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Life Finds a Way: Carnivore Movement and Conflict in Developing Landscapes

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Carnivore Movement and Conflict in Developing Landscapes

By

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Abstract

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Human-carnivore conflict (HCC) is a major conservation challenge that drives declines of large carnivore populations and impacts human livelihoods and major industries. Protected areas are often unable to support wildlife without surrounding unprotected and developed dispersal areas, where they may spend large portions of their time. Predictive mapping of carnivore predation risk based on verified livestock predation has created new tools for effective HCC management. Yet, rarely are verified conflict and ecological data integrated with social and attitudinal data describing people's perceptions of risks from carnivores, despite their importance for carnivore conservation. This dissertation explores methods of incorporating participatory spatial knowledge with carnivore ecology and behavior, land use, human infrastructure, and human activity. This research contributes to theoretical understandings of social and spatial factors contributing to HCC and carnivore management in developed landscapes, and explores the effectiveness of using participatory and multidisciplinary methods for conservation in a rapidly changing world. In Chapter 1, I introduce theories underlying this research, describe the study site, and contextualize the research questions within the global trend of carnivore responses to increasing human activity. Chapter 2 applies ecological theory to describe predation on domestic prey and devises an ecological framework for understanding and mitigating HCC. Case studies demonstrate its utility for employing appropriate conflict interventions in varying ecological contexts. Chapter 3 maps patterns of verified and perceived HCC using community participatory mapping and verified livestock predation records, and provides recommendations for incorporating ecological data and participatory social data to more effectively and holistically address conservation challenges. Chapter 4 uses fine scale telemetry data to analyze spotted hyena behaviors around human infrastructure and human activity across land cover types, human risk perceptions, land management zones, and seasons. I then discuss the broader implications of these findings for "adaptable" large carnivore species that share landscapes with people globally. Chapter 5 explores wildlife behavioral responses to one of the most widespread forms of human-wildlife conflict mitigation: the conservation fence. I show that, regardless of fence maintenance, most wildlife species are likely to cross these fences. I discuss implications of these findings for fenced protected areas globally, and offer the first known guidelines for classifying wildlife fence-specific behaviors from camera trap imagery. Finally, in Chapter 6, I make recommendations on how carnivore conservation and HCC management should be informed by ecological, social, and participatory data and methodologies.

DEDICATION

This dissertation is dedicated to my dad, Andrew James John Wilkinson, who first inspired in me a love of animals and a deep caring for humanity.

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Chapter 1. Introduction

FRONTIERS OF COEXISTENCE IN THE 21st CENTURY

We are now living in unprecedented times in which humans have altered the earth so profoundly as to have created our own epoch: the Anthropocene (Steffen et al. 2007, Steffen et al. 2011, Di Marco et al. 2018). Human disturbances, such as land use change, infrastructure placement, and high population densities, impact nearly every aspect of ecology across the globe (Hill et al. 2019, Wilson et al. 2020). Habitat loss (Hoekstra et al. 2005), invasive species (Clavero and Garcia-Bertho 2005, McGill et al. 2015), and widespread changes in animal behavior (Gaynor et al. 2018; Torres et al. 2016) are just some of the anthropogenic effects that can be observed across scales (e.g., Halpern et al. 2015, Chase et al. 2019) and geography (Davies et al. 2006). Human needs are only increasing, thus creating new frontiers of coexistence in which people and wildlife must learn to live together either for the first time (Nickel et al. 2020, Williams et al. 2020), or in new ways (Northrup and Whittemer 2013, Soulsbury and White 2015, Margulies and Karanth 2018).

As typically wide-ranging animals, large carnivores and mesopredators are two of the species groups most likely to come in contact with people due to habitat loss or fragmentation (Chapron and Lopez-Bao 2016, Di Minin et al. 2016, Carter and Linnell 2018). Many carnivores also exhibit behavioral plasticity, which means they may have some advantage in navigating the novel human-created landscapes that are the spatial hallmark of the Anthropocene (Burdett et al. 2010). However, where people and carnivores share landscapes, humans also act as apex predators, contributing to “landscapes of fear” for carnivores through direct or indirect means (e.g., Clinchy et al. 2016, Lodberg-Holm et al. 2019). Human-carnivore conflict (HCC), in which people fear actual or perceived risk from carnivores to themselves or their livestock, and actions people take to protect themselves from these risks (Treves and Karanth 2003) is another phenomenon on these shared landscapes.

Human-carnivore conflict is an ongoing critical issue around the world which significantly impacts human livelihoods (Muhly and Musiani 2009, USDA 2020) while driving declines in predator populations (Ripple et al. 2014). Instances of HCC are rising with increases in land subdivision, development, and agro-pastoral settlement in wildlife dispersal areas (Said et al. 2016). Consequently, increasing rates of HCC are prevalent in many regions of the world, and can be particularly stark in the Global South where people are experiencing poverty (Barua et al. 2013). Additionally, communities dealing with conflict must often cope with governments that are unable to compensate or provide other means of addressing HCC. There is also a tendency for many governments to historically prioritize wildlife over peoples’ livelihoods in HCC situations (Sindiga 1995). Exacerbating these issues, protected areas are often unable to support wildlife without surrounding unprotected dispersal areas, where wildlife may spend up to 70% of their time (Western and Gichohi 1993). Wildlife populations in general are experiencing major declines inside and outside of protected areas, resulting in a need for interdisciplinary and community-based research and methods of wildlife conservation to understand human interactions with wildlife in a changing world (Western et al. 2009, White et al. 2009, Nyhus 2016).

In this dissertation I draw on ecology, animal behavior, interdisciplinary technologies, and participatory methods to understand how carnivores might fare in the Anthropocene, and how they may coexist with people in ways that explicitly elevate local community needs.

COEXISTENCE THROUGH MULTIPLE LENSES

While ecology and animal behavior are key to understanding how carnivores will adapt to developing landscapes, people are an integral part of the coexistence story and of ecology. Conservation biologists are coming to understand that we need to bolster interdisciplinary work to support more holistic conservation efforts, yet few studies have incorporated participatory mapping into land use and animal behavior assessments to enhance understanding of human-carnivore conflict and carnivore movement. Because visible manifestations of HCC are often rooted in less visible and more complex social conflicts (Madden and McQuinn 2014), incorporating social factors into our broader understanding of human-carnivore conflict is key (Hemson et al. 2009, Dickman 2010, Dickman, et al. 2014). One way to meet the lack of hybrid scientific-local knowledge approaches in conservation research (Reid et al. 2016), and to overcome epistemic injustices (often toward local communities) inherent in the traditional academic approach (Fricker 2007), is to involve the community in all aspects of the research process, to the extent possible. Participatory mapping of conflict and human resource use is an ideal way to guide the research process and enhance remote sensing and GIS analyses by providing community-specific information that is unattainable otherwise and crucial for informing management decisions (Ramstad et al. 2007, Polfus et al. 2014).

In recent years, methods for predictive mapping of carnivore predation risk based on actual instances of conflict have been developed (Abade et al. 2014, Miller 2015), creating new tools for effective HCC management. However, perception of risk is as influential on human attitudes as is actual loss (Naughton-Treves and Treves 2005), and tolerance for carnivores is diminished by high perception of risk (Knopff et al. 2016), ever confirming that perceptions can influence negative actions toward carnivores. Although various studies have been conducted on perceived HCC, little work has investigated how verified conflict compares to human perceptions and experiences. Understanding the relationship between perceived and verified risks and types of conflict is necessary for effective management and mitigation (Dickman et al. 2014), and multidisciplinary methods (remote sensing, GIS, participatory mapping, surveys) should be employed to elucidate this relationship at fine scales.

A multidisciplinary and participatory approach can not only help in understanding the long-term impacts of frontiers of coexistence for carnivores (Galvez et al. 2018), but may also lead to long lasting and environmentally just solutions to our coexistence challenges (Lute and Gore 2019). This dissertation serves to explore critical questions of human-carnivore coexistence through multiple technologies and ways of knowing.

STUDY SITE

The primary data collection for this dissertation was conducted in and around Lake Nakuru National Park (LNNP) and Soysambu Conservancy in the Rift Valley of Kenya. Despite their relatively small sizes as compared to other Kenyan protected areas, LNNP and Soysambu Conservancy maintain a wide variety of large mammal species, including a number of threatened species, and portions of both protected areas are classified as UNESCO World Heritage sites. Because of the high wildlife populations in the protected areas, the high rates of human immigration into the area, and the rapid infrastructure development in the surrounding communities, this region provides an ideal opportunity to study the frontier of human-wildlife coexistence in the Anthropocene.

While Soysambu Conservancy hosts large populations of wild mammals, it is also a livestock ranch which is home to 10,000 cattle, sheep, and goats. Additionally, the colonial history of Soysambu contributes to a tension between wildlife management goals, livestock husbandry priorities, and local community grazing and resource needs. This combination of varying management objectives and nuanced local histories supported the idea development and data collection for Chapter 3 on verified and perceived livestock predation. While this region has its distinctive history, the combination of critical local histories and dense development in close proximity to wildlife likely exemplifies similar coexistence challenges around the world.

LNNP also provides a particularly unique setting with which to study human-wildlife coexistence, since it is one of only two fully fenced national parks in Kenya. Electric fences are one of the primary tools employed toward achieving coexistence around the world. The semi-permeability of the electric fence surrounding LNNP allowed for the questions and methodologies outlined in Chapter 5.

Lastly, spotted hyenas (*Crocuta crocuta*) have burgeoning populations in this region, with upwards of 60 animals per clan on average. With spotted hyenas widely considered one of the most adaptable large carnivore species, such a densely populated and rapidly developing region allowed for Chapter 4's exploration of whether, how, and to what extent this species might be adapting to anthropogenic changes. Spotted hyena adaptability can serve as a litmus test for how other carnivore species may or may not adapt to new frontiers of coexistence globally.

OVERVIEW OF DISSERTATION

My dissertation research is comprised of 4 chapters. In Chapter 2, "An ecological framework for contextualizing carnivore-livestock conflict", I use ecological theory to understand one of the main ways people and wildlife interact: carnivore-livestock conflict. I present a framework that maps basic ecological theories onto predation on domestic prey (such as cattle, sheep, and goats). I then provide a series of case studies to demonstrate the utility of this framework for choosing conflict interventions that are based in ecology and animal behavior, and are thus more effective over time.

While Chapter 2 emphasizes the basic ecology determining conflict between livestock and carnivores, in Chapter 3, "Examining drivers of divergence in recorded and perceived human-carnivore conflict hotspots by integrating participatory and ecological data", I examine how the broader socioeconomic context impacts conflict and coexistence through human tolerance and people's perceptions of risk. To assess spatial and contextual differences between verified and perceived conflict reports, I compare a long-term dataset of verified conflict between carnivores and people in Nakuru County with a participatory dataset drawn by community members dealing with conflict in the region. I explore possible ecological or anthropogenic causes in spatial differences between the two spatial datasets, and conduct pairwise analyses of interview data from the same communities in order to more deeply understand what factors predict perceived conflict and negative attitudes toward carnivores.

After laying the ecological and social groundwork for understanding human-carnivore conflict and coexistence in Chapters 2 and 3, in Chapter 4, "Spotted hyena landscape navigation on a coexistence frontier", I explore the fine-scale movements of a highly behaviorally plastic carnivore: the spotted hyena. I examine hyena navigation of landscape-level ecological, infrastructure, and human perception covariates to infer how we may build connectivity models in developed landscapes using interdisciplinary types of data. I then discuss more broadly how these findings from spotted hyenas may apply to our understanding of carnivore adaptations to people in developing landscapes.

For Chapter 5, “Quantifying wildlife responses to conservation fencing in East Africa”, I provide a case study for understanding the effectiveness of a tool widely employed to achieve coexistence between wildlife and people: the conservation fence. In this chapter, I demonstrate the semi-permeability of the conservation fence surrounding Lake Nakuru National Park, and the potential ecological impacts of taxa-specific mammalian behaviors around the fence line. I also present a classification for categorizing mammal fence-specific behaviors from still camera trap imagery, to be used by other scientists seeking to answer behavioral questions in the budding field of fence ecology. Finally, I discuss how fence maintenance may be ineffective at containing wildlife over the long term, and how these collective results indicate a need to have clear goals and realistic cost assessments for conservation fences.

Lastly, in Chapter 6, “Concluding remarks”, I review the frameworks and themes that guide and emerge from this dissertation work. I consider the ways in which interdisciplinary framing and methodologies can contribute to a more holistic understanding of conflict and coexistence, and reflect on how incorporating diverse ways of knowing may lead to lasting and socially just conservation outcomes. I conclude by examining how the stories presented through these chapters may serve as starting points for applied conservation research that meaningfully engages communities and prioritizes human perspectives while being grounded in ecological theory.

Chapter 2. An ecological framework for contextualizing carnivore-livestock conflict

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ABSTRACT

Carnivore predation on livestock is a complex management and policy challenge yet is also intrinsically an ecological interaction between predators and prey. Human-wildlife interactions occur in socio-ecological systems, in which human and environmental processes are closely linked. However, underlying human-wildlife conflict and key to unpacking its complexity are concrete and identifiable ecological mechanisms that lead to predation events. To better understand how known ecological theories map onto the interactions between wild predators and domestic prey, we developed a framework describing ecological drivers of predation on livestock. We used this framework to examine ecological mechanisms through which specific management interventions operate, and we analyzed the ecological determinants of failure and success of management interventions in three case studies on snow leopards (*Panthera uncia*), wolves (*Canis lupus*), and cougars (*Puma concolor*). Our analysis demonstrates that mitigation of human-wildlife conflict ultimately requires an understanding of how fundamental ecological theories work within domestic predator-prey systems.

INTRODUCTION

Livestock predation is one of the most pervasive and widely studied manifestations of human-carnivore conflict. With over 4.2 billion cows, sheep, goats, and pigs grazing on 30% of the planet’s land (Robinson et al. 2014, FAO 2018), conflict resulting from carnivore-livestock interactions is among the greatest threats to carnivore conservation worldwide (Ripple et al. 2014). The dynamic web of social and ecological factors underlying carnivore-livestock conflict (Dickman 2010, Redpath et al. 2013) makes livestock losses particularly difficult to address via static policy and management tools (Treves and Karanth 2003, van Eeden et al. 2018a). This task is made harder still by our frequent failure to recognize that the interaction between wild carnivore and domestic prey can be understood at its heart as an ecological event: predation.

As an inherently applied field of study, research on carnivore-livestock conflict has focused on the effectiveness of selected interventions, with less consideration of the ecology shaping the relationship between carnivores and livestock (Miller et al. 2016, Treves et al. 2016). Yet, understanding predation, and how to effectively control or mitigate the encounters between prey and predators, requires knowing the principles governing the ecological interactions among predators, prey, and their surrounding landscape (Treves et al. 2004, Trainor and Schmitz 2014, Miller 2015).

Illuminating the ecological mechanisms that drive carnivore predation on livestock will allow a deeper understanding of why mitigation tools succeed or fail and in which contexts, as well as how and why intervention effectiveness changes over space and time. Such an understanding could form the basis of a framework to guide research and management of carnivore-livestock conflict (Graham et al. 2005, Goswami 2015, Miller 2015).

Here we provide a mechanistic framework for considering the ecological determinants of carnivore-livestock dynamics by integrating foundational works on ecological theory with seminal research on carnivore-livestock interactions. Our goal is to identify the ecological mechanisms which fundamentally underlie human-wildlife conflict. We operationalize this framework through a typology of interventions and case studies that represent a diversity of carnivores, socio-political systems, and landscapes. Applying our framework, we further demonstrate a) how current tools for conflict intervention act through specific ecological pathways to prevent or reduce livestock predation, b) why management interventions implemented without a consideration of ecological basis often fail, and c) the value of combining intervention strategies to target the diverse ecological drivers of livestock predation in a given system. Finally, we discuss applications of our framework to inform future research, management, and policymaking.

FRAMEWORK: ECOLOGICAL MECHANISMS OF LIVESTOCK PREDATION

A myriad of ecological factors affects the likelihood and outcome of a predator-prey encounter and therefore influences livestock predation. We group these factors into three categories: biophysical landscape characteristics, carnivore ecology, and livestock ecology. Below we introduce these categories of ecological drivers, we then develop a framework that explores their interdependence (Figs. 1 and 2), and outline the ecological mechanisms through which they may help understand the dynamics of livestock predation. The framework we develop can be considered most simply as one in which a predation event is viewed as an outcome predicted by the "state" (e.g. condition, traits) of two actors, livestock and predator, and the interaction of these states with the stage (landscape) on which they engage.

Biophysical landscape

Numerous factors within the biophysical environment influence the behavior and distribution of livestock and carnivores. These factors often include topography, vegetation type (Rostro-Garcia et al. 2016), season and day length (Chen et al. 2016), and proximity to human activities (Michalski et al. 2006). The integration of these factors provides the context for when and where livestock and carnivores encounter each other (Miller 2015). For example, tall vegetation surrounding pastoral areas may increase predation risk by obscuring carnivore activity from humans, thus creating a 'predation refuge' or an area of reduced human threat within a carnivore's landscape of fear (Bradley and Pletscher 2005, Davie et al. 2014,). Similarly, patchy networks of habitat that overlap livestock ranges can provide locations where predators hide and stalk livestock at close distances (Rostro-Garcia et al. 2016) or increase the presence of habitat ecotones preferred by many large carnivores, and where multiple prey species, including livestock, may be found together (Polisar et al. 2003). Thus, biophysical properties of a given landscape play an important role in both prey availability (how domestic and wild prey distribute themselves across a landscape) and accessibility (where prey are most vulnerable to an attack), and shape the likelihood of success when a carnivore chooses to attack (Trainor and Schmitz 2014).

Carnivore ecology

The traits intrinsic to carnivores that determine their behavior, landscape use, and inter- and intra-specific interactions include age, sex, and group size (Linnell et al. 1999, Courchamp and MacDonald 2001), body size (Haskell et al. 2002), hunting mode (Schmitz et al. 2004), demographic status (Rasmussen et al. 2008), body condition, and the propensity for behavioral plasticity (e.g., Farr et al. 2019). Along with taxonomic-level traits, an individual carnivore's behavioral characteristics can create variable risk landscapes for livestock, whereby chance or intentional encounters with that particular individual can lead to predation (Treves and Karanth 2003). The utility of a tool for protecting livestock from predation depends in part on the carnivore species' hunting mode – i.e. whether it is a coursing predator, ambush predator, or flexible in hunting mode depending on the environment. Ultimately, the tools most likely to be effective in protecting livestock will target evolutionary features of the predator as well as unique individual and species-specific behavioral traits. For example, because they are agile climbers, leopards (*Panthera pardus*) may take advantage of sturdy footholds on enclosures made of wooden poles, whereas spotted hyena (*Crocuta crocuta*) can push through dense traditional bush enclosures, given their skill in navigating brush (Kolowski and Holekamp 2006).

