grassland	1.944 (1.494 – 2.394)	8	1.000
Distance to road	-0.619 (-0.759 – -0.479)	8	1.000
Ruggedness (2,500m^2)	0.119 (-0.019 – 0.257)	7	0.898
Distance to chaparral edge	-0.119 (-0.270 – 0.031)	7	0.892
Distance to headquarters	-0.031 (-0.139 – 0.076)	3	0.279
Viewshed	0.004 (-0.017 – 0.024)	1	0.107
Ruggedness (900m^2)	-0.003 (-0.023 – 0.017)	1	0.092
Slope	-0.002 (-0.018 – 0.014)	1	0.092
Distance to fence	-0.0002 (-0.011 – 0.011)	1	0.087

TABLE 3. FACTORS ASSOCIATED WITH SPATIAL ACTIVITY OF MOUNTAIN LIONS

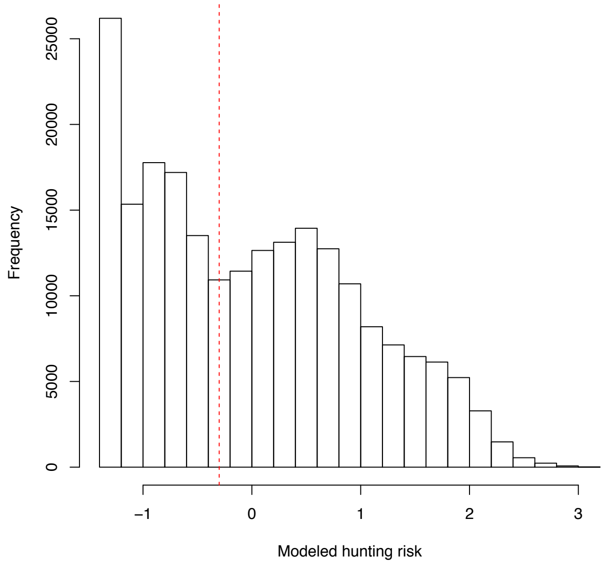
Spatial features associated with mountain lion activity, as determined from a generalized linear model of mountain lion Relative Activity Index at 52 camera traps. Model-averaged estimates and confidence intervals are reported. All covariates were standardized prior to modeling. A negative estimate for distance to BLM boundary means that mountain lion activity increased closer to BLM land. The reference value for the vegetation layer is chaparral, so negative estimates mean that mountain lions were less active in woodland and grassland as compared to chaparral.

Covariate	**Estimate (with 95% Confidence Interval)**	**Number of Top Models (<2 ∆AICc) Present**	**Relative Importance**
Intercept	-0.001 (-0.002 – 0.001)	2	1.000
Vegetation = Woodland	-0.010 (-0.014 – -0.007)	2	1.000
Vegetation = Grassland	-0.009 (-0.012 – -0.005)	2	1.000
Distance to BLM boundary	-0.001 (-0.002 – 0.001)	1	0.655

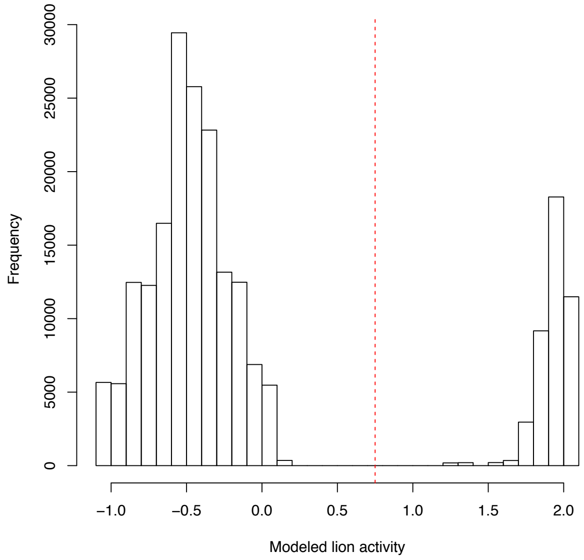
SUPPLEMENTARY FIGURE 1. HISTOGRAMS OF MODELED HUNTER RISK AND MOUNTAIN LION ACTIVITY

Histograms showing the distribution of cell values of (A) modeled hunter risk and (B) modeled mountain lion activity in the study area, after rasters have been standardized. Dashed red lines indicate the cut points used to distinguish between low and high risk.

A)

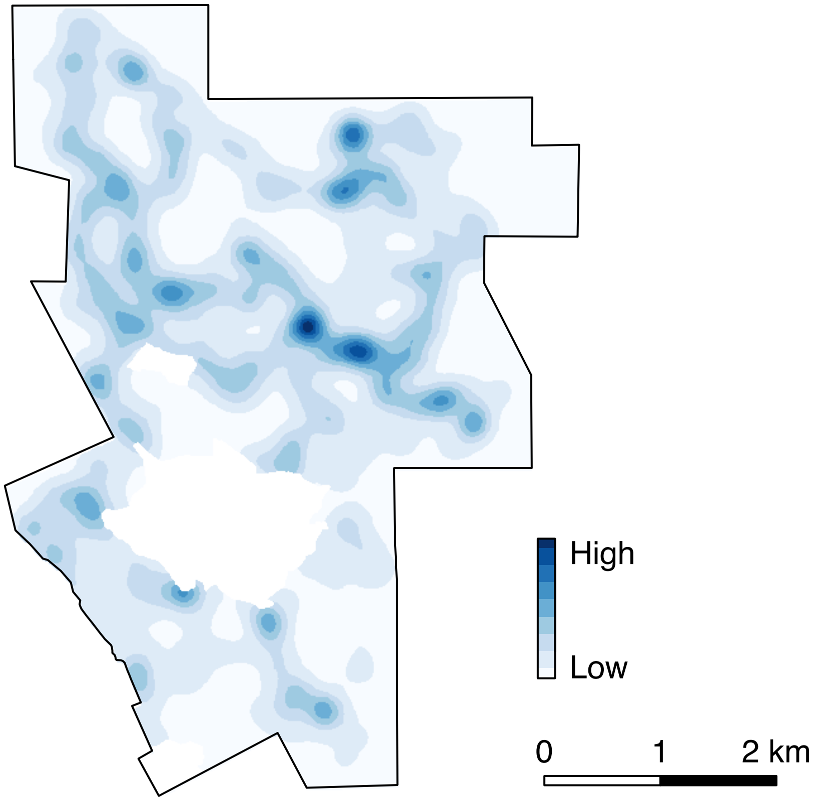


B)



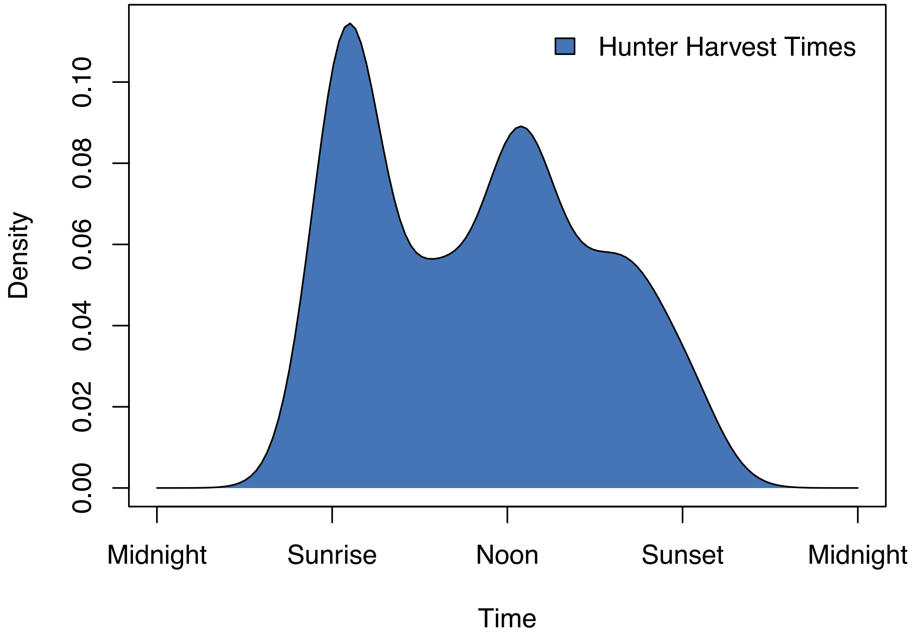
SUPPLEMENTARY FIGURE 2. SPATIAL PATTERNS OF HUNTER ACTIVITY

Kernel density estimates of hunter activity, based on GPS tracking of hunters from 2015-2017.



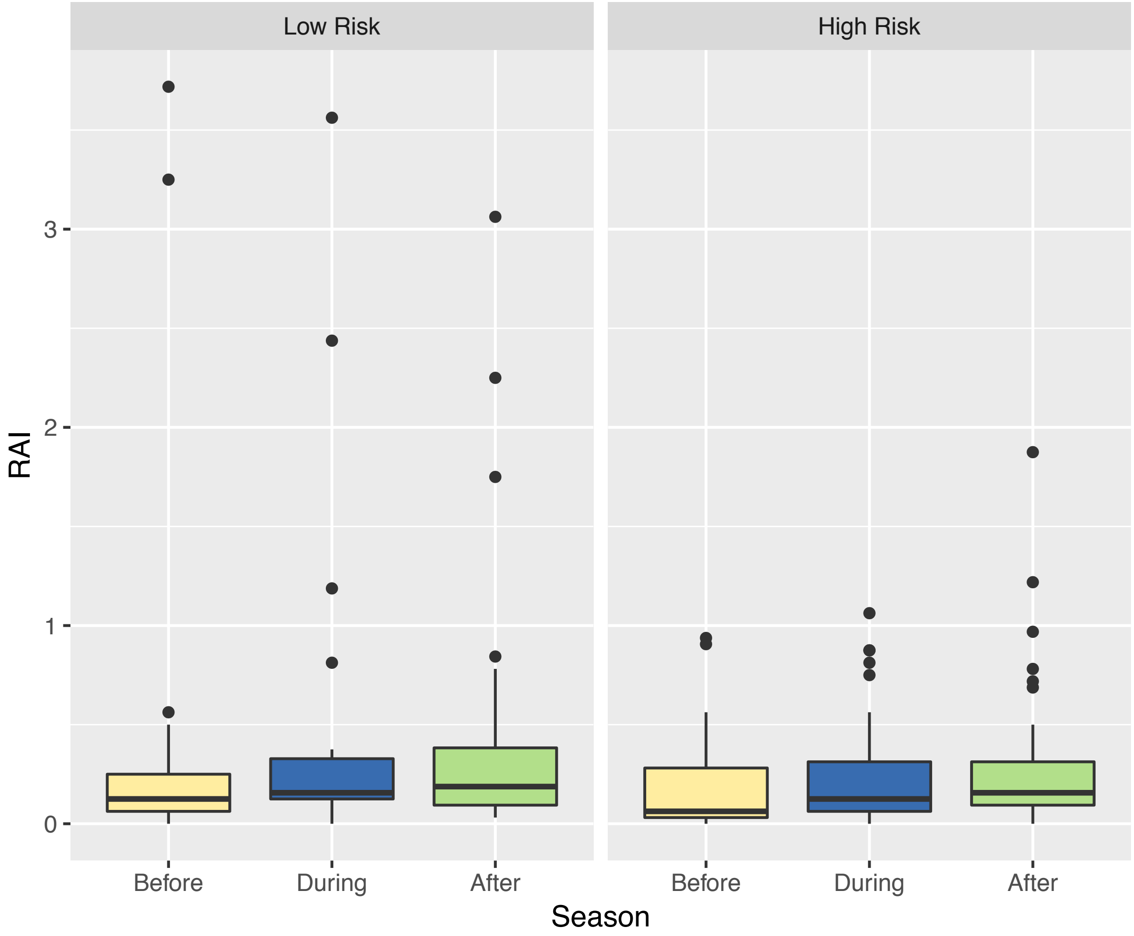
SUPPLEMENTARY FIGURE 3. HUNTER HARVEST TIMES

Kernel density distributions representing the timing of deer harvest by hunters from 2015-2017 (n = 32 kills), based on iGotU GPS data. Deer are exclusively harvested by hunters during the day. Most deer are harvested around dawn, with a smaller peak around noon.



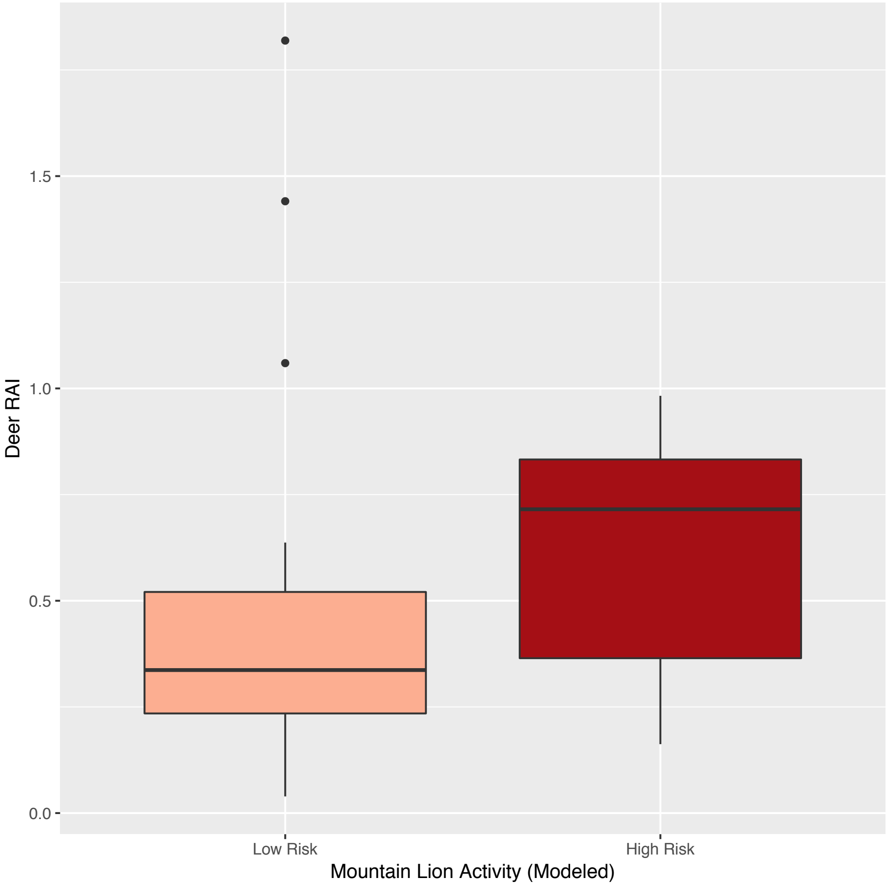
SUPPLEMENTARY FIGURE 4. DOE ACTIVITY IN RELATION TO HUNTING RISK IN SPACE AND TIME

The Relative Activity Index (RAI) of does was similar in the periods before, during, and after the hunt, and in areas of high and low hunting risk. The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points).



SUPPLEMENTARY FIGURE 5. DEER AND MOUNTAIN LION ACTIVITY

Deer RAI was slightly higher at cameras in areas of high mountain lion activity (n=7) than at cameras of low mountain lion risk (n=29). This difference was not statistically significant.



Chapter 4. The influence of human disturbance on wildlife nocturnality

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ABSTRACT

Rapid expansion of human activity has driven well-documented shifts in the spatial distribution of wildlife, but our effects on the temporal dynamics of animals have rarely been quantified. We examined anthropogenic impacts on mammal diel activity patterns, conducting a meta-analysis of 76 studies of 62 species from 6 continents. Our global study revealed a strong effect of humans on daily patterns of wildlife activity. Animals increased their nocturnality by an average factor of 1.36 in response to human disturbance. This finding was consistent across continents, habitats, taxa, and human activities. As the global human footprint expands, temporal avoidance of humans may facilitate human-wildlife coexistence. However, such responses can result in dramatic shifts away from natural patterns of activity, with consequences for fitness, population persistence, community interactions, and evolution.

INTRODUCTION

The global expansion of human activity has had profound consequences for wildlife. Research has documented the effects of habitat destruction and defaunation on species and ecosystems (Dirzo et al. 2014), but the indirect or non-lethal pathways through which humans alter the natural world have largely escaped quantification. Human presence can instill strong fear in wild animals, which may adjust their activity to avoid contact with humans (Frid and Dill 2002). As in natural predator-prey systems, such risk avoidance can have important non-lethal effects on animal physiology and fitness, affecting demography and triggering trophic cascades (Preisser et al. 2005).

The study of fear effects on animals has focused mainly on spatial avoidance, propelled by rapid advances in wildlife tracking, remote sensing, and computational methods (Frid and Dill 2002, Tucker et al. 2018). However, as the human footprint expands (Venter et al. 2016), there are fewer areas where animals can seek spatial refuge from people. In places where wild animals co-occur with humans, animals may minimize risk by separating themselves in time rather than in space (Kronfeld-Schor and Dayan 2003). Temporal partitioning is a common, even intrinsic, feature of ecological communities, shaping spatiotemporal patterns of predation and competition (Carothers and Jaksić 1984, Kronfeld-Schor and Dayan 2003, Lesmeister et al. 2015). Here we show that humans, as a diurnal apex “super-predator,” (Clinchy et al. 2016) are driving increases in nocturnal activity across diverse mammalian taxa.

METHODS

To quantify temporal shifts in wildlife activity in response to humans, we conducted a meta-analysis of published literature on the activity of mammals across gradients of human disturbance. Our dataset included 141 effect sizes for 62 mammal species, representing 21 families and 9 orders, and spanned 6 continents (Figure 1). We restricted our analysis to medium- and large-bodied mammals (>1kg in body size (Jones et al. 2009)), given their large space needs, potential for conflict with humans, and high levels of behavioral plasticity, and because data were widely-available on their 24-hour activity patterns. Within each study, we compared animal activity in low and high human disturbance treatments. We classified areas, time periods, or individual animals as being associated with low or high disturbance based on categorical descriptions of the study system, or binned distance or elapsed time from an anthropogenic disturbance.

For each species in each study, we calculated the Risk Ratio (RR) as a measure of effect size. We compared the percentage of activity that occurred at night (as measured by motion-activated cameras, telemetry devices, and direct observation) at sites or during seasons of high human disturbance (X_h) to nighttime activity under low disturbance (X_l), with RR = $\ln(X_h/X_l)$). A positive RR indicated a relatively greater degree of nocturnality in response to humans, while a negative RR indicated reduced nocturnality. We used meta-analytical random effects models to estimate the overall effect of human disturbance on nocturnality and to compare responses across types of human disturbance, species traits, habitats, continents, and study methods. We also used multivariate models to explore the relative importance of these factors using an information-theoretic approach.

RESULTS

Our analysis revealed a striking increase in nocturnal activity. Overall, mammal nocturnality increased by a factor of 1.36 [95% confidence interval: 1.23-1.51] in areas or time periods of high human disturbance relative to low-disturbance conditions. For example, an animal that typically split its activity evenly between the day and night would increase its proportion of nocturnal activity to 68% of total activity near human disturbance. Of the 141 effect sizes, 83% corresponded to an increase in nocturnality in response to humans (Figure 1b). This finding indicates a significant, widespread increase in nocturnality among mammals living alongside people.

Our analysis spanned a wide range of human activities associated with diverse stimuli representing different levels of risk to wildlife, including lethal activities (*e.g.*, hunting, retaliatory persecution), non-lethal activities (*e.g.*, hiking, natural resource extraction), and human infrastructure (*e.g.*, urban development, roads, agriculture). There was a significant increase in nocturnality in response to all forms of human presence (Figure 2), signaling the robustness of our findings. Surprisingly, non-lethal human activities generated similar shifts in wildlife diel patterns as lethal activities (Figure 2), suggesting that animals perceive and respond to humans as threats even when they pose no direct risk.

We expected temporal responses of wildlife to vary across species, given interspecific differences in biology such as variation in morphology and behavior. Body sizes of the 63 species analyzed ranged from the common opossum (*Didelphis marsupialis*, 1.13 kg) to the African elephant (*Loxodonta africana*, >3,500 kg). Mammals of all body size classes showed a strong response to human activity, although there was a slight trend toward a greater response among larger-bodied species (Figure 2), perhaps because they are more likely to be hunted and harassed or because their space needs force them into more frequent contact with people. Across trophic levels, species also exhibited similar responses to human activity (Figure 2). Even apex carnivores, which from an evolutionary perspective have typically faced little or no predation risk from other species, responded to humans by becoming more active at night. Species that are typically diurnal showed an increase in nocturnality, and even crepuscular and nocturnal species became more strongly nocturnal around humans (Figure 6a). Human activity increased wildlife nocturnality across continents and habitat types (Figure 6b,c). Study method (camera trap, telemetry, or direct observation), human disturbance treatment (space or time), and continent were included as predictors of effect size in the best multivariate models (Tables 3, 4).

DISCUSSION

The absence of increased nocturnal activity by wildlife in many of the studies examined does not necessarily indicate an absence of human impact. Differences in age, sex, reproductive status, and personality may shape responses and mask patterns at the population level (Hertel et al. 2017). For example, in one population of brown bears (*Ursus arctos*), human recreation induced temporal shifts among adult males that created additional daytime feeding opportunities for females, which are often otherwise outcompeted by males for access to resources (Nevin and Gilbert 2005). Alternatively, ecological and morphological constraints may limit behavioral plasticity, causing individuals to remain active during the daytime in the presence of humans, thereby incurring the cost of increased stress or energetically-expensive anti-predator behaviors (Gill et al. 2001). Animals living alongside humans in disturbed ecosystems may face additional constraints (*e.g.*, limited food resources) that limit their ability to respond temporally (Martin et al. 2010). At the community level, strictly diurnal species may also entirely avoid areas of human activity, opening niches for more nocturnal competitors, including invasive species (Huijbers et al. 2013).

In addition to changing diel patterns of activity in response to human disturbance, wildlife species may alter temporal patterns of specific behaviors. During the day, animals often choose more protected habitats or microhabitats in areas of human disturbance (Dupke et al. 2016), or more strongly avoid anthropogenic features like roads and buildings (Morrison et al. 2014, Stabach et al. 2016). Some species also modify daytime and nighttime movement speed and tortuosity (Oriol-Cotterill et al. 2015) and temporal patterns of anti-predator behavior like vigilance (Sönnichsen et al. 2013). Furthermore, in addition to shifting activity from the day to the night, animals often decrease their overall activity throughout the 24-hour period in response to human disturbance, spending more time resting and less time foraging or engaging in other fitness-enhancing behaviors (van Doormaal et al. 2015).

We assert that fear of humans is the primary mechanism driving the increase in wildlife nocturnality, given its prevalence across activity types, and the widespread evidence that mammals perceive and respond to risk from people (Frid and Dill 2002, Tucker et al. 2018). In some of the studies included in our analysis, fear of humans may interact with other factors, such as food provisioning (*e.g.*, anthropogenic food sources like livestock, crops, and food waste), to drive increased nocturnal activity (rather than spatial avoidance) by generalist species in areas of human disturbance (Beckmann and Berger 2003, Valeix et al. 2012). Furthermore, nighttime light cues or increased visibility around permanent human infrastructure may also promote an increase in nocturnal activity in these areas (Dominoni et al. 2016). However, for animals wary of humans or more fearful of predators in lit areas, anthropogenic light may also be perceived as a source of risk, and thus may limit the magnitude of a shift to nocturnality (Longcore and Rich 2004).

The global increase of nocturnality among wildlife in human-dominated areas demonstrates the high degree of behavioral plasticity of animals in a human-altered world, with great implications for ecology and conservation (Figure 3). On the positive side, temporal partitioning may facilitate human-wildlife coexistence at fine spatial scales and effectively increase available habitat for species that are able to adjust (Carter et al. 2012). The separation of humans and wildlife in time, if not space, may also limit contact rates between people and dangerous animals and therefore reduce some forms of negative encounters between the two, such as disease transmission and attacks on people. In situations where humans pose a lethal threat to wildlife, increased nocturnality may be advantageous to individual animals and has been linked to increased probability of survival (Murray and St Clair 2015). In this case, increased mortality among more diurnal individuals may even drive selective pressure for behavioral plasticity and nocturnal activity (Murray and St Clair 2015).

While human-wildlife coexistence may be a positive outcome of increased nocturnal activity of wildlife, there are also potentially negative and far-reaching ecological consequences of this shift. Humans may impose significant fitness costs on individual animals, analogous to predation risk effects in predator-prey systems, in which costly anti-predator behavior compromises prey reproduction and survival and alters trophic interactions (Creel and Christianson 2008). An increase in nocturnality may also eventually alter evolution through selection for morphological, physiological, and behavioral adaptations to nighttime activity. The human "super-predator" has already been implicated in evolutionary changes through selective harvest (Darimont et al. 2009), but, as with other predators (Preisser et al. 2005), the non-lethal effects of humans may have an even stronger influence on fitness and evolutionary trajectories.

Risk effects induced by a temporal response to human presence are expected to be particularly strong, as an increase in nocturnal activity can cause mismatches between morphology and environment for historically diurnal species. The diel cycle provides a reliable set of environmental cues against which ecological and evolutionary processes play out (Gaston et al. 2013). Behavior at different times of the diel cycle influences and is influenced by morphology (*e.g.*, corneal size, (Schmitz and Motani 2010), physiology (*e.g.*, opsin proteins(Zhao et al. 2009), and ecology (*e.g.,* group-living, predation risk(Stankowich et al. 2014). Although most mammals possess some sensory adaptations to nighttime activity due to our nocturnal mammalian ancestors, many species have evolved traits that optimize diurnal behavior (Hall et al. 2012, Maor et al. 2017). When active at other times, diurnally-adapted animals may suffer from reduced hunting and foraging efficiency, weakened anti-predator strategies, disruption of social behavior, poor navigational capacity, and higher metabolic costs, all of which can compromise reproduction and survival (Tuomainen and Candolin 2010, Sih 2013).

By altering typical activity patterns in some wildlife species, human disturbance initiates behaviorally-mediated trophic cascades and transforms entire ecological communities (Werner and Peacor 2003, Schmitz et al. 2004). Fear-based behavioral responses by apex predators to humans might diminish their ability to hunt and thus perform their ecological role at the top of a trophic web (Ordiz et al. 2013). Animals that are increasingly nocturnal may drastically alter their diets towards prey or forage that are more accessible at night, reshaping lower trophic levels

(Ordiz et al. 2017). Predators may also abandon kills near human settlements in the daytime, resulting in increased overall predation rates (Smith et al. 2015). Human-induced increases in nocturnality among prey species can also increase their vulnerability to nocturnal predators (Kilgo et al. 1998). Differential responses to human disturbance among mammal species also alter patterns of predation and competition. Predators may increase nocturnality in response to humans, creating temporal human shields, in which a prey species will then *decrease* nocturnality near human disturbance to avoid predation, analogous to spatial human shields (Berger 2007, Muhly et al. 2011). Alternatively, some prey species may instead seek out human-dominated areas at night to escape nocturnal predators that spatially avoid humans (Atickem et al. 2014).

Human-induced change in diel activity represents a growing field of inquiry, as evidenced by the large number of studies in our meta-analysis. However, very few studies have examined the individual, population, or community-level consequences of these behavioral changes. Given the widespread nature of increased nighttime activity, there is ample opportunity and need to study not just the magnitude of this effect but also its consequences for individual fitness, species interactions, and natural selection. Additional research and synthetic analyses are also needed for non-mammalian taxa, which may also exhibit diel shifts in response to humans (Burger and Gochfeld 1991).

As research on the pattern and consequences of increased nocturnality advances, we urge similar progress be made incorporating knowledge of temporal dynamics in conservation planning. Currently, spatial ecology informs commonly-used land-planning tools (Pressey et al. 2007), but new tools are needed that explicitly address temporal interactions. Approaches might include diurnal "temporal zoning," analogous to spatial zoning, that would restrict certain human activities during times of the day when species of conservation concern are most active or when the likelihood of negative human-wildlife encounters are highest. Similar strategies already restrict human activity at certain times of the year, such as during breeding seasons (Larson et al. 2016). Systematic approaches to understanding and managing temporal interactions between humans and wildlife can open up new domains for conservation in an increasingly crowded world.

EXTENDED MATERIALS AND METHODS

Literature search

To quantify the effects of human disturbance on mammal activity patterns, we conducted a meta-analysis of data from published and grey literature (Figure 4). We used the following search terms (matching title, abstract, and/or keywords): *((activity* OR *temporal* OR *diel* OR *nocturnal** OR *diurnal** OR *"time of day")* AND *(human* OR *people* OR *anthropogenic)* AND *(wildlife* OR *mammal** OR *animal** OR *herbivore** OR *ungulate** OR *carnivore** OR **predator*)).*

We searched the published scientific literature using the ISI Web of Science database (Research Areas: Environmental Sciences & Ecology and Zoology), including peer-reviewed and grey literature and publications in all languages (with English abstracts). To identify unpublished studies, we also searched the ProQuest Dissertations & Theses database. We sorted these results by relevance and reviewed the first 700 dissertation titles. We also searched Google Scholar, and our review of the first 500 results (sorted by relevance) did not reveal any studies that had not been already identified on Web of Science, nor did it include any studies from the unpublished, grey literature. We searched Google with a variety of search terms as well, but no relevant scientific publications appeared in the first 100 results of any searches.

To broaden our search, we also used a "snowball" method, in which we reviewed the references of all included papers, and used the ISI Web of Science database to identify papers that cited included papers. This snowball method yielded several studies from the unpublished, grey literature.

Inclusion criteria

We scanned the abstracts of all studies that referenced some aspect of wildlife ecology in the title. When the abstract mentioned human activity and/or diel activity patterns of mammals, we scanned the full paper to determine whether it met the inclusion criteria. We included all studies that presented data on the day and night activity of at least one mammal species (body size >1kg) across a gradient of human activity that enabled a dichotomous distinction between a control (low human activity) and treatment (high human activity).

Ultimately, we included a very small percentage of studies identified in the initial search (Figure 4), as many of them failed to meet our inclusion criteria. We found that using more specific, restrictive search terms often excluded relevant references, so we chose to cast a wider net. However, this approach required us to scan and reject the titles and abstracts of a large number of papers, many of which were ultimately irrelevant to the meta-analysis.

Methods for studying animal activity included camera traps, GPS or VHF telemetry, or direct observation. Recent research suggests that camera traps and telemetry provide comparable measures of diel activity pattern (Lashley et al. 2018). Gradients of human activity included distinct study areas or study time periods with different degrees of anthropogenic disturbance, or a mosaic of land use types within the study area that were subject to different degrees of disturbance. We included studies with continuous variation in human activity that could be binned into low and high activity categories. We included studies of single species as well as those of multiple species. For single-species studies that used camera traps, we contacted the authors and requested unpublished data on non-target species to reduce potential publication bias.

Extraction of nocturnality data

For each species in each study, we determined nocturnality (the percentage of activity that occurred at night) in the high human disturbance treatment ($\bar{X}_{\text{High}}$) and low human disturbance contrast ($\bar{X}_{\text{Low}}$). We adopted the definition of "active" used in each original study. Activity measures included movement in front of motion-activated cameras, accelerometers on telemetry devices, radio signals from telemetry observations, behavioral records from direct observation, distance traveled, and, when no behavioral data were available, presence in a given area. We conducted supplementary analyses excluding the 12 studies that only examined presence (rather than activity) to confirm that they did not bias our results.

To calculate nocturnality, we recorded the total number of daytime activity and nighttime activity observations in areas of high and low human disturbance in a 2x2 contingency table:

	Night	Day	Total
High Human Disturbance	$O_{HighNight}$	$O_{HighDay}$	$O_{HighNight} + O_{HighDay} = O_{High}$
Low Human Disturbance	$O_{LowNight}$	O_{LowDay}	$O_{LowNight} + O_{LowDay} = O_{Low}$

We determined observation counts based on statistics reported in the published text or tables, using counts, means, and sample sizes to calculate the number of observations for each condition. When the data were not reported in the text, we extracted data from figures using WebPlotDigitizer (http://arohatgi.info/WebPlotDigitizer/). If any of the four cells in the contingency table had a value of zero, we added a small value (0.5) to each of the cells, as is customary for the calculation of risk ratios in meta-analysis to avoid issues arising from division by zero (Viechtbauer 2010). This was only necessary for 5 (3.5%) of the 141 data sets, and each only had one cell with a zero value.

For each study, we pooled observations from each human disturbance condition together in a single contingency table to calculate $\bar{X}_{\text{High}}$ and $\bar{X}_{\text{Low}}$ as follows:

$$\bar{X}_{High} = \frac{O_{HighNight}}{O_{High}} \qquad \bar{X}_{Low} = \frac{O_{LowNight}}{O_{Low}}$$

Defining day vs. night

If the original study summarized data by day versus night, we followed the definitions of day and night used by the authors. If data were summarized hourly or provided in raw format, we defined day as the time period between sunrise and sunset, and night as the time period between sunset and sunrise. We identified sunset and sunrise times for the reported study location using the website: https://www.timeanddate.com/sun/. If the date of each observation was provided, we used date-specific sunrise and sunset times and classified each observation or binned hour of observations as day or night. Otherwise, we used the average sunrise and sunset times during the reported study period at the study location. If authors classified some observations crepuscular, we reclassified those observations as day or night based on the sunrise and sunset criteria. If this reclassification was not possible, we excluded crepuscular observations from analysis.

Defining low vs. high human activity

For each study site, we classified areas, time periods, or individual animals as associated with "low" and "high" human activity. In most cases, we followed classifications made by authors. In some cases, authors did not explicitly differentiate between low and high areas or time periods of human activity, instead typically either expressing human activity as a continuous variable or recognizing more than two categories of disturbance. In these cases, we classified areas, time periods, or individual animals as low or high human activity based on descriptions of the study system in the publication, or based on binned distance or elapsed time from an anthropogenic disturbance. The spatial and temporal scale of classification varied across studies. Examples of low vs. high human activity included: areas without vs. with recreation or hunting; inside vs.

outside of a protected area; far vs. near from settlement or roads; non-hunting vs. hunting season; before vs. after the construction of infrastructure.