Livestock ecology

While there exists extensive research on the ecological mechanisms that make wild prey susceptible to predation, there has been comparatively little research on the ecological characteristics of livestock as prey animals (Mignon-Grasteau et al. 2005). In contrast to wild prey, many aspects of livestock ecology are largely managed by humans. For instance, livestock freely make fine-scale habitat and grazing choices within their home ranges (Laporte et al. 2010), but those home ranges and broader geographic ranges are primarily determined by husbandry practices (e.g., by fencing, zoning laws, penning, herding, etc.). Therefore, livestock habitat selection is heavily driven by economic considerations, property rights, and legal access (Voisinet 1997), and little research has investigated the extent to which habitat selection by livestock influences their predation risk (De Azevedo 2007, Laporte et al. 2010).

Equating livestock to wild prey has its limitations. Thousands of years of breeding have selected for traits in livestock that may decrease their ability to identify, defend against, and avoid predation threats (Muhly et al. 2010). Selection for behavioral traits, such as docility, and physical traits, such as exaggerated meat growth, cause livestock to be more vulnerable than their wild ancestors (Florcke and Grandin 2013). Thus, absent the risks posed by the humans managing livestock, carnivores may view many types of livestock as easy prey with minimal awareness or defenses (Price 1999). These combinations of human management and livestock behavioral traits make it essential to consider species-specific, breed-specific, and context-dependent livestock behavioral ecology to understand the mechanisms governing their predation.

ECOLOGICAL MECHANISMS OF LIVESTOCK PREDATION

Several ecological mechanisms can clarify the dynamics at play in carnivore-livestock interactions and help guide management techniques that effectively address livestock predation. Below, we discuss how these mechanisms (Fig. 1 highlighted letters a-e), fit within our framework and how humans shape numerous ecological relationships by manipulating interactions between species and their environment.

(a) Density-mediated effects

One of the most direct and popular methods through which humans manipulate carnivore populations is by removing reducing animal densities through the removal of individuals (e.g., culling, translocation; see Table 1 for definitions of interventions). Humans can also indirectly influence carnivore population ecology by reducing the availability of necessary resources (e.g., habitat and prey loss). Changing the density of carnivores on a landscape can result in a non-linear reduction of livestock predation (Berryman 1992), where decreasing carnivore density reduces livestock losses. However, the population dynamics and territorial behavior of some carnivore species can prompt unexpected pulses of increased predation on livestock due to enhanced reproduction (Knowlton et al. 1999), new individuals re-colonizing empty territory (Athreya et al. 2011), or the ecological release of other predators (Newsome et al. 2017). In this way, carnivore removal may result in unpredictable, undesired repercussions due to the important role that predators play in regulating ecosystem health and maintaining food webs (Suryawanshi et al. 2017).

(b) Behaviorally mediated effects

In addition to directly reducing carnivore density, humans can indirectly affect carnivore ecology by influencing their behavior. The use of interventions that simulate the presence of people, such as visual or auditory deterrents, as well as the use of guard animals, increases the real and perceived risk to the predator, thereby changing the “landscape of fear” (Fig. 1, b) for carnivores and reshaping their distribution and behavior (Laundre et al. 2010). Humans, and in some cases the guardian animals we employ, can thus fill the ecological role of apex predators with top-down effects on carnivores, initiating behaviorally mediated trophic cascades that ultimately reduce mortality among livestock (Frid and Dill 2002).

(c) Optimal foraging theory

Optimal foraging theory (Fig. 1, c) maintains that predators and prey alike balance foraging costs and opportunities to ultimately select food resources that provide the greatest net benefit for survival and reproduction (Brown et al. 1999). As mentioned above, livestock are generally a low-cost, high-reward prey item for large predators, at least where human involvement is low. Additionally, livestock are usually among the largest prey items on a given landscape and in good physical condition due to food provisioning, offering a high caloric reward. Further, fenced or corralled animals are in predictable locations, reducing the exploratory and locomotive energy costs to the carnivore.

Human interventions for protecting livestock alter the trade-offs associated with optimal foraging. For example, predator-proof fencing can create a higher energetic cost for carnivores seeking to hunt livestock. Deterrents that mimic human presence, such as noise or lighting (e.g., Foxlights) can produce a perception of greater risks for carnivores (Lesilau et al. 2018). By increasing the costs, real or perceived, of preying on livestock, a livestock manager can create suboptimal conditions for predation, and prompt a carnivore to switch to other, less costly alternatives.

(d) Apparent facilitation and apparent competition

Livestock managers may further alter the playing field for carnivore-livestock interactions by manipulating the local abundance of alternative wild prey. Recent research indicates that the relationship between wild prey availability and livestock predation is not always linear, and that in some situations the presence of wild prey reduce carnivore predation on livestock (Khorozyan et al. 2015). For example, bolstering wild prey populations to provide more wild prey for carnivore consumption can increase *apparent facilitation* (Fig. 1, d), by which carnivores consume more wild prey and fewer livestock when there are higher densities of preferred wild prey (Suryawanshi et al. 2017). In other situations, limiting the number of wild prey will reduce carnivore densities and accordingly decrease *apparent competition* (Fig. 1, d), by which higher wild prey densities lead to increases in carnivore densities and accordingly increases in predation on livestock. Understanding the ecology of a particular carnivore and its wild prey can help livestock managers anticipate ecological outcomes and set appropriate goals to minimize conflict.

(e) Predator-prey shell games and response races

Essential to understanding livestock-carnivore interactions are two connected bodies of theory. First, the *predator-prey shell games* theory (Fig. 1, e) posits that prey move through the landscape avoiding detection by carnivores by making their location unpredictable (Mitchell 2009). Simultaneously, *behavioral response race* models (Fig. 1, e) predict that the spatial distribution of prey reflects their effort to avoid encountering predators, whereas predators seek patches where they maximize their chance of finding prey (Sih 1984, Lima 2002, Laundre 2010). Thus, observed patterns of predation are the product of dynamic, adaptive feedbacks between predator and prey decisions, as each species responds to the other’s behavior. These two theories arguably may have limited predictive application in the context of livestock, because domesticated populations have reduced ability and opportunity to respond to predation risk (Laundre 2010). However, these behavioral theories can inform management, as human intervention can take on the ‘prey response’ role by manipulating livestock breed, group size, demographics, and distribution on a landscape (Minnie et al. 2015).

By understanding spatial and temporal patterns of predation and predicting how carnivores will respond to a given intervention, managers can take action to keep livestock “ahead in the game” (Lima 2002). Furthermore, these theories offer insight into how carnivore experience and memory may change predation dynamics. For example, if there are aversive stimuli accompanying interventions, carnivores may habituate and change their perceived cost of preying on livestock.

TYPOLOGY OF INTERVENTION TECHNIQUES

Most research to date describes methods for mitigating carnivore-livestock conflict by intervention type, rather than by underlying ecological mechanisms (Eklund et al. 2017, Moreira-Arce et al. 2018, van Eeden et al. 2018b). Here we link our ecological framework to previous literature on interventions by adapting the terminology established by Miller et al. (2016) to define different forms of intervention. Rather than categorize tools as lethal/non-lethal or proactive/reactive, which biases practitioner use and limits integration among interventions, our typology focuses on the connection between tools and ecological mechanisms, emphasizing the effectiveness of using different types of tools complementarily. In this typology, interventions generally fall into the following classifications: livestock management and ecology, carnivore deterrents, carnivore removal, and land and wild prey management. We link each of these classes to the ecological concepts described previously (Table 1).

Although each of the intervention groups within the typology is distinct, the ecological pathways underlying a particular tool can have components derived from one or more concepts. For example, the effectiveness and utility of carnivore deterrent and removal interventions are generally governed by carnivore ecology and manipulation of the predator’s landscape of fear. In contrast, livestock management and ecology interventions are driven by the interaction between livestock ecology and their biophysical landscape and situated within theories such as optimal foraging theory. Similarly, indirect land and wild prey management tools are an integration of livestock ecology, carnivore ecology, and management of the biophysical landscape.

We apply the typology and demonstrate the utility of our framework with three carnivore-livestock conflict case studies (Panels 1, 2, & 3), chosen to represent different species of carnivores in varying ecological and management systems. These cases provide explicit examples of the utility of the framework for choosing intervention tools as well as predicting and assessing the effectiveness of both lethal and non-lethal methods of predator control.

PANEL 1. SNOW LEOPARDS IN ASIA: COMMUNITY INTERVENTIONS AND PREDATOR-PROOF CORRALS

Snow leopards (*Panthera uncia*) occupy large territories in the upper elevations of the Himalayas and Central Asian plateau. Their territories often overlap with high-altitude grazing lands, resulting in conflict with pastoral communities. Livestock predation consists of opportunistic attacks and intentional forays into corrals, the latter of which often results in ‘surplus kills’ with high livestock mortality. In some locations snow leopards are largely dependent on livestock. For instance, domestic prey comprise 27% of snow leopard diet in Mongolia (Johansson et al. 2015). The annual economic impact of snow leopard predation on livestock ranges between 20-75% of a household’s annual income (Jackson et al. 2010). Livestock owners’ attempts to reduce livestock losses through retaliatory killing have contributed to snow leopard decline, and human-wildlife conflict is considered a top threat to the species (IUCN 2017).

Our framework highlights how four key interventions have reduced snow leopard predation on livestock by targeting diverse ecological drivers and mechanisms underlying conflict (see Fig. 3):

(1) *Rotational grazing practices:* The use of rotational grazing, traditionally followed by many pastoral communities, has increased wild prey abundance and distribution by allowing forage growth in pastures. Increasing the availability of wild prey has

encouraged snow leopards to switch from livestock to wild prey via apparent facilitation, decreasing the likelihood that they kill livestock (Mishra et al. 2003); although, as previously discussed, apparent competition may cause the opposite to occur in some situations (Suryawanshi et al. 2013, 2017).

(2) *Moving livestock from daytime pastures to night corrals:* Moving livestock from grazing pastures during the day to protected corrals at night reduces their vulnerability to attack (Johansson et al. 2015). By collecting and protecting livestock at night, this intervention alters the distribution of livestock and also increases the risk for leopards, and thereby the cost, associated with an attack.

(3) *Improved corral design:* More efficient corral designs protect livestock from nighttime attacks. In response to snow leopard attacks, herders added mesh wire roofs reinforced with wooden beams. This technique was especially effective at decreasing mass livestock mortality events, in which predators may kill as many as 100 livestock in one event (Jackson and Wangchuk 2001). This intervention can be understood ecologically as increasing the energetic cost and risk of livestock predation for a snow leopard.

(4) *Herding in lower-risk areas:* Improving herding practices by keeping livestock in sight at all times significantly reduced opportunistic attacks (Johansson et al. 2015). Likewise, grazing livestock in high-visibility areas reduces the accessibility of livestock to snow leopards. As with other interventions focused on livestock management, improved herding alters the distribution of livestock while increasing the risk associated with an attack for carnivores.

A combination of two or more of these interventions is likely to be most effective in reducing predation on livestock (Johansson et al. 2015). Notably, in this case study, all four interventions are directly targeted at the livestock ecology of the system but may work through multiple mechanisms to indirectly affect the biophysical environment and carnivore ecology, preventing livestock predation (Fig. 3). The use of interventions that target diverse mechanisms may have resulted in a suite of secondary benefits to the ecosystem, including fewer retaliatory killings of snow leopards (Jackson and Wangchuk 2004) and higher wild prey densities (Mishra et al. 2003).

PANEL 2. WOLVES IN IDAHO: HUMAN PRESENCE, DETERRENTS, AND LIVESTOCK GUARDIAN DOGS

The Wood River Valley in Idaho is home to the largest remaining sheep-grazing sectors in the state. During the grazing season (May-October), bands of 1,000-1,500 sheep are moved from the lower elevation sagebrush desert to higher forested areas following the vegetational green-up. After the U.S. Fish & Wildlife Service reintroduced gray wolves (*Canis lupus*) to central Idaho in 1995 and 1996, wolf populations expanded their range from remote wilderness areas to working landscapes. Sheep are often grazed on public land (U.S. Forest Service and Bureau of Land Management allotments), within which grazing locations are chosen based on local forage quality. Wild ungulates simultaneously select for these conditions, increasing the chances that sheep and native prey will overlap, and that carnivores will seek out these locations as productive hunting grounds. The rocky terrain and steep topography of the region create challenging conditions for livestock operators to erect protective fencing, leaving sheep to range freely and further increasing the risk of wolf-sheep encounters.

In 2008, conservation organizations, ranchers, county commissioners, federal government agencies, and scientists came together to collaboratively implement non-lethal interventions for preventing wolf predation on sheep, forming the Wood River Wolf Project (WRWP). WRWP team members monitored numerous ecological factors – including wolf presence, grazing conditions, terrain, and available forage resources – to adaptively manage sheep activities using three interventions (see Fig. 4):

(1) *Increased human presence:* The WRWP increased human presence at temporary sheep bed-downs by employing human guards from dusk to dawn. This took advantage of wolves' natural wariness to humans and thus reshaped the carnivores' landscape of fear and resulted in them avoiding areas with sheep.

(2) *Animal husbandry and deterrents:* In locations in which wolves were highly active, WRWP technicians and herders applied non-lethal livestock management and carnivore deterrents, such as mobile fencing and flagging, strobing lights, noisemakers, and starter pistols. These interventions caused behaviorally mediated effects and influenced the predator-prey response race in the system by triggering wolves to shift their activities elsewhere. To prevent wolves from habituating to a given tool, each deterrent was restricted to a limited period of time.

(3) *Livestock guardian dogs:* Ranchers and herders were encouraged to assign at least three livestock guardian dogs to each sheep band. This intervention worked through behaviorally mediated effects by utilizing interspecific competition between the dogs and wolves to discourage the wolves from attacking sheep. Dogs were employed only during months when wolves did not have young pups (March to mid-June) to avoid prompting highly aggressive parenting instincts from local packs.

During the first seven years of these efforts, sheep losses to wolves were 90% lower in the study area where non-lethal methods were implemented compared to the area where they were not (Stone et al. 2017). In the study area, wolves predated only 0.02% of the total sheep present – the lowest rate among recolonized sheep-grazing areas in Idaho. In contrast to interventions to reduce snow leopard attacks (Panel 1), the interventions in this case study were mainly directed at factors related to carnivore ecology, and less directly affected the distribution and ecology of livestock (Fig. 4). One exception was the use of mobile fencing, a livestock husbandry technique which directly affected the location and protection of livestock on the landscape, while indirectly affecting carnivore behavior.

PANEL 3. COUGARS IN WASHINGTON STATE: LETHAL CONTROL

Between 2005 and 2010, Washington Department of Fish and Wildlife (WDFW) verified 19-42 cougar (*Puma concolor*) predation events per year on livestock and household pets. Sport hunting of adult cougars is permitted in Washington, and hunting of cougars is further permitted for landowners in response to predation of their livestock. Both of these policies represent efforts to establish legal, lethal population control measures for cougars in Washington, with the idea that fewer cougars will increase safety for domestic animals.

While lethal removal is designed to protect livestock, people, and pets from encounters with cougars, several studies have examined the effects of cougar removals and identified ecological drivers that could in fact exacerbate risks. A study of cougar population biology by Robinson et al. (2008) suggested that hunting cougars decreased the average age of independent males and increase the male to female ratio, possibly due to females leaving attractive ecological sinks in response to the threat of infanticide from younger immigrating males. In response to this hypothesis, Peebles et al. (2013) tested whether verified complaints and livestock predations decreased in the year following increased hunting of cougars. The authors demonstrated that the lethal population control approach did not account for immigration, a major factor in population biology. In particular, young male cougars immigrated twice the distance of females and dispersed regardless of natal population density (Robinson et al. 2008). Consequently, following periods of lethal population control, cougar populations shifted age and sex structure, becoming younger and more male-dominated even as habitat and livestock husbandry remained constant. Hunted areas thus were theorized to be "attractive sinks" for immigrating young males, which are the most likely age and sex class to prey on livestock (Torres et al. 1996). As a result, in the year following cougar hunting, verified complaints and livestock predations recorded by WDFW did not decrease, but rather *increased* at both the county (n=39) and Game Management Unit (n=139) levels.

A detailed understanding of the population and behavioral ecology of cougars helps identify the specific ecological mechanisms driving conflict. Without holistically considering the multiple ecological drivers underlying conflict and allowing for a suite of tools that address these drivers, interventions — both lethal and nonlethal — may not only fail to mitigate conflict but exacerbate risks by pulling the wrong ecological levers (Fig. 5). Though lethal intervention can be an effective management tool alone and/or in conjunction with non-lethal tools (Bradley et al. 2015), this case study is not unique. The hunting of carnivores for sport, population control, and conflict mitigation is prevalent around the world with mixed and sometimes counterintuitive consequences (Miller et al. 2016, Treves et al. 2016, Eklund et al. 2017, Moreira-Arce et al. 2018, van Eeden et al. 2018b).

OPERATIONALIZING THE FRAMEWORK

Livestock Managers

Understanding the ecological dynamics underlying livestock predation incidents can aid in more efficient and effective resource allocation and intervention strategies. Managers, who know their livestock operations intimately, can apply this framework to holistically understand the ecology picture of their operation and can adaptively determine which intervention tools to use, in which contexts, and for what purposes. Operationalizing this framework will be best achieved when managers target multiple ecological drivers and mechanisms and vary strategies to affect different pathways as time passes and as effectiveness of a particular intervention or set of interventions wanes.

Additionally, intervention tools are constantly being innovated. In 2017, WWF and WILDLABS implemented the first Human Wildlife Conflict Tech Challenge, in which competitors developed and field tested solutions to human-wildlife conflict (https://www.worldwildlife.org/press-releases/first-of-its-kind-tech-challenge-spurs-innovations-to-fight-human-wildlife-conflict). Some of the submissions included more effective electric fences and carnivore detection warning systems. To aid in grounding livestock protection measures in science and ecological context, managers can partner with cooperative extension specialists and researchers to pair the implementation of emerging techniques with evidence-based, systematic measures of effectiveness based in this ecological framework.

Future Research

The increasing overlap of carnivores and humans presents both an unprecedented need and opportunity for researchers to partner with livestock producers and wildlife managers to test interventions that promote coexistence. Such applied research is, by necessity, interdisciplinary and must be grounded in strong scientific inference to robustly test effectiveness (van Eeden et al. 2018a). For researchers, our framework provides a way to target specific research gaps that will aid in understanding livestock predation in a researcher's region of interest, and thus provide a clear pathway toward identifying the proper intervention tools for that context.

For example, this paper has identified that although many interventions target livestock ecology and carnivore ecology (Fig. 2; Panels 1, 2, & 3), the biophysical landscape has enormous influence on both of these actors (Fig. 2). It is thus critical to better understand the influence of the biophysical landscape on livestock predation and to determine potential intervention tools that target that landscape. African People and Wildlife's Living Walls intervention (Lichtenfeld et al. 2015), in which living *Commiphora* spp. are planted as livestock enclosure walls to replace traditional acacia bomas, is an example of a promising avenue for such research. Researchers could use remote sensing and other methods to quantify the effects of the Living Walls on surrounding acacia regeneration and browse availability, the potential role of Living Walls as microhabitat, and other effects on the biophysical landscape that may impact wild prey availability and carnivore distribution and behavior.