Additional meta-data extraction

For each study, we recorded information about methods and relevant characteristics of the site and ecosystem. We recorded the study location (latitude, longitude, country, and continent). If authors did not provide the exact latitude and longitude, we identified the approximate coordinates using site descriptions, figures, and Google Maps. If the study included multiple sites, we identified the approximate center point for all sites used. We classified the habitat, as described in the publication, into one or more of the following broad habitat categories: forest, savanna, grassland, or desert.

We recorded all types of human activities that were reported in the study system and that varied in magnitude between the low and high activity treatments. For each species in each study, we further classified human activity as lethal (hunting or lethal persecution of the target species) or non-lethal. For studies in which activity varied over space (rather than time period), we recorded the distance between the low and high human activity sites in each study. We also noted when areas of low and high activity were adjacent or arranged in a mosaic.

For each species represented in the meta-analysis, we determined the taxonomic classification, body size, trophic level, and typical activity pattern using the PanTHERIA database (Jones et al. 2009). We followed the taxonomy of Wilson & Reeder 2005 (Wilson and Reeder 2005), unless species had been reclassified and were only present in the database based on Wilson & Reeder 1993(Wilson and Reeder 1993). When information was unavailable in the PanTHERIA database, we extracted data from Animal Diversity Web (Myers et al. 2018) or used PanTHERIA data for closely-related congeners.

We classified the general methods that each study used to measure animal activity (camera trap, telemetry, or observation), and the specific measures of activity (direct observation, activity sensor, movement on camera, distance moved, presence). We classified each effect size as low, medium, or high quality, based on the study design to determine potential effects of study quality on the observed result. Low quality studies had < 10 individual animals in the study, < 20 observation sites (including camera trap locations), or limited information about sample size. Medium quality studies had 10-19 individual animals in the study or 20-99 observation sites. High quality studies had > 20 individual animals in the study or >100 observation sites. These classifications resulted in a roughly even distribution of studies across bins. To supplement this study quality analysis, we also split studies of each general study method into quartiles based on sample size, and classified each effect size by quality quartile (Q1, Q2, Q3, and Q4).

Data sources

Our initial ISI Web of Knowledge search yielded 7,610 references and the ProQuest search yielded 700 references, with an additional 50 identified from the snowball citation search (Figure 4). We ultimately included 76 of these papers in the meta-analysis. There was a mean (+ SD) of 1.91 (+ 1.78) species per study (range = 1 to 8 species), with a total of 62 species represented across studies. There was a total of 141 effect sizes included in the meta-analysis. For two studies, the results were compared to those from separate publication with a different degree of human activity; in these instances, we combined data from both studies to calculate effect sizes for the meta-analysis after determining that methods were comparable.

Effect size calculation

We calculated an effect size for each species in each study (studies of multiple species therefore yielded multiple effect sizes). We calculated log risk ratios (RR) as a measure of effect size (Figure 5), where RR is the ratio of mean nocturnality at sites or during time periods of high human disturbance ($\bar{X}_{\text{High}}$) to mean nocturnality in low disturbance locations or temporal periods ($\bar{X}_{\text{Low}}$):

$$\text{RR}= \ln\left(\frac{\overline{\text{X}}_{\text{High}}}{\overline{\text{X}}_{\text{low}}}\right)$$

A positive risk ratio (RR > 0) represents a shift to increased nighttime activity (and decreased daytime activity) in areas of high human activity. A negative risk ratio (RR < 0) represents a shift to decreased daytime activity (and increased nighttime activity) in areas of high human activity. To facilitate interpretation of our results, we back-transformed mean effect sizes and converted unlogged risk ratios to percentages to determine the percent shift towards nocturnality in areas of high human activity.

Calculating sampling variance of effect sizes

We calculated variance as follows, where O represents the total number of observations in the 2x2 contingency table above (Borenstein et al. 2008):

$$\text{Variance(RR)}=\left(\frac{1}{\text{O}_{\text{High}_{\text{night}}}}-\frac{1}{\text{O}_{\text{High}}}\right)+\left(\frac{1}{\text{O}_{\text{Low}_{\text{night}}}}-\frac{1}{\text{O}_{\text{Low}}}\right)$$

For studies that used camera traps or direct visual observation, each independent detection of a species was counted as one observation for the purposes of calculating variance. Definitions of independence varied across studies, but when possible, we used raw data to define independence as >1 hour between sightings or photographs (camera trigger events).

For telemetry studies, we counted each active GPS or VHF fix as an observation. Given that fix rate fixes are spatiotemporally autocorrelated, we subsampled high-fix rate data to create a 1-hour inter-fix interval. When we had access to raw data, comparisons of our results with analyses of the full data set indicated that subsampling did not change the effect size but did reduce sample sizes for observations and increased associated estimates of variance, for a more conservative meta-analysis. Finally, when fix intervals differed between nighttime and daytime data, we subsampled the period with more fixes to standardize data collection effort.

Data analysis

To calculate an overall mean effect size, we used a random effects linear model in the *metafor* package in R (Viechtbauer 2010). We weighted each effect size by the inverse of its variance, and included study and species as random effects to account for non-independence. For the purposes of modeling random effects, we considered publications using the same data set from the same study area to be part of the same study. We also subsampled the data to compare overall effects for each type of human activity, trophic level, body size, habitat, continent, and typical activity pattern (Figure 6).

Finally, we constructed mixed effects models with random and fixed effects to evaluate the impacts of ecological, geographical, anthropogenic, and methodological variables on effect sizes (see list of variables and explanations in Table 1). We used a forward stepwise model selection process based on AIC (Table 2). The best model included study and species as random effects, and body mass quartile, human disturbance treatment (space vs. time), study quality (camera trap, telemetry, and direct observation), and continent as fixed effects (Table 3).

Publication bias and testing robustness of results

We took several steps to address potential publication biases in the literature. When conducting the literature search, we used a broad search strategy to locate studies of wildlife activity across gradients of human disturbance. The majority of the studies included in the meta-analysis reported diel activity patterns alongside many other patterns of movement and behavior, and a temporal shift was rarely the primary study objective or key finding. We therefore expected less publication bias towards findings of increased nocturnality around human activity. For all camera trap studies that reported results for only a single species, we contacted the authors to request unpublished data on additional species that were captured on camera.

We conducted separate analyses using effect sizes only from studies of single species and only from studies of multiple species. As expected, the increase in nocturnality in response to humans was slightly greater for datasets that focused on a single species (1.41, 95% Confidence Interval: 1.27-1.58, n = 50) compared to those that included multiple species (1.31, 95% Confidence Interval: 1.13-1.53, n = 91). For both types of study, the increase in nocturnality in areas of high human activity was significant. Comparing single versus multiple study species indicated that estimates of effect size were not significantly different, nor were they different from the overall outcome when all effect sizes were included (1.36, 95% Confidence Interval: 1.23-1.51).

To further address potential bias introduced by phylogenetic relationships among the included species, we ran two additional meta-analytic models including either family or order as random effects in the model. These models performed far more poorly than those that instead only included species as a random effect. The AIC for the overall meta-analytic model was 442 when family was included and 566 when order was included, compared to an AIC of 171 for the model that includes species only.

We assessed publication bias using funnel plots, which mapped residuals for RR against the inverse of the variance (Figure 7). We conducted an Egger test to measure the asymmetry of these funnel plots; these tests revealed a correlation between observed outcomes (RR) and the corresponding sampling variances, suggesting a publication bias ($z = 3.86$, $p = 0.0001$). However, the Rosenberg's fail-safe number – the estimated number of unpublished studies that would have to be included in the meta-analysis to change the significance of the result – was very large (1,597,688, $p < 0.0001$) (Rosenthal 1979, Viechtbauer 2010). This number represents the estimated number of unpublished studies that would have to be included in the meta-analysis to change the result, suggesting that our results are robust to publication bias.

Results were robust to study methodology and did not vary with study quality, the number of species in the study, general study method, measure of animal activity, or disturbance comparison type (Table 4). All methods yielded effects with the same directionality (increased nocturnality in response to humans) and with similar magnitudes to the overall global effect.

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FIGURE 1. MAMMALS BECOME MORE NOCTURNAL TO AVOID HUMANS THROUGHOUT THE WORLD.

(A) Map illustrating the locations of the 76 studies included in the meta-analysis. (B) Paired measures of nocturnality (percentage of activity that occurs in the night) in areas of high human disturbance (red points; X_h) and low human disturbance (green points; X_l), displayed for each species in each study (n = 141; ordered from high to low X_l). The relative change in nocturnality in response to human disturbance was used to calculate effect size (RR) for the meta-analysis, where RR = $\ln(X_h/ X_l)$.

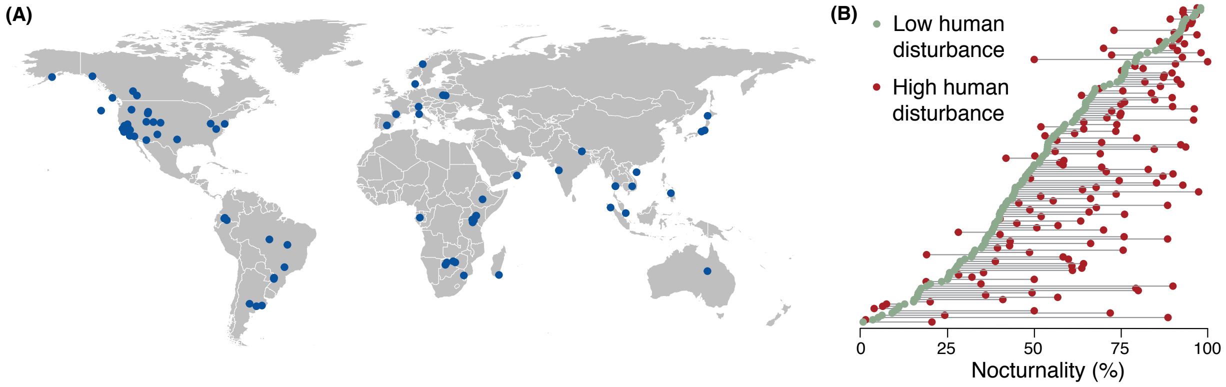

FIGURE 2. INCREASE IN LARGE MAMMAL NOCTURNALITY IN RELATION TO HUMAN ACTIVITY TYPES, TROPHIC LEVEL, AND BODY SIZE.

Points represent the estimated overall effect size (with 95% confidence intervals) for each category. Positive values indicate a relative increase in nocturnal activity in areas of higher human disturbance. The number of effect sizes in each category is indicated in parentheses (human activity categories were non-exclusive). Mammals exhibit a significant increase in nocturnal activity in response to all types of human activity, with similar patterns across trophic levels and body sizes. Back-transforming the overall (mean) RR (0.31, CI: 0.21-0.41) indicates that nocturnality increased by a factor of 1.36 (CI: 1.23-1.51) in response to human activity.

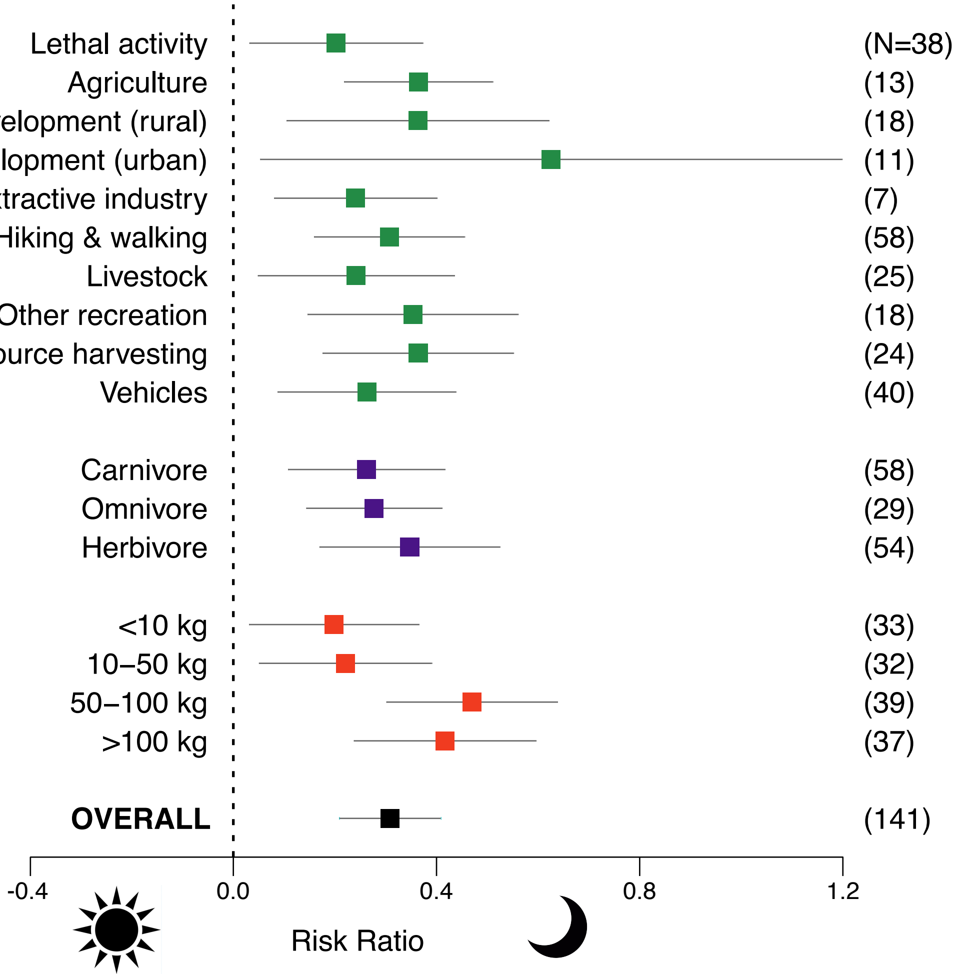

FIGURE 3. CASE STUDIES DEMONSTRATE THE DIVERSE CONSEQUENCES OF HUMAN-INDUCED INCREASES IN NOCTURNALITY.

(A) red brocket deer (*Mazama americana*) and subsistence hunting, Atlantic Forest, Argentina (Di Bitetti et al. 2008); (B) coyote (*Canis latrans*) and hiking, Santa Cruz Mountains, California, USA (Wang et al. 2015, Smith et al. 2018); (C) sable antelope (*Hippotragus niger*) and sport hunting, Hwange National Park, Zimbabwe (Crosmary et al. 2012a); (D) tiger (*Panthera tigris*) and forest product collection and farming, Chitwan National Park, Nepal (Carter et al. 2012); (E) wild boar (*Sus scrofa*) and urban development, Cracow and Białowieza Forest, Poland (Podgórski et al. 2013). Green bars represent nocturnality (percentage of total activity that occurs in the night) in areas of low human disturbance (X_l), and red bars represent nocturnality in high human disturbance (X_h).

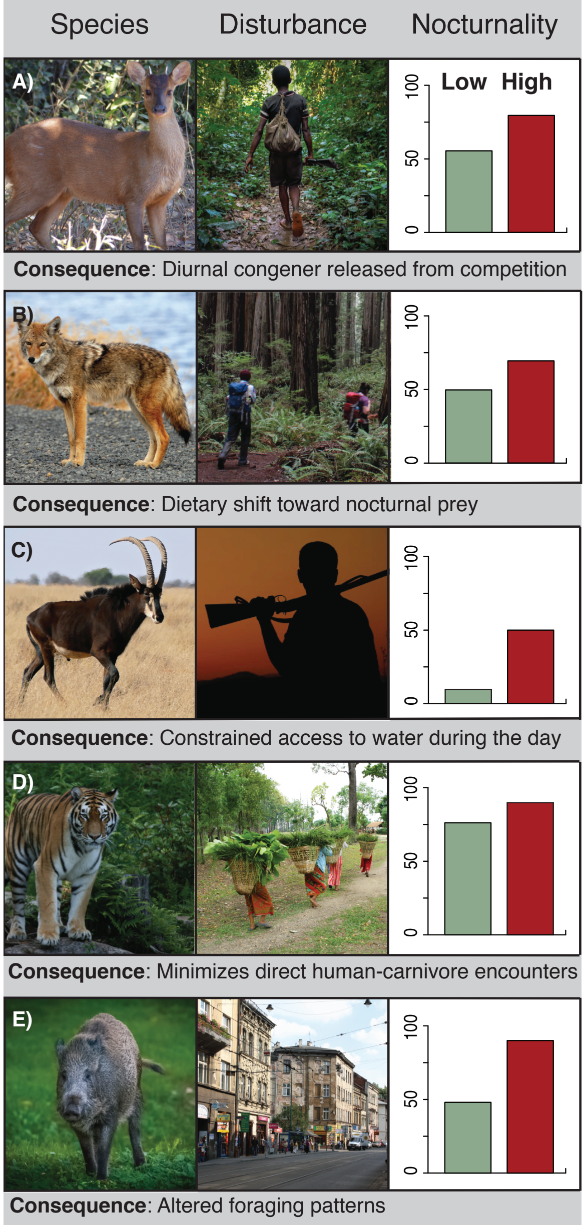

Figure 4. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow chart illustrating the procedure for identifying and including relevant publications.

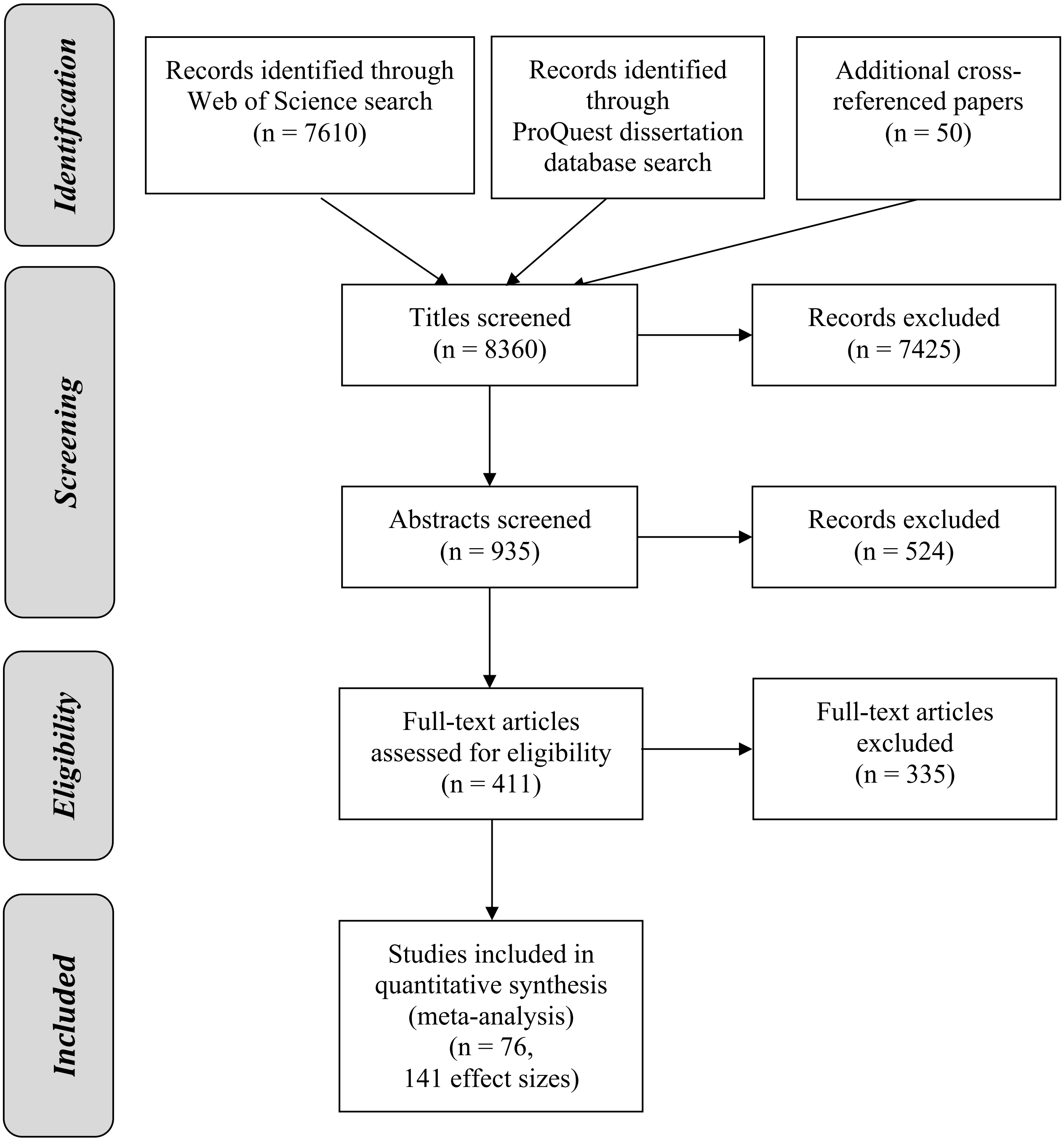

FIGURE 5. FOREST PLOT OF ALL EFFECT SIZES AND CONFIDENCE INTERVALS

Forest plot of 141 effect sizes (Risk Ratio) in blue, with 95% confidence intervals (CI) indicated. Positive values indicate a relative increase in nocturnal activity in areas of higher human disturbance. The green diamond represents the estimated global overall effect size (0.31; CI: 0.21-0.41), and the width of the diamond represents the 95% CI. Back-transforming the overall RR indicates that nocturnality increased by a factor of 1.36 (CI: 1.23-1.51) in response to human activity.

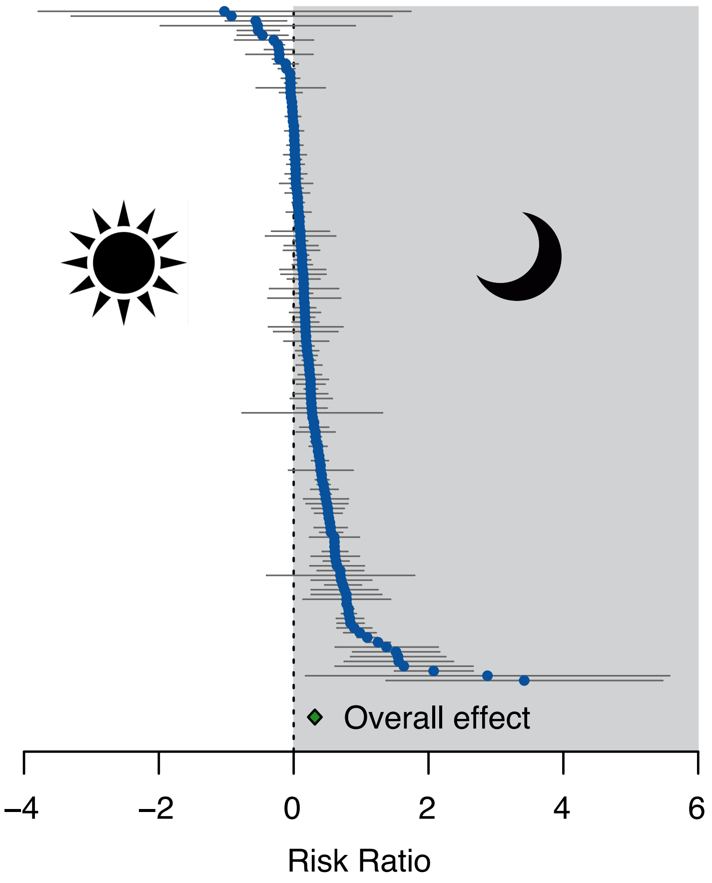

Figure 6. Effect sizes across (A) continents, (B) habitat types, and (C) typical activity patterns.

Squares denote estimated effect sizes for each category; horizontal lines depict 95% Confidence Intervals. Sample sizes (number of effect sizes) are shown in parentheses.

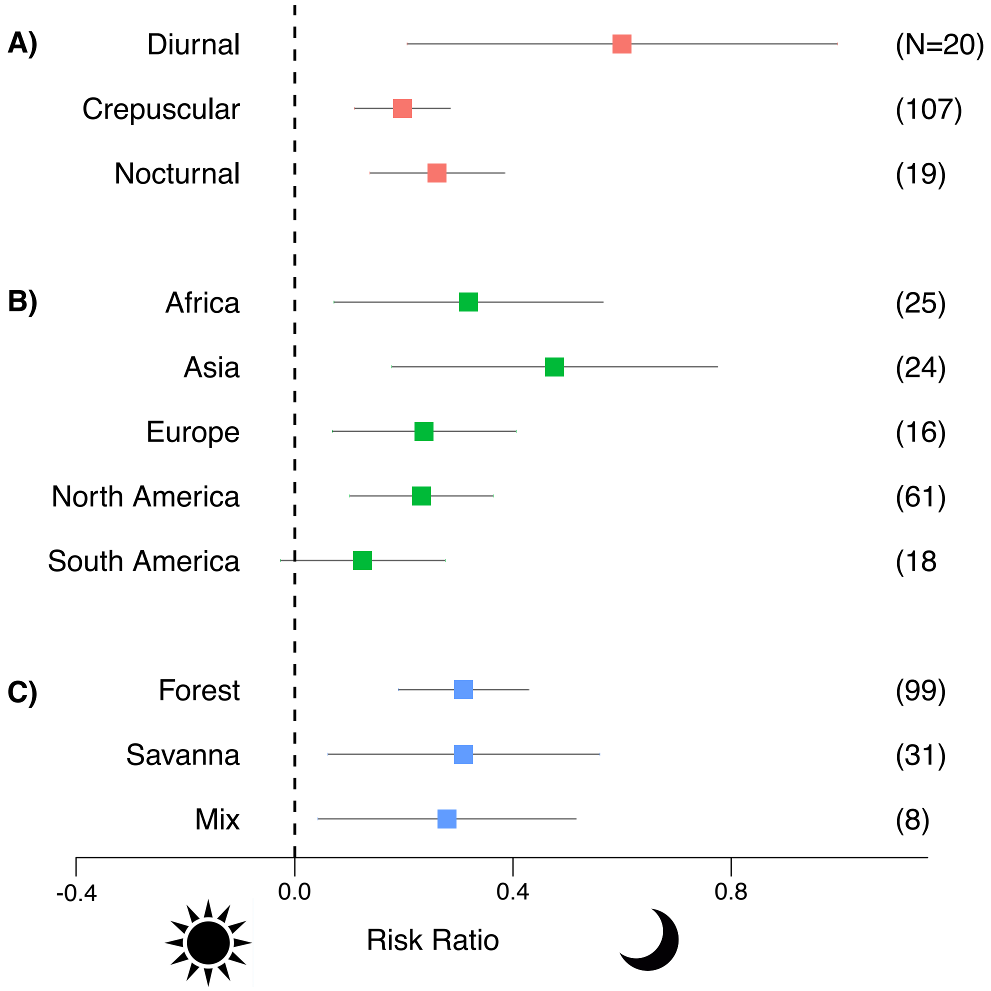

FIGURE 7. FUNNEL PLOTS DEPICTING THE RELATIONSHIP BETWEEN THE EFFECT SIZE (RISK RATIO) AND (A) STANDARD ERROR, (B) SAMPLING VARIANCE, (C) INVERSE STANDARD ERROR, AND (D) INVERSE SAMPLING VARIANCE.

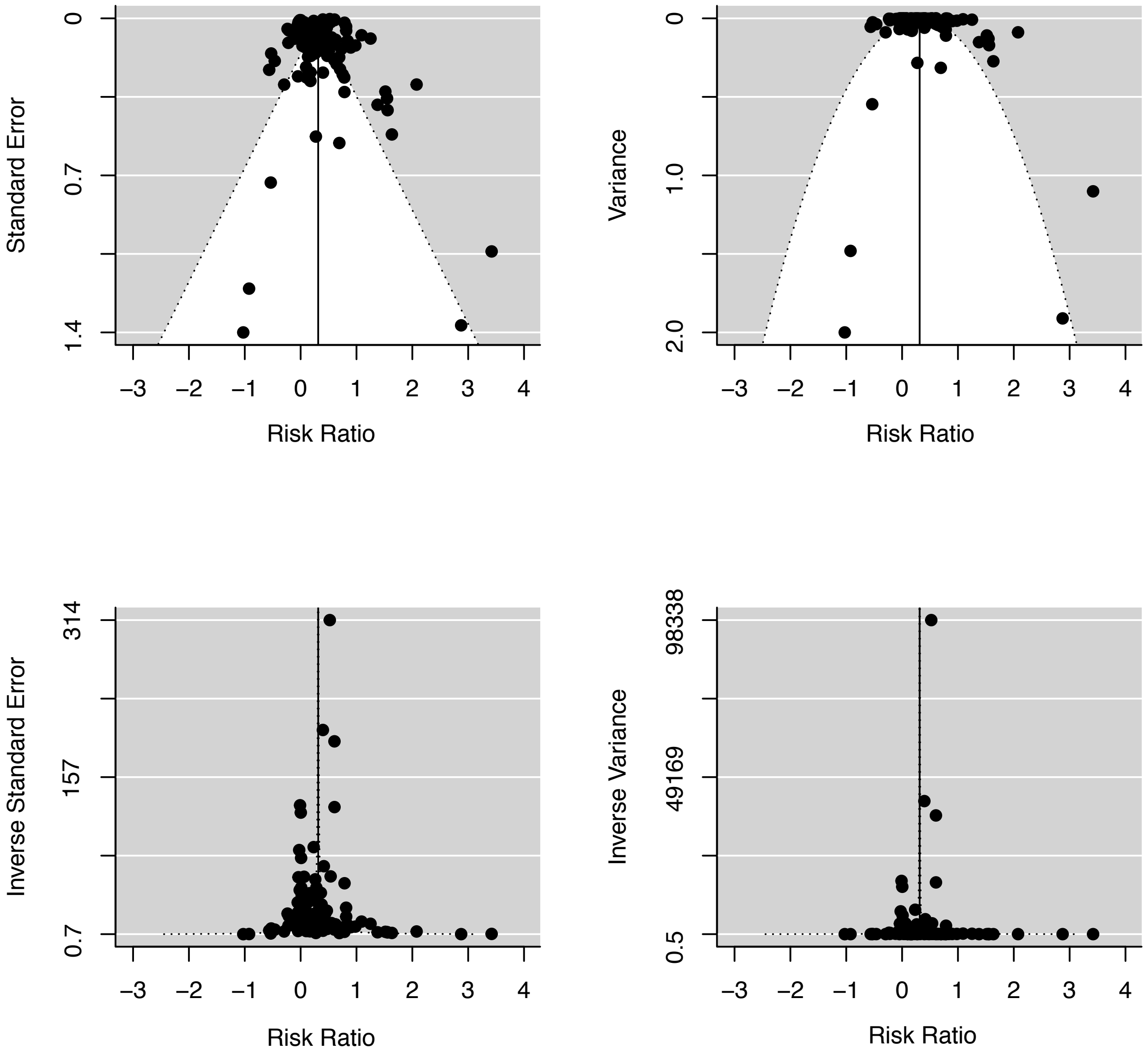

TABLE 1. DESCRIPTIONS OF META-ANALYTIC MODEL VARIABLES

These factors were tested as predictors of changes in mammalian nocturnality in response to human disturbance. All factors are categorical, unless otherwise indicated.

Category	Variable	Description	Justification
Random	Study	Source publication	Study design and methodology may influence the results; we therefore controlled for the study as a random effect.
Random	Species	Species name	We expected that populations/individuals of a given species would exhibit similar results across studies; we therefore controlled for the species as a random effect.
Ecology/ Geography	Trophic level	Carnivore, omnivore, or herbivore (from Pantheria)	Animals of different trophic levels face different risk trade-offs from human disturbance, and might therefore respond accordingly. For example, carnivores face more persecution from humans.
Ecology/ Geography	Body size quartile	Quartile of average body mass of study species, in kg (from Pantheria)	Larger-bodied species may face greater threats from humans, or perceive greater risk from human disturbance, and therefore respond more strongly. The body sizes used in this analysis do not capture sexual dimorphism or the range across populations, so we therefore used a categorical rather than continuous body mass measure. Four categories allowed for robust estimates of mean effect sizes. Dividing the 62 species into more bins would lead to the overrepresentation in bins of those species that were most commonly studied, limiting inference.
Ecology/ Geography	Activity pattern	Typical activity pattern: diurnal, crepuscular, nocturnal (from Pantheria)	Nocturnal or crepuscular species may be better able to increase their nocturnality in response to humans, while diurnal species may face greater constraints. However, diurnal species may also exhibit shifts of greater magnitude in response to humans.
Ecology/ Geography	Habitat	Habitat as described in study: desert, forest, grassland, savanna, mix	Habitat may influence the degree to which (and spatial scale at which) human disturbance is perceived and responded to; we expected greater responses in more open habitats, where the effects and sensory cues associated with disturbance may be more pervasive.
Ecology/ Geography	Continent	Continent	There may be continent-wide patterns in the effects of human disturbance on diel activity patterns in mammals, due to continental similarities in disturbance type, history of human disturbance, and wildlife communities.
Human	Disturbance type	Broad category of human activity: activity, infrastructure, or both	Animals may respond more strongly to direct human presence rather than infrastructure if they perceived humans themselves to be a threat. Furthermore, animals may exhibit a stronger temporal response to activity than infrastructure, given that human activity is less predictably avoidable in space.
Human	Lethality	Whether subject animal was target of hunting or lethal persecution: yes or no	Animals should respond more strongly to lethal disturbance than to non-lethal disturbance, given the presence of an actual threat to the animal's life.

Category	**Variable**	**Description**	**Justification**
Human	Human footprint (continuous)	Average value of human footprint in 10km radius around the center of study site (*130*)	There may be greater effects of the human footprint on human-induced nocturnality in areas with a higher human footprint, if the magnitude of overall human disturbance drove the magnitude of response. Alternatively, effects may decrease with footprint if animals become habituated to humans in these areas and are therefore less likely to perceive them as a threat.
Methods	Method	Broad method for studying animal activity: camera trap, telemetry, or observation	Study method may influence the magnitude of the effect. For example, direct observation of animals may reduce the size of the effect if human observer presence during the night and day is perceived as a threat.
Methods	Activity measure	Measure of animal activity: direct observation, activity sensor, movement on camera, distance moved, or presence	The measure of animal activity may influence the magnitude of the effect size.
Methods	Number of species	How many species were in the study (categorical): single or multiple	Studies of a single species may be more subject to publication bias, and therefore have a higher effect size than those of multiple species.
Methods	Disturbance comparison	Human disturbance treatment: space or time	The magnitude of the change in nocturnality may be greater when comparing different areas than different time periods. When using time-for-space substitution, there may be lag effects, or habituation effects, which could weaken the observed response of wildlife to human activity.

TABLE 2. RESULTS OF META-ANALYTIC LINEAR MIXED-EFFECTS MODELS OF THE EFFECTS OF HUMAN DISTURBANCE ON MAMMALIAN NOCTURNALITY

Tables include AIC, ΔAIC (difference in AIC between the model and the model with the lowest AIC), and Akaike weight (w) values. We used forward stepwise model selection. Here, we report the results of the null and full models and all models with ΔAIC < 10.

Fixed effects	Random effects	AIC	ΔAIC	w
Treatment + Continent + Method	Study + Species	156.10	0	0.223
Treatment + Continent + Method + Activity Pattern	Study + Species	157.12	1.02	0.134
Treatment + Continent + Method + Body Size	Study + Species	157.22	1.12	0.127
Treatment + Continent + Method + Lethality	Study + Species	157.53	1.43	0.109
Treatment + Continent + Method + Human Footprint	Study + Species	158.12	2.02	0.081
Treatment + Continent + Method + Number of Species	Study + Species	158.16	2.06	0.080
Treatment + Continent + Method + Trophic Level	Study + Species	159.50	3.40	0.041
Treatment + Continent + Method + Disturbance Type	Study + Species	159.68	3.58	0.037
Treatment + Continent	Study + Species	160.48	4.38	0.025
Treatment + Continent + Activity Pattern	Study + Species	160.92	4.82	0.020
Treatment + Continent + Method + Activity Measure	Study + Species	161.00	4.90	0.019
Treatment + Continent + Activity Measure	Study + Species	161.23	5.13	0.017
Treatment + Continent + Body Size	Study + Species	161.74	5.64	0.013
Treatment + Continent + Lethality	Study + Species	161.96	5.86	0.012
Treatment + Continent + Number of Species	Study + Species	162.01	5.91	0.012
Treatment + Continent + Method + Habitat	Study + Species	162.13	6.03	0.011
Treatment + Continent + Human Footprint	Study + Species	162.44	6.34	0.009
Treatment + Method	Study + Species	163.33	7.23	0.006
Treatment + Body Size	Study + Species	163.62	7.52	0.005
Treatment + Continent + Trophic Level	Study + Species	163.83	7.73	0.005
Treatment + Continent + Disturbance Type	Study + Species	164.17	8.07	0.004
Treatment	Study + Species	165.64	9.54	0.002
Treatment + Activity Pattern	Study + Species	165.69	9.59	0.002
Null model (Random effects only)	Study + Species	169.77	13.67	0.001
Full model (All variables in Table S4)	Study + Species	178.97	22.87	<0.001

TABLE 3. STANDARDIZED COEFFICIENTS OF THE FIXED EFFECTS IN THE BEST FIT META-ANALYTIC LINEAR MIXED-EFFECTS MODEL (AIC = 156.10)

The reference levels of each fixed effect are: Treatment = Location, Method = Camera trap, Continent = Africa.

Fixed effect	Estimate	SE	Z	p-value	Lower 95% CI	Upper 95% CI
Intercept	0.1554	0.1353	1.1407	0.2540	-0.1109	0.4197
Treatment = Time	-0.3537	0.0996	-3.5510	0.0004	-0.5489	-0.1585
Method = Observation	0.4345	0.1510	2.8780	0.0040	0.1386	0.7305
Method = Telemetry	0.1330	0.0804	1.6548	0.0980	-0.0245	0.2905
Continent = Asia	0.4372	0.1598	2.7365	0.0062	0.1241	0.7504
Continent = Europe	0.0260	0.1638	0.1588	0.8738	-0.2950	0.3470
Continent = North America	0.0760	0.1445	0.5255	0.5992	-0.2073	0.3592
Continent = South America	-0.0489	0.1689	-0.2894	0.7723	-0.3799	0.2822

TABLE 4. COMPARISON OF RESULTS ACROSS STUDY METHODS

Methods included study quality, the number of species in the study, general study method, animal activity measure, and disturbance comparison. Results were robust to study methodology, with all methods yielding effects of the same direction (increase in nocturnality in response to humans) and of similar magnitude. An asterisk indicates a significant increase in nocturnality in response to human activity. The effect sizes are presented as back-transformed RRs for ease of interpretation.

Methodology	Overall Effect	95% Confidence Interval	Number of Effect Sizes
Study quality (3 bins)			
Low	1.45	1.20-1.75 *	35
Medium	1.31	1.17-1.48 *	54
High	1.39	1.13-1.70 *	52
Study quality (quartiles)			
Q1 (lowest)	1.45	1.20-1.75 *	35
Q2	1.30	1.12-1.50 *	38
Q3	1.45	1.18-1.78 *	38
Q4 (highest)	1.28	1.05-1.57 *	30
Species in study			
Single	1.41	1.27-1.58 *	50
Multiple	1.31	1.13-1.53 *	91
Study method			
Camera trap	1.29	1.13-1.46 *	98
Telemetry	1.45	1.31-1.62 *	31
Observation	2.19	1.33-3.62 *	12
Animal activity measure			
Direct observation	2.00	1.32-3.03 *	14
Activity sensor	1.40	1.18-1.66 *	17
Movement (camera)	1.29	1.13-1.46 *	98
Presence	1.61	1.46-1.78 *	12
Disturbance comparison			
Location	1.42	1.28-1.58 *	127
Time	1.17	1.03-1.33 *	14

Chapter 5. Effects of human settlement and roads on diel activity patterns of elephants

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Gaynor, K. M., Branco, P. S., Long, R. A., Gonçalves, D. D., Granli, P. K., & Poole, J. H. 2018. Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology*, 56(4), 872–881.

ABSTRACT

As the human footprint expands worldwide, people and wildlife are coming into greater contact, and areas of human activity may be simultaneously associated with risk and reward for animals. To avoid human threats while exploiting opportunities, animals may adjust their spatiotemporal activity, using areas of anthropogenic disturbance at night when people are less active. We combined four camera trap datasets from Mozambique's Gorongosa National Park to evaluate the effects of roads and settlement on diel activity patterns of elephants (*Loxodonta africana*). We found high rates of elephant activity along the boundary of the park, where elephants can access cultivated crops, and along roads, which serve as movement corridors. However, elephants restricted their activity to the night and crepuscular periods in these areas of human disturbance, seeking refuge in the interior of the park away from roads and settlements during the day. Our findings suggest that a history of killing and antagonism has instilled a fear of humans in this elephant population, with implications for research, tourism, and human-elephant coexistence. Our study highlights the utility of camera traps in monitoring human-wildlife conflict and habituation and demonstrates the value of integrating disparate camera trap datasets for comparative analyses on landscape or even continental scales.

INTRODUCTION

As the human population grows exponentially and our footprint expands across the globe, people and wildlife are increasingly forced to share space (Hoare and Toit 1999, Venter et al. 2016, Jones et al. 2018). Conservation efforts have bolstered wildlife populations in many African protected areas (Craigie et al. 2010), and human development interventions outside of protected areas have promoted the growth of human populations (Wittemyer et al. 2008). People and wild animals are therefore coming into contact more frequently in these interfaces along protected areas, and encounters between humans and wildlife can have important implications for animal behavior, human-wildlife conflict, protected areas management, and conservation (Dickman 2010, Tucker et al. 2018). By simultaneously monitoring the use of both natural and anthropogenic landscapes by wildlife, we can better understand the impacts of humans on wildlife populations and manage for coexistence within shared spaces.

Wild animals often perceive humans as a threat, and therefore seek to minimize encounters with people (Frid and Dill 2002). This perception may sometimes be precipitated by actual risk, such as hunting or persecution (Ndaimani et al., 2014; Setsaas et al., 2007). However, animals may also exhibit generalized anti-predator strategies in response to human activity (e.g., tourism, settlement), especially if they have had previous negative experiences with humans

(Pangle and Holekamp, 2010; Stankowich 2008). Despite such perceptions of risk, animals may also seek out areas of human activity that provide accessible or high-quality food resources such as crops, livestock, or food waste (Chiyo and Cochrane 2005, Treves 2009). Thus, animals sometimes experience trade-offs between forage and perceived risk wherein areas of anthropogenic disturbance are associated with both threats from people and high-quality resources (Brown et al. 1999, Chiyo et al. 2011).

Where wild animals are unable to avoid people in space due to expansive human activity, and especially when animals are drawn to anthropogenic resources, they may instead avoid people in time (Rasmussen and Macdonald 2011, Oriol-Cotterill et al. 2015). There is growing evidence that mammal species across the planet adjust their diel activity patterns in response to human activities (which occur largely during daylight hours) by becoming more nocturnal (Gaynor et al. 2018a). For wide-ranging and behaviorally plastic species, such adjustments may occur at relatively fine-scale spatiotemporal scales (Carter et al. 2012), where during the daytime animals seek out areas of lower human activity and at night move into human-dominated areas (Barnes et al. 2007, Graham et al. 2009, Valeix et al. 2009a, Gunn et al. 2014).

African elephants (*Loxodonta africana*) are an ideal species for examining the effects of human activity on spatiotemporal behavior because of their learning ability, flexible activity patterns, large home range sizes, and propensity to exploit anthropogenic resources (Boettiger et al. 2011, Fullman et al. 2017). Elephants also face diverse threats from humans, including poaching (Wittemyer et al. 2014, Ripple et al. 2015, Wasser 2015). While some elephant populations can take refuge in protected areas, many also forage in human-dominated environments (Scholssberg et al. 2018). However, elephants often leave park boundaries in search of additional resources, resulting in measurable changes in movement patterns (Cook et al. 2015, Hunninck et al. 2017) and higher stress levels (Hunninck et al. 2017). The presence of elephants outside of protected areas is frequently a source of human-wildlife conflict in the form of crop damage and threats to safety, which can disrupt human livelihoods and lead to retaliation against elephants (Hoare 2000, Chiyo et al. 2005, Graham et al. 2010, Chase et al. 2016). Elephants are an important flagship species for conservation, and are a keystone species in savanna ecosystems (Coppolillo et al. 2003, Pringle 2008, Coverdale et al. 2016). Nonetheless, elephants are also declining across the African continent (Chase et al. 2016). As the human population grows throughout Africa, particularly in areas with high elephant populations (de Boer et al. 2013), it is critical to expand our toolkit for understanding how human disturbance influences the behavior of this important species. With fine-scale information on the spatiotemporal responses of elephants to human activities, conservation practitioners can better plan for coexistence (Songhurst et al. 2016).

We used data from multiple camera trap studies throughout Gorongosa National Park in Mozambique to quantify spatiotemporal patterns of elephant activity in close proximity to humans. Camera trap studies have become increasingly common for continuous monitoring and for observational and experimental research, as the cost decreases and software for automating analysis of images becomes more readily available (Burton et al. 2015, Steenweg et al. 2017). Moreover, because camera traps capture all species that pass by (including people) at all times of day, they provide a rich source of data, often beyond the initial study focus (Caravaggi 2017). Our study was opportunistic in that we took advantage of four unique camera trap projects designed for different monitoring and research purposes by different research teams in the park. The distinct goals of each of these projects led to differences in study design and camera placement, which inadvertently facilitated a larger-scale comparative study.

Our specific objectives were to use the camera trap data to examine the effects of (1) settlement and agriculture just outside of the park and (2) roads used for tourism and research inside the park on elephant diel activity patterns. We expected elephants to be more active in the interior areas of the park during the day, and show increased presence in human-dominated areas along the boundary of the park and in the park's buffer zone at night to take advantage of cultivated crops. Due to the recent history of violence against elephants within the national park, both avoidance and aggressive behavior are common responses to vehicles across elephant families (Poole and Granli 2018). Therefore, at a finer spatial scale, we expected elephants to avoid the park's roads more strongly during the day, when potential vehicle encounter rates are higher. By elucidating elephant activity patterns in human-altered landscapes, our research highlights the implications of behavioral plasticity for conservation and human-wildlife conflict and coexistence.

METHODS

Study site

Gorongosa National Park (GNP) is located in Sofala Province in central Mozambique, at the southern extent of the Great Rift Valley (Latitude: -18.82, Longitude: 34.50). The park encompasses 3,770 km^2 and supports a diversity of large mammal species that occupy a range of habitat types. The study area is characterized by *Acacia-Combretum* savanna woodlands and floodplain grasslands (Stalmans and Beilfuss 2008). Mean annual rainfall in the valley of GNP is 700-900 mm, with a rainy season that runs from November – March and a dry season from April – October (Stalmans and Beilfuss 2008). Lake Urema is located in the center of the park and provides a permanent water source throughout the year, and inundating the floodplains of the valley during the wet season. There are several perennial rivers in GNP, including the Pungue River, which forms the southern border of the park.

During Mozambique's civil war (1977-1992), wildlife populations, including elephants, declined dramatically due to killing for meat and ivory (Vines 1991, Daskin et al. 2016). Prior to the war, the park was estimated to have ~2,200 elephants (Tinley 1977), reduced to <200 individuals by 1994 (Poole and Granli 2017). Following the end of war, renewed investment in wildlife management has enabled populations to recover, largely through natural population growth. In particular, a public-private partnership between the government of Mozambique and the Gorongosa Restoration Project (Stalmans and Peel 2016) has facilitated considerable progress toward returning GNP to its former status as one of the most diverse parks in the world. The current elephant population in GNP is estimated to be between 567 (aerial total count, Stalmans and Peel, 2016) and 825 individuals (based on individual registration of adults and a mean ratio of 2.4:1 of immatures to adult female; Poole and Granli, 2018). As a result of their recent history of violence with humans, elephant family groups in GNP exhibit a high rate of aggressive behavior toward people and are fearful of both humans and vehicles, despite little evidence of elephant poaching at present (Poole and Granli 2017, 2018).

A variety of human activities occur within GNP, centered on the park's core road network. There is a small but growing tourism operation based in Chitengo, the park's headquarters, and tourist vehicles frequently travel throughout the park for wildlife viewing (multiple times per day during most of the year). Despite their aggression, elephants are a sought-after species for viewing, and tourist vehicles thus regularly seek out areas of high elephant activity. There is also a large amount of research activity in the park, and researchers use the road network as they travel around the park to collect samples, make observations of animals, and set up experiments. GNP's park rangers also use the road network, although most of their patrols are in remote, off-road areas based out of the park's ranger outposts. The park gates are only open from sunrise to just after sunset, so the vast majority of vehicle activity is restricted to daytime and dusk, with the exception of some ranger activity.

GNP is surrounded by a 5,333 km^2 buffer zone, where approximately 200,000 subsistence crop farmers currently reside (Ministério da Terra 2016). The buffer zone is a mixed-use area, where people are permitted to grow crops, harvest natural resources, raise livestock, and conduct controlled burns, along with other livelihood activities. Hunting for bushmeat and trophies is prohibited, and there are no roads with vehicle traffic in the buffer zone study area. Importantly, when asked about the problems they face living close to the national park, residents of the buffer zone overwhelmingly indicate that the primary issue is crop damage by elephants (P. Branco, unpublished data). Most crop foraging occurs along the park's southern border, where GNP's elephants are concentrated (Stalmans and Peel 2016, Poole and Granli 2017).

Data collection

As scientific activity in GNP has grown, several research projects have deployed camera traps to accomplish various monitoring and research objectives. We combined camera trap data from four projects to quantify elephant activity patterns in relation to human disturbance (Table 1). These projects included a systematic camera grid, the ElephantVoices project, the Human-Elephant Coexistence (HEC) project, and the Gorongosa Lion Project (GLP).

The systematic camera grid (5-km^2 grid cells) was set up to monitor year-round spatiotemporal patterns of large mammal activity and determine landscape-level correlates of occupancy in the core area of the park. To maximize animal detections, cameras faced open areas or small game trails with signs of animal activity, all off-road.

The ElephantVoices project used cameras to identify individual elephants and groups along the southern boundary of the park, and to look at patterns of access from the park to the Pungue River and buffer zone. Camera traps were deployed at five sites on elephant trails off of the Dingue-Dingue Road, which follows the southern boundary of the park. This road is occasionally used by park vehicles, but seldom by tourist or researcher vehicles and therefore has very little vehicle traffic.

The Human-Elephant Coexistence project was aimed at understanding and mitigating crop damage by elephants. HEC cameras were located at 13 elephant crossing locations (>200 m apart) in the park's buffer zone between the Pungue River and agricultural fields. There were 1-3 cameras at each crossing location (<100 m from each other; combined for analysis). Although some camera traps were located near deterrents (e.g., beehive fences) that were constructed halfway through the study period, the cameras were placed in such a way that they photographed the elephants before they encountered these deterrents. Thus, the mitigation experiment does not appear to have affected diel activity patterns, although cameras in that project might have experienced reduced detection rates if elephants were less likely to return to those crossing locations after encountering deterrents.

Finally, the Gorongosa Lion Project used camera traps opportunistically placed on roads to monitor the recovery of the park's lion population. For our analysis of GLP data, we used images from the 21 camera traps that faced roads. All GLP images were uploaded to WildCam

Gorongosa, a Zooniverse citizen science platform through which untrained volunteers from around the world identify the species in camera trap images. We downloaded all image records that had been classified as an elephant by at least one of 25 volunteers ($n = 6833$). We reviewed all images classified as an elephant by 10% or more of the users and excluded all images that were not elephants.

In total, data were collected from 2013 through 2017, although not all projects spanned this entire period. All projects used Bushnell TrophyCam camera traps with infrared sensors set to be triggered by motion, and detection distances and habitat types were similar across data sets. We reviewed all photographs to identify those with elephants (GLP photographs were first screened by citizen scientists). For all projects, camera traps were deployed within the park's road network in the southern region of GNP, bounded by Lake Urema on the north and the buffer zone in the south (Figure 1). This area of the park corresponds to the area of highest human activity and highest elephant densities, as determined from elephant sightings during seven dry season aerial surveys (2010-2016) that covered all or most of the park area (Stalmans and Peel 2016). Despite the concentration of human infrastructure, elephants remain in this area as it provides prime habitat and may have historically experienced lower levels of illegal poaching.

Data analysis

For each of the four data sets, we identified each independent observation of elephants, defined as an image taken >15 minutes from any other image. We chose 15 minutes based on expert assessment; extensive visual observations of elephant groups and examination of camera trap footage indicated that elephants in the same known group were rarely separated by >15 minutes at a given location. We considered the observation time to be the time of the first photograph. Combining photographs limited pseudoreplication and allowed us to compare relative activity rates across projects, given differences in the number of photographs taken during each trigger event and the delay time between trigger events.

To quantify differences in elephant activity between the core and exterior of the park, we compared the grid dataset (interior) with the combined ElephantVoices and HEC datasets (edge). To evaluate the effects of roads on elephant diel activity patterns we compared a subset of the grid dataset (off-road) with the GLP dataset (on roads). To control for non-random placement of GLP cameras across habitat types and areas of the park, we included only the 13 grid cameras (of the 60 cameras) that were located within the same 5-km^2 grid cell as a GLP camera.

We used kernel density estimation to model diel activity patterns of elephants, as described by Ridout and Linkie (2009). We converted the times of each observation to radians to account for the circularity of the temporal data. To account for seasonal differences in sunset and sunrise time, we scaled the times so that $\pi/2$ corresponded to sunrise and $3\pi/2$ corresponded to sunset. Based on the distribution of observation across the 24-hour cycle, we generated a smoothed non-parametric kernel density distribution of elephant activity for each project.

We compared pairs of density distributions (interior vs. edge of park, on vs. off road) by calculating the temporal overlap value, d-hat. The value d-hat represents the area under the curve formed by taking the minimum of the two activity density distributions at each time point. A value of 0 indicates no temporal overlap, whereas a value of 1 indicates complete overlap. We used the d-hat4 formula for estimating overlap, as recommended by Ridout and Linkie (2009) for sample sizes >50, and calculated an approximate 95% bootstrap confidence intervals. We used the *overlap* package in R for these analyses (Ridout and Linkie 2009). Although there was an uneven survey effort across projects, the sample size was >100 detections for all datasets, and considered to be sufficiently large for these analyses (Ridout and Linkie 2009).

We used counts of elephant observations at each of the 99 camera sites to further examine patterns of elephant activity in response to human disturbance. We determined the time period of each observation based on the sunrise and sunset times on the day of the observation. We defined four diel time periods: dawn (30 min period before sunrise), day (sunrise to sunset), dusk (30 minute period after sunset), and night (between dusk and dawn). We also combined dawn and dusk detections to determine the total number of crepuscular detections.

Based on this count data, we calculated a Relative Activity Index (RAI) for elephants at each camera. Daily RAI (RAI_D) was equal to the total number of observations divided by the number of trap-nights (based on the dates of deployment). We calculated mean RAI_D for each treatment (interior vs. edge of park, on vs. off road). We also calculated an hourly RAI (RAI_H) for each of the four diel time periods, defined as the number of independent detections per trap-hour (day: 12 hours, night: 11 hours; dawn and dusk: 0.5 hours each).

We used generalized linear models to examine the effects of roads and settlement on elephant observation counts. For all models, we used a negative binomial distribution to account for the overdispersion of the count data. We then used Wald chi-square tests, with the Anova function in the *car* R package, to test the significance of the fixed effects on elephant activity (Fox and Weisberg, 2011). To compare overall numbers of elephant detections across projects and human disturbances, we ran separate models with fixed effects of road treatment (on vs. off) and settlement (park interior vs. boundary), in which the dependent variable was the overall count of elephant observations, and the unit of analysis was the camera site. We controlled for differences in camera trap sampling effort by including effort (number of trap-nights) as an offset in the model. To examine temporal differences, we also ran separate models for each project and treatment, in which we included time period as a fixed effect, camera site as a random effect, and effort (number of trap-hours) as an offset.

We did not conduct any spatially-explicit analyses, given the differences in spacing of the camera traps. While the grid cameras were systematically deployed and >2km apart, the other cameras were all opportunistically placed.

RESULTS

The four projects generated a total of 1,983 independent elephant detection events, over a total of 19,904 trap nights. Elephants were detected at 93 of the 99 camera sites. The number of elephant observations differed across the four datasets ($\chi^2 = 47$, df = 3, $p < 0.0001$, Supplementary Figure 1). Elephant RAI_D (mean ± SD) was highest for the ElephantVoices project (0.47 ± 0.17), followed by the GLP (0.23 ± 0.27) and the Human-Elephant Coexistence cameras (0.10 ± 0.08). RAI_D was lowest on the grid cameras (0.06 ± 0.09).

Distinct diel patterns of activity were evident among elephants in each of the four datasets (Figure 2). Elephant activity was higher at night and during crepuscular periods than during the day for the ElephantVoices and HEC datasets (EV $\chi^2 = 175$, df = 2, $p < 0.0001$; HEC $\chi^2 = 61$, df = 2, $p < 0.0001$), with sharp peaks in activity just after sunset, and less pronounced peaks just before sunrise. In the grid dataset, elephant activity was highest during crepuscular periods, intermediate during the day, and lowest at night ($\chi^2 = 37$, df = 2, $p < 0.0001$). Elephant activity at GLP cameras was highest during crepuscular periods and the night and lower during the day, though there was no significant difference between time periods ($\chi^2 = 5$, df = 2, p = 0.09).

Inside the park, elephants were active throughout the 24-period, though there were significant differences across diel periods with most activity occurring during the day ($\chi^2 = 37$, df = 2, $p < 0.0001$). In contrast, elephants showed crepuscular activity patterns at the park edge, with significant differences across diel periods ($\chi^2 = 233$, df = 2, $p < 0.0001$). The overlap coefficient of the activity distributions of elephants in the interior versus the edge of the park was 0.46 (± 95% CI 0.40-0.48), representing the percentage of the total area under the activity density curves that is shared by the inside and outside park activity distributions (Figure 3). Mean RAI was higher at the boundary of the park (0.203 ± SD 0.200) than in the interior of the park (0.062 ± SD 0.087; Figure 5). There was a significant effect of settlement proximity on elephant observation counts ($\chi^2 = 27$, df = 1, $p < 0.0001$).

Elephant diel activity patterns on versus off of roads differed (Figure 4). On roads, elephants showed a peak in activity before sunrise, a reduction in activity during the daytime, and an increase in activity again at sunset and into the early hours of the morning, although differences across diel categories were not significant ($\chi^2 = 5$, df = 2, p = 0.09). Off road, elephants were more active during the middle of the day and late afternoon, with significant differences across diel periods ($\chi^2 = 9$, df = 2, p = 0.01). The overlap coefficient of the activity distributions of elephants on roads versus off roads in the park was 0.79 [95% CI: 0.73-0.84]. In the core of the park, there was no significant effect of roads on elephant observation counts ($\chi^2 = 3$, df = 1, p = 0.09). Mean RAI at cameras on roads was 0.24 (± SD 0.29), and mean RAI at cameras off roads was 0.10 (± SD 0.16; Figure 5).

DISCUSSION

Our findings suggest that elephants in Gorongosa National Park adjust the timing and location of their activity to avoid encounters with vehicles in the park and with people living in the buffer zone. Despite a likely fear of humans, however, this population of elephants did not entirely avoid areas of human disturbance; elephants exploited agricultural areas as food and water sources and used roads as movement corridors. By adjusting the timing of their movements at multiple spatial scales, elephants were able to navigate a landscape of multiple anthropogenic activities and opportunities while minimizing direct contact with people.

Although elephants in the park were more likely to be detected on roads than on trails, our study suggests that they adjusted the timing of their movement on roads to avoid vehicle encounters. We found that elephants were more active during the day than during the night on the grid cameras, which were placed away from roads, whereas elephants were more active at crepuscular and nocturnal periods on the GLP cameras that were placed on the road system. Elephants appear to be reducing their use of roads during areas of peak vehicle traffic, which are restricted to daytime and dusk periods. Such fine-scale temporal avoidance of vehicles has also been observed among Asian elephants (*Elephas maximus*; Katugaha et al. 1999). Our finding could also be attributed in part to the non-random distribution of GLP (road) cameras.

Previous studies have reported that elephants avoid roads in places where they experience persecution, such as the Congo Basin, where road avoidance by elephants restricts their habitat access, home range size, and movement ability (Blake et al. 2008). The elephant population of GNP was heavily poached during Mozambique's civil war, which may account for their avoidance of vehicles (Poole and Granli 2018). Many elephants in GNP exhibit distress, flight, and aggression in the presence of vehicles, and their response to vehicles has the potential to hinder tourism and elephant research in GNP. There is evidence that some elephants are slowly becoming habituated to the presence of vehicles, and in the assumed absence of direct threats to elephants inside the park, this habituation may continue to increase (Poole and Granli 2018). The continued use of camera traps throughout GNP will enable us to document and monitor potential changes in behavior through time, and inform ongoing efforts to habituate the park's elephants to human presence.

Despite their tendency to avoid vehicles, cameras placed on the road system (GLP cameras) still detected similar overall levels of elephant activity than cameras placed off of roads (grid cameras). This suggests that despite perceived risk from vehicles, elephants use low-traffic unpaved roads (Granados et al. 2012) as movement corridors, as has been documented for many other large mammal species (Abrahms et al. 2016). In fact, many of the roads in Gorongosa National Park originated as elephant trails. Elephants sometimes respond vocally to the sound of vehicles (Poole 1987), doing so in one documented case from up to 3 km away (Poole et al. 2005), and, therefore, may choose to reactively avoid vehicles when they encounter them, rather than proactively avoid roads altogether.

Elephants in GNP are far more likely to be active in and around human settlements during the night, when people are generally less active. Our findings are consistent with the results of GPS telemetry studies that found that elephants utilize settled areas most often at night (Graham et al. 2009, Cook et al. 2015) and have relatively higher nocturnal movement speeds in response to poaching (Ihwagi et al. 2018) or human settlement (Galanti et al. 2006). In GNP, elephants cross park boundaries to forage in maize fields in the communities along the Pungue River (P. Branco, unpublished data). The overall higher activity rates at the boundary of the park as compared to the interior can be attributed to study design and elephant movement patterns. The cameras on the boundary of the park were placed on elephant paths with the goal of capturing elephants, and as elephants have been found to show strong site fidelity to crossing paths, these cameras had high detection rates (Gerhardt et al. 2014).

By entering the settled areas of the buffer zone mainly at night, elephants reduce the risk of direct contact with people and maximize their crop foraging opportunities, as has been reported in similar studies in Kenya (Graham et al. 2010) and Tanzania (Gunn et al. 2014). Direct encounters with humans can pose a risk to elephants, which may be chased away or harassed by people defending their fields, and can also pose a risk to people (Moss 2001, Sitati et al. 2003). However, although nocturnal activity among elephants in settled areas benefits elephants by reducing direct contact with people, this activity pattern makes it more difficult for local farmers to protect their crops, resulting in high rates of crop damage (Parker et al. 2007). Camera traps set up in strategic locations, like those used by the ElephantVoices and Human-Elephant Coexistence projects in GNP, can be used to document, monitor, and potentially mitigate crop foraging and conflict. Such efforts will be increasingly important, as elephants in GNP are expanding their range and are beginning to raid crops in other areas of the buffer zone.

In addition to implications for tourism and human-wildlife conflict, behavioral responses of animals to human disturbance can have important consequences for wildlife populations and their conservation. When animals perceive risk from people, they may avoid areas of human activity, and these behavioral adjustments may alter foraging and reproduction and have costly consequences for individual fitness and survival (Sawyer et al. 2017). Avoidance of human activity may also decrease the effective amount of habitat available for wild animals (Gibeau et al. 2002, Eldegard et al. 2012). For wide-ranging species like elephants, avoidance of humans in both space and time may increase movement distances and travel costs (Graham et al. 2009). However, such effects likely are context-dependent. For example, as we found in this study, animals such as elephants may sometimes be able to exploit anthropogenic infrastructure and resources, which could compensate for increased costs of movement in anthropogenic landscapes (Chiyo et al. 2011). Future research is needed to understand the costs and benefits of spatiotemporal responses to human activity, and their implications for conservation at the human-wildlife interface (Songhurst et al. 2016, Goldenberg et al. 2017).

Our study demonstrates the utility of camera traps as an alternative to telemetry for studying spatiotemporal activity patterns of wildlife. While camera traps do not yield fine-scale spatial data, they provide insight into the 24-hour activity patterns and can be systematically deployed to facilitate spatial analysis. Our results also highlight the value of integrating datasets for comparative analyses. We compared different regions of a study system to examine the dynamics of elephant behavior in and around a national park. Similar analyses could be conducted at larger scales to compare different systems or even regions throughout the African continent, highlighting similarities and differences in drivers of animal activity. As the use of camera traps throughout Africa grows, there will be opportunities to integrate disparate datasets to improve our understanding of the continent's wildlife and address conservation challenges.

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Figure 1. Map of the study area in the southern portion of Gorongosa National Park, Mozambique.

Locations of camera traps from all four projects in relation to roads and the park boundary. The smoothed kernel density of elephants in the park was calculated in ArcGIS using the location of elephants (weighted by group size) recorded during seven aerial surveys of the park from 2000-2016, during the dry season (208 records of 1932 elephants).

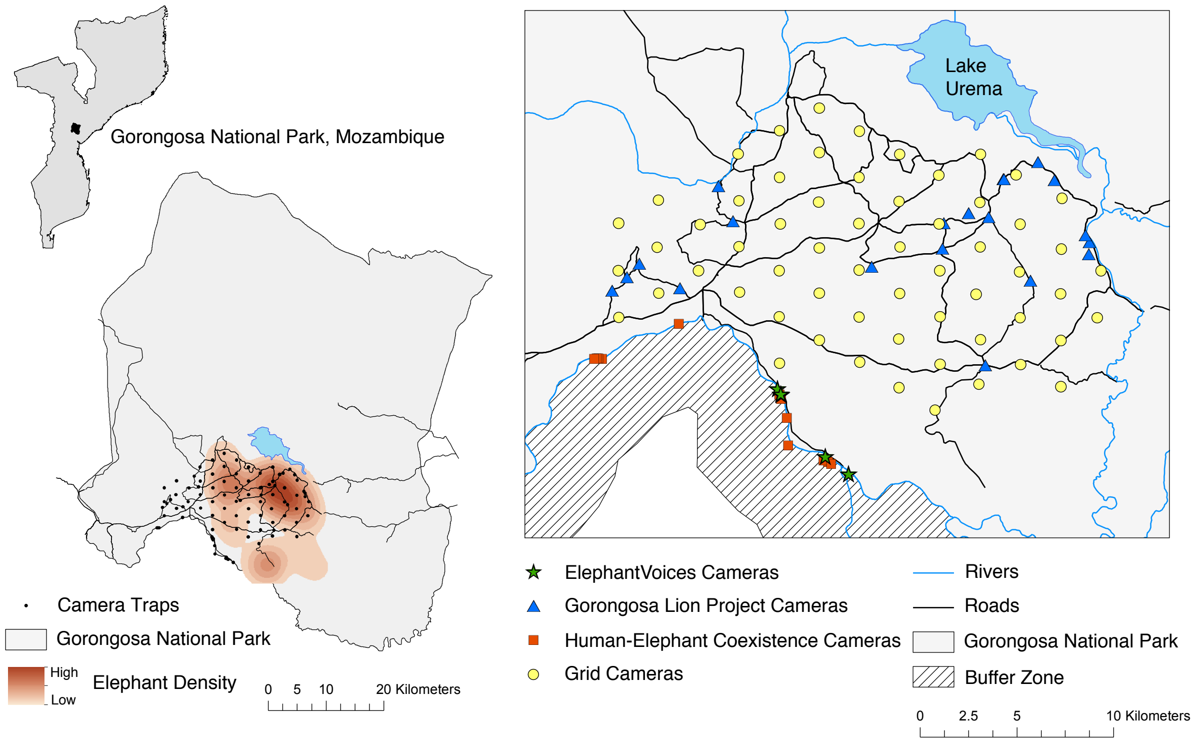


FIGURE 2. DIEL DISTRIBUTION OF ELEPHANT ACTIVITY FOR EACH PROJECT.