The potential for interdisciplinary insights to support effective mitigation of livestock-carnivore conflict appears promising. New online information-sharing platforms are being developed to encourage communication about research and provide usage tips on cutting-edge, science-based approaches between diverse stakeholders involved in management decision-making. EviWild (https://eviwild.slu.se), created by the Swedish Wildlife Damage, is a database where researchers can share evidence-based management strategies with practitioners. ENCOSH (http://encosh.org), created by the Human Initiative to Save Animals (HISA), is a participatory network for practitioners to share successful approaches and tips about living with wildlife. A mechanistic understanding of carnivore-livestock interactions, facilitated by the framework outlined in this article, could play an important role in these initiatives by informing the design of experimental tests of effectiveness that leverage and account for ecological relationships. For example, by studying carnivore behavior and physiology in a particular system, researchers can determine whether and how intervention tools should target the landscape of fear for the carnivore species in question, i.e., whether livestock guardian dogs, noisemakers, or fladry would make the most sense for the traits of a given carnivore species or individual. Knowing which mechanisms to study can thus lead researchers to provide useful, targeted information to managers. Future studies should build on the ideas developed here to explore how ecological frameworks can inform the mitigation of other forms of human-wildlife conflict, such as agricultural crop raiding by wild herbivores and wildlife attacks on people, as well as key components of conflict, such as human attitudes and socioeconomics.

CONCLUSIONS

The complex web of social and ecological factors underlying carnivore-livestock conflict has challenged efforts to devise efficient and effective solutions. In an effort to untangle some of the ecological complexity behind carnivore predation on livestock, we developed a framework linking common management interventions to the ecological mechanisms through which these interventions operate. Recognizing the linkages between management action and ecological outcome is vital to improve not only our mechanistic understanding of when, where, and how livestock predation occurs, but also to allow more targeted and effective application of tools grounded in the science of ecology. While traditional perspectives on carnivore-livestock conflict often considered management tools along axes of 'proactive to reactive' or 'lethal to non-lethal', our framework provides an alternative perspective that will help target the underlying causes of predation, thus enabling more effective implementation of conflict mitigation interventions. The case studies we provide offer material examples of how ecologically driven tools have been successful, as well as examples of failures when ecological mechanisms were ignored in devising interventions. We hope future efforts can refer to this framework to foster a common vocabulary across studies and mitigation efforts, and as a comprehensive yet accessible means to target specific interventions within the ecological context. By functionally linking the vast bodies of literature on the ecology of predation, the ecology and management of livestock, and the ecology of the biophysical landscape, we hope to open new avenues of research as well as help practitioners save time and money while reducing livestock losses.

ACKNOWLEDGEMENTS

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FIGURE 1. ECOLOGICAL FRAMEWORK TO CONTEXTUALIZE CARNIVORE-LIVESTOCK CONFLICT

Livestock predation is the result of ecological interactions between aspects of the biophysical landscape, carnivore ecology, and livestock ecology. Here, we draw on ecological concepts to describe these interactions, including (a) density-mediated trophic cascades; (b) landscape of fear for carnivores and behaviorally-mediated trophic cascades; (c) optimal foraging theory (as applies to carnivore-livestock interactions), which includes the real or perceived cost of hunting livestock; (d) apparent competition or apparent facilitation; and (e) predator-prey shell games and response races, including humans serving as the "response" on behalf of the livestock prey.

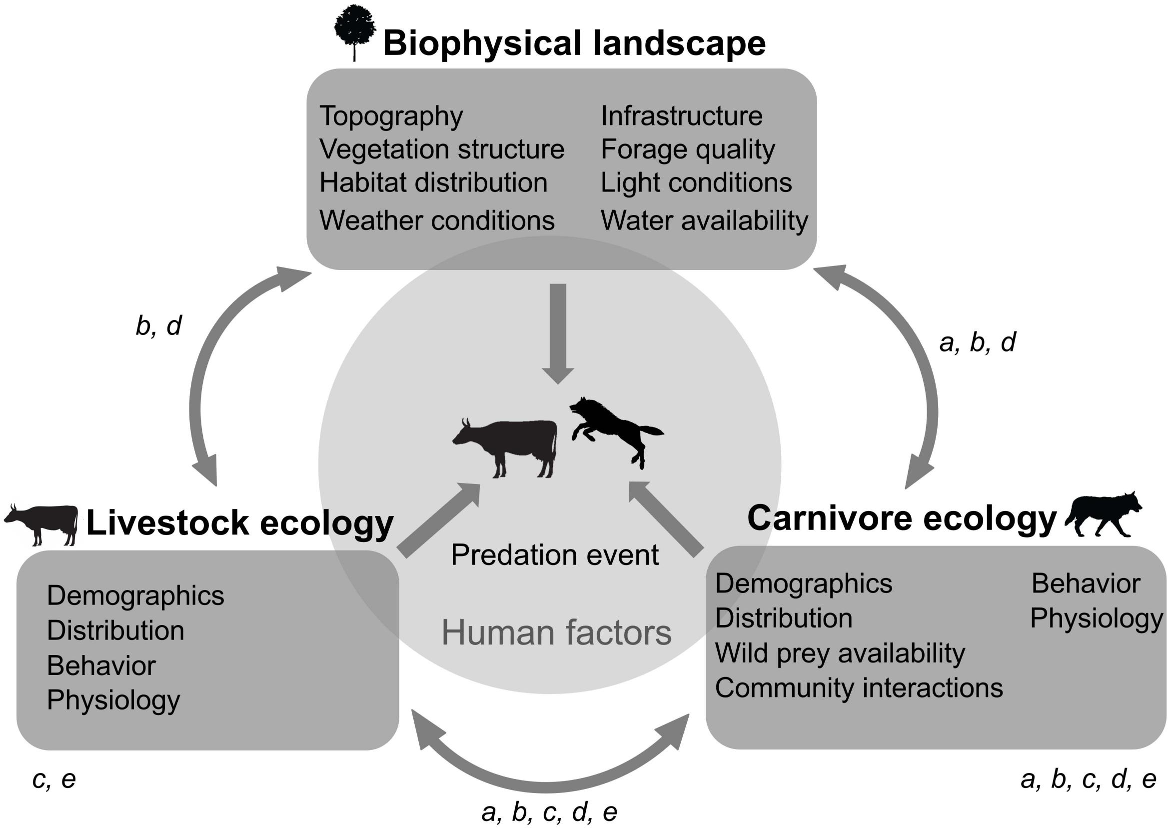

FIGURE 2. INTERACTIONS BETWEEN DRIVERS OF CARNIVORE-LIVESTOCK CONFLICT

Interactions between individual drivers of carnivore-livestock conflict, which are nested within broad categories of the biophysical landscape, livestock ecology, and carnivore ecology. Symbols next to the individual drivers represent the influence of one or more broad categories on that driver. An individual driver can be influenced by other drivers within and outside of its category.

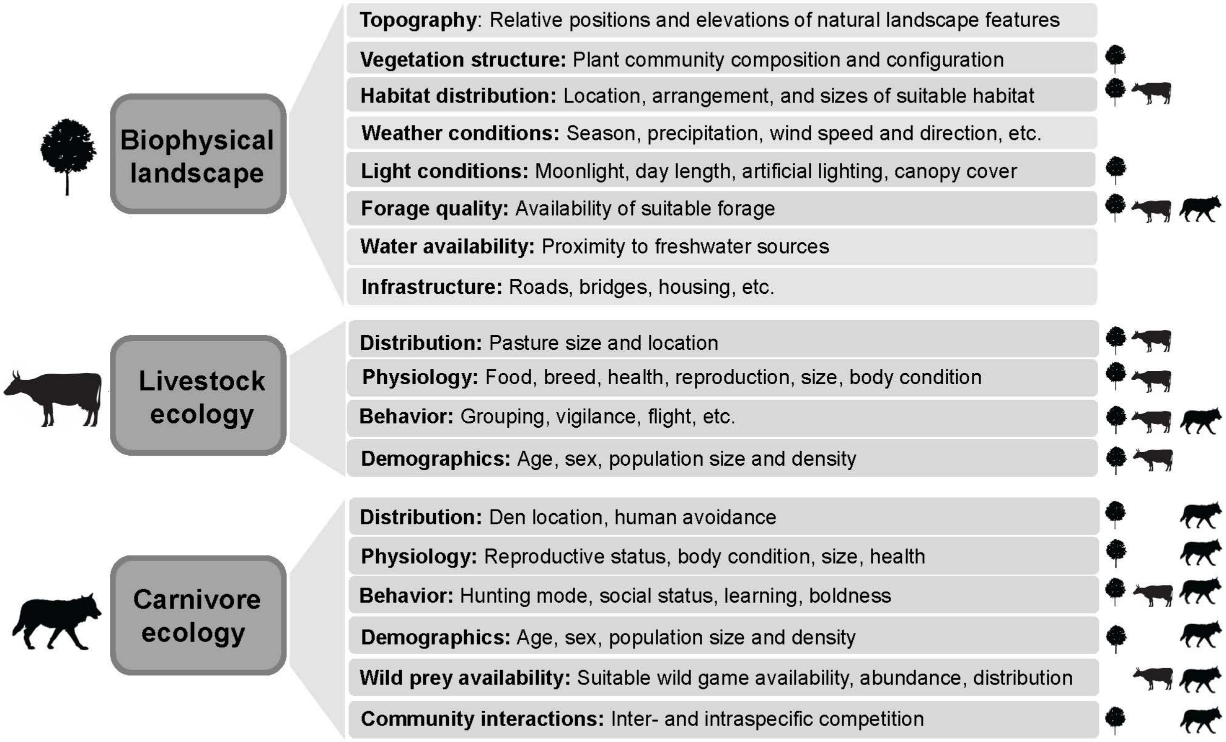

FIGURE 3. APPLYING THE FRAMEWORK TO SNOW LEOPARD PREDATION

Interventions applied to snow leopard predation on livestock in the Himalayas and Central Asian Plateau, contextualized in an ecological framework (panel 1). Arrows indicate pathways through which interventions operate. Small diamonds indicate mechanisms through which interventions operate. Rotational grazing, better-designed corrals, decreasing stragglers in daytime pastures, and avoiding grazing in low-visibility terrain all operate through (c) altering optimal foraging dynamics (as applies to carnivore-livestock interactions), by increasing the cost of hunting livestock for predators. Decreasing stragglers in daytime pastures and avoiding grazing in low visibility terrain also affect the dynamics of (e) predator-prey shell games and response races, with humans determining the predictability of prey locations in relation to habitat patch risk. Rotational grazing also (d) increases apparent facilitation by increasing the wild prey availability via increasing pasture available for wild prey.

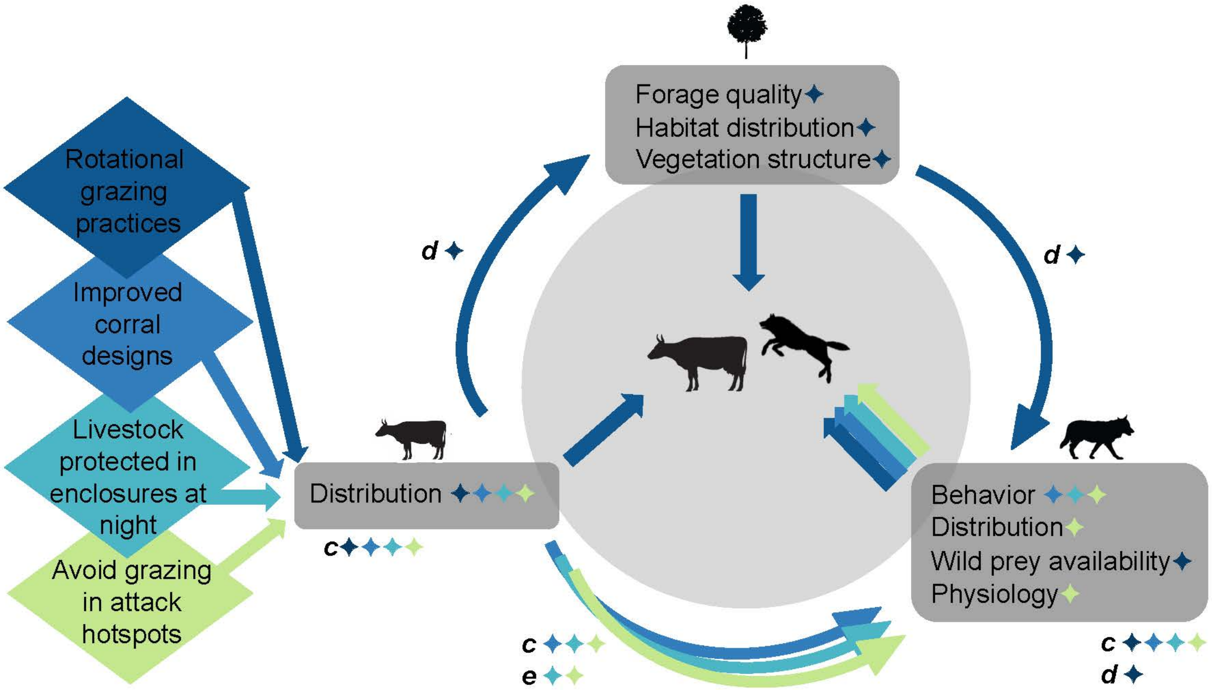

FIGURE 4. APPLYING THE FRAMEWORK TO WOLF PREDATION

Interventions applied to reduce wolf predation on sheep in Idaho, USA, contextualized in an ecological framework (panel 2). Arrows indicate pathways through which interventions operate. Small diamonds indicate mechanisms through which interventions operate. Increased human presence, livestock guardian dogs, and husbandry/deterrents all reshape (b) landscapes of fear for carnivores and behaviorally mediated trophic cascades – by influencing the fear and behavior of carnivores, and (c) optimal foraging– by influencing the cost of preying upon livestock. Husbandry/deterrents also change (e) predator-prey shell games and response races with humans as the adaptive prey response of livestock.

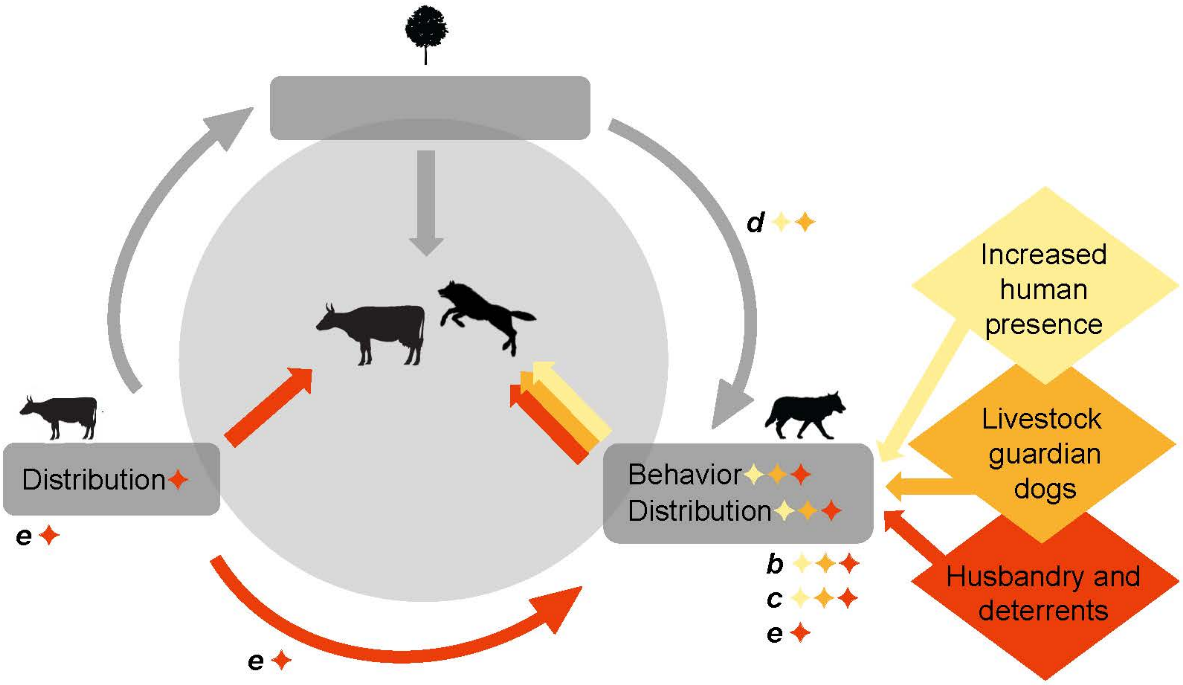

FIGURE 5. APPLYING THE FRAMEWORK TO COUGAR PREDATION

Human-cougar conflict in Washington, USA is primarily managed through lethal control of cougar populations (panel 3). This intervention can be understood ecologically as a manipulation of predator ecology, with little impact on prey or landscape ecology. Arrows indicate pathways through which population control operated. Small diamonds indicate mechanisms through which cougar population control operated. In this case study, direct cougar population control increased predation on livestock through (a) density mediated cascades which affected cougar behavior, distribution, and demographics.

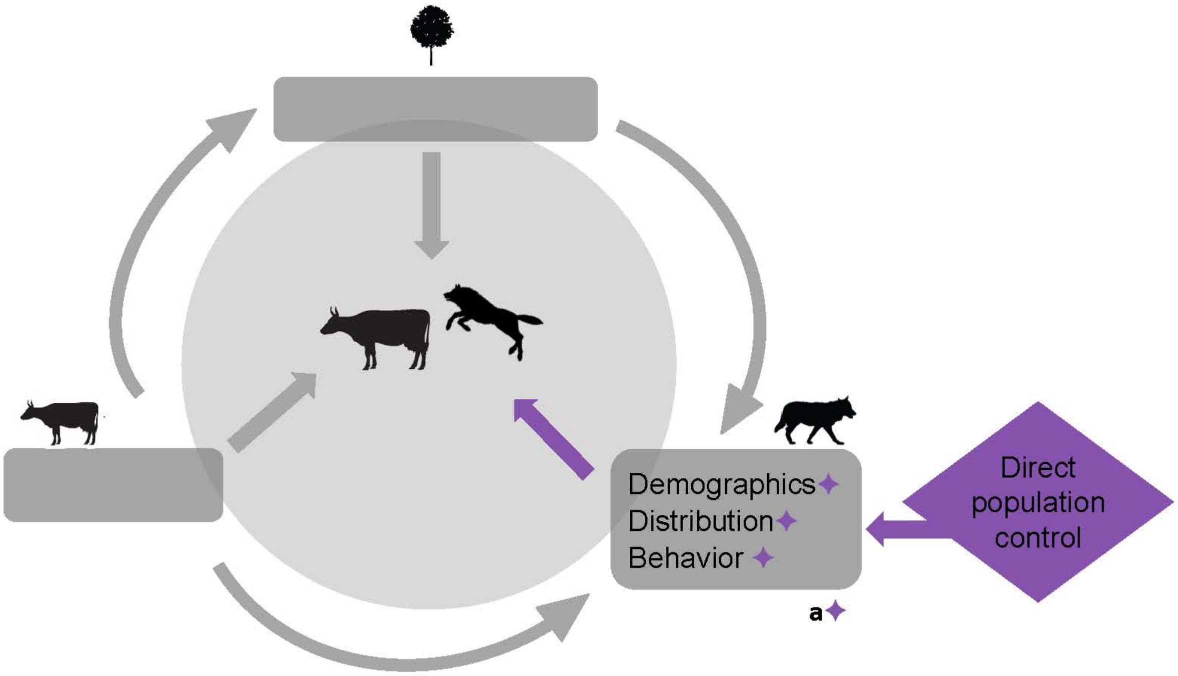

TABLE 1. TYPOLOGY OF LIVESTOCK-CARNIVORE INTERVENTION TECHNIQUES

A typology of livestock-carnivore conflict intervention techniques, linking specific tools with ecological concepts described by the framework.