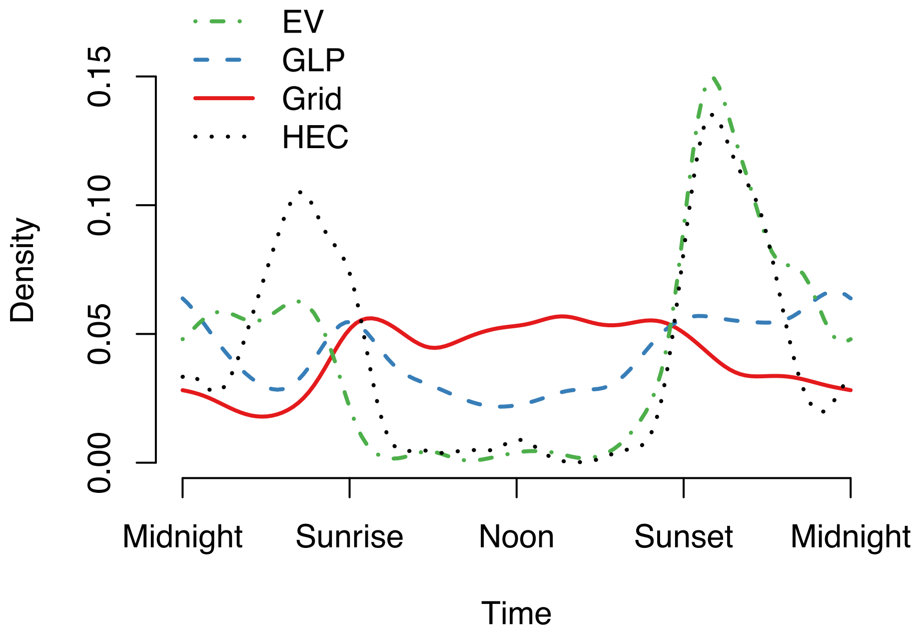


Figure 3. Effects of settlement on elephant diel activity.

Diel distribution of elephant activity inside the park (grid dataset) versus at the park boundary (ElephantVoices and HEC datasets). The grey region shows the overlap between the two distributions, and its area represents the overlap value (d-hat).

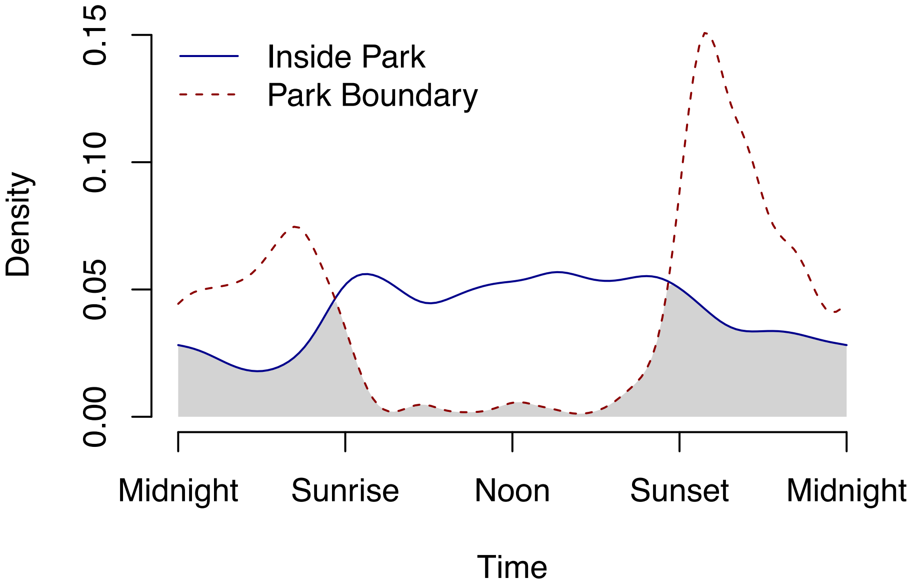


FIGURE 4. EFFECTS OF ROADS ON ELEPHANT DIEL ACTIVITY.

Diel distribution of elephant diel activity on roads (GLP dataset) versus off roads (grid data, subset to include only cameras in proximity to GLP cameras) inside Gorongosa National Park. The grey region shows the overlap between the two distributions, and its area represents the overlap value (d-hat).

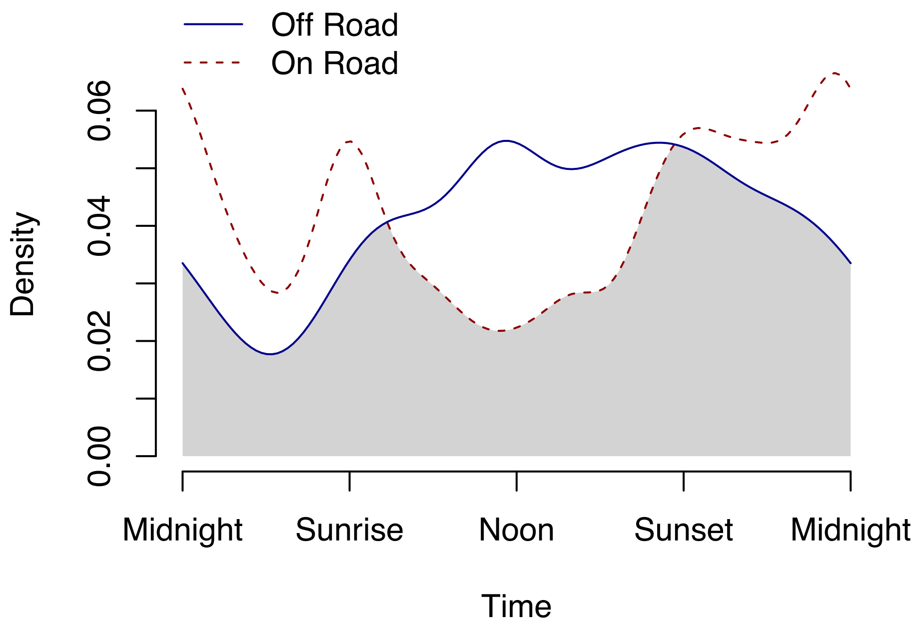
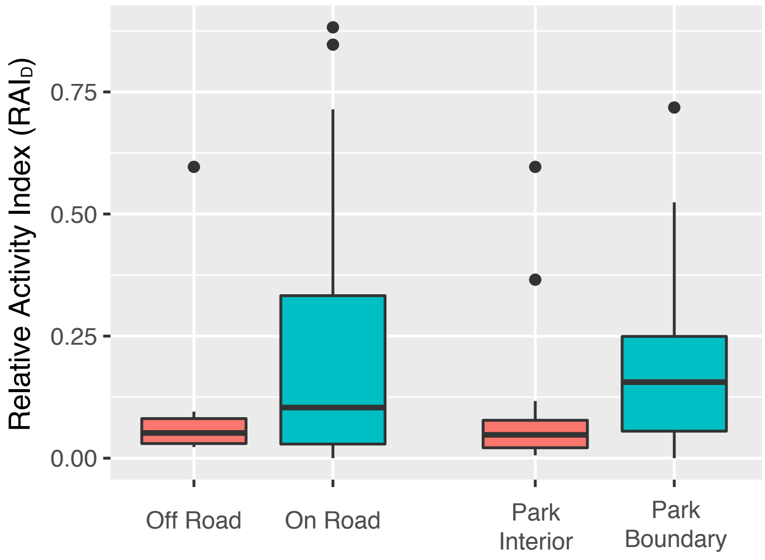


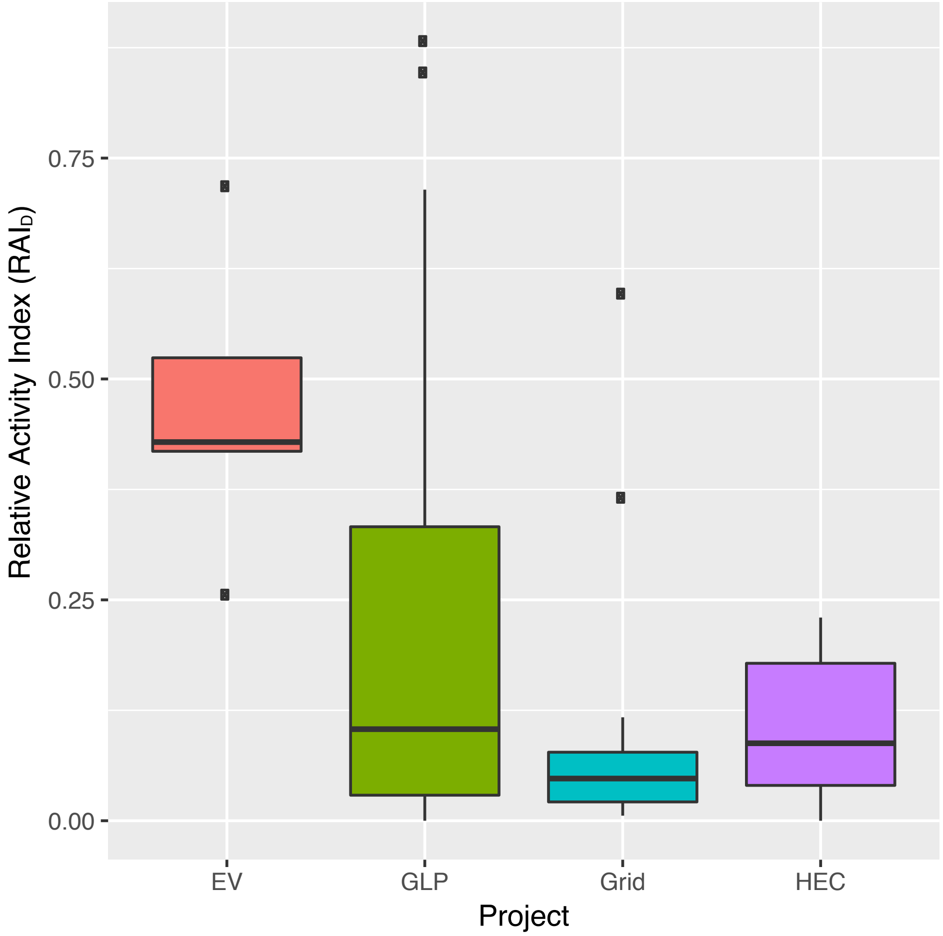
FIGURE 5. EFFECTS OF SETTLEMENTS AND ROADS ON DETECTION RATES.

The Relative Activity Index of elephants (independent detections per camera trap-night), for cameras off roads (subset grid dataset) and on roads (GLP dataset), and for cameras inside the park (grid dataset) and at the park boundary (ElephantVoices and HEC datasets). The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points).



SUPPLEMENTARY FIGURE 1. ELEPHANT RAI BY PROJECT

The Relative Activity Index of elephants (independent detections per camera trap-night), for each of the four projects. The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points).



SUPPLEMENTARY FIGURE 2. ELEPHANT RAI ACROSS DIEL PERIODS, BY PROJECT

The hourly Relative Activity Index of elephants (independent detections per camera trap-hour) across diel time periods, for each of the four projects. The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points).

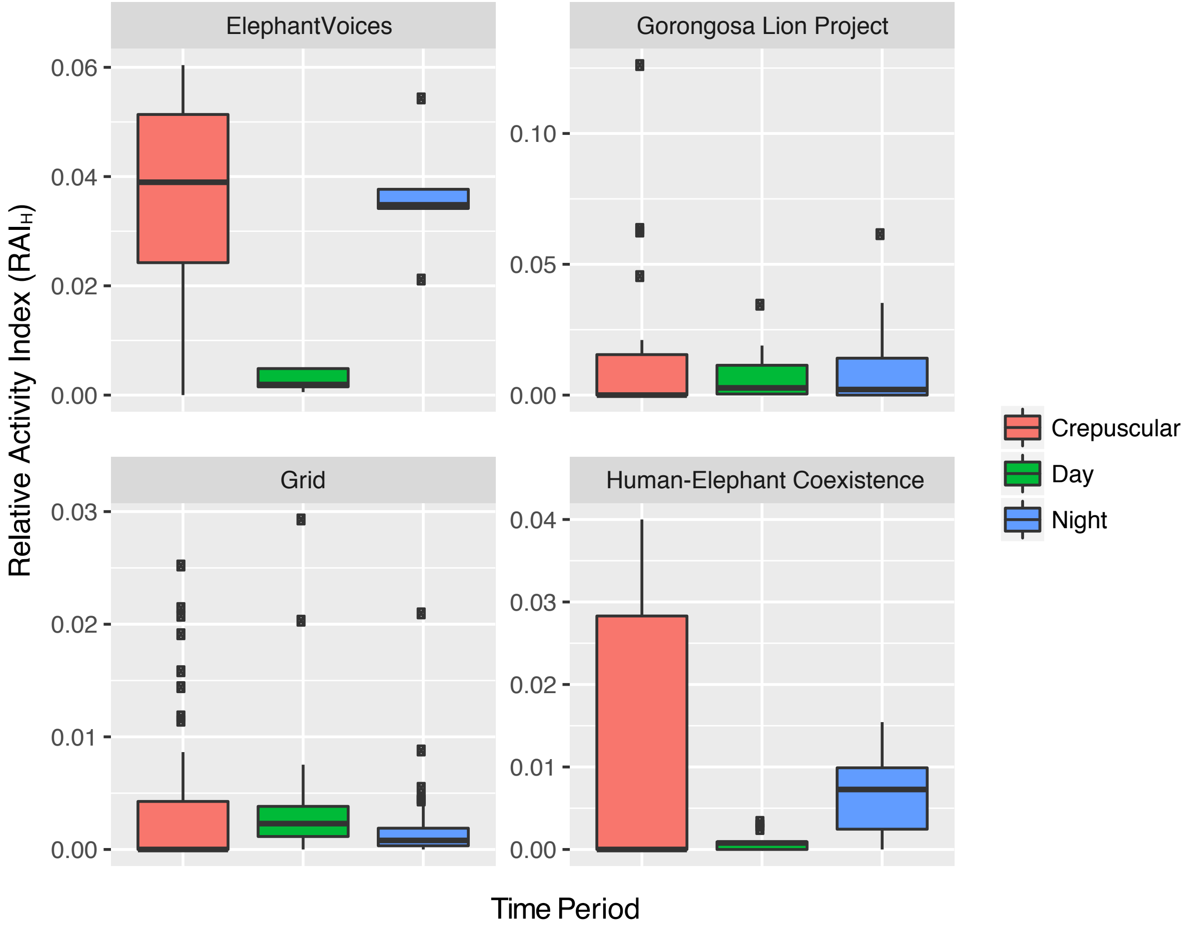


TABLE 1. SUMMARY OF CAMERA TRAP DATA COLLECTED BY THE FOUR PROJECTS INCLUDED IN OUR ANALYSES.

	ElephantVoices	**Gorongosa Lion Project**	**Grid**	**Human-Elephant Coexistence**
Study purpose	Elephant identification and monitoring	Monitoring of lions and other carnivores	Systematic large mammal survey	Elephant crop-foraging and response to deterrents
Camera placement	On elephant river crossing trails	On roads	Game trails off road	On elephant river crossing trails
Study location	Park boundary (park side)	Park interior	Park interior	Park boundary (buffer zone side)
# camera sites	5	21	60	13
# camera sites with elephant detections	5 (100%)	20 (100%)	60 (100%)	11 (87%)
Study period	May 2015 – November 2016 (seasonal)	August 2013 – May 2015 (seasonal)	June 2016 – July 2017 (continuous)	August 2017 – December 2017 (continuous)
Total camera trap-nights	803	2,290	15,599	1,353
# of elephant detection events (>15 min apart)	406	421	1,022	134

Chapter 6. Seasonal dynamics of an ungulate assemblage in a savanna floodplain landscape

ABSTRACT

African savannas are spatially heterogeneous and highly seasonal, resulting in a wide range of niches that diverse ungulate species occupy. Some of these savanna systems experience extreme flooding, which inundates grassland habitat, reducing its seasonal availability. The resulting concentration of animals in woodlands leads to the seasonal re-assortment of the mammal assemblage, potentially restructuring patterns of niche partitioning. In the Anthropocene, human activity is reshaping the dynamics of these systems through both local disturbance and global change. Here, we examined the effects of seasonal flooding, landscape heterogeneity, and human disturbance on the spatial distribution and spatiotemporal partitioning of ungulates in Gorongosa National Park, Mozambique. We conducted a two-year camera trap study to explore how environmental and anthropogenic spatial features interact with species traits to drive patterns of ungulate occupancy, relative density, and species co-occurrence across seasons.

Ungulate species showed strong associations with multiple environmental features (e.g., tree cover, water availability, fire history, termite mounds) with specific habitat preferences varying across species. In general, the effects of environmental heterogeneity on ungulate distributions were far greater than anthropogenic impacts. In the wet season, relative densities of waterbuck and other grazers increased dramatically in the woodland study area, as the floodplain was inundated; this reassortment resulted in greater spatial overlap among taxa, particularly species with similar diets. We did not find evidence that increased competition in the wet season leads to greater spatial or temporal partitioning among ungulates. However, as lions concentrate in woodlands during the wet season, there may be apparent competition dynamics, through which one species negatively impacts another as a result of its shared predator. As the ungulate assemblage in this system recovers from its near-extirpation during Mozambique's civil war, insights into its ecological dynamics can inform continued restoration efforts.

SPATIAL HETEROGENEITY AND UNGULATE DIVERSITY IN AFRICAN SAVANNAS

African savannas are some of the most iconic ecosystems on the planet, hosting a diversity of large mammal species and a mosaic of distinctive landscape features (Dobson 2009). These ecosystems are also experiencing rapid transformation as a result of global climate change and human population growth (Wittemyer et al. 2008). Many African savannas increasingly represent novel systems due to local extinctions, fragmentation, anthropogenic disturbance, and in some cases, targeted restoration efforts. To better conserve these ecosystems in the face of global change, we must know how they function, and understand how landscape heterogeneity interacts with a species' biology to drive patterns of spatial and temporal distributions.

Spatiotemporal heterogeneity is a hallmark of savanna ecosystems, which are characterized by a mixture of grassland and woodland habitats as well as extreme seasonality in annual rainfall (Anderson et al. 2016). At finer spatial scales, termite mounds and their associated nutrient-rich soils create hotspots of high-quality browse amidst the grassland and woodland matrix habitat. Fire is also an important feature of savanna habitats, resulting in the immediate loss of vegetative cover and the subsequent regrowth of high-quality forage (Bond and Keeley 2005, Eby et al. 2014). Water availability is heterogenous, and watering holes are important resources for many species. Increasingly, many savanna ecosystems around the world are also characterized by spatial variation in human activities, including roads and other infrastructure, ecotourism, law enforcement, research, hunting, and other livelihood activities. Such activities can change the distribution of animal species through both numerical and behavioral effects, mediated by habitat degradation, removal of individual animals, or avoidance of anthropogenic disturbance by animals (Frid and Dill 2002, Darimont et al. 2015).

Over evolutionary history, the landscape heterogeneity of savannas and associated diversity of niches have generated a wide range of forms and strategies among ungulate species (Cromsigt and Olff 2006, Hopcraft et al. 2011, Owen-Smith 2014, Schuette et al. 2016). African ungulates exhibit a large degree of variation in body mass, diet, sociality, anti-predator strategies, and water dependence, among other traits (Jarman 1974, Toit and Olff 2014, Hempson et al. 2015). In studies of other African savanna systems, body size and foraging strategy have been found to influence the effect of spatial heterogeneity on ungulate density and distribution (Bhola et al. 2012, Anderson et al. 2016). Trait diversity thus promotes the coexistence of ungulate species, allowing them to partition resources within savanna systems and minimize competition (Belovsky 1997, Kleynhans et al. 2010).

SEASONAL DYNAMICS OF FLOODPLAIN SYSTEMS

Many of the most notable African savanna systems, including Botswana's Okavango Delta and Zambia's Kafue National Park, are characterized not only by spatial heterogeneity but also by extreme flooding. In these systems, floodplain grasslands are often completely underwater for portions of the year, resulting in the seasonal loss of an entire ecotype. The seasonal movement of grazing ungulates off of floodplains leads to an annual re-assortment of the spatial distribution of ungulate species, thereby reshaping assemblages in the surrounding landscape and potentially altering patterns of herbivore competition. Many herbivore grazers utilize the floodplain in the dry season, but are concentrated into surrounding woodland savanna during the wet season as the submerged floodplains become inaccessible, potentially reshaping patterns of competition among ungulates (Bennitt et al. 2014).

Given this flooding and the associated loss of grassland habitat, the seasonal dynamics of floodplain systems differ dramatically from those of other African savanna systems that experience extreme wet and dry seasons. In systems that do not flood, the wet season and associated vegetation growth afford opportunities for herbivores to disperse away from permanent water sources (Okello and Kiringe 2008). For example, in the dry season in the Masai Mara, medium- and large-bodied herbivores concentrate in the reserve and in areas with greater water availability (Bhola et al. 2012). In the dry season in Serengeti, constrained resource availability leads to broader habitat use among herbivore species and increased interspecific competition (Bukombe et al. 2017). In floodplains, however, competition may be increased during the wet season, as herbivore biomass becomes concentrated in a smaller area and high-quality forage is particularly in demand given the nutritional requirements of lactating females, the presence of which often coincides with the wet season (Fynn et al. 2014). The inaccessibility of submerged floodplains may thus transform patterns of niche partitioning among African ungulate species.

As global climate change alters precipitation regimes in tropical areas, flooding dynamics may come to play a larger role in savanna ecosystems (Andersson et al. 2011). With more frequent droughts punctuated by more dramatic floods, animals may be seasonally concentrated into smaller or larger areas, potentially reshaping community interactions. Furthermore, as the human footprint expands (Venter et al. 2016) and populations grow around protected areas (Wittemyer et al. 2008), human activity may also be constraining animal movement and limiting dispersal during floods. It is therefore important to understand how environmental heterogeneity and anthropogenic disturbance interact to influence animal communities in these dynamic savanna systems.

RESEARCH QUESTIONS

We set out to understand the seasonal dynamics of a floodplain savanna ecosystem, and to answer the following questions and evaluate the following hypotheses:

I. How does seasonal flooding of the grassland affect the occupancy and density of species in the surrounding woodland?
    - *Hypothesis*: There will be an influx of ungulates into the woodland, particularly grazing and water-dependent species, as grassland habitat becomes less accessible.

II. What environmental and anthropogenic spatial features are associated with ungulate species occurrence and relative densities?
    a) How does this effect of landscape heterogeneity on species distributions differ in the dry and wet seasons?
    b) How does the relative importance of these factors differ among species with different ecological and life history traits?
    - *Hypothesis*: Associations with woody cover and other landscape features will vary widely across herbivore species, in accordance with diet, group size, water-dependence, and anti-predator strategy (Jarman 1974). For example:
        - Water-dependent species will be found closer to the floodplain in the dry season, and closer to seasonal pans in the wet season.
        - Smaller-bodied browsers, which are more selective in their diets, will be found more often in areas with higher fire frequency and termite mound density, both of which promote growth of nutritious forage (Eby et al. 2014).
    - *Hypothesis:* Animals will avoid areas of higher human disturbance, and this avoidance will be greater during the dry season when people are more active.

III. How do seasonal dynamics influence patterns of species co-occurrence in space and time?
    - *Hypothesis:* As animals concentrate in the woodland in the wet season, spatiotemporal overlap among competitors will increase.

GORONGOSA NATIONAL PARK: A CASE STUDY

Mozambique’s Gorongosa National Park (henceforth, Gorongosa) provides an ideal opportunity to study interactions between seasonal flooding, spatial heterogeneity, anthropogenic disturbance, and spatiotemporal niche partitioning by ungulates. Located at the southern extent of Africa's Great Rift Valley, Gorongosa's defining feature is the vast floodplain surrounding Lake Urema, which is located in the center of the park. This floodplain is inundated each year from approximately December through April (Figure 1); after the flood recedes in the dry season (approximately July through October), the Lake Urema floodplain is highly productive, supporting high densities of grazing ungulates. The woodland savannas around the floodplain are dominated by *Acacia-Combretum* assemblages, and also include palmveld, miombo woodland, and closed-canopy forest (Stalmans and Beilfuss 2008). Together, the floodplain and savannas host a rich mammal assemblage representing 18 ungulate species across 16 genera.

Seasonal flooding dynamics

In the dry season, Lake Urema covers an area of approximately 23 km^2. The lake is fed by several rivers in a 9,300 km^2 catchment (Steinbruch and Weise 2014). The floodplain of the lake and surrounding rivers encompasses roughly 750 km^2, though the degree to which it is inundated in the wet season varies greatly with annual rainfall. Up to 40% of Gorongosa floods each year, and within the Rift Valley, as much as 60% of the area can be inundated, resulting in a dramatic loss of terrestrial habitat during the wet season.

In the dry season, most large mammals concentrate on the floodplain. For example, an aerial survey of Gorongosa during the 2016 dry season (October) documented 69% of the park's medium and large mammal biomass on the floodplain (Stalmans and Peel 2016). While pre-war aerial surveys and historical accounts indicate that many of these animals left the floodplain during the wet season (Tinley 1977), little is known about current dynamics of seasonal wildlife movements in Gorongosa.

Community dynamics in a novel, recovering system

The study area represents a changing ecosystem that includes a large mammal assemblage that is markedly different from historical baseline conditions (Stalmans et al. 2019). During Mozambique's civil war (1977-1992), wildlife populations declined dramatically in the midst of political and economic instability as well as food insecurity, which drove increased bushmeat hunting (Hatton et al. 2001, Gaynor et al. 2016, Daskin and Pringle 2018). Following the end of the armed conflict, a restoration effort led by the Government of Mozambique and an NGO, the Gorongosa Restoration Project, facilitated the recovery of many large mammal populations through increased enforcement and, to a lesser extent, through limited reintroductions (Stalmans et al. 2019). However, the megaherbivore species that were dominant before the war, including buffalo, hippo, and elephant, have not returned to their pre-war numbers and the system is now dominated by antelope (Stalmans et al. 2019). Most notably, waterbuck populations have exploded in number and now account for >60% of herbivore biomass in the park, with waterbuck abundance an order of magnitude higher than pre-war estimates (Stalmans et al. 2019).

While the causes of this asymmetric recovery remain unknown, it has been suggested that waterbuck survived the war at higher densities and their population has been growing unchecked in the absence of predation or food limitation (Stalmans et al. 2019). Although Gorongosa once hosted a diverse guild of large carnivores, including leopards (*Panthera pardus*), lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*), all species but lions went locally extinct during the armed conflict. Lions were the only large carnivore species in the focal area during our study period, with a growing population of around 100 individuals

(Bouley et al. 2018). In the absence of an intact carnivore guild, it is unlikely that herbivore populations in Gorongosa are limited by top-down forces (Atkins et al. 2019, Stalmans et al. 2019). Small- and medium-sized ungulates may therefore be released from the predator limitation that is common in other African savanna systems (Sinclair et al. 2003).

In the absence of top-down forces given predator extirpation, herbivores may instead be food-limited (Sinclair 1985, Sinclair et al. 2003). Previous research in Gorongosa has revealed that dietary breadth is greater for abundant species, a finding that has been attributed to niche expansion resulting from more intense intraspecific competition (Pansu et al. 2018). Pansu et al. (2018) also found that dietary specialization among species is higher in the woodland savanna than in the grassland floodplain, presumably because the structural complexity of the former habitats makes certain plants inaccessible to smaller-bodied species. It is possible that in the current, restructured herbivore assemblage that more abundant species may outcompete and therefore suppress the recovery of other species, suggesting that it is important to understand patterns of ungulate niche partitioning (Stalmans et al. 2019).

Anthropogenic impacts on the system

As wildlife populations in Gorongosa National Park have recovered from armed conflict, human activity has also increased. The park is surrounded by a 5,330 km^2 buffer zone that is occupied by around 200,000 subsistence farmers (Ministério da Terra, 2016). The buffer zone is a mixed-use area, where people are permitted to grow crops, harvest natural resources, raise livestock and conduct controlled burns, along with other livelihood activities. Unlike in other well-studied African savanna systems (Schuette et al. 2016), there is no livestock grazing in or around Gorongosa. All hunting for bushmeat or trophies is prohibited in the park and buffer zone, but illegal hunting occurs throughout the park (Gonçalves 2017). It is possible that the expansion of human settlement at the park's borders is constraining seasonal movement for some woodland species, although historically, most movement of animals between the wet and dry season was confined to the Rift Valley (Tinley 1977).

Although the park is largely undeveloped, there is a dense network of roads in the southern region of the park, in the woodland south of the floodplain. There is a small but growing tourism operation based in Chitengo, the park's headquarters, and tourist, research, and ranger vehicles frequently travel throughout the park, with vehicle activity peaking in the dry season but declining markedly in the wet season, when many roads are closed. There are also several settlements located inside the park, including Chitengo. There is a large ranger presence in the park, primarily aimed at reducing hunting and other illegal activities.

These human disturbances are heterogeneous in both space and time. Little is known about the extent to which human disturbance is changing the distribution of mammal species in Gorongosa, either through changes in behavior associated with avoidance of human activity (Frid and Dill 2002) or through bottom-up (via changes in habitat) or top-down (via hunting) effects on local population densities (Ogutu et al. 2009). By examining the effects of both habitat heterogeneity and human activity on ungulate assemblage dynamics, we can better understand the changing ecology of this system as both wildlife and people recover from civil war.

OVERVIEW OF METHODS

To evaluate spatiotemporal patterns of ungulate activity in Gorongosa National Park, we conducted a camera trap survey in the woodland south of Lake Urema from 2016-2018. Data collection encompassed two dry seasons (July – September) and two wet seasons (December – March). We used a grid configuration to place 60 cameras in an area of 300km^2 in the woodland floodplain (Figure 2). We selected this study region because it contained a high density of large mammals and was accessible via the park's road network. Flooding prevented camera trap monitoring of the floodplain itself, and thus we focused on the seasonal dynamics of the surrounding, unflooded areas.

We examined dry and wet season patterns of ungulate occupancy and relative activity in response to environmental and anthropogenic spatial features. We evaluated the effects of nine covariates that we hypothesized would affect species distribution, including tree cover, fire history, density of termite mounds, density of seasonal watering holes (pans), lion activity, poaching, and distance to lake, rivers, and roads (Supplementary Figure 1).

We used two complementary modeling approaches: a multispecies occupancy model that provided insights into broad patterns of species presence and absence while controlling for imperfect detection (Rich et al. 2016), and linear mixed models of species Relative Activity Index (a simple measure of detections per trap-night) to explore patterns of relative species densities (Palmer et al. 2018). We then explored how ungulate ecological and life history traits (diet, sociality, water dependence) mediated the observed seasonal relationships between spatial heterogeneity and species occupancy and relative density. We also evaluated pairwise patterns of spatial co-occurrence, spatial Relative Activity Index correlations, temporal overlap, and dietary overlap among all ungulate species in the wet and dry season to understand how patterns of spatiotemporal niche partitioning changed seasonally.

We documented 38 species in our study area (Supplementary Table 1), including 18 ungulates (Supplementary Table 2; listed in decreasing order of camera trap detections; Supplementary Table 3): warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), bushbuck (*Tragelaphus scriptus*), impala (*Aepyceros melampus*), oribi (*Ourebia ourebi*), nyala (*Tragelaphus angasii*), elephant (*Loxodonta africana*), bushpig (*Potamochoerus larvatus*), Southern reedbuck (*Redunca arundinum*), greater kudu (*Tragelaphus strepsiceros*), Natal red duiker (*Cephalophus natalensis*), sable antelope (*Hippotragus niger*), African buffalo (*Syncerus caffer*), common wildebeest (*Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*), common duiker (*Sylvicapra grimmia*), hippopotamus (*Hippopotamus amphibius*), and common eland (*Taurotragus oryx*). More detailed information about study design and analytical methods can be found in Extended Methods section at the end of this chapter; more information about the study species is provided in the appendices.

I. HOW DOES SEASONAL FLOODING OF THE GRASSLAND AFFECT THE OCCUPANCY AND DENSITY OF SPECIES IN THE SURROUNDING WOODLAND?

Seasonal influx of floodplain species

Each year, the woodlands of Gorongosa experience an influx of biomass during the wet season, as animals move out of the inundated floodplain of Lake Urema. This influx was apparent from the camera trap data: in general, the species that concentrate on the floodplain in the dry season (as determined from the 2016 aerial survey) showed an increase in their Relative Activity Index in the woodland during the wet season. These floodplain species were found in close proximity to the lake in both the dry season and the wet season, but this pattern was even stronger in the wet season, suggesting that dispersal from the floodplains is responsible for the observed wet season increase in their woodland activity (linear regression for dry season: $r^2 = 0.07$, $F(1,16) = 1.29$, $p = 0.27$; wet season: $r^2 = 0.19$, $F(1,16) = 3.80$, $p = 0.07$).

Much of this seasonal influx was driven by waterbuck, which accounted for 58% of the animals counted in the aerial survey and 75% of the non-elephant biomass. During the 2016 dry season, the aerial survey revealed that 76% of waterbuck were on the floodplain. While waterbuck occupancy remained close to 1.00 in both the dry and wet seasons due to the uniform presence of waterbuck at all cameras on the study site, waterbuck detections in the camera trap grid nearly doubled in the wet season as compared to the dry season (Figure 3; paired t-test: $t = -3.85$; $df = 91$, $p < 0.0001$). This pattern held for both years of the study, and notably, waterbuck detections increased from the first year to the second year of the study in both seasons, a pattern indicative of their continued population growth. Seasonal models of waterbuck Relative Activity Index (RAI = detections / trap-night) predicted higher activity throughout almost the entire study area in the wet season, with effects strongest close to Lake Urema but extending well into the woodland (Figure 4).

Most ungulate species had a higher occupancy probability in the wet season than the dry season, suggesting that more species are concentrating in the woodland study area as a result of seasonal flooding (Supplementary Figure 2). African buffalo showed the most striking difference, with both occupancy probabilities and RAI increasing dramatically in the wet season (Supplementary Figure 2, 3; RAI paired t-test: $t = -2.49$, $df = 91$, $p = 0.01$). However, the ecological impacts of buffalo dispersal are likely limited, particularly when compared to those of the waterbuck, given the low densities of buffalo in the study system. Prior to the civil war, buffalo were the most abundant species in Gorongosa in terms of both number and biomass, and it is likely that their seasonal movement patterns played an important role in driving historical dynamics. Further research is needed to understand the ecological implications of the replacement of buffalo with waterbuck as the dominant floodplain migrant in this reassembled ecosystem.

Although detection rates for hippopotamus were low (20 detections across 6 cameras), hippopotamus were detected exclusively in the wet season. Hippopotamus are highly water-dependent and the expansion of Lake Urema likely results in a complete seasonal shift of their distribution. As massive bulk grazers that transfer substantial nutrients from terrestrial to aquatic systems (Stears et al. 2018), hippopotamus may have large impacts on dynamics of the woodland in the wet season. Their ecological role was likely even more important before their hunting-induced decline during the civil war, when hippopotamus numbers were much higher; today, based on aerial counts, hippopotamus densities remain around 15% of their estimated densities in the 1970s, (Stalmans et al. 2019).

Limited evidence for displacement of woodland species

Three species – greater kudu, nyala, common duiker – displayed a lower occupancy probability in the woodland study area in the wet season than the dry season, although these differences were not significant (95% credible intervals overlapped; Supplementary Figure 2). In addition to bushbuck, these species also had a lower Relative Activity Index in the wet season than in the dry season (Kudu paired t-test: t = 2.18, df = 91, p = 0.03; Nyala: t = 1.77, df = 91, p = 0.08; Common duiker: t = 1.81, df = 91, p = 0.07; Bushbuck: t = 1.65, df = 91, p = 0.10; Supplementary Figure 3). These browser or mixed-feeder species are all strongly associated with woodland habitat throughout the year and it is possible that they were displaced to other woodland areas further from the floodplain (and thus outside of the camera trap grid) as a result of the wet season influx of floodplain grazing species. However, the observed differences in seasonal occupancy and density were small, suggesting that any displacement is likely minimal.

II. WHAT ENVIRONMENTAL AND ANTHROPOGENIC SPATIAL FEATURES ARE ASSOCIATED WITH UNGULATE OCCURRENCE AND RELATIVE DENSITIES?

Environmental features and species traits interact to drive species distributions

In both the wet and dry seasons, we observed strong effects of environmental heterogeneity on the distribution of ungulate species, with the influence of environmental features varying according to ecological and life history traits (Supplementary Table 4, 5). Tree cover was an important predictor of relative densities of many species, with some taxa found in areas of greater tree cover (nyala, red duiker) and others found in more open areas (oribi, reedbuck, wildebeest, impala, and hartebeest). Generally, tree cover had a negative effect on the Relative Activity Index (RAI = detections / trap-night) of grazing species, a positive effect on the RAI of browsing species, and no effect on the RAI of mixed feeders (Figure 5). Similarly, dietary diversity (or niche breadth), as measured by Pansu et al. (2018) in Gorongosa, was positively associated with higher tree cover, as browsers and mixed feeders tend to feed on a greater number of plant species than the grazers.

Proximity to Lake Urema and its associated floodplains also influenced the distribution of many water-dependent species in the neighboring woodland; waterbuck, warthog, eland, elephant, and bushbuck all had higher Relative Activity Indices closer to the lake, while sable antelope, nyala, hartebeest, and wildebeest were all more active further from the lake. Thus, heterogeneity in tree cover and water availability appears to facilitate the coexistence of a diversity of ungulate species.

Seasonal differences in species-habitat associations

In most cases, the effects of environmental features on the occupancy and relative activity of a species were consistent across seasons, suggesting that species occupy similar niches in wet and dry seasons. Some exceptions included nyala, which showed a strong association with termite mounds in the dry season only, and elephants and kudu, both of which had higher relative activity indices in areas with more frequent fire in the dry season only. Both fire and termite mounds are associated with nutrient-rich forage for browsers and it is possible that this relatively higher-quality forage is a more important resource in the dry season, when resources are scarcer and there is less nutritious, early-growth browse available.

In contrast, species with a greater percentage of grass in their diets had a stronger association with fire frequency in the wet season only (Figure 6; Linear regression for dry season: $r^2 = 0.019$, $F(1,11) = 0.22$, $p = 0.65$; wet season: $r^2 = 0.24$, $F(1,11) = 3.56$, $p = 0.09$). However, this relationship was not significant, apparently due to an outlier: bushbuck were exclusively browsers with no grass in their diets, but were very strongly associated with areas of high fire frequency in the dry and wet seasons. Fire clears indigestible, dry grass in the dry season, promoting the growth of nutritious grass after the first rains. It is likely that grazing species are therefore drawn to these areas of the woodland in the wet season, particularly given that floodplain grasses are unavailable during the flood.

Patterns of association with rivers and lakes differed seasonally for some of the water-dependent species (Figure 7). While buffalo were found closer to lakes and rivers in the dry season, this pattern was absent in the wet season, when water was more available throughout the woodland in seasonal watering holes. Similarly, waterbuck activity was higher near rivers in the wet season, but not in the dry season.

Weak anthropogenic effects

We found limited evidence that human activity influenced the occupancy and relative activity of ungulates in Gorongosa. In general, environmental features were much more important than anthropogenic features in determining patterns of species occupancy and relative activity. The only exception was for red duiker, which were found further from roads in both the wet and dry seasons; these small, solitary antelope are generally skittish and are known to flee quickly from vehicles in Gorongosa. At the community level, animal occupancy was higher near roads in the dry season than in the wet season, contrary to our prediction that road closures in the wet season would reduce road avoidance by wildlife. As my coauthors and I have demonstrated previously (Chapter 5), animals may be using roads for travel but avoiding vehicles in time rather than space (Gaynor et al. 2018b). The absence of an effect of roads on species activity may also be confounded by the fact that the roads were created to facilitate dry-season wildlife viewing by tourists and thus roads may be located in areas of high wildlife densities. Finally, although not all roads are used equally (and some, in fact, are rarely used), we did not assess the relative degree of vehicle traffic on the different roads in the study area; it is possible that animals may be avoiding the most heavily-trafficked roads during periods of peak use but that this tendency was not evident in our data set.

While illegal bushmeat hunting continues to pose one of the major threats to wildlife in Gorongosa (Bouley et al. 2018), we found limited evidence to suggest that hunting is driving fine-scale spatial patterns of distribution and activity in ungulates. However, our measure of hunting was coarse, having been generated by participatory mapping exercises with rangers. In these interviews, rangers noted that hunting is very dynamic and that spatial patterns change year-to-year and across seasons. Additional research is needed to understand how hunting may be shaping the recovery of Gorongosa's ungulates through fine-scale numerical and behavioral effects on populations (Stalmans et al. 2019).

We were unable to examine the effects of human settlements on ungulate distribution, as there were few settlements near the study area (with the exception of park headquarters) and distance to the nearest settlement was correlated with other spatial variables. A 2015 pilot study conducted around two communities located in the park (Muaredzi and Muanza-Baixo) revealed no relationship between settlement distance and wildlife activity (Gaynor 2016). A recent study conducted in a forestry concession located adjacent to Gorongosa's buffer zone found that species richness declined in proximity to settlements (Easter et al. 2019), although this disturbed landscape still had a high level of species richness and provided habitat for species that are not found in the park itself, including leopards. As settlements expand around Gorongosa's borders and within areas of the park itself, it will be important to understand how human activities around settlements are shaping the environment and influencing wildlife recovery.

III. HOW DO SEASONAL DYNAMICS INFLUENCE PATTERNS OF SPECIES CO-OCCURRENCE IN SPACE AND TIME?

Little spatiotemporal partitioning among competitors

Although different ungulate species were associated with distinctive spatial features as discussed above, we found that the majority of ungulate species were positively associated with one another in both space and time. Species with more similar diets were somewhat more likely to be found at the same cameras (Figure 8), likely because they are drawn to areas that contain their shared resources. This pattern was slightly stronger in the wet season, but overall the correlation between spatial and dietary overlap was not statistically significant (Dry: $r^2 = 0.045$, $F(1,76) = 0.55$, $p = 0.46$; Wet: $r^2 = 0.045$, $F(1,76) = 3.58$, $p = 0.06$). Although we found that animals with similar diets tended to share rather than partition space, it is possible that competitors are partitioned resources at finer spatial scales. Other studies have shown that while some African herbivore species have a high degree of overlap at broad scales of space use, they have little overlap at scale of individual foraging areas (Owen-Smith et al. 2015).

We did not find evidence that dietary similarity was correlated with overlap of diel activity patterns (Supplementary Figure 4), suggesting that animals did not partition time to avoid their competitors (Kronfeld-Schor and Dayan 2003). While temporal partitioning may be beneficial in reducing scramble competition, it is likely less important in contest competition systems in which resources are spatially dispersed and slowly renewing, as is the case for many of the grazer and mixed-feeder species in Gorongosa. In fact, temporal overlap with competitors may confer anti-predator benefits through the detection and dilution effects of mixed-species herds (Schmitt et al. 2014), although we found no evidence of a positive relationship between temporal and dietary overlap.

Stronger overlap in the wet season

As predicted, we found that spatiotemporal overlap among ungulates was higher in the wet season, as compared to the dry season. As animals are concentrated into a smaller area, they may be constrained in their ability to avoid each other in space, despite the potential for increased competition. Patterns of spatial overlap between ungulate species were generally higher in the wet season than in the dry season (Figure 9). When comparing all pairwise interactions of ungulates, we found significantly higher SIF, a measure of co-occurrence ($t = -2.37$, $df = 54$, $p = 0.02$), and higher correlations between Relative Activity Index (RAI), a measure of relative densities ($t = -3.75$, $df = 54$, $p < 0.001$), in the wet season than in the dry season (Supplementary Figure 4). It is possible that dietary specialization increases in the wet season as species carve out unique dietary niches in the woodland, but we were not able to examine seasonal differences in dietary overlap since diet samples were only collected in the dry season.

It is possible that the greater availability of high-quality forage in the wet season reduces competition and thus counteracts the effects of increased density of ungulates in the woodland. Other studies of ungulates in Southern Africa have documented strong dietary niche partitioning only in the dry season, when resources are scarce (Kleynhans et al. 2010). Generally, competition may play less of a role in Gorongosa's ungulate communities than we had initially hypothesized. It is possible that, as species recover, they are not regulated either by bottom-up nor top-down effects. The system is highly dynamic, and during our study, the population trajectories of several species were exhibiting exponential growth (Stalmans and Peel 2016). As populations continue to grow, it is likely that competition will play a greater role in structuring the ungulate assemblage and continued seasonal monitoring may reveal changes in spatiotemporal partitioning as competition intensifies.

Potential apparent competition

The concentration of herbivores in the woodland during the wet season may also be driving apparent competition among species, through which dominant floodplain-associated species negatively impact woodland species through the increase in abundance of lions, a common predator. As previously reported for the Gorongosa lion population, lion home ranges shift from the floodplain to the woodland in the wet season and their home range sizes decrease (Bouley et al. 2018). Lions are also excluded from the inundated floodplains and may track dispersing prey into the woodlands; floodplain species comprise the majority of lion prey (Bouley et al. 2018).

Low overall predator densities in Gorongosa likely mean that the numerical effects of predation on any given ungulate species are small. However, we found some evidence to suggest that seasonal differences in predation risk may change prey behavior. We found that some species, including sable antelope (a strongly-preferred prey species of lions, Bouley et al. 2018), reedbuck, and oribi dramatically change their diel activity patterns from the dry to the wet season (Figure 10). The overlap between the diel activity distributions of lions and both reedbuck and oribi was significantly greater in the dry season than in the wet season (oribi: dry season overlap coefficient dhat = 0.704, bootstrapped 95% confidence interval = 0.583 – 0.834, wet season dhat = 0.367, 95% CI = 0.915 – 0.464; reedbuck: dry season dhat = 0.871, 95% CI = 0.830 – 1.044, wet season dhat = 0.519, 95% CI = 0.354 – 0.689). Overlap between the diel activity patterns of sable antelope and lions was also greater in the dry season than the wet season, although this difference was not statistically significant (confidence intervals overlapped; dry season dhat = 0.795, 95% CI = 0.700 – 0.960, wet season dhat = 0.574, 95% CI = 0.430 – 0.789).

These ungulate species typically give birth around the beginning of the wet season, and newborn and juvenile ungulates are particularly vulnerable to predation. In the dry season, they are crepuscular, and have a high degree of overlap with lion activity. However, in the wet season, they become primarily diurnal, despite increased daytime temperatures at this time of year. It is possible that this shift in diel pattern is related to lion avoidance. It is unlikely, however, that it is related to avoidance of waterbuck, as waterbuck are primarily diurnal.

CONCLUSION: THE DYNAMICS OF A RECOVERING SYSTEM

We documented seasonal changes in ungulate distributions in the woodlands of Gorongosa, where the annual inundation of the neighboring floodplain excludes animals from a large portion of the available terrestrial habitat. Waterbuck, already a dominant species in the woodland during the dry season, nearly doubled in number in the woodland during the wet season. As a consequence of this seasonal concentration of ungulates, we found stronger spatial overlap among all species during the dry season compared to the wet season. Despite the potential for increased competition during the wet season, there was no evidence that species partitioned space or time at the scales examined in our study, regardless of dietary overlap or shared life history traits. Each ungulate species was generally associated with the same habitat features in the dry and the wet season, although we saw some seasonal effects of water availability and forage (mediated by fire) for some species. The tight coupling between species traits and environmental niches may have limited seasonal reassembly of ungulate species but may also have facilitated coexistence and even facilitation at fine spatial scales among species using different resources within their overlapping home ranges (Arsenault and Owen-Smith 2002).

Given the recent re-establishment of large mammal populations in Gorongosa, it is unlikely that we are observing the dynamics of a community in a stable state. Both bottom-up and top-down pressures on ungulate communities are growing, potentially leading to increased competition among ungulate species. Predation will also likely play a larger role in driving the distribution of fearful prey as carnivores return to the landscape. Since the completion of this study, lion populations in Gorongosa have increased, African wild dogs have been reintroduced, a leopard was seen in the study area, and additional reintroductions are planned for the near future. While hunting has declined in recent years, other forms of human activity have increased, including tourism, research activity in the park, and human settlement at park borders, each of which has the potential to influence ungulate activity. Growing ungulate populations, in turn, will continue to reshape the landscape through foraging feedbacks such as changing patterns of tree cover and forage quality (Holdo et al. 2009, Daskin et al. 2016, Anderson et al. 2016). Seasonal patterns of spatiotemporal partitioning may shift in response to these landscape changes; continued monitoring of the Gorongosa ungulate assemblage will provide important insights into the ecological dynamics of large mammal restorations in African habitats.

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EXTENDED METHODS

Study site

Gorongosa is located in central Mozambique, at the southern extent of Africa's Great Rift Valley (Latitude: -18.82, Longitude: 34.50). The continuous core of the park encompasses 3,700km^2 (excluding the discontinuous portion of the park on Mount Gorongosa, and the newlyincorporated Coutada 12). The 40-km-wide valley in the center of the park is bordered to the east and west by steep terrain. Average annual rainfall is 700-900mm in the valley, and greater on the surrounding plateaus, peaking in December to February.

Camera trap grid

We deployed a grid of 60 Bushnell TrophyCam camera traps within the 300 km^2 study region (Figure 1; Supplementary Table 6, 7). We divided the study area into 5 km^2 hexagonal grid cells and placed one camera at the center point of each grid cell, similar to the Snapshot Serengeti protocol (Swanson et al. 2015). We mounted each camera on a suitable tree within 100 meters of the center point, at a height of 1 meter. To maximize animal detections and minimize false triggers, we faced cameras towards open areas or small game trails with signs of animal activity. Each camera was within 2 km of a road, but no cameras faced roads.

The grid operated continuously from June 2016 – June 2018, although some cameras were inoperable for limited periods due to water or elephant damage, overgrown vegetation blocking the lens, or depleted batteries. In June 2017, 14 of the least-accessible cameras were removed from the grid.

Each camera took 2 photographs per trigger event with a delay of 30 seconds between triggers. For analyses that involved counts of independent detections, we considered all records of a given species without a break of >15 minutes to be part of the same detection.

Trained undergraduate volunteers at the University of California, Berkeley, identified the animal in each photograph to species. K.G. confirmed all identifications and generated a record of detections from the photographs using the *camtrapR* package in R (Niedballa et al. 2016).

Defining seasons

For the purposes of our analyses, we defined the dry season as July 1 to September 30 (3 months), and the wet season as December 1 to March 31 (4 months). Although the time period for the wet season was one month longer than the dry season, there were fewer total camera trap-nights in the wet season due to more frequent camera inoperability during this season (Supplementary Table 6, 7).

These season designations correspond to patterns of annual rainfall during the study period, as recorded at Gorongosa headquarters. From 2016 and 2017, total rainfall from July through September was < 15mm (or around 2% of total annual rainfall). For the rain-years of 2016-2017 and 2017-2018 (spanning October-September), > 70% of the total annual rainfall fell from December through March. The second year of the study received nearly twice as much rain as the first, much of it falling late in the wet season (total rainfall 2016-2017 = 685 mm; 2017-2018 = 1286 mm). Although December 2017 was a low rainfall month, we chose to include it in the wet season, as early rains in October-November 2017 had led to early flooding of the Gorongosa floodplain. The first year of our study was a somewhat dry year, while the second year was a particularly wet year. We were unable to distinguish between the effects of different rain and flooding regimes given that we were only comparing two years, and had small sample sizes for the second year.

Spatial data

We compiled spatial data on environmental and anthropogenic features that we expected to be related to large mammal occupancy and density (Supplementary Figure 1). We generated raster layers corresponding to tree cover, fire, termite mounds, seasonal watering holes, lion activity, poaching, and distances to lake, rivers, roads, and settlement. For rasters not already at a 10 x 10 m resolution, we resampled each raster at this scale. We then cropped each raster to the study area, and standardized each raster by scaling each variable so that the mean was 0 and the standard deviation was 1. We then extracted the value of each raster layer at each of the 60 camera trap locations. We examined correlations between all covariates and excluded any for which $r > 0.7$ (Dormann et al. 2012). All analyses were done using the *raster* package in R (Hijmans & van Etten 2017).

We used remotely-sensed satellite imagery to generate tree cover, fire, and seasonal watering hole layers. We used the 2010 tree cover layer from the Global Forest Change database (Hansen et al. 2013). To quantify fire history in the study area, we used the 500-meter resolution Burned Area product from NASA's MODIS satellites (MCD64A1) (Giglio et al. 2016). We calculated fire return interval (or fire frequency) in the period from 2000-2016. We manually digitized seasonal watering holes, which have a unique and recognizable visual signature, using a DigitalGlobe image from 2015, via ESRI ArcMap World Imagery. We ground-truthed the layer in the field, visiting 50 points that we had visually identified as watering holes from satellite imagery, with 100% accuracy in identifying watering holes. It is possible but unlikely that some small watering holes were missed. We then generated raster layers corresponding to the distance to the nearest watering hole and to the area covered by watering holes within 100m, 250m, 500m, and 1km of each pixel. After exploratory analysis, we decided to use a radius of 250m^2, because it best predicted community-level occupancy in the multi-species models described below.

When setting up the camera traps, we counted the number of termite mounds within a 100 meter radius of each camera. To extrapolate termite mound model results to the entire study area, we used spatial data on termite mound locations generated through both supervised and object-based training procedures, using 1.8m resolution WorldView-2 (© Digital Globe; Longmont, CO, USA) satellite imagery from July and August 2010. This classification involved the separation of mounds from surrounding habitat based on spectral properties and shape. We compared the classification output to information on the locations of known mounds (n = 126) and other habitat patches (n = 1041), as recorded in the field (overall accuracy: 62%; sensitivity to mounds: 61%; specificity to mounds: 64%).

To quantify relative lion activity in the study area in each season, we used the 10%, 25%, 50%, 75%, and 95% home-range isopleths for all male and female lions, generated from GPS collar data collected as described by Bouley et al. (2018). All prides and male coalitions in the study area were collared for at least one year between 2013-2016.To generate a raster of relative lion activity density, we summed all isopleths for all collared individuals in the wet and late dry seasons, using only the most recent isopleths for each individuals for animals followed for multiple years.

To understand spatial variation in poaching pressure, we used participatory maps generated by focus groups of park rangers, as described by (Gonçalves 2017). In the participatory mapping exercise, the relative degree of poaching was classified as high, medium, or low throughout the park, based on ranger perception of reported incidents, snares and traps found, and wildlife mortality. We created a raster with three levels corresponding to low, medium, and high poaching.

We also generated rasters corresponding to the distance to Lake Urema, distance to the nearest river, distance to the nearest settlement, and distance to nearest road. The locations of settlements in and around the park were compiled by M. Stalmans of the Gorongosa Department of Scientific Services from a number of sources, including aerial surveys and remotely-sensed imagery. The locations of roads were recorded on the ground with a GPS unit while driving along the roads in the park. We ultimately removed distance to settlement from analysis, as it was correlated with distance to river, which we hypothesized was a more important predictor of animal activity in this system.

Analysis of species distribution and activity

We used two complementary modeling approaches to examine spatial covariates of seasonal species distributions: 1) a multispecies occupancy modeling approach developed to understand broad patterns of species richness and species presence or absence, and 2) predictors of species detection rates (Relative Activity Indices) to explore differences in relative densities of ungulate species over space and time.

Occupancy modeling

The occupancy modeling framework developed by (Rich et al. 2016) accounts for imperfect detection of animals by camera traps, allows for the examination of covariates of interest for both occurrence and detection probabilities, and draws on observations of all species in the community to inform occurrence probabilities of individual taxa (Dorazio and Royle 2005). This approach was recently used by Easter et al. (2019) to quantify patterns of species richness in a forestry concession in the greater Gorongosa ecosystem.

For each species detected at each camera, we generated a detection history corresponding to the number of days in which that species was detected. We then used this detection history to estimate the probability of species i occurring at camera site j, while accounting for imperfect detection. In our model, we defined occurrence of a given species at a site, $z_{i,j}$, as a binary variable equal to 1 if the range occupied by species i included camera site j, and 0 if it did not. We assumed that occurrence was a Bernoulli random variable, where $\Psi_{i,j}$ is the probability of a species i occurring at site j, and thus $z_{i,j} \sim \text{Bern}(\Psi_{i,j})$. We treated each day as a repeat survey at a given camera site, to distinguish between true absences and non-detections in cases in which a species was present but not detected by the camera trap. We then estimated the conditional probability of detecting species i at camera site j on survey occasion (day) k as $X_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where $p_{i,j,k}$ is the detection probability given that the species was truly present at the site.

We used a generalized linear mixed modeling approach, following (Zipkin et al. 2009, 2010, Rich et al. 2016); this consisted of fitting one model for each season (dry and wet) with spatial covariates selected based on *a priori* justification. Occupancy covariates included tree cover, fire frequency, termite mound density, watering hole density, lion activity, poaching, and distance to lake, rivers, and roads. We also included four detection covariates that we thought might influence the detection probability of different species: camera height, camera angle, detection distance, and grass cover in the immediate area.

We fitted a single model to the entire community, assuming that species-specific parameters were random effects derived from a normally-distributed, community-level hyperparameter. We incorporated detections from all species in this model, although in subsequent analyses we focused on ungulates. We also split species into groups according to diet (herbivore, omnivore, and carnivore), after which coefficients were modeled as functions of community-level mean, group-level mean, and species-specific effect for each covariate. More information on the specifics of the modeling framework can be found in Rich et al. (2016).

Relative activity index

We also used information on relative detection rates to explore spatial and seasonal changes in relative densities of ungulate species, complementing the occupancy modeling approach. While hierarchical occupancy modeling accounts for imperfect detection of species, it only addresses presence or absence and thus fails to account for differences in species abundance. For common species that are widespread in space, a comparison of relative activity across camera sites may provide greater insight into seasonal dynamics of space use. To that end, for each camera in each season, we calculated a Relative Activity Index (RAI), corresponding to the number of detections per trap-night. RAI has been found to be a suitable proxy for densities of African ungulates in the Serengeti (Palmer et al. 2018). We did not use the RAI modeling framework for the carnivore species, as it is less suited for rare, solitary, or territorial species, for which there is often a bimodal distribution in detection rates across camera sites.

We used linear mixed models to evaluate the effects of landscape covariates on RAI, running separate models for each species in each season (n = 116 cameras in the dry season; n = 82 cameras in the wet season). Before modeling, we first standardized RAI for each species in each season by setting the mean to 0 and the standard deviation to 1; this was done so that we could compare covariate estimates across species and seasons. Using the *dredge* function in the MuMIn package (Bartón 2018), we evaluated all possible combinations of fixed effects to identify the top models based on AIC, including the same covariates as we did in the occupancy model above: tree cover, fire frequency, termite mound density, water hole density, lion activity, poaching, and distance to lake, rivers, and roads. We included camera location as a random effect in each model to account for the inclusion of two years of data for most of the cameras. Fixed effects included tree cover, fire frequency, termite mound density, water hole density, distance to lake, distance to river, lion activity, and distance to road. We then averaged the coefficients from all models within 2 AIC of the top model, and calculated 95% confidence intervals for each covariate.

To map activity patterns for waterbuck in the dry and wet seasons, we used the model-averaged coefficients to predict waterbuck RAI for each 100 x 100 meter cell in the study area given the average values of the covariate rasters in that cell. For this analysis, we used raw RAI values rather than standardized RAI values to facilitate comparisons between seasonal RAI. We compared dry and wet season RAI for each species using paired t-tests, where dry and wet season RAI were paired for a camera in a given year (n = 92 camera-years). The summary results of these tests are presented in Supplementary Figure 3.

Linking species traits to spatial patterns

To examine the relationship between species traits and spatial predictors of activity and distribution, we compiled information on all ungulate species in the study area from a variety of sources. We gathered information on sociality, broad dietary strategy, and water dependence from the PanTHERIA database (Jones et al. 2009) and from the supplementary materials of

(Hempson et al. 2015). We also used site-specific information on dietary niche width and percent grass in diet from (Pansu et al. 2018), who conducted a DNA-metabarcoding study in Gorongosa National Park concurrently with our camera trap study. Finally, we used data from the 2016 dry season (October) aerial survey of Gorongosa (Stalmans and Peel 2016) to understand species distributions at a larger spatial scale during the dry season, since our camera trap grid was confined to the woodland savanna. For each species, we calculated the percentage of individuals of each species that were on the floodplain versus the woodland savanna.

Analysis of species interactions

To evaluate seasonal differences in niche partitioning among ungulate species in Gorongosa, we calculated pairwise overlap between ungulate species in space and time, and incorporated information on dietary overlap from (Pansu et al. 2018). We then used several linear regression models for the wet and dry season to examine relationships between spatial, temporal, and dietary overlap.

As with the analysis of spatial predictors of species distribution, we also used two different modeling approaches to determine pairwise spatial overlap. First, we used a Bayesian hierarchical co-occurrence modeling framework to assess pairwise patterns of species co-occurrence. As described by (Davis et al. 2018), we used a Bayesian modeling framework to calculate Species Interaction Factors (SIF) for each pair of ungulate species based on conditional occupancy and detection probabilities for each member of the pair (e.g. the probability that species A is present given that species B is present or absent, and vice versa). If the species are independent of one another, SIF is equal to 1; SIF > 1 if the species co-occur more frequently than expected, and SIF 0-1 if species co-occur less frequently than expected (avoidance). We log-transformed SIF values for subsequent analysis, so that a negative value corresponded to avoidance, and a positive value to attraction. Second, we conducted a linear regression of Relative Activity Indices. For all pairs of species A and B, we calculated Pearson's r correlation coefficients between the Relative Activity Index of species A and species B at a given camera site in a given year.

To calculate diel temporal overlap between species, we first used the times of each independent detection to generate a kernel density distribution of diel activity patterns across camera sites, as described by Ridout and Linkie (Ridout and Linkie 2009). To account for the circularity of the temporal data and for daily differences in sunset and sunrise time, we scaled all times to radians so that $\pi/2$ corresponded to sunrise and $3\pi/2$ to sunset. For each pair of species, we then calculated a coefficient of temporal overlap, d-hat, using the overlap package in R (Ridout and Linkie 2009b). The value d-hat represents the area under the curve formed by taking the minimum of two activity density distributions (0 represents no temporal overlap, and 1 complete overlap). We used the dhat4 formula, as recommended by (Ridout and Linkie 2009) for sample sizes >50.

We also incorporated two pairwise measures of interspecific dietary niche overlap from (Pansu et al. 2018): Pianka's index of dietary niche overlap and the Bray-Curtis dissimilarity index. To minimize the influence of outliers caused by infrequently-detected species, we restricted analysis to the 10 most commonly-detected ungulate species for which diet data was also available: warthog, waterbuck, bushbuck, impala, oribi, nyala, elephant, reedbuck, greater kudu, and sable. All data for the diet study were collected during the dry season.

FIGURE 1. SEASONAL RAINFALL IN GORONGOSA, 2016-2018.

Total monthly rainfall in Chitengo, the headquarters of Gorongosa National Park, during each month of our study. We compared wildlife distributions in the dry season (July – September) and wet season (December – March).

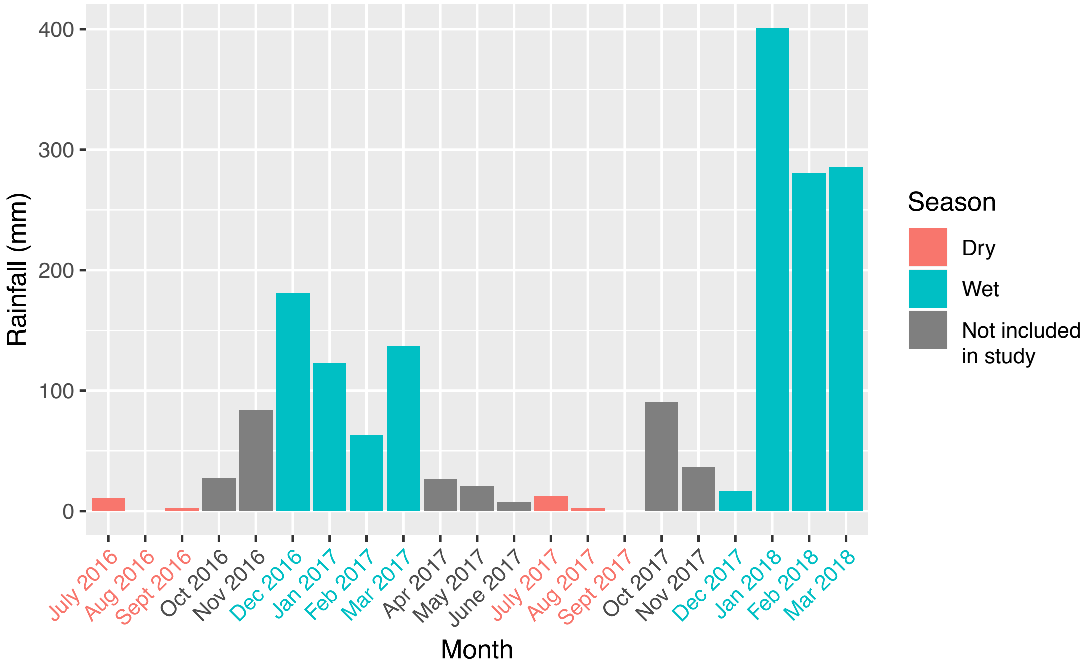


FIGURE 2. STUDY SITE.

Map of Gorongosa National Park, showing the locations of the lake, floodplain, and camera traps. In the dry season, Lake Urema is restricted to the area shown in dark blue. In the wet season, much of the floodplain, in light blue, is seasonally inundated as Lake Urema and the surrounding rivers flood. The camera trap grid is located south of Lake Urema, in savanna woodland. Inset shows the location of Gorongosa National Park within Mozambique.

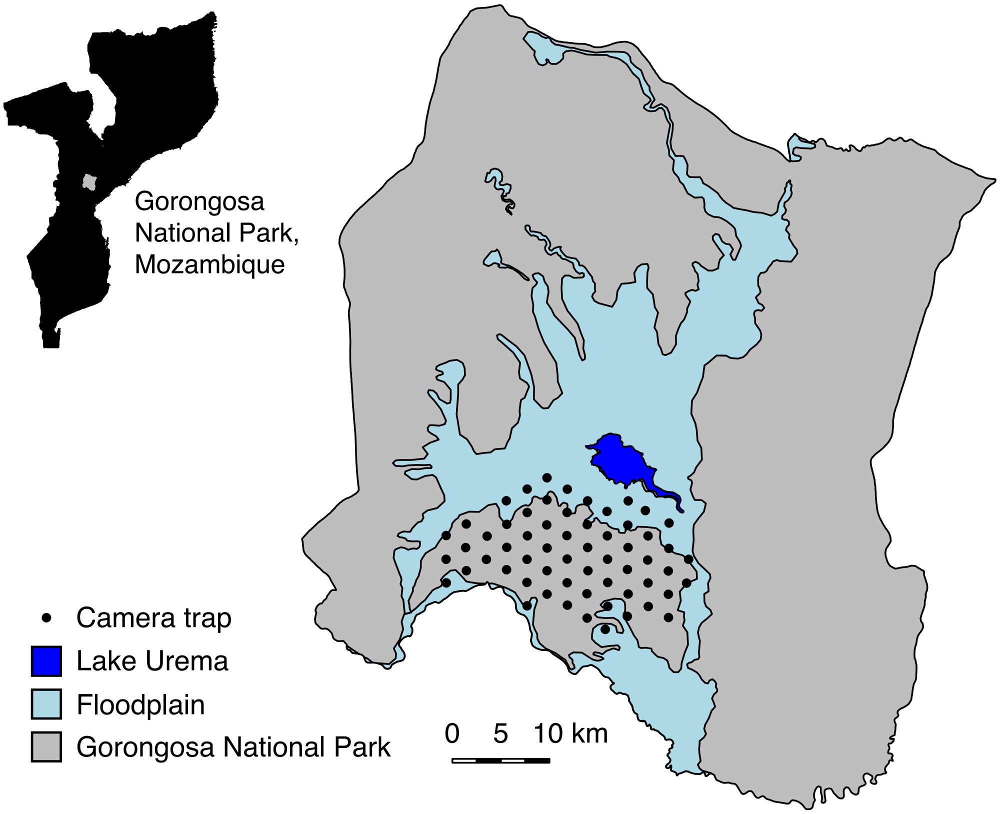


FIGURE 3. RELATIVE ACTIVITY INDEX OF WATERBUCK.