Intervention Classification	Ecological category(s)	Description	Examples	Ecological concepts
Livestock management	Livestock ecology	Animal husbandry approaches governing livestock management and species/breed, as well as biological characteristics that influence space use and behavior of livestock	• Stocking rate[a] • Rotational grazing[b] • Breed selection[c] • Guarding[d,e,f,g] • Calving barns[h] • Livestock enclosures[g,i,j] • Space use[b,h] • Fencing[b,h]	• Optimal foraging theory • Prey switching • Landscape of fear • Predator-prey shell games and response races
Carnivore deterrent	Carnivore ecology	Physical objects and sensory stimuli that target and disrupt specific elements of carnivore behavior and/or ecology	• Guarding[d,e,f,g] • Fladry[k,l] • Flashing lights[m] • Audio recordings[m] • Chemical deterrents[n] • Turbo fladry[o]	• Landscape of fear • Behaviorally mediated trophic cascades • Habituation
Carnivore removal	Carnivore ecology	Techniques that reduce the number, or change the demographics, of carnivores in a given area.	• Hunting[p] • Targeted removal[q] • Translocation[r,s] • Sterilization/ contraception[b,t]	• Landscape of fear • Optimal foraging theory • Prey switching • Population ecology

Indirect land/ wild prey management	Biophysical environment Livestock ecology Carnivore ecology	Management approaches that separate carnivores and livestock by altering wild prey habitat use and behavior as well as and land management in and around the grazing area.	• Protected areas/buffer zones[u,v,w] • Restricted grazing[b] • Brush clearing[x] • Zoning for designated land use[y] • Habitat enhancement[z] • Fencing[b,h] • Prey hunting[z,aa] • Diversionary feeding[bb]	• Apparent competition/ apparent facilitation • Optimal foraging theory

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[a] Blaum et al. 2009; [b] Boitani & Powell 2012; [c] Landa et al. 1999; [d] Andelt 1992; [e] Woodroffe et al. 2007; [f] Gehring et al. 2011; [g] Rigg et al. 2011; [h] Pimenta et al. 2017; [i] Mazzoli et al. 2002; [j] Kolowski & Holekamp 2006; [k] Musiani et al. 2003; [l] Davidson-Nelson & Gehring 2010; [m] Shivik et al. 2003; [n] Smith et al. 2000; [o] Lance et al. 2011; [p] Wagner & Conover 1999; [q] Blejwas et al. 2002; [r] Bradley & Pletscher 2005; [s] Milligan et al. 2018; [t] Bromley & Gese 2001; [u] Rao et al. 2002; [v] Maddox 2003; [w] Linnell et al. 2005; [x] Bradley and Pletscher 2005; [y] Linnell et al. 2005; [z] Breitenmoser et al. 2005; [aa] Linnell et al. 2012; [bb] Kavcic et al. 2013

Chapter 3. Examining drivers of divergence in recorded and perceived human-carnivore conflict hotspots by integrating participatory and ecological data

ABSTRACT

Human-carnivore conflict is a global challenge with complex and context-specific causes and consequences. While spatial analyses can use ecological principles to predict patterns of conflict, solutions to mitigate conflict must also be locally adaptable, sustainable, and culturally-sensitive. In Nakuru County, Kenya, rapid development and land subdivision have exacerbated conflict by isolating wildlife in protected areas that are increasingly adjacent to human settlements. In an effort to understand local perspectives on carnivore conflict, and to apply this information towards locally based conservations actions, we conducted gender-stratified interviews and participatory mapping sessions with 378 people in 16 villages near two ecologically isolated protected areas in Kenya: Lake Nakuru National Park and Soysambu Conservancy. Specifically, we developed a method for associating interview responses and demographic information with spatial participatory data to examine how local perceptions of conflict compared to spatially-explicit records of livestock depredation in the region from 2010-2018. We mapped kernel densities of recorded and perceived risk of human-carnivore conflict and then tested for potential social and ecological predictors of divergences found between the two datasets. Mismatched hotspots of observed and perceived risk of conflict were correlated with several ecological and socioeconomic factors. Regions with higher NDVI exhibited more perceived conflict, while the opposite held true for verified conflict. Road density was positively correlated with both types of conflict, and both types of conflict increased closer to protected areas. Livestock ownership, visitation to Lake Nakuru National Park, if the participant's child walked to school, and male gender identity were associated with more perceived conflict reports. Education level and national park visitation were associated with more positive attitudes toward carnivores. Our results show that while observed and perceived conflict may ultimately be equally important for understanding and managing human-carnivore conflict, they may be driven by markedly different social and ecological processes. We suggest that integrating the spatially explicit experiences and perspectives of local communities with more traditional ecological methods is critical to identifying lasting and socially just forms of conflict mitigation.

INTRODUCTION

Human-carnivore conflict (HCC) is a primary driver of large carnivore declines globally (Ripple et al., 2014) and creates a significant challenge to rural livelihoods in many areas (Muhly and Musiani, 2009). For example, in the United States, over $168 million in livestock losses per year are attributed to depredation by carnivores (USDA, 2020). Livelihood impacts of HCC are most pronounced in regions where carnivore populations remain viable or have recovered, and where marginal incomes place producers near poverty (Dickman et al., 2011). Along with affecting livelihoods, human-wildlife conflict is known to have a number of indirect social and emotional impacts on affected communities, such as diminished psychological wellbeing and food insecurity (Barua et al., 2013). Conflicts between people and carnivores are exacerbated by a combination of sociopolitical factors (e.g., regional livelihoods, poverty, global wildlife policies; Treves and Karanth 2003) and local histories of people's relationships with wildlife (e.g., Megaze et al. 2017), as well as increased development that has intensified habitat fragmentation and human-wildlife interactions (Were et al. 2013, Weldemichel and Lein 2019).

Conservation biologists lean heavily on an understanding of ecology when researching and managing human-carnivore conflict (Wilkinson et al. 2020). In recent years, there has been considerable momentum behind using ecological data in combination with innovative spatial tools for addressing conflict using scientific evidence (Miller, 2015, Miller and Schmitz 2019). Predation risk mapping, for example, layers verified conflict events across ecological (e.g., habitat structure and productivity) and anthropogenic (e.g., human infrastructure and activity) variables in order to overcome HCC's inherent context-dependency, and to anticipate future carnivore conflict (e.g., Broekhuis et al. 2017). For instance, in arid ecosystems, conflict has been observed to increase in the rainy season when wildlife are not reliant on permanent water bodies and are able to disperse widely (Koziarski et al. 2016). Yet, in fenced arid ecosystems, wildlife transgressions of fences to exit protected areas may be higher in the dry season (Kesch et al. 2015), possibly because seasonal vegetation resources are more limited within fenced ecosystems than in unfenced ecosystems (Bartzke et al. 2018). Thus, HCC in different regions with varying human development may exhibit measurable, context-specific, and spatially-explicit patterns across key ecological variables. Additionally, anthropogenic structures and activity have altered wildlife behavior and ecology around the globe at numerous scales (Gaynor et al. 2018, McInturff et al. 2020), and may be consequential covariates when mapping carnivore conflicts with people. Risk mapping and other spatial methods have thus proven to be highly useful tools for quantifying correlates of verified conflict and employing ecological theory to create targeted mitigation strategies that address HCC (Melzheimer et al. 2020).

While global increases in HCC are regularly studied by examining the associations between ecological covariates and verified on-the-ground conflict reports, there is increasing understanding that the perception of risk held by local communities may more meaningfully predict their attitudes towards carnivores and their retaliatory or preventative actions (Dickman et al. 2014). Though interactions between wildlife and humans are situated within a broad range of social, institutional, and ecological landscapes, a key element of any human-carnivore interaction is human behavior (Lischka et al. 2018). Behavior of people when interacting with wildlife is, among other factors, driven by emotion, experience, and resulting attitudes and perceptions (Carter et al. 2012a), making human emotions and perceptions critical for understanding and resolving HCC.

A number of studies have acknowledged that perceptions of conflict can diverge from ecological findings and yet still provide tangible contributions to conservation efforts (Siex and Struhsaker 1999, Dickman et al. 2014). Some of these have employed surveys to better understand the drivers of people's perceptions of conflict in space and time (e.g., Holmern et al. 2007). These studies and others suggest the most important observed social drivers of HCC perception, realization, and management outcomes among stakeholders are gender, education level, livestock ownership and adoption of tools for guarding livestock, and visitation and access to nearby protected areas (Tessema et al. 2010, Knopff et al. 2016, Mkonyi et al. 2017). For example, men and women may have different motivations, goals, and risk perceptions regarding human-wildlife conflict and management (Gore and Kahler 2012), and women may bear disproportionate burdens of conflict due to gendered relations of space and identity (Ogra 2008). Additionally, education level may influence attitudes toward wildlife and conservation (Akama et al. 1995, Megaze et al. 2017), and may also be an indicator of modernization, which is hypothesized to increase positive attitudes toward carnivore conservation (Bruskotter et al. 2017).

Livestock ownership also plays a potentially major role in perceptions of conflict since livestock owners are most likely to fear predation's impact on their livelihoods. These same stakeholders may be more likely to discuss conflict history or their perceptions of risk with neighbors (Kellert 1985), which can contribute to spreading of perceived risks (Dickman et al. 2014). Relatedly, the adoption of common interventions designed to reduce carnivore conflicts (such as fladry, lights, noisemakers, etc.; van Eeden et al. 2018) may also impact people's perceptions of carnivore, conflict, and risk (Eklund et al. 2020). Number of livestock owned (Hemson et al. 2009) as well as number of children or family size (Khumalo and Yung 2015), may also be indicators of financial precarity that influence conflict risk perceptions. Finally, national park visitation, as both a means of ecological education and connection to wildlife living on the landscape, may have the potential to affect community members' understanding of and thus reaction to carnivores (Espinosa and Jacobson 2012, Mkonyi et al. 2017). These social factors can be as critical as ecological variables when understanding and predicting patterns of HCC across different landscapes.

While these and other socioeconomic factors help predict local perceptions of conflict, the application of information on perceptions to structure and implement programs HCC is rare (Lozano et al. 2019). Moreover, the participatory methodologies necessary to assess and apply human perceptions are scarce in human-wildlife conflict research (Gray et al. 2020). This is despite the known importance of considering spatial, ecological, and social variables together for long-term conflict mitigation (White et al. 2009), and the common acknowledgement that conservation conflicts are best managed when science and solutions are co-created with affected communities (Redpath et al. 2013, Treves et al. 2009). In fact, examples abound of cases where a lack of participatory and integrative approaches have contributed to ineffective, short-lived, and/or unjust solutions to conflict (Meguro and Inoue 2011, Eklund et al. 2020). For targeted and effective outreach and management of HCC, we need to address this disconnect by working toward an understanding of how and why verified and perceived HCCs diverge (Dickman 2010), as well as how conflict risk perceptions cluster spatially and are driven by various social and ecological factors (Bruskotter and Wilson 2014).

We sought to bridge this gap by using a unique combination of verified conflict reports and participatory perception data to answer the following questions: 1) How do verified and locally perceived carnivore conflict compare spatially?, 2) How are similarities and differences in the two datasets correlated with ecological variables and infrastructure?, and 3) Are there social predictors (e.g., demographics, livestock ownership, and attitudes toward carnivores) of the level and distribution of perceived carnivore conflict? We examined these questions in the region surrounding Lake Nakuru National Park and Soysambu Conservancy in the Rift Valley of Kenya. This location provided an ideal system for this study because of its high rate of human immigration and land subdivision, and the resulting proximity of wildlife to people, human activities, and infrastructure (Kassilly et al. 2008, Mubea and Menz 2012, Wilkinson et al. 2021). We predicted 1) that verified and perceived conflict would exhibit observable spatial differences, and 2) that these disparities would be driven by a variety of ecological factors, such as season, vegetation, road density, and distance to protected areas, as well as social factors, such as participant education level, gender, livestock ownership and activities, and national park visitation (Table 1).

METHODS

Study site

We conducted our study in Nakuru County, in the Rift Valley, southwest Kenya (Figure 1) from June 2018-March 2019. The study area (~500km^2, 0°26' S, 36°1' E) includes two major wildlife protected areas: Lake Nakuru National Park (LNNP, 188 km^2), which is one of two fully fenced national parks in Kenya, and Soysambu Conservancy (190 km^2), which is semi-fenced and functions simultaneously as a wildlife conservancy and a livestock ranch with over 10,000 cattle, sheep, and goats. The two large alkaline lakes in the region, Lake Nakuru and Lake Elmenteita, are designated UNESCO World Heritage sites. The region supports many species of large mammals, including threatened and endangered species such as black rhinoceros (*Diceros bicornis*) and Rothschild's giraffe (*Giraffa camelopardalis rothschildi*); large carnivore species, such as African lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), and leopard (*Panthera pardus*); and several mesocarnivore species, such as serval (*Leptailurus serval*) and black-backed jackal (*Lupulella mesomelas*). Many carnivore populations in the region (both inside and outside of protected areas) are stable or increasing despite heavy historical persecution (Ogutu et al. 2017).

Outside of protected areas, the Nakuru-Elmenteita watershed is home to dense human populations, with considerable immigration into the region. Small-scale agriculture and pastoralism, as well as increased urbanization, are common in the settled areas surrounding LNNP and Soysambu Conservancy, and there is a mix of ethnic representation (mostly Kikuyu, Kalenjin, and Maasai). Nakuru town, which is directly adjacent to the northern border of LNNP, is home to an estimated 570,674 people (Kenya National Bureau of Statistics 2019) and is considered to be one of the fastest growing cities in East Africa. In many places throughout the study area, human settlements directly abut the conservancy and park boundaries.

Participatory data

Data collection

In order to gather community perspectives on carnivores and conflict, we selected 16 sub-villages, within 5 broader village areas, located within 5km of the protected area boundaries (Figure 1). Though participatory mapping is subject to inherent logistical, access, and scalability limitations (Brown 2012), we addressed these challenges in a number of ways through iterative pre-testing and sampling considerations. Because the study area was large and many of the households were unmapped, we used semi-random heterogeneity sampling (Blankertz 1998) to identify 378 participants (180 women, 198 men) for participatory mapping and interview sessions. Participants were informed a) they could leave mapping and interview sessions at any time, b) that participation in the exercise was not mandatory, and c) that compensation was not provided. To reduce bias in responses, participants were informed that the interviewers and facilitators were students, and that the students held no direct authority in addressing human-wildlife conflict issues.

For each participatory mapping session, we aimed for 12 participants, with no more than 6 participants drawing on a single map (for legibility purposes). However, this wasn't always feasible, as the mapping sessions were popular and occasionally drew crowds. Thus, in a few circumstances, up to 8 participants drew on a single map. Mapping sessions were gender-stratified, with men and women gathering on different days to encourage open conversation and a broad range of perspectives (Pfeiffer and Butz 2005).

Each interviewee's session began with a short (~10 minutes) one-on-one interview, with a Kenyan master's student serving as an interviewer, using the application Open Data Kit (ODK; https://getodk.org/), carried out on Android devices (Motorola Moto E). Interviews were conducted in English or Kiswahili, depending on the interviewee's preference. Information gathered included demographic data, risk perceptions about carnivores, attitudes toward carnivores and carnivore conservation, livestock ownership, experience with carnivore-livestock conflict, educational experience, national park visitation, and employment (Appendix 1), with a combination of multiple choice, check all that apply, numerical, and open-ended questions. Prior to the interview, each participant was assigned a unique pen color for the day. During the initial interview, a photo was taken of their pen within the ODK application. This allowed us to associate a participant's spatial data with their interview data while maintaining anonymity.

For the participatory mapping portion of the sessions, paper maps were developed and printed using *Field Papers* (www.FieldPapers.org). Field Papers is an open source tool to print base maps that can be annotated in the field and then scanned, allowing annotation to be digitized into a GIS database. During the sessions, participants were first given a minimum of 15 minutes of map orientation, though these orientation exercises and conversations often lasted longer than 30 minutes. Participants were encouraged to teach one another by using laminated, highly detailed atlases of the region, and finding locations of interest to the community such as the national park, particular intersections, Nakuru town, and village centers. We asked participants to use the assigned pens and paper maps we provided to draw their answers to 24 general questions regarding places of importance, livestock predation, carnivore presence, desired carnivore conservation and movement, risk perceptions regarding carnivores, and other factors (Appendix 1). For each question on each map, a unique (to that map) symbol (falling into the categories of point, line, or polygon) was requested. Participants were encouraged to draw on top of one another's symbols as needed.

Participatory data preparation

To digitize maps, participatory maps were photographed, and a QR code allowed the map images to be georeferenced directly using FieldPapers.org. Georeferenced map images were then uploaded into ArcGIS Pro (Version 2.5) in order to trace each question's spatial responses (points, lines or polygons) into GIS layers, with each layer representing the collected answers to one question. During the digitization process, pen colors on each session's maps were again cross-referenced with photographs of pen colors that had been automatically labeled with each interview's unique identification number. These identification numbers were assigned to each feature in each layer's attribute table. Interview data were then joined with attribute tables for each layer, and each question's layers were subsequently merged into a single master layer that included data from all sessions for that question.

Verified conflict data

Human-carnivore conflict (HCC) data for 2008-2018 were provided by the Kenya Wildlife Service. The dataset contains HCC incidents (such as carnivore attacks on livestock and threats to people) reported to the Nakuru Community Wildlife Service (CWS) station. The station houses trained rangers who respond to conflict issues and also undertake community outreach around the park and adjacent localities within the county. Conflict cases are reported by the local community through a dedicated telephone hotline or the institutional call center, both of which are open 24 hours a day. Once a conflict report is received at the station, a CWS team is dispatched to verify. The details of the nature of each conflict are collected by the rangers and later recorded in an occurrence book. The information collected includes the date, location name, conflict species, the nature of the conflict, and the management action taken. Data recorded in the occurrence book are later entered into a database at the station. We obtained these verified conflict data from the main human-wildlife conflict database and georeferenced each record to the approximate village or sub-village level using landmarks and location names provided in the original dataset. While this dataset consisted of historical records of conflict which were initially collected solely for monitoring purposes (see Easterday et al. 2018), the data were cleaned and georeferenced points were iteratively verified with Kenya Wildlife Service staff prior to analysis.

Spatial explanatory variables for conflict reports

The ecological and anthropogenic spatial covariates that we tested as predictors of conflict reports included distance to protected area, road density (kernel density, per km^2), mean vegetation greenness (as measured by NDVI- normalized difference vegetation index, via Landsat 8, for 2018), and slope (via Shuttle Radar Topography Mission, 30m).