Average Relative Activity Index (RAI = detections / trap-night) of waterbuck across cameras in each season, with bars representing Standard Error. Waterbuck activity in the woodland study area nearly doubled between the dry and wet seasons during both years of the study, with a general increase from year 1 to year 2, reflecting continued population growth.

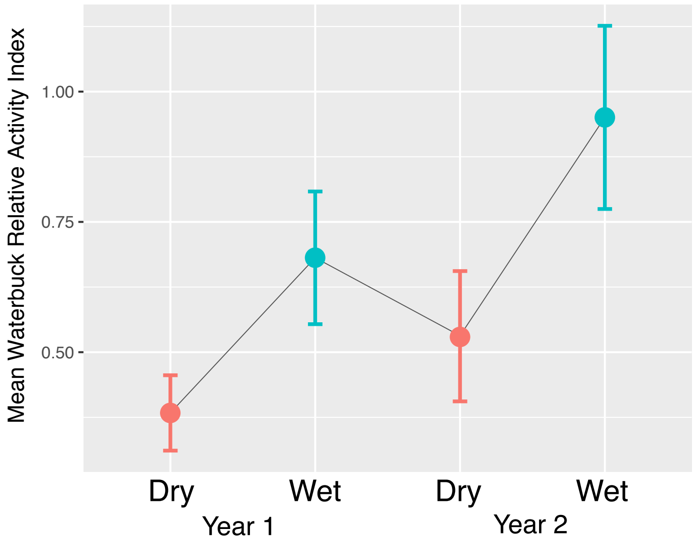


FIGURE 4. MODELED RELATIVE ACTIVITY INDEX OF WATERBUCK IN THE DRY AND WET SEASON.

Map illustrates the predicted waterbuck Relative Activity Index (RAI = detections / trap-night) in the woodland camera trap study area south of Lake Urema. The map is based on the top dry and wet season models of waterbuck RAI, and the values of the underlying spatial raster layers associated with the predictors in these models. Waterbuck activity increases throughout the study area, particularly near Lake Urema, as animal disperse from the inundated floodplain.

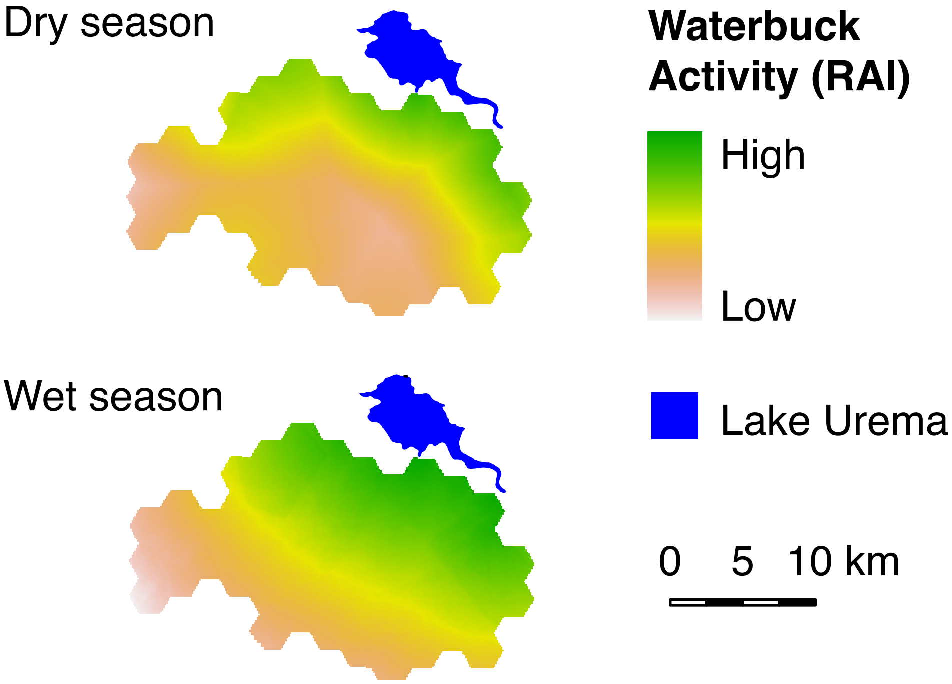


FIGURE 5. FORAGING STRATEGY AND TREE COVER ASSOCIATION.

Points represent the mean of model-averaged coefficients for tree cover as a predictor in the models of Relative Activity Index (RAI = detections / trap-night), averaged across species within each foraging strategy. Error bars correspond to standard error of the mean. Generally, the RAI of grazing species decreased with tree cover, while the RAI of browsing species increased with tree cover.

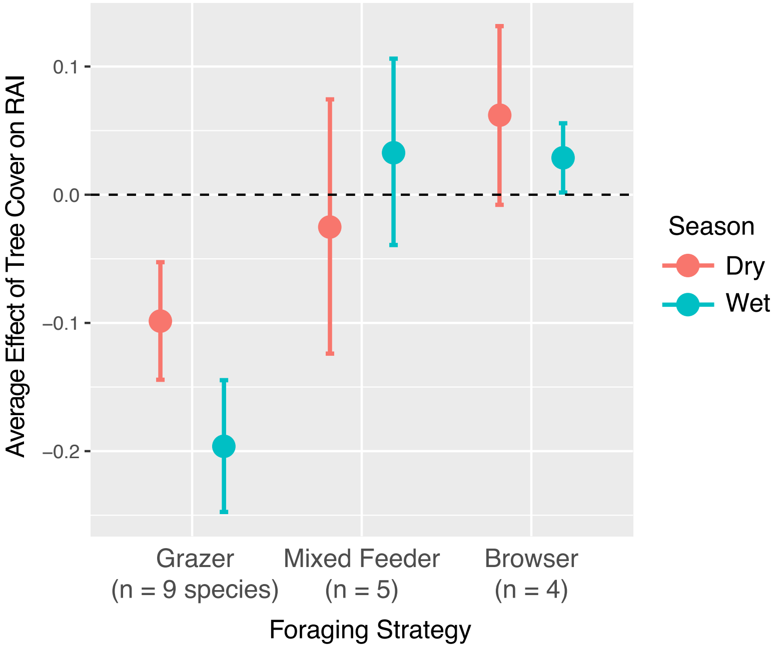


FIGURE 6. FIRE AND GRAZING.

Relationship between percent grass in diet and the effect of fire frequency on Relative Activity Index (RAI = detections / trap-night). There is one point for each species (for which diet data were available), representing the model-averaged coefficient corresponding to the effect of fire frequency on RAI. In the wet season, species with a higher percentage of grass in their diet were more strongly associated with areas that burn more frequently.

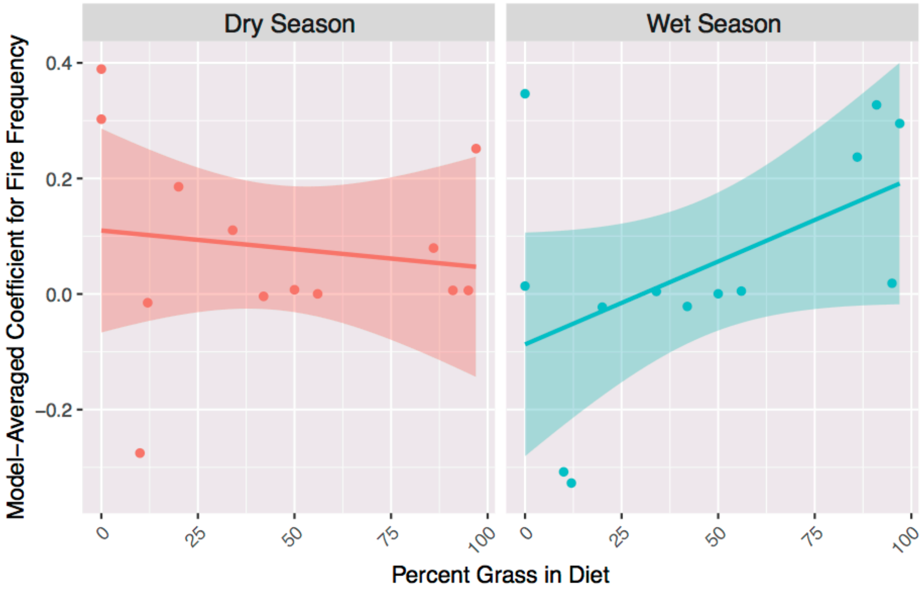


FIGURE 7. WATERBUCK AND BUFFALO ASSOCIATE WITH RIVERS AND LAKES IN DRY SEASON.

Model-averaged coefficients and 95% confidence intervals representing the effect of distance to river and lake on the seasonal Relative Activity Index (RAI = detections / trap-night) of buffalo and waterbuck. In the dry season, the RAI of waterbuck and buffalo is higher in proximity to rivers and lakes. A negative value represents greater activity when in closer proximity to the feature (smaller distance).

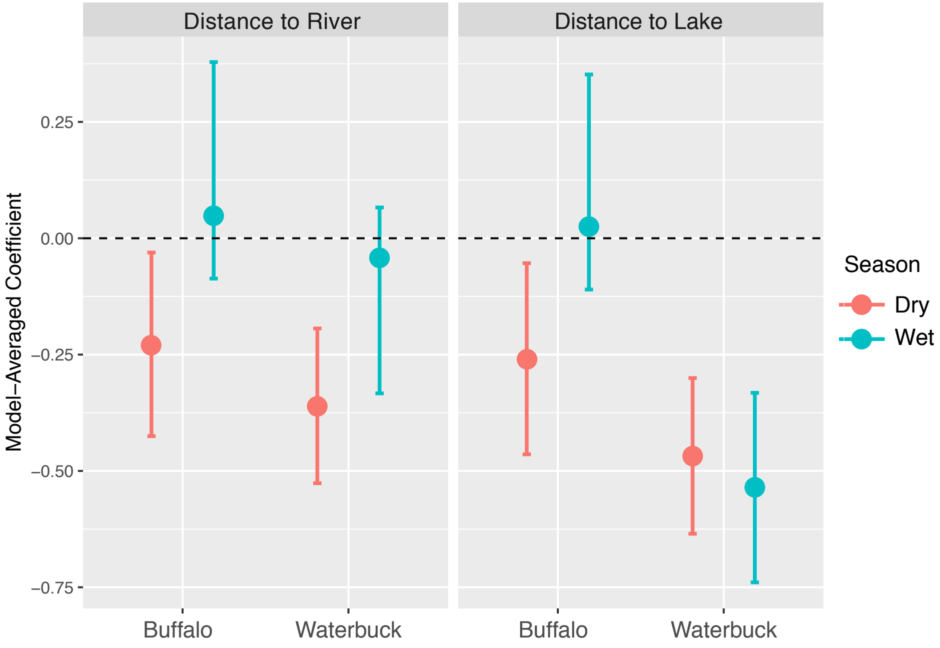


FIGURE 8. SPATIAL AND DIETARY OVERLAP.

Relationship between pairwise dietary overlap and pairwise spatial associations among ungulate species. Each point represents a pair of species (for which diet data were available for both species). There is a weakly positive, although not statistically significant, relationship between pairwise dietary overlap and correlation between relative activity index.

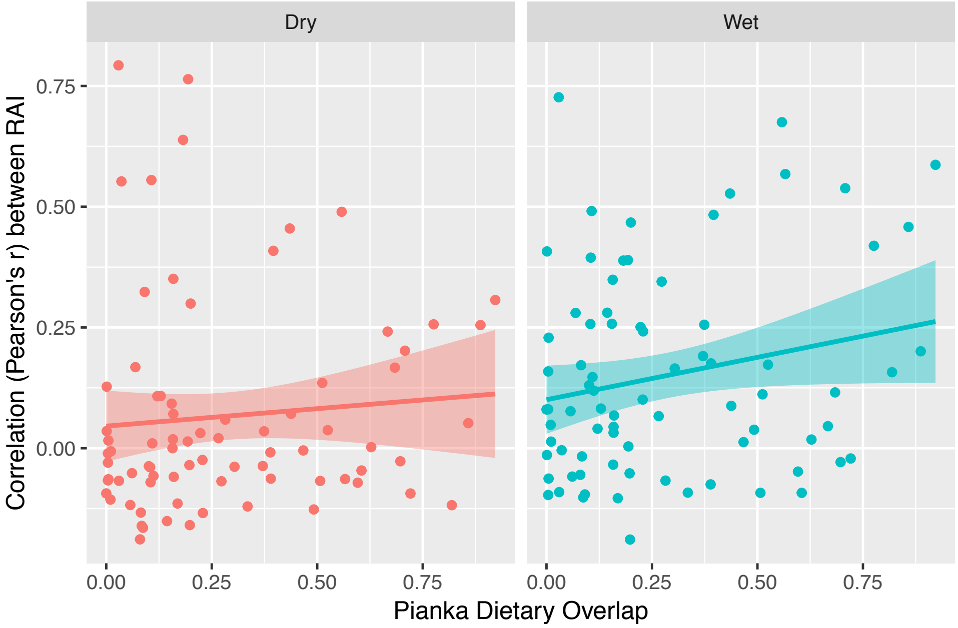


FIGURE 9. SEASONAL DIFFERENCES IN SPECIES ASSOCIATIONS.

Seasonal differences in pairwise Pearson's r correlation coefficients between the Relative Activity Index of species at a given camera site. The color of the circle represents the season in which spatial correlation was higher between those species, and the size of the circle corresponds to the magnitude of the difference between wet and dry season correlation.

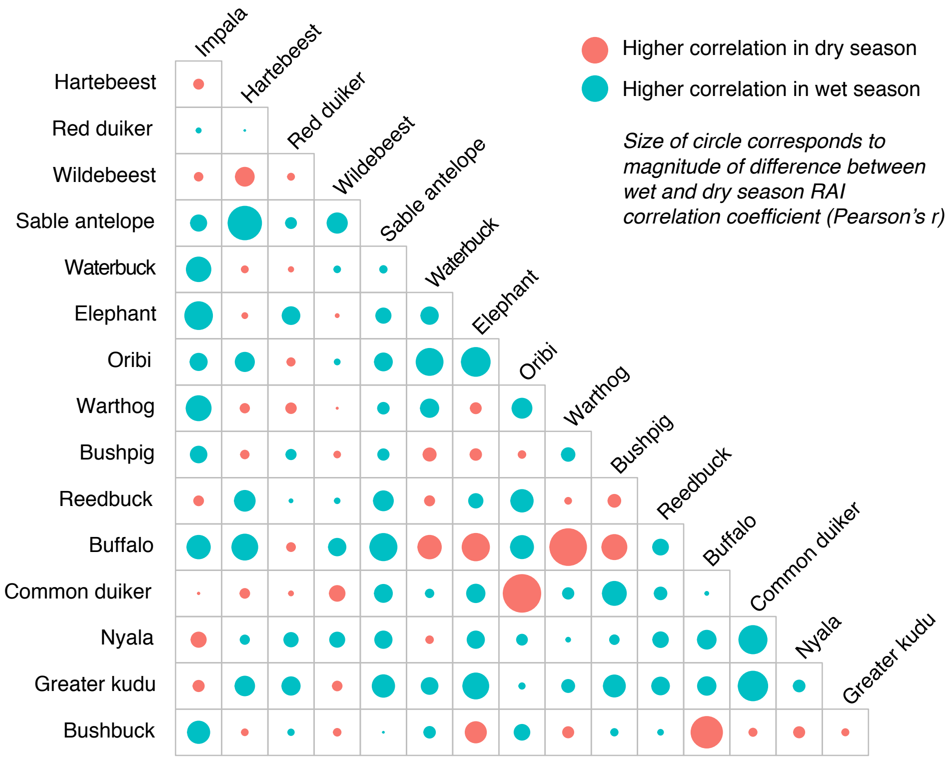
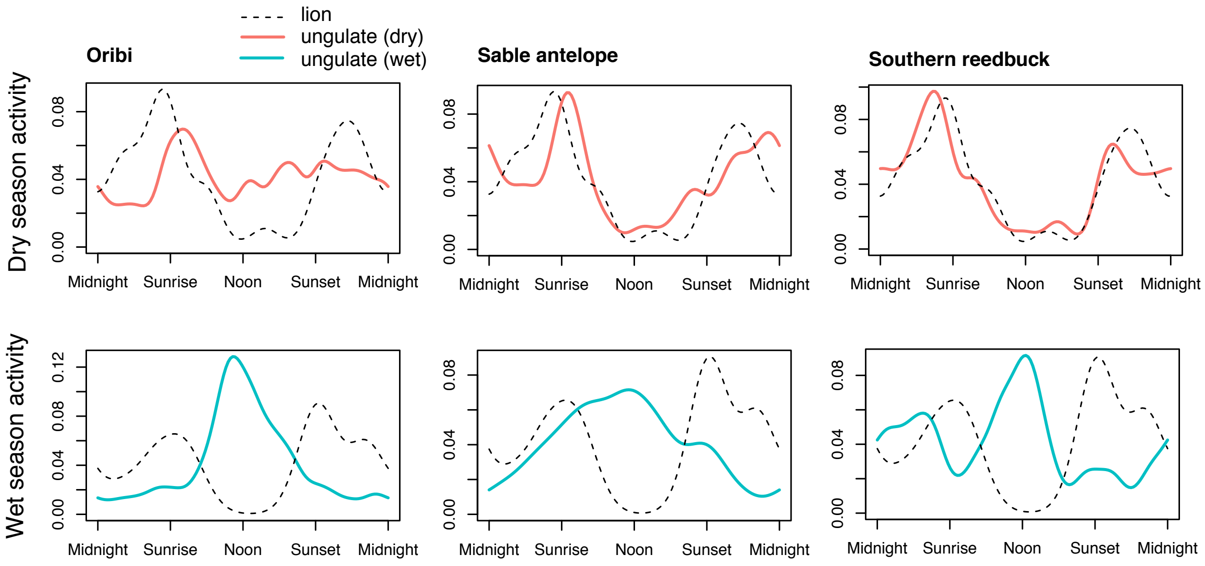


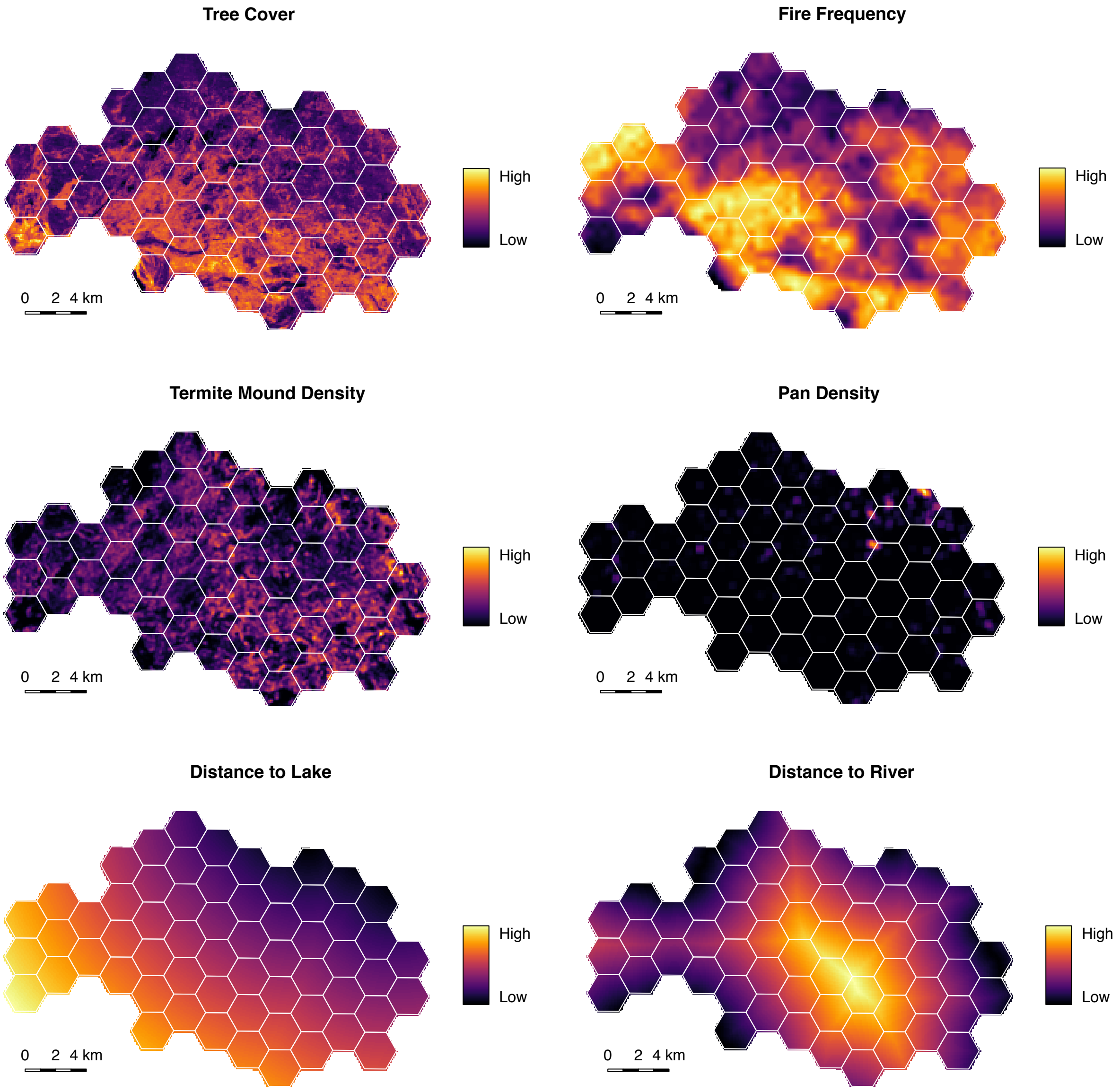
FIGURE 10. SEASONAL CHANGES IN DIEL OVERLAP BETWEEN UNGULATES AND LIONS.

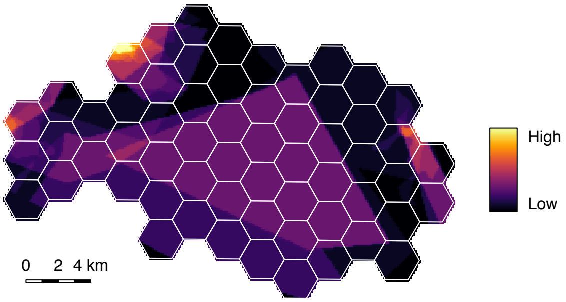
Kernel density distributions representing the timing of ungulate and lion detections, where the area under the curve is equal to 1. In the dry season, oribi, sable antelope, and reedbuck have a relatively high degree of temporal overlap with lions (dotted line), exhibiting crepuscular and nocturnal activity. In the wet season, lions remain crepuscular/nocturnal, but all three antelope species change their activity patterns to be more diurnal.



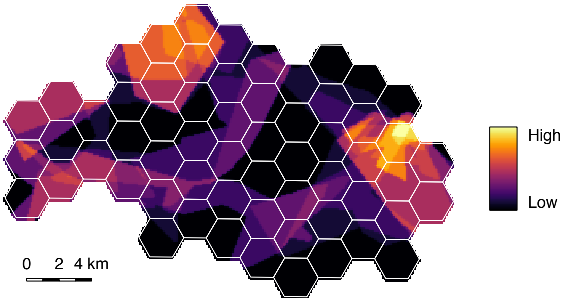
SUPPLEMENTARY FIGURE 1: SPATIAL COVARIATES

Maps of environmental and anthropogenic spatial features in the study area. These features were used as covariates in models of mammal occupancy and relative activity. All features have been standardized to have a mean of 0 and standard deviation of 1, and all values presented here are relative values. The hexagonal grid is overlaid on each map; grid cells are 5km^2 in area, and camera traps are located at the center point of each grid cell.

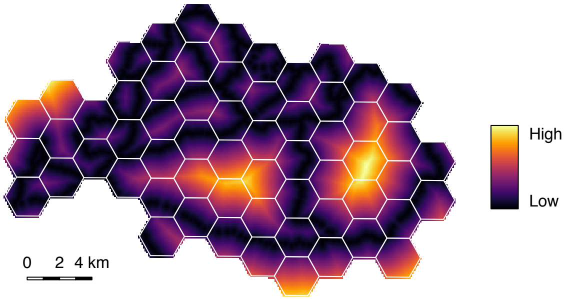




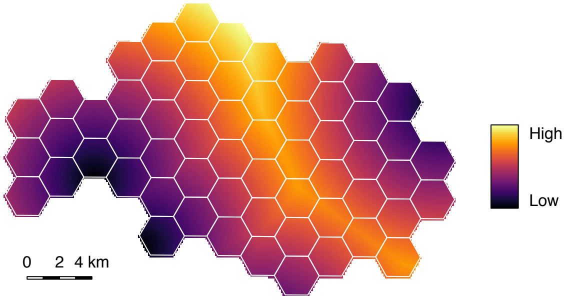
Lion Activity (Dry Season)



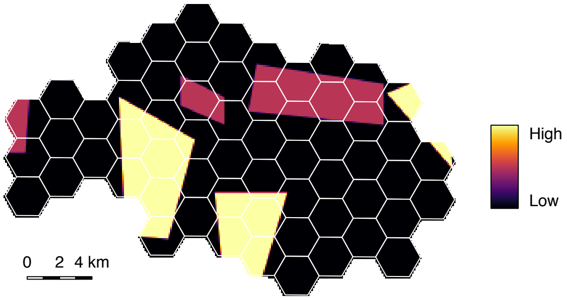
Lion Activity (Wet Season)



Distance to Road



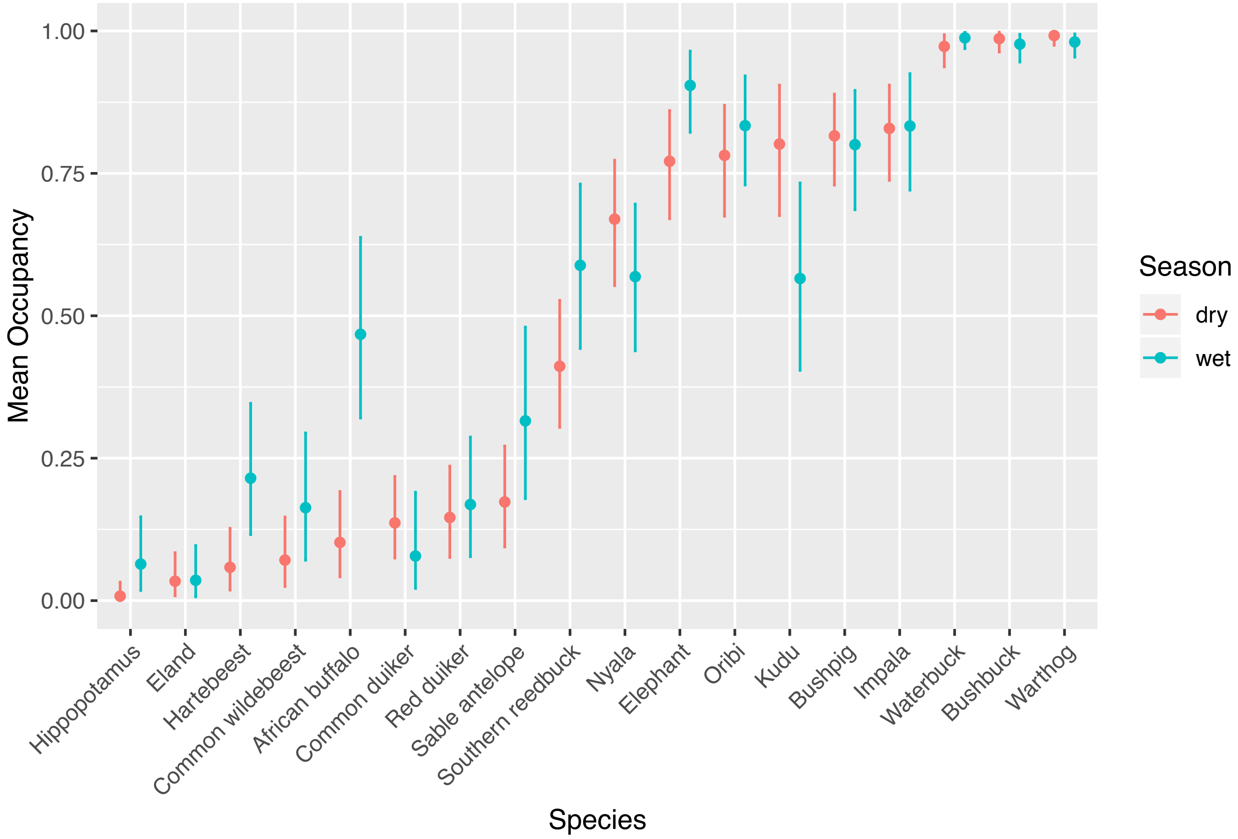
Distance to Settlement



Poaching

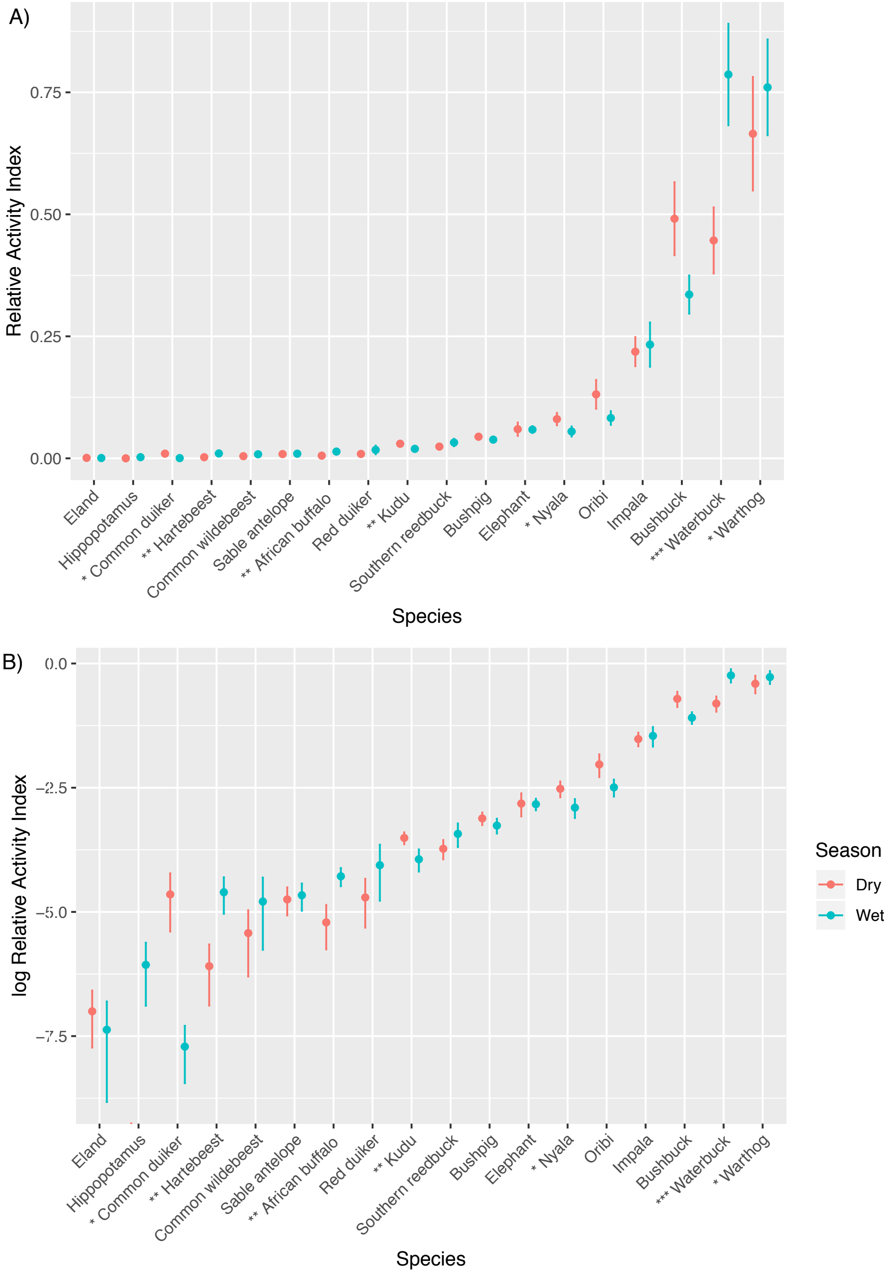
SUPPLEMENTARY FIGURE 2: SEASONAL OCCUPANCY OF UNGULATE SPECIES

Mean occupancy probabilities for ungulate species in the dry and wet seasons, with 95% credible intervals, as calculated using a Bayesian multispecies hierarchical model. Occupancy can be interpreted as the probability of a species using a given camera site in the study area during the study period, accounting for imperfect detection rates. Species are ordered by increasing dry season occupancy.



SUPPLEMENTARY FIGURE 3: SEASONAL RELATIVE ACTIVITY INDICES OF UNGULATE SPECIES

Mean Relative Activity Index (RAI) of each ungulate species in the dry and wet season across camera sites, with bars representing Standard Error. RAI represents the number of independent detections (>15 minutes apart) per trap-night. Species are ordered by increasing dry season RAI. The significance level of paired t-tests comparing RAI at a given camera-year in the dry and wet season is indicated with asterisks next to the species name (* $p < 0.10$; ** $p < 0.05$; *** $p < 0.001$). A) A small number of species comprised the majority of detections (warthog, waterbuck, bushbuck, and impala), with a long tail of more rare species. B) Here, the y-axis (RAI) is plotted on a log scale so that seasonal differences are more visible for the rare species.