Data Analysis

Summary and comparison of verified and perceived conflict

To determine spatial differences between the verified and perceived datasets, we used ArcGIS Pro to conduct kernel density estimations (KDE) for the entire verified conflict and perceived conflict datasets, respectively. From the KDE analyses (search radius = 3km) we created difference maps comparing the verified and perceived datasets across all stratifications by subtracting the verified conflict KDE from the perceived conflict KDE. We thresholded difference maps to the upper and lower quantiles to determine areas of highest disagreement among the two datasets, and conducted generalized linear regressions to assess perceived and verified conflict density in relation to distance to protected area, road density, NDVI, and slope.

Correlates of local clustering of perceived conflict

In order to determine whether people with positive attitudes toward carnivores and who guard their livestock nonetheless exhibited significant clustering in their perceived carnivore conflict reports, we first used global logistic regressions to identify predictors (Table S1) of 1) attitudes toward carnivores and 2) nighttime livestock guarding behavior. We then employed a geographically weighted logistic regression (GWLR; Brunsdon et al. 1996) to test for local clustering. The initial regressions revealed a best-supported model (AUC = .805) that included the following variables to retain for GWLR: cow ownership, sheep or goat (hereafter *shoat*) ownership, whether the participant collected water in the evening (i.e. landscape traversal at night), number of reasons reported for hyenas to be conserved, belief that hyenas have access to too few wild prey, and perceptions of carnivore-related threats to children on their way to school (Table 2).

Trends in verified conflict reports

We used linear regression to test for trends in HCC reports over time for each carnivore species, for each livestock species and for humans, and for all carnivore species in aggregate using *R* (R Core Team 2018). For all non-spatial analyses, verified conflict data from 2013 were excluded because reports were only recorded for one month of that year.

Predictors of perceived conflict/risk and attitudes toward carnivores

To determine correlates of perceptions, we assessed the correlates of two variables: perceived carnivore conflict and attitudes toward spotted hyenas. As a widely reviled carnivore species in sub-Saharan Africa (Glickman, 1995), and as one of the most populous and visible carnivores in this region (Wilkinson et al., *In Press*), spotted hyenas served as the best proxy for examining what drives differences in attitudes toward conflict-prone carnivores among Nakuru County residents. Pair-wise analyses were conducted for all relevant explanatory variables (age, education, national park visitation by participant, national park visitation by participant's child, livestock ownership, whether participant actively guards livestock at night, number of livestock owned). To determine whether perceived carnivore conflict or attitudes could be predicted using these variables, a logistic regression was then run for each dependent variable across all explanatory variables. After eliminating any collinear variables, we used the *dredge* function in the *MuMin* package in *R* to conduct model selection, and retained model variables within 2 delta AIC of the top model for model averaging (Burnham and Anderson 2002). To test the robustness of the top model, we bootstrapped a calculation of the area under the receiver operating characteristics curve (AUC; Pearce and Ferrier 2000). We randomly split the data into 20% testing and 80% training data, and calculated AUC using the *performance* function in the *ROCR* package. AUC values below 0.7 were considered poor, values between 0.7-0.8 were considered acceptable, and values greater than 0.8 were considered good or excellent (Hosmer and Lemeshow 2000).

Finally, to assess underlying values and beliefs that may lead to positive or negative attitudes toward carnivores, we conducted descriptive statistics and pairwise analyses of responses to follow-up questions in which we had asked people to describe why they did or did not believe spotted hyena conservation was important (see Appendix 1).

RESULTS

Spatial patterns of verified and perceived carnivore conflict

Overall patterns and correlates

Verified and perceived conflict reports exhibited marked differences in spatial distribution and density. Kernel density estimates revealed a maximum of 3.34 verified and 3.44 perceived conflict reports per km^2 within the study area (Figures 2a, 2b). The difference map ($KDE_{perceived}$ - $KDE_{verfied}$) showed a maximum of 3.02, and a minimum of -3.44, with a mean difference of .044, meaning differences in the mapped reports across the study area skewed slightly toward perceived conflict. However, the minimum indicated a region on the map where there were no perceived conflict reports at all (Figure 2c).

KDE analyses exhibited 198.88 km^2 of high divergence (quantified as first [-3.44 to -0.444] and eighth [0.709 to 3.02] quantiles of difference) between the two datasets: 87.02 km^2 (~9.8% of the KDE study extent) skewing toward perceived conflict, and 111.856 km^2 (~12.6%

of the study area) skewing toward verified conflict (Figure 2a). Within these areas of maximum divergence, mean NDVI for the lower quantile (i.e. areas skewed toward verified conflict) was 0.283 (σ=.038), while mean NDVI for areas skewed toward perceived conflict was 0.316 (σ=.015). NDVI was positively correlated with perceived conflict kernel density ($\beta = 0.477$, $p < 0.01$), and negatively correlated with verified conflict kernel density ($\beta = -0.413$, $p < 0.01$). Mean road density within areas of maximum divergence was 2.46 ($\sigma = 1.113$) for areas skewed toward perceived conflict, and 2.23 ($\sigma = 0.341$) for areas skewed toward verified conflict. Road density was positively correlated with both perceived ($\beta = 0.115$, $p < 0.001$) and verified ($\beta = 0.103$, $p < 0.001$) conflict density. Distance to protected area was strongly negatively correlated with perceived ($\beta = -13.327$, $p < 0.001$) and verified ($\beta = -13.794$, $p < 0.001$) conflict, while slope showed a slight negative correlation with both perceived ($\beta = -0.009$, $p < 0.05$) and verified ($\beta = -0.016$, $p < 0.001$) conflict.

Correlates of local clustering of perceived conflict

Those engaged in nighttime guarding of cattle did not differ from others in their spatial perceptions of HCC hotspots (Figure 3a), but geographically weighted logistic regression revealed local clusters (Figures 3b, 3c). GWLR results indicated that positive attitudes toward hyenas and beliefs that wild prey was scarce correlated with local clusters of perceived conflict that were reported despite guarding behavior (Figures 3b, 3c).

Those who reported positive attitudes toward spotted hyenas similarly did not exhibit marked clustering in their perceptions of HCC hotspots. Similar to the guarding behavior results, GWLR revealed that park visitation, perceptions of carnivore-related threats to children, and nighttime livestock guarding correlated with varying local clusters of perceived conflict reports in relation to attitudes (Figure 4).

Trends in verified conflict reports

There was an upward trend in overall verified conflict reports over time, but it was nonsignificant ($\beta = 0.6818$, $p = 0.74$) (Figure 5a). Carnivore species exhibited different trends over time: there was a slight downward trend in proportion of conflicts attributed to leopards ($\beta = -0.0399$, $p < 0.01$), an upward trend in the proportion of conflicts attributed to servals ($\beta = 0.0189$, $p < 0.01$), as well as nonsignificant upward trends in proportion of conflicts attributed to spotted hyena ($\beta = 0.0091$, $p = 0.428$) and lion ($\beta = 0.0119$, $p = 0.331$) (Figure 5b). As far as livestock attacked, verified conflict reports concerning sheep ($\beta = -0.0145$, $p < 0.05$), and dogs ($\beta = -0.0129$, $p < 0.05$) decreased over time (Figure 5c). A higher number of verified conflict reports were reported during the dry season, but this result was nonsignificant (Suppl. Fig 1).

Predictors of perceived conflict/risk and attitudes toward carnivores

Gender and national park visitation were the strongest predictors of the number of conflict reports (Table 3). Pairwise analyses showed that livestock owners who have more children were less likely to indicate more perceived livestock attacks on the map ($\beta = -0.101$, $p < 0.05$). Livestock owners with a higher education level were slightly more likely to report more conflict events on the map ($\beta = 0.157$, $p < 0.01$). On average, men reported higher numbers ($\bar{x} = 1.725$) of perceived livestock attacks than women reported ($\bar{x} = 1.13$, $p = 0.001$). Unexpectedly, participants who had visited the national park were likely to report more perceived livestock attacks ($\bar{x}=1.41$) than participants who had not visited the park ($\bar{x}=.82$, $p= 0.001$). If a participant guarded their livestock at night, they reported slightly fewer livestock attacks ($\bar{x} = 1.289$ livestock attacks) than those who did not actively guard their livestock at night ($\bar{x} = 1.484$), though the result showed low significance ($p = .064$).

When asked whether they feared risks to children from carnivores on their children's way to school, people who actively guard their livestock at night ($X^2 = 6.1274$, $p <0.05$) or whose children walk to school [which is 86.2% of participants who had children] ($X^2 = 4.3355$, $p < 0.05$) were more likely to perceive risks to children. Carnivore species feared as risks to children were spotted hyena (34.4% of participants), leopard (33.9%), lion (27.5%), and black-backed jackal (20.1%).

Attitudes toward carnivore conservation

Main predictors of attitudes

Education, national park visitation, and whether participants guarded their livestock at night were the strongest predictors of attitudes toward carnivore conservation (Table 4), with 70.8% of participants believing that spotted hyenas should be conserved. According to pairwise analyses on attitudes toward spotted hyena conservation (as a proxy for carnivore conservation more generally), if a participant had visited the national park, they were more likely to have positive views of hyena conservation than if they had not visited the park (Fisher test, two-sided, $p < 0.001$; Figure 6a). Additionally, if a participant's child had visited the park, they were more likely to have positive views of hyena conservation (Fisher test, two-sided, $p = 0.001$). This was true despite 82 participants in the latter group (i.e., 44% of the 186 participants with children who have visited the national park) never having visited the national park themselves. Attitudes toward hyena conservation were also more likely to be positive with increasing education level ($\beta = 0.3241$, $p < 0.001$; Figure 6b), and for livestock-owning participants who actively guard their livestock at night (Fisher test, two-sided, $p < 0.01$).

If a participant owned any species of livestock, they were less likely to believe hyenas should be conserved (Fisher test, two-sided, $p = 0.01$). Participants who self-identified as farmers and herders for their primary livelihood (Fisher test, two-sided, $p < 0.01$), or said their children face risks from carnivores on the way to school (Fisher test, two-sided, $p = 0.01$), were also considerably less likely to report positive attitudes toward hyena conservation. Participants who owned at least one shoat in particular were significantly less likely to believe hyenas should be conserved ($\beta = -0.322$, $p < 0.01$), and cattle owners followed the same pattern ($\beta = -0.5011$, $p < 0.01$).

Reasons for positive and negative attitudes toward hyena conservation

Participants who said it was important for spotted hyenas to be conserved believed this due to ecotourism (83.3%), ecological reasons (43.2%), cultural reasons (15.2%), or other reasons such as for children to view in the future ("For the next generation"), or because hyenas were created by God ("They are God's creatures"). Participants who said it was not important for spotted hyenas to be conserved largely believed this due to the species' role in livestock attacks (89%), attacks on people (38%), or belief that hyenas are a bad omen (11%).

Of participants who supported hyena conservation, if the participant was older ($\beta = -0.2003$, $p< 0.01$), owned higher numbers of cattle ($\beta = -0.3439$, $p < 0.05$), or owned higher numbers of shoats ($\beta = -0.2372$, $p < 0.05$), they were less likely to say that ecotourism money was the reason to conserve spotted hyenas. Women ($X^2 = 4.1778$, df = 1, $p < 0.05$), participants with higher education levels ($\beta = 0.2279$, $p < 0.001$), and participants whose children had visited the national park ($X^2 = 7.9898$, df = 2, $p < 0.05$) were more likely to report ecotourism money as a reason to conserve spotted hyenas.

Meanwhile, participants who had visited the national park were more likely to report ecological reasons to justify why it was important to conserve spotted hyenas ($X^2 = 4.637$, df = 1, $p < 0.05$), as were participants with higher education levels ($\beta = 0.1351$, $p < 0.05$).

DISCUSSION

This study used a uniquely interdisciplinary dataset to advance our understanding of the social and ecological drivers of human-wildlife conflict. Our analyses provided three main conclusions: 1) verified and perceived conflict exhibit quantifiably different spatial patterns, 2) information from verified conflict reports may be tied to anthropogenic ecosystem changes, and 3) park visitation, education level, and gender may be strong predictors of risk perceptions and attitudes toward carnivores and can thus serve as conservation targets or mechanisms for managers in conjunction with spatial information.

Mismatch in perceived and verified conflict

There were clear spatial differences between the perceived and verified conflict datasets. Areas of mismatch between verified and perceived conflict density comprised approximately 20% of the conflict study area, with clear local regions where conflict skewed toward perceived or skewed toward verified. Though the effect was slim, NDVI was positively correlated with perceived conflict and negatively with verified conflict. This could be due to overinflation of perceived conflict in highly vegetated regions that carnivores could be more likely to use as habitat (e.g. Kolowski and Holekamp 2006, Broekhuis et al. 2017).

Road density, meanwhile, was positively correlated with both verified and perceived conflict. This could be because where there are people, there are more roads, and in this region human population density is increasing due to a boom in immigration (Were et al. 2013). Because wildlife in this densely developed area are likely more nocturnal (Gaynor et al. 2018), people are likely experiencing carnivore conflicts at night near their homes (Ugarte et al. 2019), rather than during the day while animals are out to pasture in open or less road-dense areas. However, there is also broader literature showing that isolation of people from nocturnal animal activity may reduce conflict (e.g., Carter et al. 2012b), so further research is needed in this area. As we consider carnivore management in increasingly human-dominated landscapes, it is important to take into account how human activity and infrastructure is correlated with concentrations of conflict risk (e.g., Said et al. 2016), and translate these findings into thoughtful conservation-friendly infrastructure development.

While many people in our study reported using tools for nighttime livestock protection, livestock guarding was not a significant predictor of spatial patterns of perceived conflict. This aligns with our understanding that many HCC interventions are implemented without evidence of their effectiveness (Moreira-Arce et al. 2018). However, people's beliefs about two factors - wild prey availability and carnivore-related threats to children - correlated with spatial patterns of perceived conflict that was reported despite guarding efforts. Similarly, spatial trends of perceived conflict and their correlates were evident for regions where people still perceived livestock depredations despite their positive attitudes toward carnivores. These analyses can help us to understand not only what might compel people to overreport conflict, but also which regions to target for locally-specific drivers of conflict.

Trends in verified conflict

Verified human-carnivore conflict reports in Nakuru County exhibited several trends that ran counter to our predictions and may be a result of anthropogenic ecosystem change. For instance, seasonality was not a strong predictor of verified conflict, though the verified reports skewed slightly toward the dry season. This runs counter to a common belief that wildlife are able to disperse more widely during the rainy season in arid ecosystems (Koziarski et al. 2016), but correlates with reports of wildlife leaving fenced protected areas more frequently in the dry season (Kesch et al. 2016, Wilkinson et al. 2021).

Despite being one of the most abundant carnivore species in the region, black-backed jackals were not reported in the verified dataset. This result matched with the perceived data regarding participants' fears of carnivore-related threats to children on their way to school; jackals were the species least likely to be feared by participants. However, jackals are known to prey on vulnerable young livestock (Kamler et al. 2012), and have been seen doing so in this particular study area (C.E.W. observation). Additionally, verified reports attributed to serval increased while leopard reports decreased. Because of the rapid development and deforestation in the region over the past decade (Mubea and Menz 2012), it is possible that this trend evidence of mesopredator release following declines in leopard populations (Prugh et al. 2009). Future research on HCC should look more deeply into ecological and social drivers of observed trends in verified reports to better inform conflict management and to provide insight into broader ecological trends in conflict-prone regions.

Predictors of perceived conflict, perceived risk, and attitudes

Visitation to Lake Nakuru National Park was one of the strongest predictors of lower perceived conflict, less perceived risk, and positive attitudes toward carnivores. This held true even if the participant themselves hadn't visited but their child had. Educational efforts regarding conservation are known for being frequently touted, but rarely evaluated. Our results could be an important data point regarding the effectiveness of environmental education in communities dealing with conflict. This result is especially surprising given the intense immigration into the region. It is possible that visitation to the national park can drive formation of a "sense of place"—or connection to the environment in this region—and thus a stronger connection to wildlife. Sense of place (Hausmann et al. 2016) is solidified when people are young, which could be influencing the strength of the effect of children's national park visitation. Importantly, domestic tourism is not only important for connecting people with their protected areas, but is also one of many ways to address sub-Saharan Africa's over-reliance on international tourism which is subject to collapse during stochastic events such as COVID-19 (Lindsey et al. 2020). Kenya and other countries with similar reliance on tourism revenue could take these results as another benefit to enhancing their domestic tourism infrastructure to make protected areas more accessible to its citizens, particularly the local communities living near conservation areas (Sindiga 1996, Okello et al. 2012).

While national park visitation could be influencing people's wildlife-related knowledge, formal education level was arguably the strongest predictor in our perceived conflict and attitude models. Our results show that having any amount of primary school education made a participant more likely to have positive views toward carnivores, and less likely to report perceived risk of livestock conflict. This aligns with other studies that have found education levels to be linked with positive attitudes and reduced risk perceptions regarding carnivores (Knopff et al. 2016, Koziarski et al. 2016). However, nearly 15% of our participants reported having received no schooling, which could be due to the lack of compulsory education during the schooling years of older participants (whereas now basic education in Kenya is compulsory and free), or in part due to school accessibility and transportation. In this region, some primary and secondary students are known to walk long distances to attend school (C.E.W. observation). Education is an avenue for learning about the environment and perhaps changing attitudes toward wildlife. The strong link we see between education and perceptions of carnivores and conflict may be an additional compelling argument for increasing access to basic education and conservation awareness programs where communities are sharing landscapes with carnivores.

Lastly, across education levels and park visitation rates, gender played an important role in predicting the nature of perceptions and attitudes. For instance, women were more likely to voice that money from ecotourism was an important reason to conserve spotted hyenas. This could be because in many parts of sub-Saharan Africa, women serve as crucial links from the community to the national parks and reserves through selling handmade crafts and food to tourists (Twining-Ward et al. 2018). In fact, women participants in this study often enthusiastically reported they would "benefit from wildlife if we were able to sell our [goods] to tourists", even if they hadn't yet had the opportunity to do so. Notably, women also reported fewer perceived conflicts than men (i.e. less likely to overreport, and/or differences in daily experiences; Gore and Kahler 2012), which could further reflect their importance as a specific demographic to target for co-created conflict solutions.

CONCLUSION

Human-carnivore conflict is a global challenge that is influenced by synergistic ecological and social dynamics. This study quantified differences in verified and perceived conflict and identified predictors of those differences. Despite the high levels of perceived conflict reported by interviewees, participants had largely positive attitudes toward carnivore conservation, even though there has been increased immigration into the region and a considerable subset of our interviewees were not long-term residents. Previous research has shown that the longer a person resides in the area, the more positively they feel toward certain species of large carnivores (Mkonyi et al. 2017), but our findings demonstrate more nuance in this than originally thought.