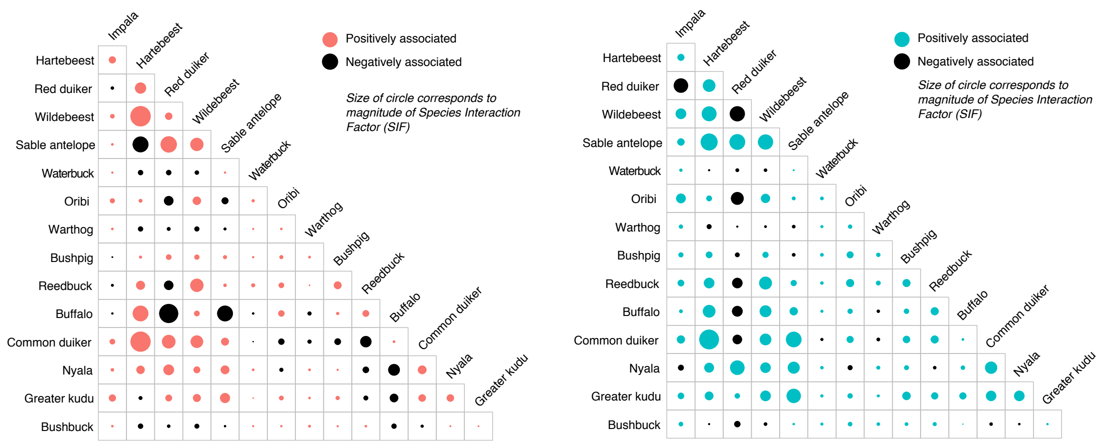
SUPPLEMENTARY FIGURE 4: PAIRWISE SPATIAL AND TEMPORAL OVERLAP AMONG UNGULATE SPECIES

Pairwise spatial relationships among ungulate species in Gorongosa National Park. Figures illustrate the direction and magnitude of the spatial and temporal association between the species in the dry season and wet season, and differences between seasons. A-C) Patterns of species co-occurrence, as determined through a series of two-species hierarchical occupancy models. The resulting measure (Species Interaction Factor) corresponds to the probability of one species being present given the presence of the other species. D-F) Patterns of spatial association as measured through Pearson's r correlation coefficients between the Relative Activity Indices of species across camera sites. G-I) Overlap in kernel density distributions of diel activity, ranging from completely opposite activity to completely synchronized activity.

Spatial co-occurrence (Species Interaction Factor)

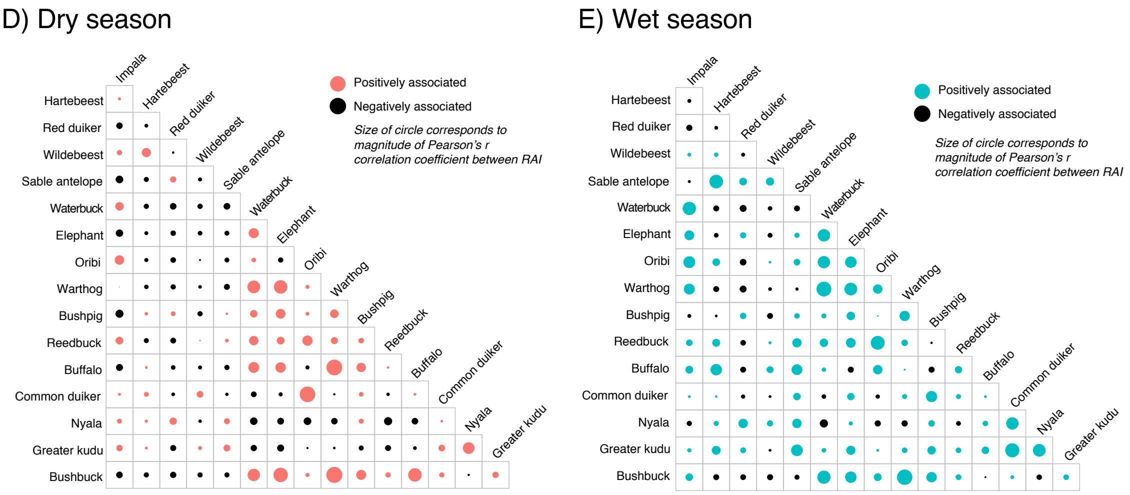
A) Dry season

B) Wet season



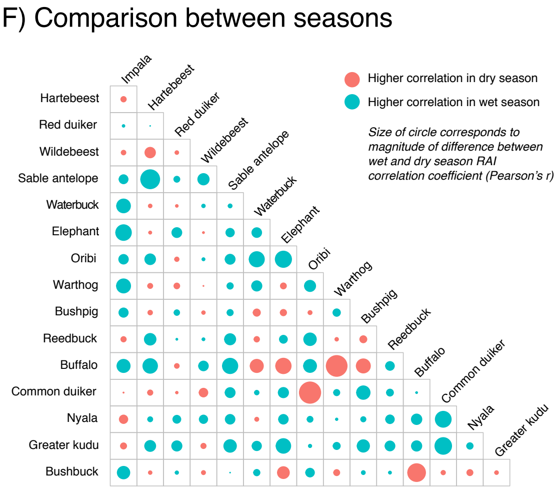
C) Comparison between seasons

Spatial correlation of relative activity


D) Dry season

E) Wet season

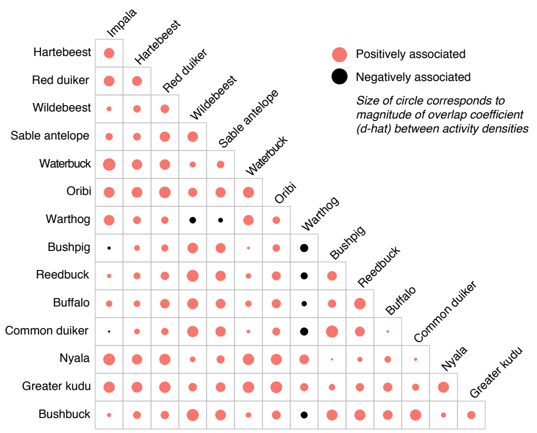
Size of circle corresponds to magnitude of Pearson's r correlation coefficient between RAI


F) Comparison between seasons

Size of circle corresponds to magnitude of difference between wet and dry season RAI correlation coefficient (Pearson's r)

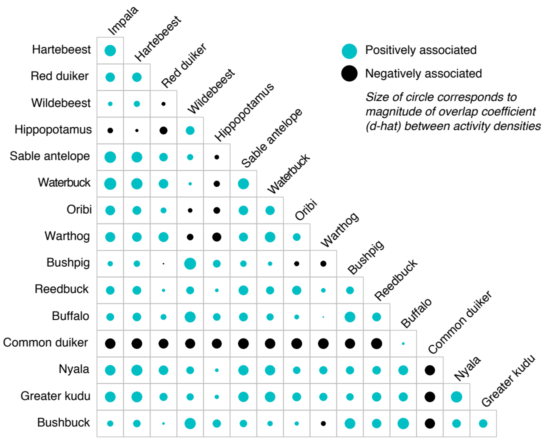
Temporal overlap

G) Dry season



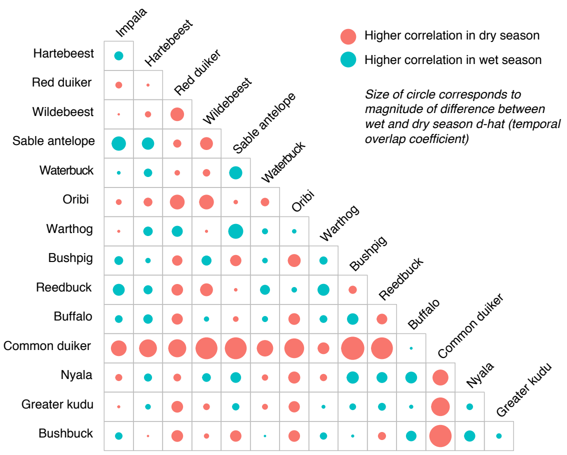
Size of circle corresponds to magnitude of overlap coefficient (d-hat) between activity densities

H) Wet season



Size of circle corresponds to magnitude of overlap coefficient (d-hat) between activity densities

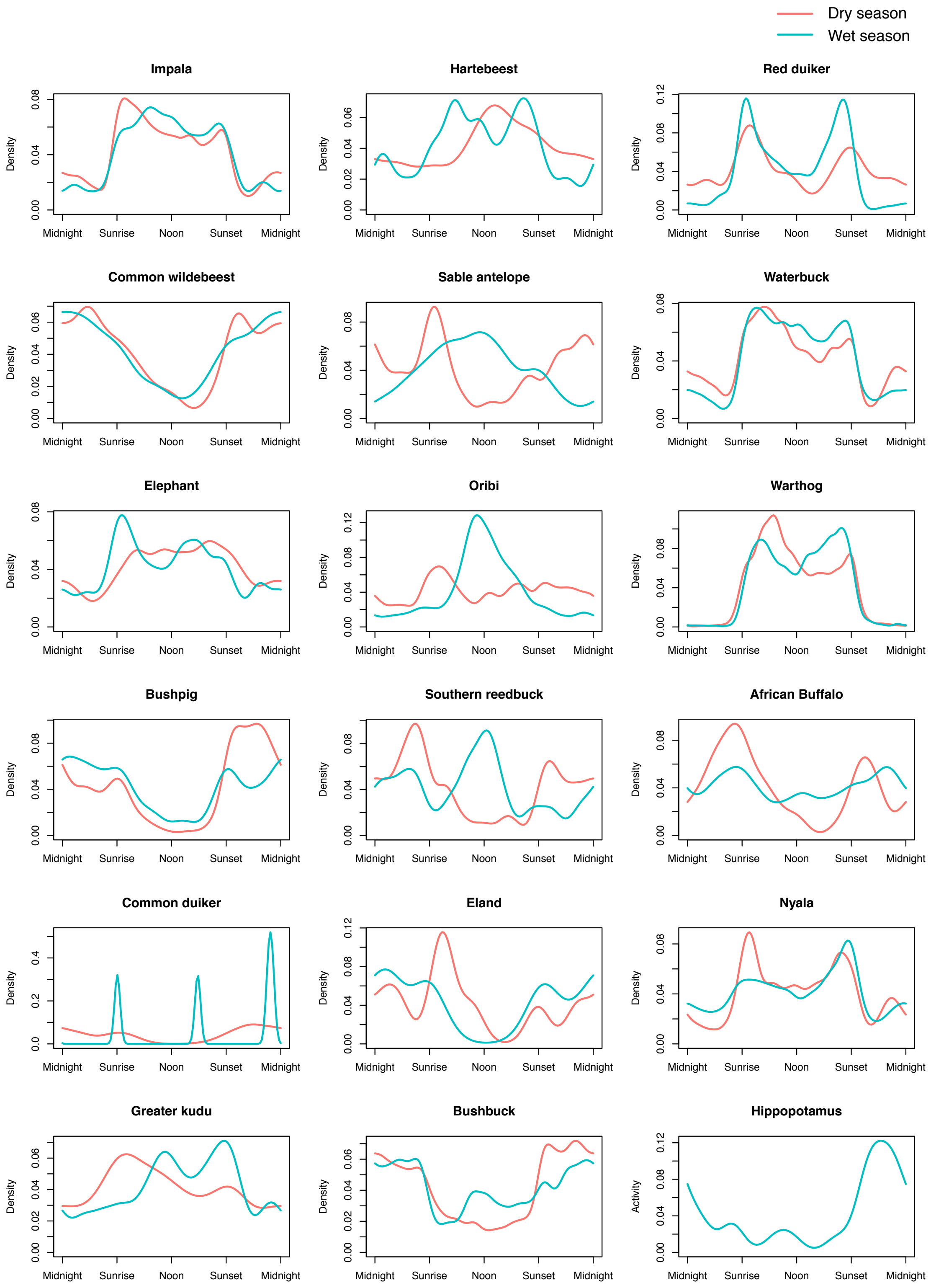
I) Comparison between seasons



Size of circle corresponds to magnitude of difference between wet and dry season d-hat (temporal overlap coefficient)

SUPPLEMENTARY FIGURE 5: SEASONAL DIEL ACTIVITY PATTERNS OF UNGULATES

Kernel density distributions for diel activity patterns of ungulate species in Gorongosa National Park in the dry and wet seasons, scaled to sunrise and sunset times.



SUPPLEMENTARY TABLE 1: STUDY SPECIES

All mammal species (excluding small rodents) that were documented by camera traps in Gorongosa National Park, Mozambique from 2016-2018. We detected a total of 38 mammal species. Detections were dominated by five species (warthog, waterbuck, baboon, bushbuck, and impala) comprising 78% of all detections (Supplementary Table 3). Diet classification and body size are from the PanTHERIA database.

Common name	**Genus and species**	**Family**	**Order**	**Diet classification**	**Body size (kg)**
Impala	*Aepyceros melampus*	Bovidae	Cetardiodactyla	Herbivore	52.59
Hartebeest	*Alcelaphus buselaphus*	Bovidae	Cetardiodactyla	Herbivore	160.94
Natal red duiker	*Cephalophus natalensis*	Bovidae	Cetardiodactyla	Herbivore	12.72
Common wildebeest	*Connochaetes taurinus*	Bovidae	Cetardiodactyla	Herbivore	198.62
Sable antelope	*Hippotragus niger*	Bovidae	Cetardiodactyla	Herbivore	236.41
Waterbuck	*Kobus ellipsiprymnus*	Bovidae	Cetardiodactyla	Herbivore	204.39
Oribi	*Ourebia ourebi*	Bovidae	Cetardiodactyla	Herbivore	17.19
Southern reedbuck	*Redunca arundinum*	Bovidae	Cetardiodactyla	Herbivore	43.29
Common duiker	*Sylvicapra grimmia*	Bovidae	Cetardiodactyla	Herbivore	15.64
African buffalo	*Syncerus caffer*	Bovidae	Cetardiodactyla	Herbivore	592.67
Common eland	*Taurotragus oryx*	Bovidae	Cetardiodactyla	Herbivore	562.59
Bushbuck	*Tragelaphus scriptus*	Bovidae	Cetardiodactyla	Herbivore	43.29
Nyala	*Tragelaphus angasii*	Bovidae	Cetardiodactyla	Herbivore	87.62
Greater kudu	*Tragelaphus strepsiceros*	Bovidae	Cetardiodactyla	Herbivore	206.06
Elephant	*Loxodonta africana*	Elephantidae	Cetardiodactyla	Herbivore	3824.54
Hippopotamus	*Hippopotamus amphibius*	Hippopotamidae	Cetardiodactyla	Herbivore	1536.31
Warthog	*Phacochoerus africanus*	Suidae	Cetardiodactyla	Herbivore	82.50
Bushpig	*Potamochoerus larvatus*	Suidae	Cetardiodactyla	Omnivore	69.06

Common name	**Genus and species**	**Family**	**Order**	**Diet classification**	**Body size (kg)**
Serval	*Leptailurus serval*	Felidae	Carnivora	Carnivore	12.00
Lion activity	*Panthera leo*	Felidae	Carnivora	Carnivore	158.62
Marsh mongoose	*Atilax paludinosus*	Herpestidae	Carnivora	Omnivore	3.60
Bushy-tailed mongoose	*Bdeogale crassicauda*	Herpestidae	Carnivora	Carnivore	1.72
Slender mongoose	*Galerella sanguinea / Herpestes sanguineus*	Herpestidae	Carnivora	Omnivore	0.54
Dwarf mongoose	*Helogale parvula*	Herpestidae	Carnivora	Carnivore	0.28
Egyptian (large grey) mongoose	*Herpestes ichneumon*	Herpestidae	Carnivora	Omnivore	2.98
White-tailed mongoose	*Ichneumia albicauda*	Herpestidae	Carnivora	Carnivore	3.63
Banded mongoose	*Mungos mungo*	Herpestidae	Carnivora	Carnivore	1.26
Honey badger	*Mellivora capensis*	Mustelidae	Carnivora	Omnivore	9.00
Civet	*Civettictis civetta*	Viverridae	Carnivora	Omnivore	12.08
Common genet	*Genetta genetta*	Viverridae	Carnivora	Omnivore	1.76
Hare	*Lepus microtis*	Leopridae	Lagomorpha	Herbivore	1.76
Pangolin	*Manis temminckii*	Manidae	Pholidota	Carnivore	11.94
Samango	*Ceropithecus albogularis*	Cercopithecidae	Primates	Omnivore	5.04
Vervet	*Chlorocebus pygerythrus*	Cercopithecidae	Primates	Omnivore	3.70
Baboon	*Papio cynocephaus*	Cercopithecidae	Primates	Omnivore	15.82
Bushbaby	*Otolemur crassicaudatus*	Galagidae	Primates	Herbivore	1.21
Porcupine	*Hystrix africaeaustralis*	Hystricidae	Rodentia	Herbivore	14.94
Aardvark	*Orycteropus afer*	Orycteropodidae	Tubulidentata	Carnivore	56.18

SUPPLEMENTARY TABLE 2: UNGULATE TRAITS

Behavioral and ecological traits for ungulate species in Gorongosa National Park.

Common name	**Foraging strategy[1]**	**Percent grass in diet[2]**	**Group size[3]**	**Water dependence[3]**	**% biomass on floodplain in dry season[4]**
Impala	Mixed feeder	10	Gregarious	High	50%
Hartebeest	Grazer	91	Gregarious	High	29%
Natal red duiker	Browser	NA	Solitary/pairs	None	20%
Common wildebeest	Grazer	95	Megagroups	High	27%
Sable antelope	Grazer	86	Family	High	23%
Waterbuck	Grazer	50	Family	High	76%
Oribi	Grazer	42	Family	None	74%
Southern reedbuck	Grazer	56	Solitary/pairs	High	83%
Common duiker	Browser	NA	Solitary/pairs	None	13%
African buffalo	Grazer	34	Megagroups	High	17%
Common eland	Mixed feeder	NA	Gregarious	None	0%
Bushbuck	Browser	0	Family	Low	15%
Nyala	Mixed feeder	12	Family	Low	25%
Greater kudu	Browser	0	Solitary/pairs	Low	53%
Elephant	Mixed feeder	20	Gregarious	High	50%
Hippopotamus	Grazer	NA	Gregarious	High	100%
Warthog	Grazer	97	Family	High	65%
Bushpig	Mixed feeder	NA	Family	High	51%

[1]Tinley 1977; [2]Pansu et al. 2018; [3]Hempsen et al. 2013; [4]Stalmans et al. 2019

SUPPLEMENTARY TABLE 3: TOTAL DETECTIONS OF EACH SPECIES

The number of camera trap detections for each species during the study (wet and dry seasons combined) and the number of cameras (out of 60) at which the species was detected.

Common name	Total Detections	Total Number (%) of Camera Sites
Warthog	11,930	60 (100%)
Waterbuck	10,437	60 (100%)
Baboon	9,210	60 (100%)
Bushbuck	6,770	60 (100%)
Impala	3,864	54 (90%)
Common genet	1,904	59 (98%)
Oribi	1,786	56 (93%)
Nyala	1,112	43 (72%)
Elephant	962	60 (100%)
Civet	938	58 (97%)
Porcupine	881	49 (82%)
Bushpig	705	58 (97%)
Vervet	623	40 (67%)
Southern reedbuck	448	47 (78%)
Greater kudu	405	53 (88%)
Natal red duiker	265	15 (25%)
Hare	220	36 (60%)
Marsh mongoose	215	42 (70%)
Sable antelope	157	33 (55%)
Honey badger	137	20 (33%)
African buffalo	134	35 (58%)
Common wildebeest	127	39 (65%)
Slender mongoose	123	24 (40%)
Aardvark	96	26 (43%)
Hartebeest	91	16 (27%)
Common duiker	89	16 (27%)
White-tailed mongoose	88	28 (47%)
Bushy-tailed mongoose	69	21 (35%)
Banded mongoose	59	26 (43%)
Egyptian (large grey) mongoose	47	38 (63%)
Lion activity	45	40 (67%)
Samango	39	18 (30%)
Serval	32	15 (25%)
Bushbaby	31	14 (23%)
Dwarf mongoose	21	13 (22%)
Hippopotamus	20	6 (10%)
Common eland	15	5 (8%)
Pangolin	14	26 (43%)

SUPPLEMENTARY TABLE 4: PREDICTORS OF RAI

Model-averaged coefficients and relative importance of spatial predictors of standardized Relative Activity Index for ungulate species. The relative importance of each covariate is the sum of the Akaike weights of the models in which that covariate appears (for all models within 2 deltaAIC of the top model). Covariates are listed in order of descending importance for the dry season, and covariates with an importance >0.50 are bolded.

Impala				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.113 (-0.332 – 0.106)**	**1.00**	**-0.001 (-0.239 – 0.236)**	**1.00**
Tree cover	**-0.368 (-0.605 – -0.130)**	**1.00**	**-0.156 (-0.505 – 0.049)**	**0.68**
Fire frequency	**-0.275 (-0.506 – -0.044)**	**1.00**	**-0.308 (-0.581 – -0.034)**	**1.00**
Pan density	**-0.300 (-0.775 – 0.066)**	**0.85**	0.002 (-0.444 – 0.517)	0.04
Poaching	0.013 (-0.115 – 0.328)	0.13	0.019 (-0.142 – 0.359)	0.17
Lion activity	-0.014 (-0.338 – 0.121)	0.13	**0.206 (-0.008 – 0.472)**	**0.89**
Distance to road	-0.012 (-0.347 – 0.137)	0.12	-0.007 (-0.352 – 0.196)	0.10
Distance to Lake Urema	-0.010 (-0.331 – 0.146)	0.11	**-0.093 (-0.452 – 0.077)**	**0.50**
Termite mound density	-0.003 (-0.216 – 0.221)	0.08	-0.014 (-0.335 – 0.154)	0.16
Distance to river	0.0001 (-0.216 – 0.221)	0.08	0.002 (-0.213 – 0.314)	0.04

Hartebeest				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.005 (-0.191 – 0.181)**	**1.00**	**-0.032 (-0.235 – 0.170)**	**1.00**
Termite mound density	**0.266 (0.078 – 0.454)**	**1.00**	-0.006 (-0.263 – 0.125)	0.08
Distance to Lake Urema	**0.281 (0.076 – 0.486)**	**1.00**	**0.109 (-0.052 – 0.393)**	**0.64**
Tree cover	**-0.132 (-0.401 – 0.044)**	**0.74**	**-0.274 (-0.515 – -0.033)**	**1.00**
Lion activity	0.030 (-0.092 – 0.322)	0.27	-0.003 (-0.241 – 0.159)	0.07
Pan density	0.032 (-0.224 – 0.515)	0.22	0.001 (-0.367 – 0.400)	0.06
Fire frequency	0.006 (-0.128 – 0.274)	0.09	**0.327 (0.073 – 0.581)**	**1.00**
Distance to river	-0.002 (-0.217 – 0.17)	0.07	0.004 (-0.163 – 0.262)	0.07
Poaching	-0.001 (-0.203 – 0.181)	0.07	-0.027 (-0.335 – 0.113)	0.24
Distance to road	0.0001 (-0.198 – 0.202)	0.07	-0.026 (-0.339 – 0.120)	0.23

Red Duiker				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**0.074 (-0.155 – 0.302)**	**1.00**	**0.073 (-0.179 – 0.324)**	**1.00**
Distance to road	**0.288 (0.029 – 0.547)**	**1.00**	**0.445 (0.158 – 0.733)**	**1.00**
Tree cover	**0.269 (0.020 – 0.518)**	**1.00**	**0.110 (-0.084 – 0.470)**	**0.57**
Fire frequency	-0.088 (-0.450 – 0.080)	0.48	**-0.342 (-0.654 – -0.030)**	**1.00**
Termite mound density	0.014 (-0.135 – 0.323)	0.15	0.002 (-0.228 – 0.283)	0.07
Lion activity	0.013 (-0.156 – 0.336)	0.14	-0.010 (-0.323 – 0.189)	0.16
Poaching	0.010 (-0.170 – 0.323)	0.13	**0.300 (0.034 – 0.567)**	**1.00**
Distance to Lake Urema	-0.008 (-0.318 – 0.187)	0.12	0.006 (-0.241 – 0.321)	0.14
Pan density	0.006 (-0.401 – 0.517)	0.11	0.001 (-0.487 – 0.524)	0.07

Distance to river	-0.001(-0.261 – 0.217)	0.05	0.024 (-0.145 – 0.380)	0.20

Common Wildebeest				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.023 (-0.232 – 0.186)**	**1.00**	**-0.019 (-0.233 – 0.195)**	**1.00**
Tree cover	**-0.281 (-0.524 – -0.038)**	**1.00**	**-0.287 (-0.538 – -0.036)**	**1.00**
Distance to Lake Urema	**0.312 (0.086 – 0.538)**	**1.00**	**0.277 (0.049 – 0.505)**	**1.00**
Termite mound density	-0.011 (-0.294 – 0.124)	0.13	-0.006 (-0.280 – 0.140)	0.09
Distance to river	0.008 (-0.146 – 0.291)	0.11	0.003 (-0.179 – 0.271)	0.07
Distance to road	0.007 (-0.162 – 0.285)	0.11	0.025 (-0.107 – 0.347)	0.21
Poaching	-0.006 (-0.271 – 0.155)	0.11	-0.002 (-0.248 – 0.187)	0.07
Fire frequency	0.006 (-0.170 – 0.288)	0.10	0.019 (-0.136 – 0.351)	0.17
Pan density	-0.007 (-0.488 – 0.343)	0.10	-0.007 (-0.509 – 0.321)	0.08
Lion activity	-0.001 (-0.242 – 0.213)	0.09	-0.041 (-0.345 – 0.083)	0.31

Hippopotamus (note: there were no hippopotamus detections in the dry season)		
	Wet season	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.008 (-0.215 – 0.199)**	**1.00**
Fire frequency	**-0.248 (-0.487 – -0.008)**	**1.00**
Poaching	0.040 (-0.094 – 0.358)	0.30
Pan density	-0.059 (-0.593 – 0.178)	0.28
Distance to Lake Urema	-0.034 (-0.359 – 0.094)	0.26
Tree cover	-0.026 (-0.370 – 0.108)	0.20
Distance to river	-0.015 (-0.315 – 0.106)	0.15
Lion activity	0.009 (-0.113 – 0.29)	0.10
Termite mound density	-0.003 (-0.256 – 0.129)	0.05
Distance to road	-0.002 (-0.287 – 0.177)	0.04

Sable antelope				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.012 (-0.229 – 0.204)**	**1.00**	**0.034 (-0.225 – 0.293)**	**1.00**
Distance to river	**0.176 (-0.017 – 0.427)**	**0.86**	0.005 (-0.195 – 0.344)	0.07
Distance to Lake Urema	**0.142 (-0.018 – 0.421)**	**0.71**	**0.172 (-0.058 – 0.528)**	**0.73**
Termite mound density	**-0.096 (-0.377 – 0.037)**	**0.56**	-0.008 (-0.336 – 0.180)	0.10
Distance to road	**-0.104 (-0.438 – 0.058)**	**0.55**	**0.129 (-0.072 – 0.517)**	**0.58**
Fire frequency	0.080 (-0.069 – 0.433)	0.44	**0.237 (-0.022 – 0.597)**	**0.82**
Pan density	-0.089 (-0.699 – 0.153)	0.33	-0.014 (-0.666 – 0.380)	0.10
Tree cover	0.046 (-0.075 – 0.427)	0.26	**-0.194 (-0.555 – 0.042)**	**0.76**
Lion activity	-0.041 (-0.413 – 0.086)	0.25	-0.012 (-0.359 – 0.159)	0.12
Poaching	0.0001 (-0.204 – 0.219)	0.02	0.0002 (-0.263 – 0.277)	0.03

Waterbuck				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.031 (-0.195 – 0.132)**	**1.00**	**-0.075 (-0.269 – 0.120)**	**1.00**

Distance to river	**-0.360 (-0.526 – -0.194)**	**1.00**	-0.039 (-0.333 – 0.066)	0.29
Termite mound density	**-0.169 (-0.326 – -0.011)**	**1.00**	-0.007 (-0.260 – 0.131)	0.11
Distance to Lake Urema	**-0.468 (-0.635 – -0.300)**	**1.00**	**-0.536 (-0.739 – -0.332)**	**1.00**
Distance to road	-0.042 (-0.291 – 0.069)	0.38	-0.028 (-0.320 – 0.097)	0.26
Tree cover	0.016 (-0.116 – 0.290)	0.18	-0.038 (-0.359 – 0.099)	0.29
Pan density	-0.021 (-0.444 – 0.196)	0.17	-0.021 (-0.543 – 0.247)	0.14
Fire frequency	0.007 (-0.143 – 0.243)	0.15	0.0004 (-0.203 – 0.237)	0.02
Lion activity	-0.004 (-0.236 – 0.147)	0.08	0.060 (-0.056 – 0.336)	0.43
Poaching	0.0003 (-0.164 – 0.173)	0.07	0.019 (-0.097 – 0.286)	0.20

Elephant

	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.014 (-0.228 – 0.200)**	**1.00**	**-0.014 (-0.199 – 0.170)**	**1.00**
Distance to Lake Urema	**-0.314 (-0.547 – -0.082)**	**1.00**	**-0.377 (-0.568 – -0.185)**	**1.00**
Distance to river	**-0.313 (-0.535 – -0.091)**	**1.00**	**-0.310 (-0.501 – -0.118)**	**1.00**
Fire frequency	**0.186 (-0.030 – 0.460)**	**0.86**	-0.023 (-0.356 – 0.106)	0.18
Poaching	-0.011 (-0.318 – 0.138)	0.13	**0.206 (0.012 – 0.400)**	**1.00**
Termite mound density	-0.005 (-0.260 – 0.161)	0.10	-0.001 (-0.187 – 0.166)	0.10
Lion activity	-0.006 (-0.302 – 0.190)	0.10	-0.002 (-0.212 – 0.179)	0.10
Pan density	-0.007(-0.499 – 0.359)	0.10	-0.016 (-0.475 – 0.223)	0.13
Distance to road	0.003 (-0.219 – 0.278)	0.09	-0.002 (-0.211 – 0.179)	0.10
Tree cover	-0.001 (-0.268 – 0.246)	0.09	-0.009 (-0.303 – 0.153)	0.12

Oribi

	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.057 (-0.270 – 0.156)**	**1.00**	**-0.103 (-0.325 – 0.119)**	**1.00**
Tree cover	**-0.276 (-0.514 – -0.037)**	**1.00**	**-0.479 (-0.729 – -0.229)**	**1.00**
Termite mound density	**-0.103 (-0.368 – 0.049)**	**0.65**	**-0.125 (-0.394 – 0.038)**	**0.70**
Distance to road	-0.063 (-0.373 – 0.076)	0.42	-0.017 (-0.335 – 0.115)	0.16
Distance to river	-0.033 (-0.338 – 0.093)	0.27	-0.004 (-0.283 – 0.157)	0.07
Pan density	-0.059 (-0.652 – 0.191)	0.25	**-0.341 (-0.822 – 0.030)**	**0.86**
Poaching	-0.009 (-0.293 – 0.138)	0.12	-0.003 (-0.262 – 0.167)	0.07
Lion activity	-0.009 (-0.328 – 0.141)	0.09	0.004 (-0.158 – 0.277)	0.07
Distance to Lake Urema	0.007(-0.150 – 0.301)	0.09	-0.004 (-0.290 – 0.174)	0.07
Fire frequency	-0.004 (-0.290 – 0.153)	0.06	-0.021 (-0.351 – 0.105)	0.17

Warthog

	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.038 (-0.220 – 0.144)**	**1.00**	**-0.027 (-0.210 – 0.157)**	**1.00**
Fire frequency	**0.252 (0.045 – 0.458)**	**1.00**	**0.295 (0.082 – 0.508)**	**1.00**
Distance to river	**-0.259 (-0.449 – -0.069)**	**1.00**	**-0.313 (-0.507 – -0.119)**	**1.00**
Distance to Lake Urema	**-0.485 (-0.680 – -0.290)**	**1.00**	**-0.658 (-0.859 – -0.457)**	**1.00**
Lion activity	-0.017 (-0.309 – 0.105)	0.17	0.015 (-0.100 – 0.288)	0.16
Pan density	-0.012 (-0.460 – 0.252)	0.12	-0.006 (-0.420 – 0.312)	0.11
Tree cover	-0.007 (-0.282 – 0.157)	0.12	-0.013 (-0.307 – 0.128)	0.14
Poaching	0.004 (-0.163 – 0.241)	0.11	0.003 (-0.166 – 0.223)	0.11
Distance to road	0.004 (-0.181 – 0.248)	0.11	0.004 (-0.172 – 0.247)	0.11

Termite mound density	-0.003 (-0.202 – 0.150)	0.11	0.001 (-0.168 – 0.193)	0.10

Bushpig				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**0.002 (-0.235 – 0.238)**	**1.00**	**0.026 (-0.206 – 0.258)**	**1.00**
Distance to road	**-0.178 (-0.508 – 0.040)**	**0.76**	0.002 (-0.218 – 0.263)	0.09
Distance to river	**-0.109 (-0.444 – 0.060)**	**0.57**	-0.004 (-0.273 – 0.196)	0.09
Fire frequency	**0.107 (-0.075 – 0.468)**	**0.55**	-0.009 (-0.343 – 0.179)	0.10
Lion activity	0.069 (-0.096 – 0.452)	0.39	-0.005 (-0.283 – 0.171)	0.10
Termite mound density	0.015 (-0.141 – 0.330)	0.16	-0.001 (-0.237 – 0.217)	0.09
Pan density	0.020 (-0.310 – 0.617)	0.13	0.014 (-0.299 – 0.561)	0.10
Distance to Lake Urema	-0.008 (-0.343 – 0.156)	0.08	-0.009 (-0.311 – 0.147)	0.11
Poaching	0.001 (-0.236 – 0.27)	0.05	**0.251 (0.018 – 0.483)**	**1.00**
Tree cover	-0.002 (-0.319 – 0.183)	0.03	0.003 (-0.213 – 0.290)	0.09