We were able to explore complexity in patterns of conflict using spatial analyses to understand where verified and conflict datasets diverge, what socioecological factors might predict spatial patterning in conflict reports, and which correlates of perceived conflict are more important in particular local regions. While the question of the exact mechanisms by which the social variables affect attitudes about carnivore conservation is beyond the scope of this study, our results provide empirical evidence to reinforce the understanding that working with communities to explore these mismatches can promote socially just and sustainable management of human-carnivore conflicts (Redpath et al. 2013). Additionally, our findings highlight the fact that land subdivision, fragmentation, and fencing within the landscape should be addressed through inclusive spatial planning to avoid exacerbating conflicts while supporting conservation measures and local community livelihoods (Said et al. 2016). Future research on human-carnivore conflict in developing landscapes should recognize that incorporating participatory methods and social science with ecological data is critical for inclusivity in addressing longstanding conservation conflicts and preventing the emergence of new ones (Weldemichel and Lein 2019).

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FIGURE 1. MAP OF THE STUDY AREA

Map of the study area, including villages surveyed.

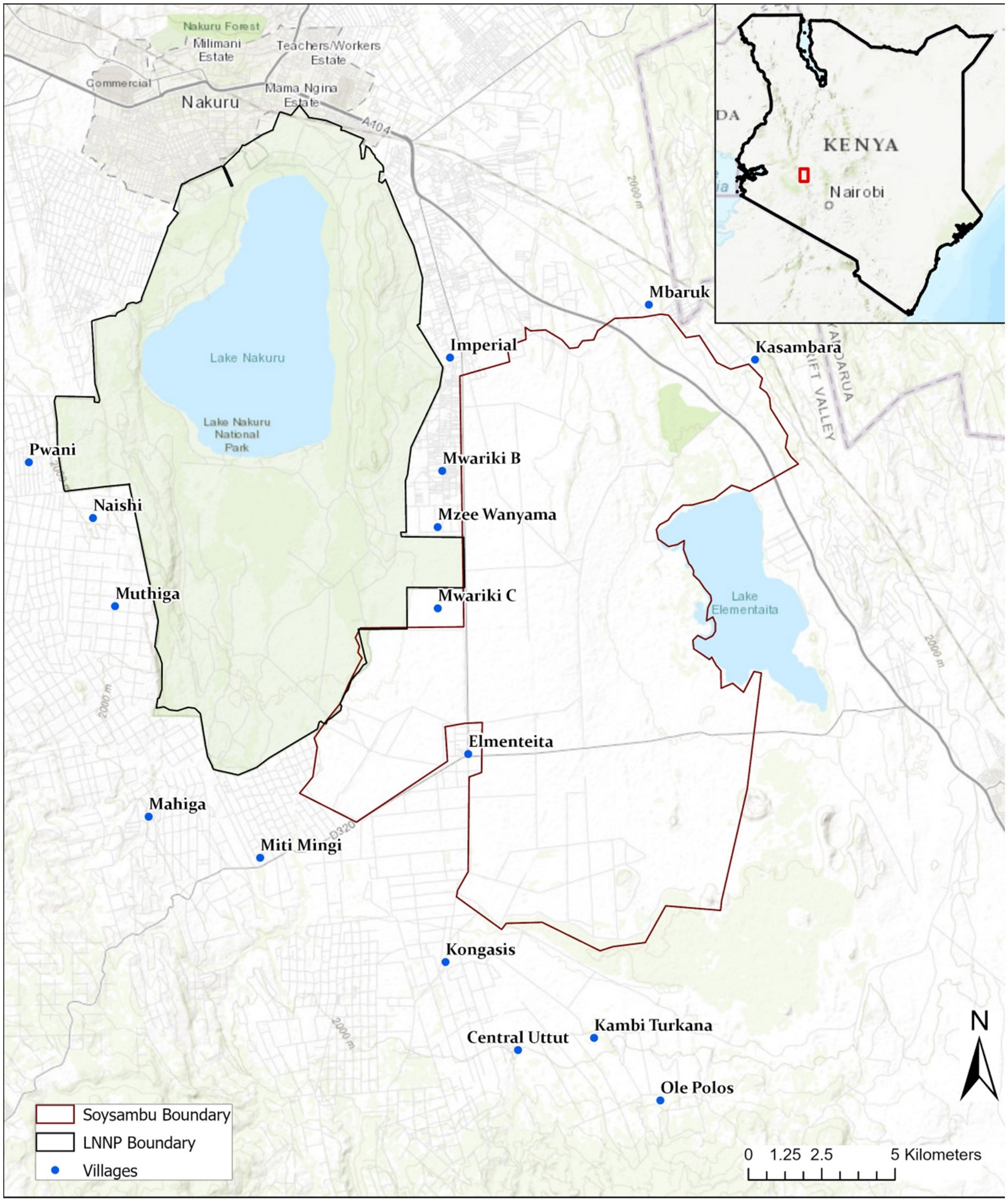


FIGURE 2. DIFFERENCES IN VERIFIED AND PERCEIVED CONFLICT REPORTS

Kernel density estimates of a) perceived and b) verified conflict reports, and c) difference map showing $\text{KDE}_{\text{perceived}}$ - $\text{KDE}_{\text{verfied}}$.

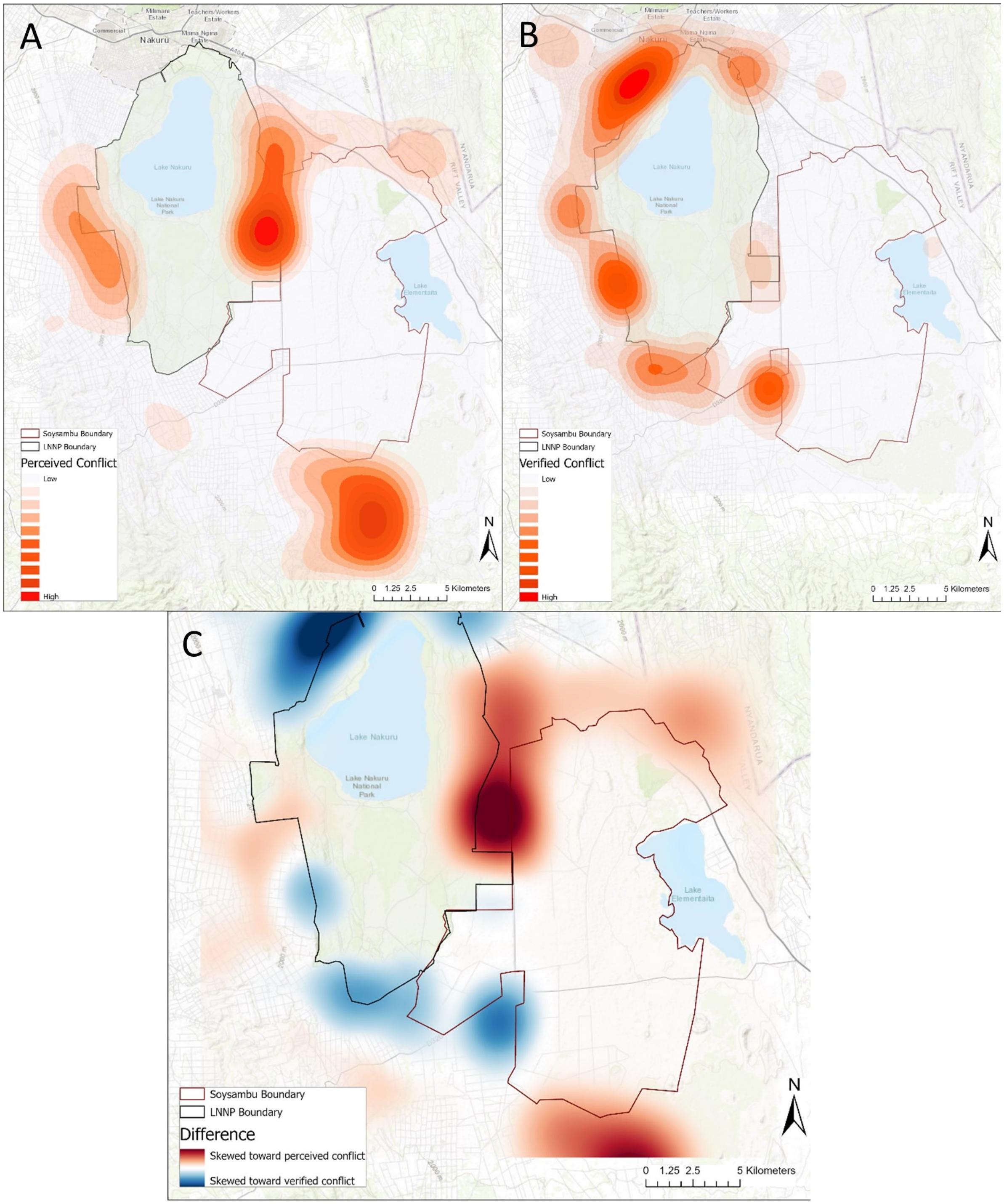


FIGURE 3. GEOGRAPHICALLY WEIGHTED LOGISTIC REGRESSION AND NIGHTTIME LIVESTOCK GUARDING

A) Perceived livestock reports color-coded by whether participant engaged in nighttime livestock guarding behavior, and geographically weighted logistic regression coefficients for clusters correlated with b) belief that wild prey for hyenas is scarce, and c) number of reasons participant believes spotted hyenas should be conserved, in relation to nighttime guarding behavior across locations of perceived livestock conflict.

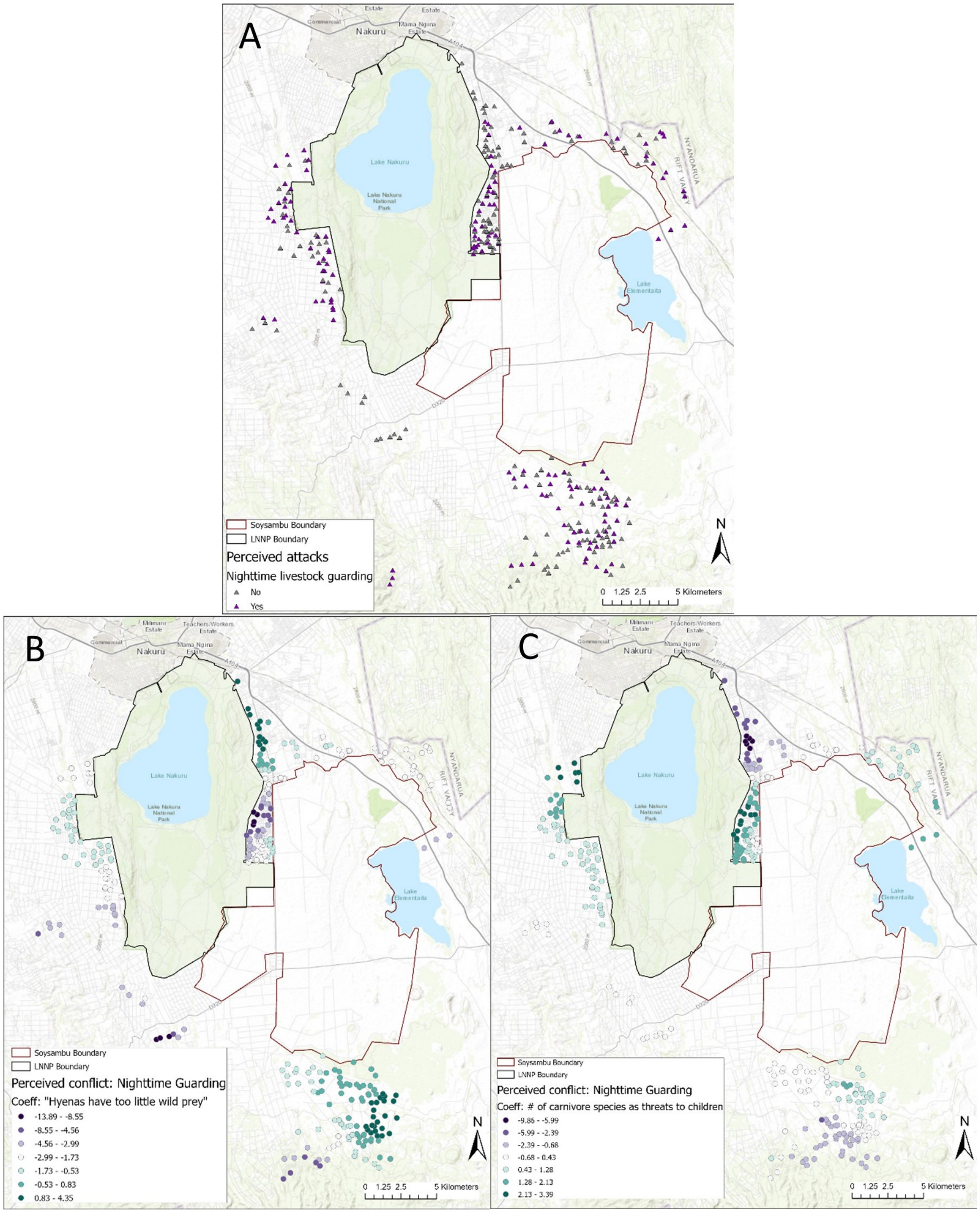


FIGURE 4. GEOGRAPHICALLY WEIGHTED LOGISTIC REGRESSION AND NATIONAL PARK VISITATION

Geographically weighted logistic regression coefficients for clusters correlated with a) national park visitation by participant, b) national park visitation by participant's child(ren), c) whether participant perceives carnivore-related threats to their children on their way to school, and d) nighttime livestock guarding, in relation to attitudes toward carnivores across locations of perceived livestock predation.

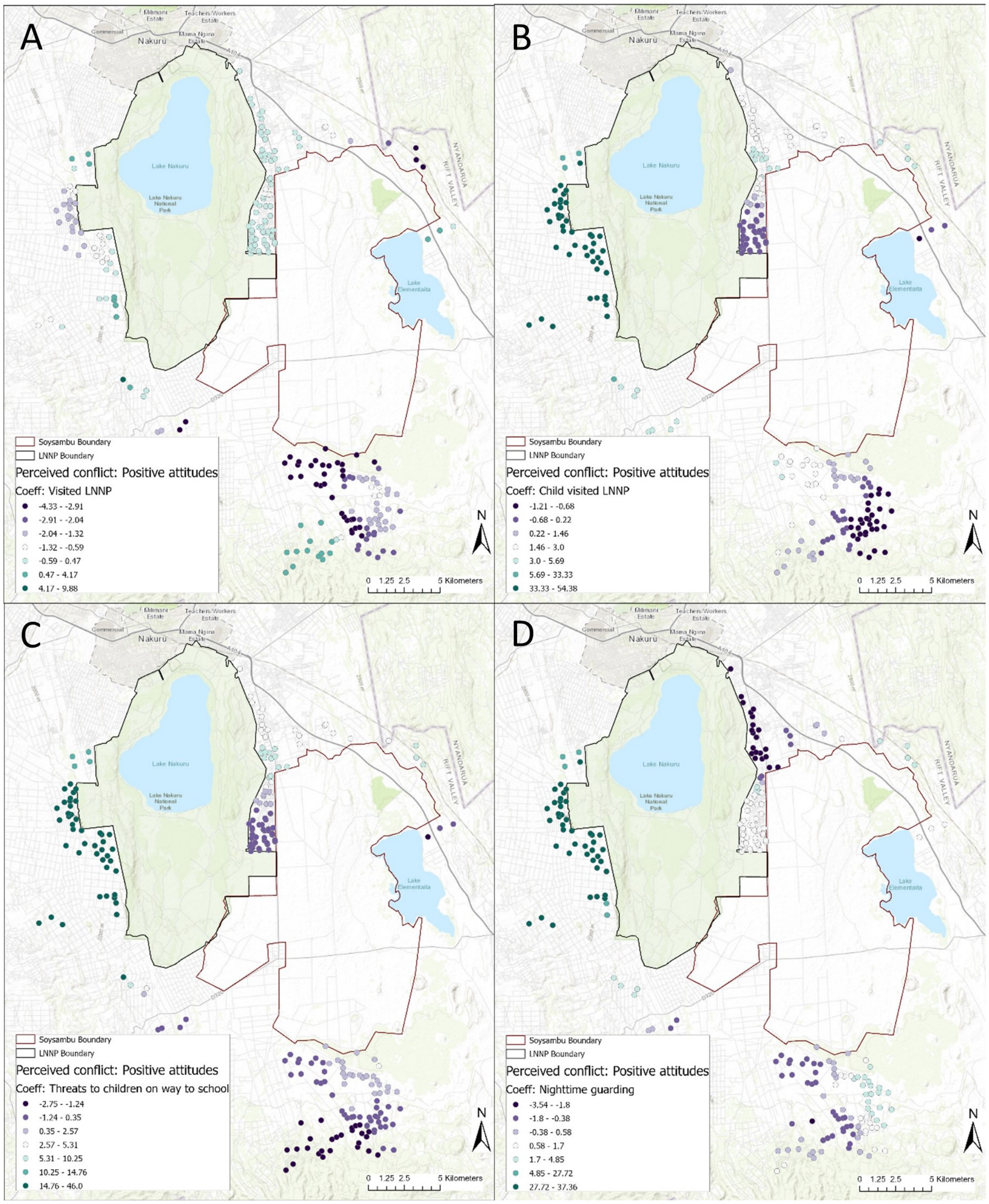


FIGURE 5. ATTITUDES TOWARD SPOTTED HYENA CONSERVATION

A) Frequency of participants answering the following questions: 1) Do you actively guard your livestock at night? , 2) Have you ever visited Lake Nakuru National Park, and 3) Do you think it is important to conserve the spotted hyena? Livestock guarding (p<0.01) and park visitation (p<0.001) were two of the most significant predictors of attitudes toward spotted hyenas. B) Proportion of participants with varying education levels answering the question "do you think it is important to conserve the spotted hyena?"

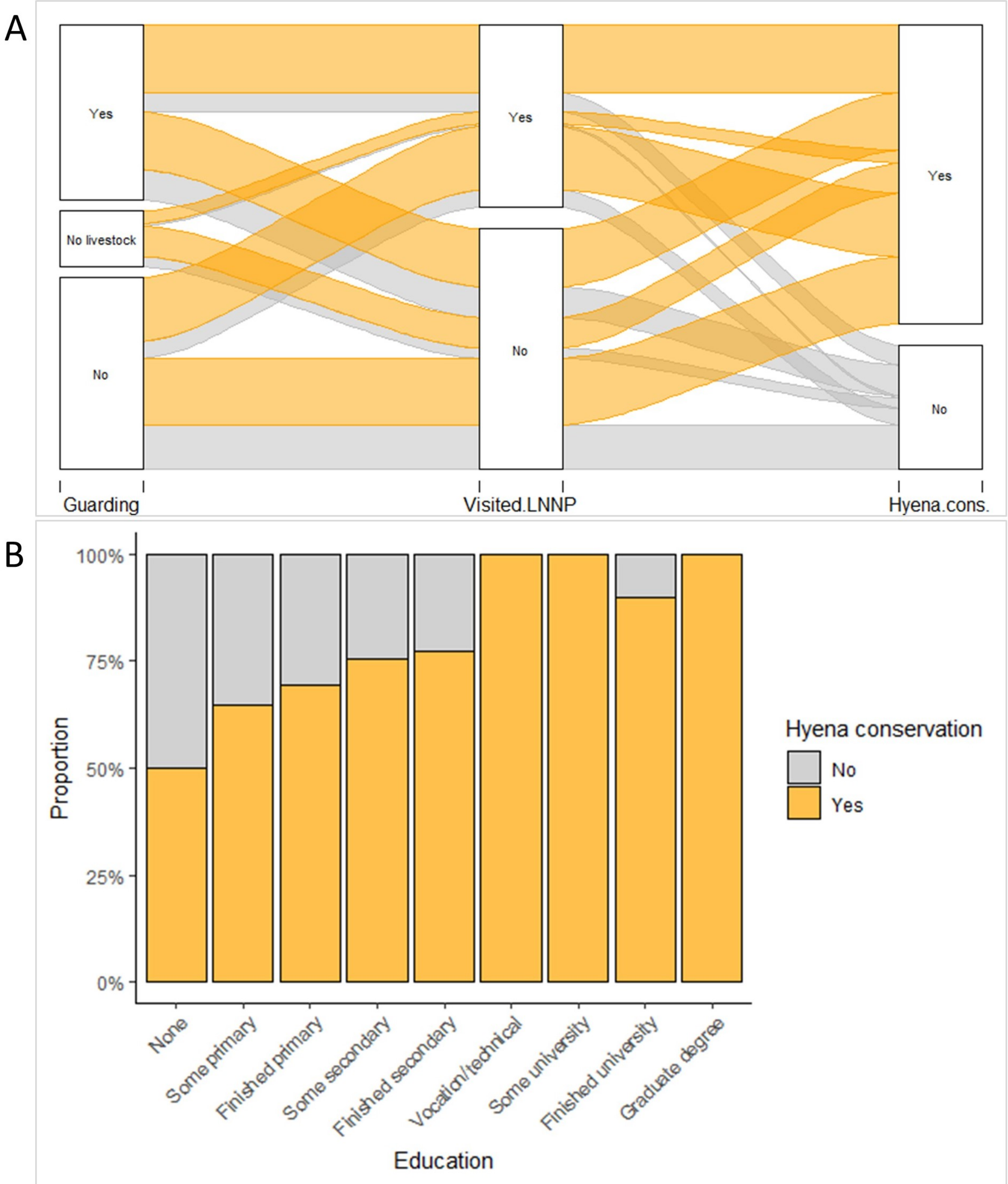


FIGURE 6. TRENDS IN VERIFIED CONFLICT REPORTS

A) Total verified conflict reports, b) relative proportions of carnivore species reported over time, and c) relative proportions of reports regarding threats to livestock or humans over time for Nakuru County.

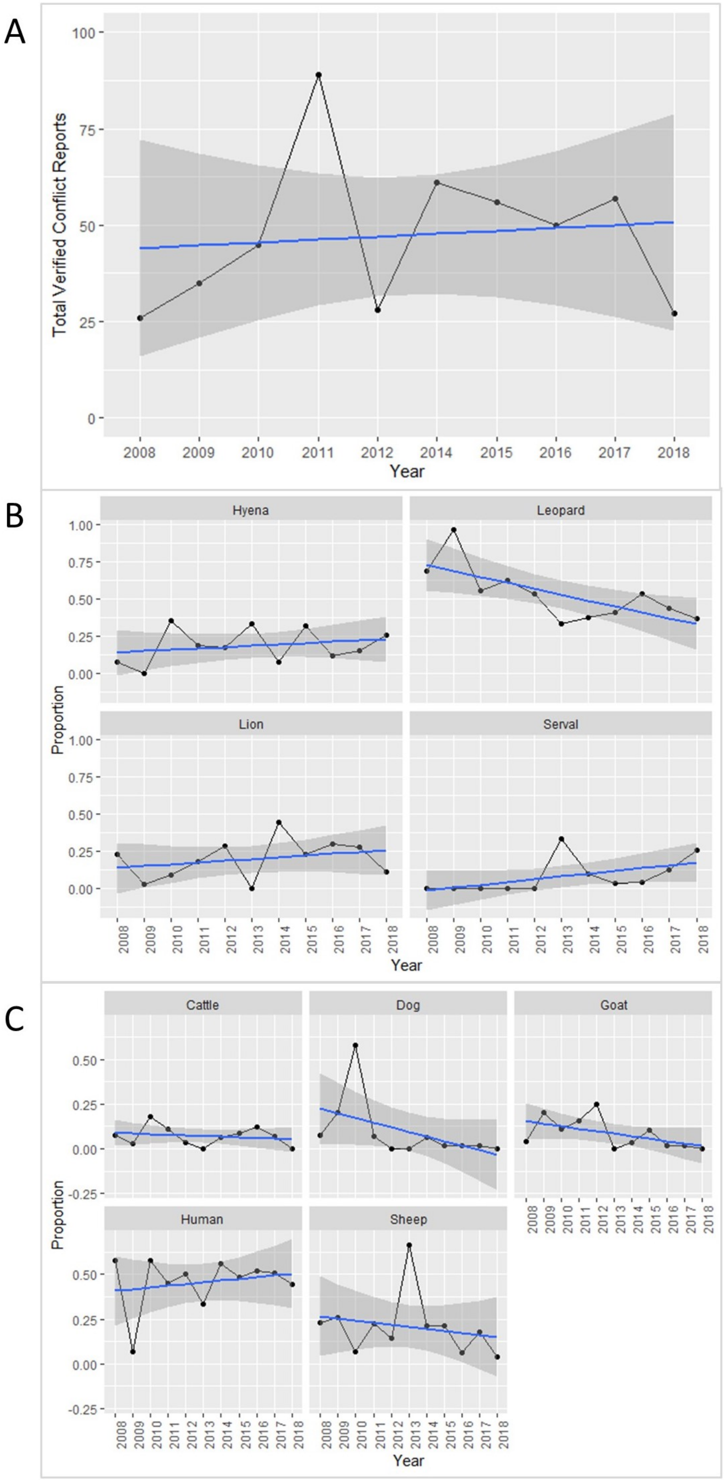


TABLE 1. HYPOTHESES

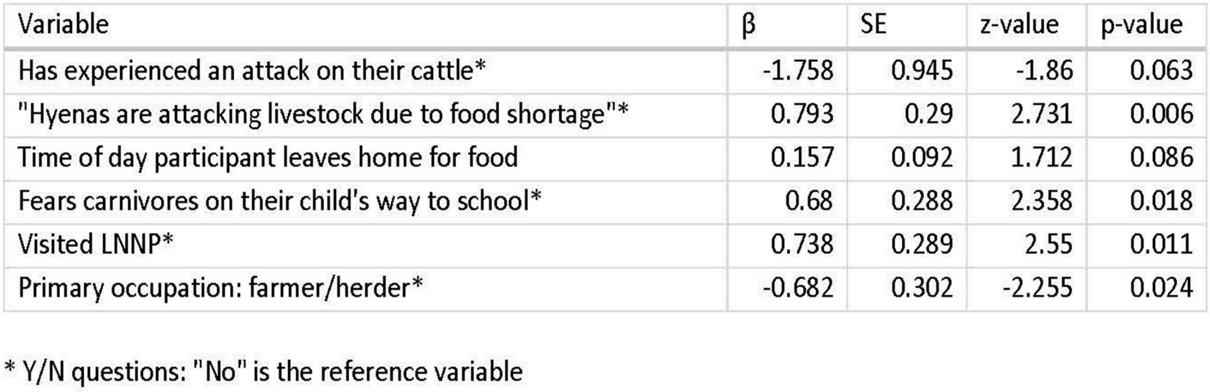
Hypotheses related to verified conflict, perceived conflict, and attitudes toward carnivores.

Variable	Hypotheses	References
Education level	Increasing education level is correlated with 1) more positive attitudes toward carnivores conservation, and 2) fewer perceived conflict reports.	Akama et al., 1995; Bruskotter et al., 2017; Megaze et al., 2017
National park visitation by participant or child	Participants who have visited the national park, or whose children have visited the national park are more likely to 1) have positive attitudes toward carnivores, and 2) report fewer perceived conflicts.	Espinosa and Jacobson, 2012; Hausmann et al., 2016; Mkonyi et al., 2017
Active nighttime livestock guarding	Livestock owners who employ tools to actively guard their livestock at night are more likely to 1) have positive attitudes toward carnivores, and 2) report fewer perceived conflicts.	Rust et al., 2013
Perceived threats to children	Participants who believe carnivores pose a threat to children on their way to school are more likely to 1) have negative attitudes toward carnivores, and 2) report more perceived conflicts.	Bruskotter and Wilson, 2014; Bruskotter et al., 2017
Number of children	Increasing number of children is correlated with 1) negative attitudes toward carnivores, and 2) more perceived conflict reports.	Bruskotter et al., 2017; Khumalo and Yung, 2015
Gender	1) Women are more likely to have negative attitudes toward carnivores. 2) Men are more likely to report more perceived conflicts.	Gore and Kahler, 2012; Ogra, 2008
Livestock ownership	1) Livestock owners are more likely to a. have negative attitudes toward carnivores, and to b. report more perceived conflicts. 2) These effects are stronger with increasing number of livestock owned.	Hemson et al., 2009; Kellert, 1985
Season	1) Verified conflict increases during the rainy season. 2) Perceived conflict shows no difference between seasons.	Bartzke et al., 2018; Koziarski et al., 2016

Vegetation greenness (NDVI)	1) NDVI is positively correlated with both perceived and verified carnivore conflict.	Bartzke et al., 2018; Koziarski et al., 2016; Ugarte et al., 2019
Road density	1) Road density is positively correlated with both perceived and verified conflict.	Ugarte et al., 2019
Distance to protected area	1) Distance protected area is negatively correlated with both perceived and verified conflict, with a stronger effect for verified conflict.	Gray et al., 2020; Mkonyi et al., 2017; Ugarte et al., 2019; Weldemichel and Lein, 2019

TABLE 2. PREDICTORS OF ATITUDES TOWARD SPOTTED HYENA CONSERVATION

Variables retained in best-performing model of predictors of attitudes toward spotted hyena conservation (AUC = .805).

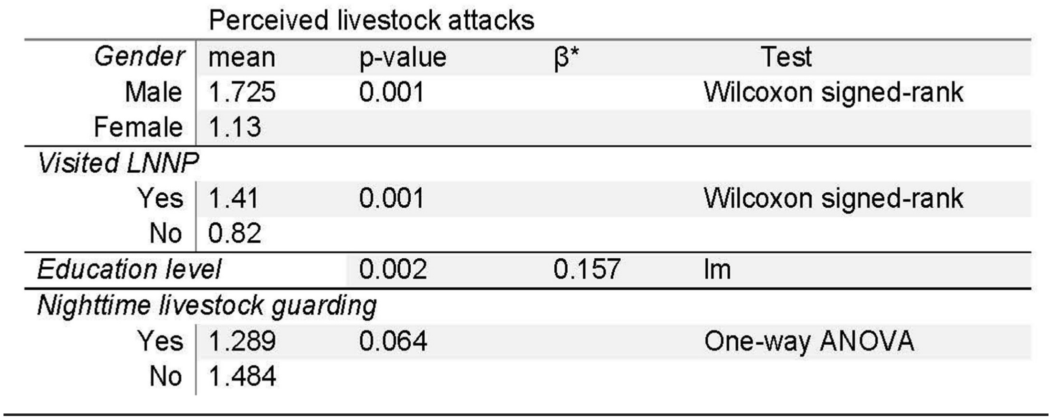


Variable	β	SE	z-value	p-value
Has experienced an attack on their cattle*	-1.758	0.945	-1.86	0.063
"Hyenas are attacking livestock due to food shortage"*	0.793	0.29	2.731	0.006
Time of day participant leaves home for food	0.157	0.092	1.712	0.086
Fears carnivores on their child's way to school*	0.68	0.288	2.358	0.018
Visited LNNP*	0.738	0.289	2.55	0.011
Primary occupation: farmer/herder*	-0.682	0.302	-2.255	0.024

* Y/N questions: "No" is the reference variable

TABLE 3. PREDICTORS OF PERCEIVED CONFLICT REPORTS

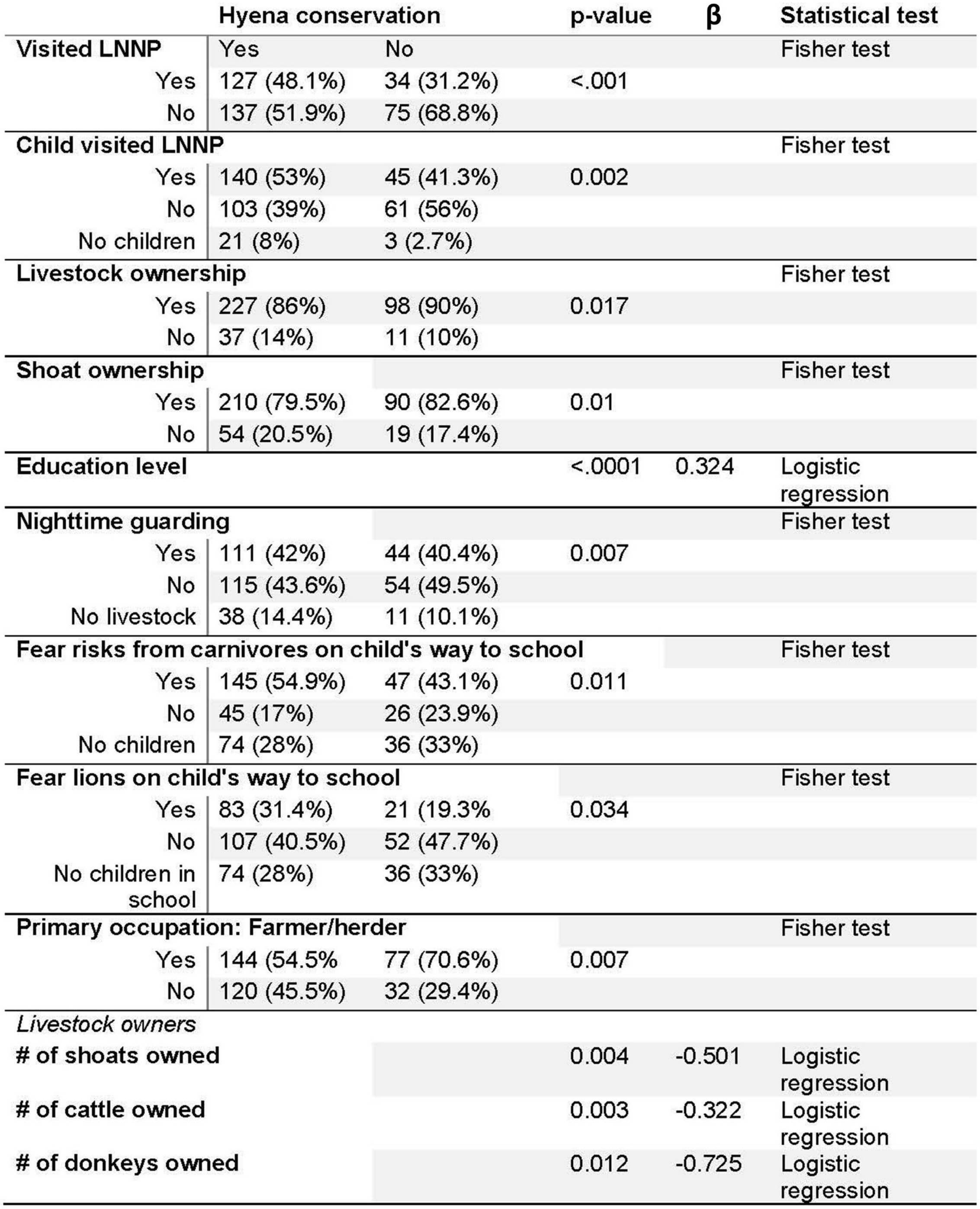
Statistically significant results of pairwise analyses examining predictors of perceived conflict reports.



	Perceived livestock attacks			
Gender	mean	p-value	β*	Test
Male	1.725	0.001		Wilcoxon signed-rank
Female	1.13			
Visited LNNP				
Yes	1.41	0.001		Wilcoxon signed-rank
No	0.82			
Education level		0.002	0.157	lm
Nighttime livestock guarding				
Yes	1.289	0.064		One-way ANOVA
No	1.484			

TABLE 4. PREDICTORS OF ATTITUDES TOWARD SPOTTED HYENA CONSERVATION: PAIR-WISE TESTS

Statistically significant results of pairwise analyses examining predictors of attitudes toward spotted hyena conservation.



	Hyena conservation		p-value	β	Statistical test
Visited LNNP	Yes	No			Fisher test
Yes	127 (48.1%)	34 (31.2%)	<.001		
No	137 (51.9%)	75 (68.8%)			
Child visited LNNP					Fisher test
Yes	140 (53%)	45 (41.3%)	0.002		
No	103 (39%)	61 (56%)			
No children	21 (8%)	3 (2.7%)			
Livestock ownership					Fisher test
Yes	227 (86%)	98 (90%)	0.017		
No	37 (14%)	11 (10%)			
Shoat ownership					Fisher test
Yes	210 (79.5%)	90 (82.6%)	0.01		
No	54 (20.5%)	19 (17.4%)			
Education level			<.0001	0.324	Logistic regression
Nighttime guarding					Fisher test
Yes	111 (42%)	44 (40.4%)	0.007		
No	115 (43.6%)	54 (49.5%)			
No livestock	38 (14.4%)	11 (10.1%)			
Fear risks from carnivores on child's way to school					Fisher test
Yes	145 (54.9%)	47 (43.1%)	0.011		
No	45 (17%)	26 (23.9%)			
No children	74 (28%)	36 (33%)			
Fear lions on child's way to school					Fisher test
Yes	83 (31.4%)	21 (19.3%	0.034		
No	107 (40.5%)	52 (47.7%)			
No children in school	74 (28%)	36 (33%)			
Primary occupation: Farmer/herder					Fisher test
Yes	144 (54.5%	77 (70.6%)	0.007		
No	120 (45.5%)	32 (29.4%)			
Livestock owners					
# of shoats owned			0.004	-0.501	Logistic regression
# of cattle owned			0.003	-0.322	Logistic regression
# of donkeys owned			0.012	-0.725	Logistic regression

Chapter 4. Spotted hyena landscape navigation on a coexistence frontier

ABSTRACT

Rapid land use changes and human population increases are restricting movements of wide-ranging species such as carnivores worldwide. “Coexistence frontiers”, or areas where human development and activity is increasing rapidly or appearing for the first time, constitute novel environments where carnivores must learn to navigate and coexist with people. Many carnivores exhibit behavioral plasticity that gives them an advantage in navigating these environments and traversing human-dominated landscapes, but we have a limited understanding of whether, how, and to what extent these animals adapt to survive and thrive on landscapes shaped by infrastructure, human activity, and human acceptance. As an oft-forgotten, widely reviled, and behaviorally plastic apex predator, the spotted hyena (*Crocuta crocuta*) is a model species for understanding how carnivores navigate coexistence frontiers in an urbanizing world. We used fine scale (5-min fix rates) GPS collar data and supplemental camera trap imagery in conjunction with resource selection and step selection functions to assess spotted hyena space use and navigation of ecological and anthropogenic covariates in Lake Nakuru National Park and Soysambu Conservancy, Kenya. Our results show that environmental covariates—including NDVI, terrain, and proximity to water bodies—had stronger effects on landscape-scale resource selection, while infrastructure and likelihood of conflict with humans or livestock factored strongly in patch-scale step selection. We also found that hyena selection for these covariates changes seasonally and across land management types. Through a barrier behavior analysis, we show that hyenas may perceive the protected area boundaries’ electric fences as risky but may cross them out of need. We also document an exceptionally high number of spotted hyena individuals (199) approaching the national park fence at just 8 sites during the study period. Our results show that “adaptability” may have different meanings depending on context and scale. These results also point to the need to incorporate socio-ecological factors into multiscale analyses of carnivore movement in order to effectively plan for human-carnivore coexistence in a changing world.