Southern Reedbuck				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.052 (-0.283 – 0.180)**	**1.00**	**-0.046 (-0.257 – 0.166)**	**1.00**
Tree cover	**-0.253 (-0.536 – -0.001)**	**0.94**	**-0.284 (-0.530 – -0.037)**	**1.00**
Distance to river	**-0.141 (-0.433 – 0.043)**	**0.72**	-0.019 (-0.314 – 0.113)	0.19
Termite mound density	-0.083 (-0.410 – 0.060)	0.47	**-0.076 (-0.345 – 0.058)**	**0.53**
Pan density	-0.070 (-0.722 – 0.209)	0.27	**-0.171 (-0.686 – 0.099)**	**0.58**
Lion activity	-0.007 (-0.349 – 0.224)	0.12	0.026 (-0.096 – 0.325)	0.22
Distance to Lake Urema	0.004 (-0.197 – 0.301)	0.08	0.004 (-0.164 – 0.275)	0.08
Poaching	-0.001 (-0.243 – 0.217)	0.08	0.004 (-0.161 – 0.266)	0.07
Distance to road	-0.001 (-0.270 – 0.217)	0.04	-0.002 (-0.257 – 0.177)	0.04
Fire frequency	0.0002 (-0.235 – 0.250)	0.04	0.005 (-0.161 – 0.291)	0.08

African buffalo				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.007 (-0.198 – 0.183)**	**1.00**	**-0.041 (-0.258 – 0.176)**	**1.00**
Distance to river	**-0.228 (-0.425 – -0.031)**	**1.00**	0.050 (-0.087 – 0.379)	0.34
Distance to Lake Urema	**-0.259 (-0.464 – -0.054)**	**1.00**	0.025 (-0.110 – 0.352)	0.21
Fire frequency	**0.110 (-0.044 – 0.399)**	**0.62**	0.004 (-0.151 – 0.306)	0.06
Poaching	0.064 (-0.057 – 0.357)	0.43	-0.002 (-0.249 – 0.184)	0.05
Pan density	0.063 (-0.157 – 0.574)	0.30	**-0.241 (-0.731 – 0.072)**	**0.73**
Termite mound density	-0.005 (-0.226 – 0.139)	0.11	-0.062 (-0.354 – 0.065)	0.43
Distance to road	-0.006 (-0.308 – 0.139)	0.07	0.004 (-0.154 – 0.287)	0.05
Lion activity	0.003 (-0.165 – 0.267)	0.05	0.031 (-0.110 – 0.349)	0.26
Tree cover	0.001 (-0.217 – 0.241)	0.05	**-0.169 (-0.482 – 0.034)**	**0.75**

Common duiker				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.001 (-0.199 – 0.197)**	**1.00**	**-0.005 (-0.214 – 0.205)**	**1.00**

Distance to Lake Urema	0.076 (-0.046 – 0.359)	0.49	0.014 (-0.121 – 0.291)	0.17
Fire frequency	0.059 (-0.088 – 0.404)	0.38	0.002 (-0.181 – 0.255)	0.06
Lion activity	-0.029 (-0.331 – 0.095)	0.25	-0.004 (-0.263 – 0.157)	0.07
Distance to road	-0.030 (-0.364 – 0.111)	0.24	0.0002 (-0.213 – 0.220)	0.06
Poaching	-0.023 (-0.346 – 0.112)	0.19	0.002 (-0.186 – 0.243)	0.06
Distance to river	-0.019 (-0.312 – 0.094)	0.17	-0.0002 (-0.215 – 0.207)	0.06
Tree cover	-0.008 (-0.332 – 0.123)	0.08	0.004 (-0.167 – 0.293)	0.07
Pan density	0.004 (-0.269 – 0.494)	0.03	-0.012 (-0.469 – 0.293)	0.13
Termite mound density	-0.001 (-0.218 – 0.160)	0.03	**0.101 (-0.053 – 0.342)**	**0.70**

Eland				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.015 (-0.205 – 0.175)**	**1.00**	**-0.018 (-0.244 – 0.209)**	**1.00**
Fire frequency	**0.249 (0.032 – 0.466)**	**1.00**	0.080 (-0.066 – 0.451)	0.42
Distance to river	**-0.236 (-0.434 – -0.038)**	**1.00**	0.003 (-0.210 – 0.297)	0.06
Distance to Lake Urema	**-0.229 (-0.431 – -0.026)**	**1.00**	**-0.122 (-0.441 – 0.055)**	**0.63**
Poaching	-0.007 (-0.273 – 0.156)	0.13	0.024 (-0.113 – 0.344)	0.21
Tree cover	-0.007 (-0.288 – 0.174)	0.12	0.036 (-0.111 – 0.420)	0.23
Lion activity	-0.006 (-0.266 – 0.169)	0.12	**0.187 (-0.018 – 0.435)**	**0.90**
Distance to road	-0.006 (-0.274 – 0.178)	0.12	0.028 (-0.125 – 0.367)	0.23
Termite mound density	-0.003 (-0.213 – 0.153)	0.11	0.005 (-0.149 – 0.304)	0.06
Pan density	0.003 (-0.339 – 0.401)	0.11	-0.004 (-0.575 – 0.315)	0.03

Nyala				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**0.005 (-0.209 – 0.219)**	**1.00**	**0.062 (-0.172 – 0.296)**	**1.00**
Termite mound density	**0.273 (0.054 – 0.492)**	**1.00**	0.016 (-0.134 – 0.335)	0.15
Tree cover	**0.254 (0.030 – 0.521)**	**0.92**	**0.293 (0.021 – 0.564)**	**1.00**
Distance to Lake Urema	0.055 (-0.068 – 0.408)	0.33	**0.340 (0.077 – 0.603)**	**1.00**
Fire frequency	-0.015 (-0.320 – 0.149)	0.18	**-0.327 (-0.596 – -0.058)**	**1.00**
Pan density	-0.010 (-0.551 – 0.309)	0.09	-0.004 (-0.509 – 0.433)	0.11
Distance to river	0.003 (-0.182 – 0.263)	0.08	0.005 (-0.207 – 0.289)	0.11
Lion activity	0.003 (-0.200 – 0.278)	0.08	-0.0002 (-0.236 – 0.233)	0.11
Distance to road	-0.003 (-0.262 – 0.196)	0.08	0.008 (-0.195 – 0.332)	0.12
Poaching	-0.001 (-0.235 – 0.202)	0.07	-0.005 (-0.290 – 0.205)	0.11

Greater Kudu				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.031 (-0.250 – 0.187)**	**1.00**	**0.015 (-0.237 – 0.268)**	**1.00**
Fire frequency	**0.303 (0.063 – 0.542)**	**1.00**	0.014 (-0.138 – 0.381)	0.11
Poaching	-0.041 (-0.376 – 0.087)	0.28	0.005 (-0.183 – 0.307)	0.08
Tree cover	-0.030 (-0.363 – 0.116)	0.25	-0.002 (-0.296 – 0.237)	0.07
Pan density	-0.040 (-0.604 – 0.241)	0.22	-0.022 (-0.679 – 0.265)	0.11
Distance to river	0.002 (-0.184 – 0.259)	0.06	0.010 (-0.150 – 0.355)	0.10
Distance to Lake Urema	0.002 (-0.199 – 0.259)	0.06	0.003 (-0.213 – 0.287)	0.08
Termite mound density	0.001 (-0.190 – 0.237)	0.06	0.005 (-0.181 – 0.309)	0.08
Distance to road	-0.001 (-0.266 – 0.238)	0.06	0.006 (-0.190 – 0.332)	0.08

Lion activity	-0.001 (-0.245 – 0.224)	0.06	-0.003 (-0.291 – 0.202)	0.08

Bushbuck				
	Dry season		***Wet season***	
Covariate	**Estimate (95% Confidence Interval)**	**Importance**	**Estimate (95% Confidence Interval)**	**Importance**
Intercept	**-0.038 (-0.226 – 0.149)**	**1.00**	**-0.033 (-0.235 – 0.170)**	**1.00**
Fire frequency	**0.389 (0.169 – 0.609)**	**1.00**	**0.347 (0.099 – 0.594)**	**1.00**
Distance to river	**-0.362 (-0.558 – -0.165)**	**1.00**	**-0.283 (-0.487 – -0.079)**	**1.00**
Distance to Lake Urema	**-0.502 (-0.706 – -0.299)**	**1.00**	**-0.510 (-0.728 – -0.292)**	**1.00**
Poaching	-0.041 (-0.327 – 0.079)	0.33	0.001 (-0.204 – 0.223)	0.08
Tree cover	0.017 (-0.138 – 0.316)	0.19	0.003 (-0.199 – 0.271)	0.09
Pan density	-0.026 (-0.511 – 0.228)	0.19	0.078 (-0.132 – 0.639)	0.31
Lion activity	-0.008 (-0.290 – 0.138)	0.10	0.001 (-0.201 – 0.228)	0.08
Termite mound density	-0.001 (-0.195 – 0.171)	0.08	-0.008 (-0.259 – 0.117)	0.11
Distance to road	0.0004 (-0.214 – 0.224)	0.08	**-0.145 (-0.417 – 0.032)**	**0.75**

SUPPLEMENTARY TABLE 5: PREDICTORS OF OCCUPANCY

Mean estimated effect size, with 95% credible interval, for each covariate hypothesized to influence occupancy. Effects with a 95% credible interval that did not overlap 0 are in bold. The community- and group-level hyper-parameters informed species-level coefficients. Group associations of each species can be found in Supplementary Table 1. Only ungulate species are reported in the table, but the full model included all 38 species detected on camera traps.

Dry season									
	Termite mound density	**Fire frequency**	**Poaching**	**Distance to road**	**Distance to Lake Urema**	**Tree cover**	**Pan density**	**Distance to river**	**Lion activity**
Impala	0.292 (-0.263 – 0.898)	0.247 (-0.288 – 0.723)	-0.142 (-0.393 – 0.135)	**-0.607 (-1.128 – -0.225)**	**0.571 (0.022 – 1.207)**	-0.737 (-1.383 – -0.116)	-0.298 (-0.999 – 0.427)	-0.193 (-0.667 – 0.246)	-0.183 (-0.485 – 0.103)
Harte-beest	0.01 (-0.605 – 0.62)	**0.655 (0.086 – 1.328)**	-0.133 (-0.387 – 0.166)	-0.303 (-0.746 – 0.191)	**0.817 (0.053 – 1.664)**	-0.322 (-1.132 – 0.468)	-0.196 (-1.154 – 0.801)	-0.026 (-0.631 – 0.613)	-0.128 (-0.409 – 0.271)
Red duiker	-0.037 (-0.568 – 0.434)	0.171 (-0.431 – 0.668)	-0.108 (-0.353 – 0.207)	-0.083 (-0.495 – 0.501)	0.502 (-0.086 – 1.14)	0.387 (-0.253 – 1.076)	-0.501 (-1.593 – 0.373)	-0.132 (-0.654 – 0.390)	-0.179 (-0.465 – 0.132)
Wilde-beest	-0.311 (-1.036 – 0.332)	0.524 (-0.023 – 1.123)	-0.170 (-0.456 – 0.090)	-0.355 (-0.831 – 0.086)	**0.848 (0.136 – 1.629)**	**-0.970 (-1.852 – -0.194)**	-0.328 (-1.360 – 0.598)	0.125 (-0.429 – 0.743)	-0.144 (-0.428 – 0.208)
Sable antelope	-0.289 (-0.847 – 0.224)	0.479 (0.003 – 0.982)	-0.157 (-0.427 – 0.091)	**-0.382 (-0.804 – -0.004)**	0.493 (-0.068 – 1.089)	0.588 (-0.043 – 1.260)	-0.701 (-2.069 – 0.172)	0.129 (-0.351 – 0.621)	-0.184 (-0.481 – 0.100)
Water-buck	0.054 (-0.617 – 0.782)	0.440 (-0.213 – 1.078)	-0.158 (-0.453 – 0.140)	-0.334 (-0.775 – 0.156)	0.048 (-0.755 – 0.877)	-0.406 (-1.338 – 0.485)	-0.342 (-1.287 – 0.547)	-0.351 (-1.068 – 0.253)	-0.221 (-0.579 – 0.077)
Elephant	-0.190 (-0.606 – 0.235)	0.244 (-0.256 – 0.685)	-0.175 (-0.452 – 0.065)	-0.362 (-0.740 – 0.006)	-0.203 (-0.749 – 0.310)	-0.141 (-0.729 – 0.432)	-0.212 (-0.905 – 0.615)	-0.128 (-0.575 – 0.318)	-0.245 (-0.616 – 0.022)
Oribi	0.034 (-0.464 – 0.552)	**0.655 (0.175 – 1.221)**	-0.130 (-0.370 – 0.160)	-0.250 (-0.618 – 0.202)	-0.370 (-0.968 – 0.185)	**-1.187 (-1.906 – -0.534)**	-0.553 (-1.385 – 0.167)	0.111 (-0.353 – 0.603)	-0.190 (-0.505 – 0.088)
Warthog	-0.088 (-0.859 – 0.752)	0.234 (-0.590 – 0.924)	-0.146 (-0.422 – 0.161)	-0.435 (-0.981 – 0.042)	0.084 (-0.900 – 1.040)	-0.120 (-1.222 – 1.044)	-0.297 (-1.311 – 0.666)	-0.120 (-0.854 – 0.600)	-0.198 (-0.537 – 0.111)

Dry season									
	Termite mound density	**Fire frequency**	**Poaching**	**Distance to road**	**Distance to Lake Urema**	**Tree cover**	**Pan density**	**Distance to river**	**Lion activity**
Bushpig	0.398 (-0.085 – 0.949)	0.189 (-0.294 – 0.736)	-0.084 (-0.355 – 0.230)	-0.033 (-0.432 – 0.366)	0.268 (-0.262 – 0.803)	-0.121 (-0.699 – 0.475)	0.431 (-0.321 – 1.273)	-0.145 (-0.625 – 0.286)	-0.035 (-0.334 – 0.293)
Reedbuck	-0.294 (-0.715 – 0.130)	**0.517 (0.090 – 0.965)**	-0.142 (-0.391 – 0.122)	-0.296 (-0.641 – 0.072)	0.421 (-0.038 – 0.894)	**-0.916 (-1.519 – -0.357)**	-0.196 (-0.847 – 0.463)	-0.082 (-0.499 – 0.323)	-0.171 (-0.441 – 0.114)
Buffalo	0.132 (-0.340 – 0.639)	**0.629 (0.135 – 1.209)**	-0.158 (-0.424 – 0.103)	-0.383 (-0.872 – 0.039)	-0.380 (-1.014 – 0.209)	**-0.950 (-1.813 – -0.179)**	0.151 (-0.56 – 1.092)	-0.497 (-1.140 – 0.068)	-0.183 (-0.476 – 0.104)
Commonn duiker	-0.107 (-0.613 – 0.358)	**0.541 (0.062 – 1.036)**	-0.133 (-0.374 – 0.156)	-0.318 (-0.713 – 0.097)	0.340 (-0.186 – 0.892)	0.073 (-0.531 – 0.695)	-0.454 (-1.469 – 0.324)	-0.121 (-0.613 – 0.357)	-0.200 (-0.536 – 0.086)
Eland	-0.246 (-1.027 – 0.467)	**0.627 (0.043 – 1.327)**	-0.143 (-0.412 – 0.164)	-0.351 (-0.854 – 0.138)	-0.184 (-1.000 – 0.539)	-0.647 (-1.691 – 0.321)	-0.178 (-1.093 – 0.794)	-0.400 (-1.155 – 0.228)	-0.210 (-0.565 – 0.091)
Nyala	0.408 (-0.056 – 0.917)	0.188 (-0.296 – 0.621)	-0.211 (-0.53 – 0.032)	-0.237 (-0.583 – 0.173)	0.364 (-0.124 – 0.867)	0.339 (-0.213 – 0.900)	**-0.745 (-1.735 – -0.034)**	0.398 (-0.055 – 0.875)	-0.156 (-0.428 – 0.153)
Greater kudu	-0.023 (-0.536 – 0.554)	**0.615 (0.057 – 1.262)**	-0.187 (-0.494 – 0.064)	**-0.411 (-0.841 – -0.031)**	**1.067 (0.391 – 1.847)**	-0.468 (-1.238 – 0.326)	-0.715 (-1.726 – 0.017)	-0.128 (-0.575 – 0.318)	-0.145 (-0.404 – 0.187)
Busbuck	-0.489 (-1.256 – 0.201)	0.191 (-0.614 – 0.815)	-0.141 (-0.410 – 0.173)	-0.426 (-0.949 – 0.011)	-0.275 (-1.265 – 0.610)	0.092 (-0.914 – 1.196)	-0.278 (-1.228 – 0.742)	-0.031 (-0.716 – 0.699)	-0.198 (-0.539 – 0.111)

	Wet season								
	Termite mound density	**Fire frequency**	**Poaching**	**Distance to road**	**Distance to Lake Urema**	**Tree cover**	**Pan density**	**Distance to river**	**Lion activity**
Impala	0.097 (-0.455 – 0.701)	0.074 (-0.56 – 0.708)	0.005 (-0.286 – 0.263)	0.166 (-0.245 – 0.599)	0.033 (-0.588 – 0.619)	**-1.800 (-2.721 – -1.007)**	0.169 (-0.595 – 1.2800)	0.193 (-0.357 – 0.697)	**1.058 (0.269 – 2.094)**
Hartebeest	-0.146 (-0.662 – 0.340)	0.247 (-0.402 – 0.949)	0.043 (-0.223 – 0.345)	0.129 (-0.339 – 0.559)	0.933 (0.230 – 1.800)	-0.639 (-1.449 – 0.105)	-0.131 (-1.200 – 0.791)	0.231 (-0.355 – 0.804)	0.262 (-0.390 – 0.914)
Red duiker	0.554 (-0.032 – 1.255)	-0.187 (-1.133 – 0.742)	-0.088 (-0.443 – 0.242)	0.439 (-0.221 – 0.941)	0.438 (-0.390 – 1.400)	0.279 (-0.772 – 1.385)	0.634 (-0.583 – 1.708)	0.509 (-0.262 – 1.260)	0.828 (-0.059 – 1.788)
Wildebeest	-0.114 (-0.726 – 0.455)	0.679 (-0.025 – 1.572)	0.035 (-0.240 – 0.345)	0.160 (-0.295 – 0.651)	0.722 (-0.030 – 1.599)	**-0.898 (-1.798 – -0.067)**	-0.154 (-1.319 – 0.825)	0.314 (-0.292 – 0.922)	0.617 (-0.094 – 1.407)
Hippopotamus	-0.175 (-0.862 – 0.433)	-0.406 (-1.384 – 0.392)	0.037 (-0.252 – 0.361)	0.076 (-0.512 – 0.527)	-0.383 (-1.376 – 0.460)	-0.821 (-1.994 – 0.230)	-0.145 (-1.230 – 0.828)	0.071 (-0.726 – 0.701)	0.147 (-0.649 – 0.930)
Sable antelope	-0.041 (-0.570 – 0.491)	0.457 (-0.241 – 1.210)	0.024 (-0.253 – 0.306)	0.171 (-0.264 – 0.647)	**0.965 (0.184 – 2.030)**	-0.362 (-1.210 – 0.421)	-0.269 (-1.516 – 0.655)	0.495 (-0.052 – 1.140)	-0.368 (-1.224 – 0.342)
Waterbuck	0.080 (-0.608 – 0.908)	-0.316 (-1.304 – 0.525)	-0.018 (-0.367 – 0.254)	0.162 (-0.332 – 0.684)	-0.167 (-1.148 – 0.730)	-0.761 (-1.882 – 0.382)	-0.013 (-1.066 – 1.137)	0.314 (-0.431 – 1.057)	0.382 (-0.625 – 1.397)
Elephant	0.127 (-0.435 – 0.830)	0.086 (-0.699 – 0.888)	0.043 (-0.234 – 0.367)	0.138 (-0.365 – 0.602)	-0.429 (-1.228 – 0.276)	-0.379 (-1.233 – 0.469)	0.085 (-0.742 – 1.200)	-0.061 (-0.743 – 0.523)	**0.793 (0.009 – 1.757)**
Oribi	0.035 (-0.510 – 0.612)	0.238 (-0.382 – 0.925)	0.022 (-0.240 – 0.293)	0.185 (-0.225 – 0.646)	-0.151 (-0.805 – 0.454)	**-1.738 (-2.645 – -0.960)**	0.233 (-0.544 – 1.465)	**0.475 (0.006 – 1.030)**	**0.900 (0.150 – 1.840)**

	Wet season								
	Termite mound density	**Fire frequency**	**Poaching**	**Distance to road**	**Distance to Lake Urema**	**Tree cover**	**Pan density**	**Distance to river**	**Lion activity**
Warthog	0.336 (-0.319 – 1.248)	-0.352 (-1.242 – 0.458)	-0.013 (-0.332 – 0.245)	0.236 (-0.210 – 0.790)	0.268 (-0.571 – 1.135)	**-1.287 (-2.413 – -0.254)**	0.053 (-0.937 – 1.205)	0.535 (-0.086 – 1.287)	0.133 (-0.757 – 0.985)
Bushpig	0.067 (-0.454 – 0.575)	0.198 (-0.453 – 0.903)	-0.062 (-0.385 – 0.284)	**0.613 (0.102 – 1.231)**	-0.362 (-0.955 – 0.223)	0.178 (-0.536 – 0.935)	0.769 (0.031 – 1.661)	**0.603 (0.061 – 1.165)**	**0.895 (0.265 – 1.615)**
Reedbuck	**-0.508 (-1.047 – -0.002)**	0.528 (-0.111 – 1.231)	0.026 (-0.236 – 0.293)	0.134 (-0.309 – 0.566)	0.243 (-0.344 – 0.851)	**-1.133 (-1.897 – -0.444)**	0.091 (-0.639 – 1.049)	0.174 (-0.360 – 0.672)	0.281 (-0.298 – 0.879)
Buffalo	-0.409 (-0.955 – 0.066)	-0.011 (-0.597 – 0.580)	0.038 (-0.234 – 0.336)	-0.005 (-0.600 – 0.395)	0.208 (-0.426 – 0.839)	-0.497 (-1.149 – 0.142)	-0.512 (-1.797 – 0.339)	0.472 (-0.034 – 1.063)	0.400 (-0.140 – 0.996)
Commonn duiker	0.300 (-0.345 – 1.162)	0.108 (-0.812 – 1.049)	0.030 (-0.257 – 0.329)	0.127 (-0.415 – 0.627)	0.570 (-0.373 – 1.700)	-0.309 (-1.546 – 0.895)	-0.134 (-1.369 – 0.926)	0.256 (-0.515 – 0.950)	0.309 (-0.626 – 1.249)
Eland	0.015 (-0.703 – 0.751)	0.353 (-0.547 – 1.373)	0.039 (-0.231 – 0.328)	0.226 (-0.231 – 0.839)	-0.298 (-1.440 – 0.673)	-0.165 (-1.445 – 1.112)	-0.088 (-1.212 – 1.029)	0.251 (-0.520 – 1.009)	0.833 (-0.099 – 1.980)
Nyala	0.174 (-0.229 – 0.640)	-0.188 (-0.757 – 0.339)	-0.008 (-0.330 – 0.250)	0.322 (-0.062 – 0.870)	0.432 (-0.103 – 0.997)	0.393 (-0.200 – 1.037)	-0.279 (-1.205 – 0.409)	**0.687 (0.181 – 1.243)**	-0.035 (-0.567 – 0.467)
Greater kudu	0.028 (-0.446 – 0.544)	0.416 (-0.234 – 1.173)	0.046 (-0.209 – 0.354)	0.109 (-0.370 – 0.531)	0.278 (-0.390 – 1.025)	-0.398 (-1.233 – 0.377)	-0.222 (-1.290 – 0.679)	**0.691 (0.163 – 1.342)**	0.489 (-0.148 – 1.137)
Busbuck	0.021 (-0.604 – 0.774)	0.059 (-0.809 – 0.922)	0.006 (-0.299 – 0.282)	0.204 (-0.253 – 0.787)	0.147 (-0.723 – 1.001)	**-1.134 (-2.224 – -0.103)**	0.039 (-0.945 – 1.193)	0.178 (-0.564 – 0.880)	0.556 (-0.343 – 1.559)

SUPPLEMENTARY TABLE 6. CAMERA OPERATION BY YEAR AND SEASON

Sampling effort for each season and each year of the camera trap study, including the number of camera sites and mean and total camera trap-nights.

		Number of cameras	**Mean (± SD) trap-nights per camera**	**Total of trap-nights**
Dry season	Year 1 (2016)	60	82 ± 14	4,906
	Year 2 (2017)	56	89 ± 10	4,093
	Total	116	85 ± 13	8,999
Wet season	Year 1 (2016-2017)	45	73 ± 40	4,000
	Year 2 (2017-2018)	37	77 ± 44	2,840
	Total	82	75 ± 42	6,840

SUPPLEMENTARY TABLE 7: CAMERA TRAP LOCATION AND OPERATION DATES

Locations of the 60 camera traps in the study grid, and the number of days for which each camera trap was operating in each season of each year. The dry season was July to September, and wet season from December to March. Cameras that were operating for fewer than 10 days in a season were excluded from analysis.

Camera	**Latitude**	**Longitude**	**2016 Dry Season Operation** (n = 60 cameras)	**2016-2017 Wet Season Operation** (n = 56 cameras)	**2017 Dry Season Operation** (n = 45 cameras)	**2017-2018 Wet Season Operation** (n = 37 cameras)
A06	-18.94847	34.31120	86	31	NA	NA
A08	-18.97055	34.31128	86	61	92	69
A10	-18.99254	34.31170	86	20	92	0
B05	-18.93760	34.33081	88	79	NA	NA
B07	-18.95957	34.33033	88	121	92	121
B09	-18.98108	34.33122	86	40	92	91
C06	-18.94877	34.35125	88	37	92	29
C08	-18.97041	34.35071	88	121	92	121
D03	-18.91569	34.36975	92	26	92	40
D05	-18.93763	34.37036	87	50	92	121
D07	-18.97986	34.37051	82	121	92	121
D09	-18.95907	34.37054	27	24	NA	NA
E02	-18.90468	34.39004	92	81	92	38
E04	-18.92648	34.39024	87	121	71	NA
E06	-18.94814	34.39065	92	58	47	NA
E08	-18.97007	34.39047	92	47	92	17
E10	-18.99155	34.39053	85	121	92	NA
E12	-19.01331	34.39089	79	121	NA	NA
F01	-18.89402	34.40934	87	NA	92	121
F03	-18.91463	34.40951	92	25	92	59
F05	-18.93785	34.40944	27	36	88	NA
F07	-18.95938	34.41000	88	95	92	NA
F09	-18.98048	34.41010	22	26	NA	NA
F11	-19.00232	34.41034	85	34	92	56
G02	-18.90452	34.42932	87	NA	92	24
G04	-18.92615	34.42925	92	121	92	121
G06	-18.94765	34.42924	88	121	92	121
G08	-18.96947	34.42969	81	114	92	121
G10	-18.99154	34.42987	85	121	NA	NA
G12	-19.01238	34.43031	83	97	NA	NA
H03	-18.91520	34.44920	87	121	92	121
H05	-18.93732	34.44904	88	121	92	50

Camera	**Latitude**	**Longitude**	**2016 Dry Season Operation** (n = 60 cameras)	**2016-2017 Wet Season Operation** (n = 56 cameras)	**2017 Dry Season Operation** (n = 45 cameras)	**2017-2018 Wet Season Operation** (n = 37 cameras)
H07	-18.95859	34.44962	86	26	48	NA
H09	-18.98015	34.45014	86	121	NA	NA
H11	-19.00162	34.44932	83	121	NA	NA
H13	-19.02429	34.44970	83	64	NA	NA
I04	-18.92486	34.46830	88	121	92	121
I06	-18.94756	34.46877	86	26	92	28
I08	-18.96937	34.46918	81	38	92	112
I10	-18.99097	34.46956	81	29	92	11
I12	-19.01319	34.46984	83	24	92	121
I14	-19.03467	34.46753	81	40	NA	NA
J03	-18.91491	34.48890	88	17	92	14
J05	-18.93744	34.48872	82	69	92	48
J07	-18.95831	34.48913	86	42	92	121
J09	-18.97872	34.48870	81	54	NA	NA
J11	-19.00152	34.48963	81	NA	92	121
J13	-19.02231	34.48900	82	44	92	40
K04	-18.92375	34.50578	75	72	92	83
K06	-18.94731	34.50857	80	121	92	121
K08	-18.96980	34.50842	80	25	92	32
K10	-18.99110	34.50899	80	121	92	121
K12	-19.01297	34.50941	82	38	92	32
L05	-18.93517	34.52907	82	34	92	31
L07	-18.95881	34.52905	80	121	66	NA
L09	-18.97978	34.52872	80	NA	NA	NA
L11	-19.00148	34.52897	82	121	92	121
L13	-19.02311	34.52930	80	121	NA	NA
M08	-18.96881	34.54853	82	79	NA	NA
M10	-18.99093	34.54668	82	92	92	NA

Chapter 7. Concluding remarks

LANDSCAPES OF FEAR IN THE ANTHROPOCENE

In this dissertation, my coauthors and I examined how spatial heterogeneity, predation risk, and human activity interact to shape the spatiotemporal distribution of wild animals. The concept of the landscape of fear, introduced in Chapter 2, provided a valuable lens for exploring these dynamics. As exemplified through the remaining chapters, the links between landscape heterogeneity, predation risk, the landscape of fear, and prey response are non-linear, and governed by behavioral constraints and trade-offs. Understanding these non-linearities can shed light on the relative importance of the landscape of fear in driving population and community dynamics across systems.

The landscape of fear framework can also inform our understanding of the multiple pathways through which human activity reshapes landscapes of fear, many of which we explored in this dissertation. Anthropogenic disturbance can transform the underlying physical landscape, and thus alter the playing field for predator-prey interactions. As documented in the Chapter 3 Hopland case study, human infrastructure like roads and settlements can facilitate hunting by people and drive spatial patterns of harvest risk for deer. Development and land conversion can also introduce spatial constraints that limit prey's ability to avoid predators. Even patterns of global climate change can have local effects on habitat; in Gorongosa, for example, more extreme patterns of flooding as a result of climate change may reshape interactions between predators and prey, as explored in Chapter 6.

Human disturbance itself is often associated with stimuli that are perceived as risky, thus generating landscapes of fear. In some cases, human hunters act as another predator on the landscape, as in the Chapter 3 Hopland study. However, novel anthropogenic landscapes of fear drive responses in animals even in the absence of underlying risk, as documented in the Chapter 4 meta-analysis on animal activity patterns in response to human disturbance. Furthermore, the Gorongosa elephant case study presented in Chapter 5 highlights how human activity can also be associated with resources for wild animals, and people can thus shape both sides of the cost-benefit trade-off associated with novel landscapes of fear.

As non-lethal apex super-predators, humans can thus alter the distribution of predators through landscapes of fear, with cascading consequences for prey species. As discussed in Chapter 3, infrastructure creates a "human shield" in which deer can find refuge from predation from mountain lions. People also directly affect the density of predators on the landscape through removal or reintroduction; policies and conservation interventions in both California and Gorongosa are facilitating the return of large carnivores, reinstating landscapes of fear for prey.

THE ROLE OF TEMPORAL PARTITIONING

While landscapes of fear are typically associated with static spatial patterns of risk, risk often varies temporally, and temporal niche partitioning emerged as a central theme throughout this dissertation. Time is an important ecological resource (Kronfeld-Schor and Dayan 2003), and the diel cycle facilitates co-existence not only between predators and prey, but also between animals and people. The role of temporal risk avoidance may be especially important when ecological or anthropogenic constraints limit the ability of animals to respond spatially to risk. As we documented in Chapter 3, deer in Hopland, which persist at high densities with strong site fidelity, did not adjust their space use or overall activity in response to risk from hunters or mountain lions. Instead, deer changed their diel activity patterns in response to spatial and seasonal patterns of risk, minimizing temporal overlap with their predators. In Gorongosa, shifts in temporal activity patterns may also be a mechanism for reducing apparent competition during times of year when spatial constraints concentrate antelope species and lions into smaller areas, as our findings in Chapter 6 suggest.

As human activity expands worldwide and constrains space for large mammal communities, temporal niche partitioning may play an even greater role in ecological dynamics of disturbed and recovering systems. Globally, animals respond to human disturbance by increasing their relative nocturnal activity to avoid people by day, as described in Chapter 4. Animals may also balance risks and rewards associated with human activity by adjusting their spatiotemporal activity around human disturbance on fine scales, as documented for the Gorongosa elephants in Chapter 5.

IMPLICATIONS FOR HUMAN-WILDLIFE COEXISTENCE

Given that humans are playing an outsized role in ecological communities, it is critical that we understand the dynamics of human-wildlife coexistence on an increasingly crowded planet. To that end, this work contributes to a growing body of evidence documenting strong behavioral responses of animals to human presence. The striking global pattern of wildlife avoidance of human activity suggests an important behavioral mechanism through which anthropogenic disturbance is reshaping ecological communities. By understanding how animals perceive and respond to risk associated with their environments and with human stimuli, we may be better able to design management interventions that facilitate coexistence.

Despite our understanding of human impacts on animal behavior, little is known about the long-term, downstream consequences of these behavioral shifts for animal populations or species interactions. Human disturbance may create ecological traps, if animals perceive risk from human activity that is actually benign and suffer fitness consequences as a result. In Hopland, for example, female deer exhibit subtle shifts in their activity patterns in response to hunters, despite the fact that only males can be harvested. Consequently, female deer experience greater temporal overlap with mountain lions, and their risk avoidance behavior may thus actually put them at greater risk. Future research that examines the role of human activity in reshaping species interactions and initiating behaviorally-mediated trophic cascades may shed light on consequences of disturbance at larger scales.

While this dissertation examined the dynamics of human-wildlife coexistence through an ecological lens, interactions between people and natural systems are also defined by social, economic, and political dynamics. Research that examines the feedbacks of socioecological systems and investigates human-wildlife interactions as part of a coupled human-natural system will provide a more complete picture of the salient factors that facilitate or inhibit human-wildlife coexistence. Identifying and implementing solutions that advance goals of biodiversity conservation along with the well-being of people necessitates interdisciplinary collaboration and integrated policies and management strategies. I hope that the body of work in this dissertation can contribute to these broader dialogues about how to best manage landscapes and wildlife communities in the Anthropocene.

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