INTRODUCTION

Land use change and anthropogenic development are proliferating around the world, restricting movements of wide-ranging species such as large carnivores (Crooks et al. 2011, Ripple et al. 2014). Carnivores and people are coming into increasing contact with one another due to these changes, exacerbated by the human population growth that is intrinsic to these shifts. In human-dominated landscapes, a number of tools have been employed to mitigate carnivore interactions with people, including fencing of protected areas or other structures and policies to separate humans from wildlife (McInturff et al. 2020). However, physical structures are often permeable, meaning wildlife must navigate these and other infrastructure and activities on the landscape. On "coexistence frontiers", where human development is either appearing or rapidly increasing for the first time, carnivores are learning to traverse novel landscapes with novel risks. For these regions in particular, it is critical to identify areas in which carnivores may be able to thrive alongside humans, or at a minimum be able to move through human-dominated landscapes to reach viable habitat (e.g., McClure et al. 2016).

Changing land uses, infrastructure, and human activity can have profound impacts not just on carnivore movement, but also on carnivore behavior and conflicts with people (Ripple et al. 2014), including retaliatory killing of carnivores (Ogada 2014). Human perceptions and acceptance of carnivores are likely to be an important factor in determining how carnivore species may be able to navigate landscapes (Behr et al. 2017). Yet, on coexistence frontiers, humans may not have developed tolerance or acceptance for species with which they have not come into routine contact before (Lute and Carter 2020). Spatial and ecological scale also matter for contextualizing human coexistence with carnivores (Carter and Linnell 2016). For instance, human development may have community level effects through pushing some species into remaining natural habitats (Parsons et al. 2018), despite carnivores exhibiting adaptations to human development on individual and patch-level scales. Through these and other processes, human-dominated landscapes adjacent to nearby protected areas can result in a source-sink dynamic, where animals from protected areas that venture into more densely populated areas are more likely to die through anthropogenic causes (Lamb et al. 2020). Thus, for carnivores, which are often highly mobile, landscape permeability is essential to maintain populations.

Many large carnivores and mesopredators are anecdotally and empirically known for their behavioral plasticity and resulting ability to adapt to novel environments and landscapes. Some carnivore species have been able to exploit urban environments so successfully that they achieve higher population densities than under natural conditions (Bateman and Fleming 2011). Meanwhile other species living in human-dominated environments may actively avoid anthropogenic features such as roads (e.g., Young et al. 2019) and fences, or change their activity patterns to adjust for human presence (e.g., Gaynor et al. 2018). Carnivores may avoid or be attracted to human infrastructure at different scales (Poessel et al. 2014).

While certain species may exhibit overall tendencies for adapting to these novel environments and structures, it is important to consider variation in individual boldness and behavioral propensities when assessing how carnivore species navigate human-dominated landscapes over time (Newsome et al. 2015). Carnivore populations may take several generations or more to adapt to novel human-dominated environments through learning and natural selection (Breck et al. 2019). However, human tolerance may be a strong enough limiting factor that it can override adaptability for carnivore populations or individuals navigating developing landscapes (Moss et al. 2016). Put simply, carnivores sharing space with people must navigate three main elements present on the landscape: ecological factors, human infrastructure, and human acceptance. To assess whether and how carnivores are adapting on coexistence frontiers, it is thus necessary to understand interactions between humans and carnivores within these broad socio-ecological contexts, rather than just considering ecological variables (O'Neal Campbell 2014, Lute et al. 2020).

As a widely controversial (Glickman 1995) and behaviorally plastic apex predator (Holekamp and Dloniak 2010), spotted hyenas (*Crocuta crocuta*, hereafter "hyenas") are a model species for understanding the nature of carnivore adaptability to human-caused landscape change and to human perceptions. Hyenas are broadly thought to be one of the most adaptable carnivores, but little is known about the extent and mechanisms of their adaptations to human activities, infrastructure, and tolerance. Green et al. (2018) found that hyena populations in Masai Mara, Kenya increased in an area of anthropogenic disturbance, possibly linked to increased consumption of livestock. In densely populated areas in Ethiopia where native prey is depleted, hyenas have become almost entirely dependent on anthropogenic food (e.g., Yirga et al. 2012). Yet, other studies have found negative, neutral, or nuanced responses to people. In one study in Kenya, hyena activity shifted in response to livestock grazing and other anthropogenic activities (Kolowski et al. 2007), while in another study, in South Africa, hyena propensity to visit anthropogenic sites varied depending on season, age, or individual (Belton et al. 2018). Understanding how hyenas and other behaviorally plastic carnivores do or do not adapt to anthropogenic landscape change is key to forecasting the resilience of movements, food webs, and ecosystems in rapidly developing landscapes.

We sought to provide insight into this adaptable carnivore's abilities to navigate coexistence frontiers by examining the following questions: 1) How do spotted hyenas navigate ecological and anthropogenic covariates on the landscape in this developing region?, 2) Do spotted hyenas exhibit differences in movement around anthropogenic structures, human activity, and tolerance as compared to ecological factors?, 3) Do hyenas living in different management types (i.e., fully protected vs. multi-use) select for different landscape features? We employed resource selection functions (RSFs) and step-selection functions (SSFs) to determine hyena space use and landscape navigation at different scales (Reinking et al. 2019). We then used this information to infer whether and how to consider a suite of socio-ecological factors when designing for hyena landscape permeability, and present implications of these inferences for human-carnivore coexistence globally.

METHODS

Study site

Our study was conducted in Nakuru County, in the Rift Valley of southwest Kenya from February 2019-June 2020. The study area (0°26' S, 36°1' E) includes two major wildlife protected areas: Lake Nakuru National Park (LNNP, 188 km^2), which is one of two fully fenced national parks in Kenya, and Soysambu Conservancy (190 km^2), which is mostly fenced and functions as both a wildlife conservancy and a livestock ranch with over 10,000 cattle sheep, and goats. Fences used in both protected areas are typically ~2m tall and consist of parallel electrified wires, though some stretches of fence are composed of other materials, are in various states of maintenance, or have an additional component of woven wire mesh to reduce wildlife digging. The two large alkaline lakes in the region, Lake Nakuru and Lake Elmenteita are designated UNESCO World Heritage sites. The region supports many species of large mammals, including large carnivore species such as African lion (Panthera leo), spotted hyena, and leopard (Panthera pardus); and several mesocarnivore species, such as serval (Leptailurus serval) and black-backed jackal (Lupulella mesomelas). Many carnivore populations in the region remain stable despite heavy historical persecution (Ogutu et al. 2017). The region is characterized by woodland, savanna, and dense brush habitats, as well as two rainy and two dry seasons each year.

Field methods and data

Collar deployment and programming

From February-March 2019, 3 female and 4 male spotted hyenas were collared, representing 5 clans in LNNP and Soysambu Conservancy. Six of these collars (still representing 5 clans) remained in function for the majority of this study. Fixes were only taken between 6pm-7am, which are the active hours of hyenas in this study area. Hourly fix rates were taken from February-April 2019, after which 5-minute fix rates were used until May 2020. After this point, the collars were reprogrammed for 1 hour fix rates, 24 hours per day.

Covariates

The following covariates were used in analyses of hyena landscape use and navigation: normalized difference vegetation index (NDVI; 30m, Landsat 8 Surface Reflectance Tier 1, rainy and dry seasonal averages for 2019), slope (30m, Shuttle Radar Topography Mission [STRM]), elevation (30m, STRM), distance to rivers, distance to lakes, distance to boundaries, distance to verified livestock predation locations, distance to regions people perceive as being risky due to hyenas, and distance to participatory mapped livestock predation locations during the study period. The latter two variables were derived using participatory mapping data from communities living within 2 km of the protected area boundaries, while the verified predation dataset was from the local wildlife authority, Kenya Wildlife Service (Wilkinson et al. *In Review*). Because killing of or retaliation against wildlife is illegal in Kenya, participatory mapped livestock predation and participatory mapped risks from spotted hyenas can serve as proxies for spatially-explicit intolerance or acceptance of spotted hyenas by local communities. Euclidean distance was used for all distance layers, and road layers were derived through Open Street Maps and by hand tracing.

Analyses

Landscape use

To determine individual home ranges, we used the 'adehabitatHR' package in R (R Core Team 2018) to assess 50% and 95% kernel utilization distributions (KUD) and calculated overlap among home ranges.

To determine landscape feature selection by spotted hyenas, we then derived resource selection functions (RSFs) using the 'lme4' package in R. Random points generated were equal to the number of GPS points used, and we found no evidence of collinearity among our covariates (Dellinger et al. 2013). We assessed resource selection using generalized linear mixed-effects models with a logit link. Using the raster package and base R, we resampled and scaled the following covariates for use in the RSFs: normalized difference vegetation index (NDVI; 30m, Landsat 8), elevation, slope, distance to rivers, distance to lakes, distance to roads, and distance to protected area boundaries. NDVI in this study site can serve as a proxy for land cover, because areas of higher NDVI are generally brush or forest, whereas lower NDVI areas are typically grasslands. After initial data exploration, individual interaction with distance to boundary (i.e., variation in boldness) was included as a random effect in our candidate models. We assessed a global model (for all hyenas) and compared global seasonal (rainy and dry) models, as well as models for hyenas whose dens were in LNNP, and for hyenas whose dens were in Soysambu Conservancy. We also assessed and compared models with the following combinations of variables: ecological variables only, ecological and infrastructure, infrastructure only, infrastructure and human perception/experience, and human perception/experience only. Models were ranked based on their Akaike Information Criterion (AIC) (Burnham and Anderson 2002), and models within Δ AIC ≤ 2 were retained to use when assessing coefficient values.

Landscape navigation

To understand how hyenas are navigating the landscape, we derived step selection functions (SSFs) using the amt package in R. We prepared the hyena data by creating tracks from the data using the mk_track() package, resampled the data to only the 5 minute fix rates, and filtered to assure bursts would have a minimum of 2 points. Five random steps were generated for each step used. Scaled covariates and model comparisons reflected those conducted for the RSF analyses. We fit conditional logistic regressions on the covariates, while also considering hyena ID as a cluster term and log of step length (i.e., speed of movement) as an interaction term with boundaries and roads. We used quasi-likelihood independence model criterion (QIC) to rank models and determine top models. We then used acf.test() on the model that best predicted the data to determine the lag at which autocorrelation is no longer observed, and employed destructive sampling to address autocorrelation, removing 2 points between each individual's clusters. Models were then fit on the destructively sampled data. Last, we created a function for individual SSF models and the parameters from the global model to visualize the data.

Barrier interactions

To gain a detailed understanding of hyena behaviors around fences and determine locations of weak or robust fences on the protected area boundaries, we used the Barrier Behavior Analysis

(BaBA) methodology developed by Xu et al. (2020). BaBA examines animal movements within set buffers around fences to determine whether, where, and how often animals exhibit normal movement (quick cross, average movement), altered movement (bounce, trace, or back and forth), or trapped movement at boundaries. To assess appropriate sensitivity for the BaBA results, we used BaBA with 50m, 100m, and 150m fence buffer distances within which GPS locations were classified as a fence encounter (Xu et al. 2020).

Finally, to supplement our understanding of hyena interactions with and crossing of the boundary fences, we used images of spotted hyenas from camera traps placed on eight key crossing points at the LNNP fence (see Wilkinson et al. 2021 for detailed methodology). Spotted hyenas in camera trap images were individually identified using spot patterns. Hyena images were compared to individuals previously listed in both the LNNP and Soysambu Conservancy hyena ID books (Supplementary Fig. 1). Hyenas appearing at the fence were first compared to the clan with a range closest to the camera trap site but then expanded to all others in the book if not identified. If we could not make a definitive identification, the hyena was labeled as unknown. These unknown individuals were later added to the Lake Nakuru or Soysambu Conservancy ID Books under a new ID code and used for further identification of images. We assessed frequency of fence approaches at each site and by specific individuals, as well as the number of different fence crossing sites visited by each individual.

RESULTS

Landscape use

Spotted hyena 50% and 95% home ranges (Figure 1) comprised between 6.06-27.29 km^2 (($\overline{x}$ = 11.6) and 31.38-132.91 km^2 ($\overline{x}$ = 61), respectively. Dry season 50% and 95% home ranges comprised 5.88-23.73 km^2 ($\overline{x}$ = 10.99) and 30.71-143.59 km^2 ($\overline{x}$ = 87.89), respectively. Rainy season 50% and 95% home ranges comprised 6.06-23.85 km^2 ($\overline{x}$ = 11.46) and 28.53-111.92 km^2 ($\overline{x}$ = 58.08), respectively. When taking into account and excluding the two individuals from the same clan, proportion of 95% home range overlap spanned between 0.108 and 0.317.

For both RSFs and SSFs all variables were retained for global models after testing for pairwise correlation (maximum correlation was 0.52, while most pairwise correlations were below 0.2). The global model including all covariates for the RSFs revealed selection for higher NDVI, distance to rivers, distance to boundaries, and distance to participatory mapped livestock predation, and selection against elevation, steep slopes, distance to roads, distance to lakes, distance to verified livestock predation, and distance to areas of people's participatory mapped risk from hyenas (Table 1). Of these, selection for distance to participatory mapped livestock predation (β = 0.0.271, $p < 0.001$) and selection against distance to verified livestock predation showed the strongest effects (β = -0.255, $p < 0.001$). Seasonal RSFs comparing all covariates across the rainy and dry seasons showed that in the dry season hyenas exhibit an increase in landscape-level selection for NDVI, distance to rivers, distance to verified livestock predation, and distance to people's participatory mapped risk, and a decrease in selection for elevation, distance to boundaries, and distance to participatory mapped livestock predation (Figure 2a). When comparing models containing combinations of ecological, infrastructure, and human experience/perception covariates, the model that best predicted the data was the model with all covariates, followed by the model containing only ecological and infrastructure covariates. When comparing global models across land management types, hyenas with dens in Soysambu showed stronger selection for or against human experience/acceptance covariates than did hyenas with dens in LNNP (Figure 3a). Soysambu hyenas also showed statistically significant selection for distance to boundaries at the landscape level ($\beta = 0.236$, $p < 0.001$), which was not exhibited as strongly by LNNP hyenas ($\beta = 0.122$, $p = 0.46$).

Landscape navigation

The global model including all covariates for the SSFs revealed step selection for higher NDVI, distance to rivers, distance to boundaries, and distance to areas of people's participatory mapped risk from hyenas, and selection against distance to lakes, steep slopes, distance to roads, elevation, distance to verified livestock predation, and participatory mapped livestock predation (Table 2). Of these, selection for distance to boundaries showed the strongest effect ($\beta = 0.273$, $p < 0.01$), yet there was marked individual variation in selection for all covariates (Figure 4). Seasonal SSFs comparing all covariates across the rainy and dry seasons showed that in the dry season hyenas exhibit an increase in patch-level selection for distance to boundaries, and a decrease in selection for distance to lakes and roads, and elevation (Figure 2b).

When comparing models containing combinations of ecological, infrastructure, and human experience/perception factors, the two models within Δ AIC ≤ 2 were the infrastructure only model and the model containing infrastructure and human experience/perception covariates. When comparing global models across land management types, Soysambu hyenas differed from LNNP hyenas in that they showed selection against distance to roads ($\beta = -0.19$, $p < 0.001$), while LNNP hyenas differed from Soysambu in that they showed selection against NDVI ($\beta = -0.077$, $p < 0.001$) and distance to verified conflict ($\beta = -0.552$, $p < 0.001$), and for distance to boundaries ($\beta = 0.62$, $p < 0.001$, Figure 3b). A case study on a single hyena that was known to frequently cross between the two protected areas (Suppl Table 1) showed a selection for distance to boundaries during the dry season ($\beta = 0.186$, $p < 0.001$) and against distance to boundaries in the rainy season ($\beta = -0.068$, $p < 0.01$), as well as an increase in speed of movement (i.e. log of step length) when selecting for boundaries during the rainy season ($\beta = 0.062$, $p < 0.001$) as compared to the dry season ($\beta = 0.035$, $p < 0.001$).

Barrier interactions

A 50-meter fence buffer best captured *quick cross* events, or events where hyenas quickly crossed a fence when they approached it. Spotted hyena individuals encountered fences on average 193 (σ=168.5) times during the study period. Overwhelmingly, hyenas encountering fences either exhibited *quick cross* (n=583, or 49% of all fence encounters) or *bounce* (n=507, 42.7%), with *average movement* (n=45, 3.8%), *trace (*3 times, 0.25%), and *back and forth* (n=7, 0.59%) exhibited occasionally (Figure 5a). *Bounce* is a behavior in which hyenas that encounter the fence immediately walk away semi-perpendicularly from the fence, toward the same direction they originated from. There was marked individual variation in overall fence encounters, as illustrated by high standard deviations in average fence encounter frequency. Both *quick cross* and *bounce* behaviors were more numerous in the dry season ($\bar{x}$ = 54.8 and $\bar{x}$ = 48.7, respectively) than in the rainy season ($\bar{x}$ = 42.3 and $\bar{x}$ =35.8, respectively), though this result was insignificant (Mann-Whitney p = .48 and p = .699; Figure 5b). Judging by differences in hyena behaviors around different fence segments, some fence segments may be more permeable than others. The highest concentration of quick cross behaviors appeared to be on the fence lines between the two protected areas (Suppl. Fig. 2), indicating high permeability for those fence segments. Meanwhile the bounce behaviors had a considerably wider spread along the boundaries (Suppl. Fig. 2), indicating regions where hyenas may have wanted to cross but could not due to fence impermeability. Notably, fence behaviors revealed several crossing points connecting LNNP to the conservancy.

Camera trap data revealed 199 individual hyenas spanning at least 3 clans approaching the fence across the 8 studied sites, with one site having a minimum of 67 different individuals appearing at the fence (Table 3; Suppl. Fig. 3). Across all sites, 63 individuals appeared at the fence in more than 10 images during the study period.

DISCUSSION

Spotted hyenas in this rapidly developing landscape appear to be selecting habitats for and against both environmental and anthropogenic covariates at different scales. We found that electric fences may constitute a risk to hyenas while simultaneously being highly permeable to this species, which has implications for coexistence and movement for this apex predator. Additionally, the hyenas in this region exhibited a number of landscape use and navigation propensities that differ from previous studies on this species conducted in landscapes that are on the high or low extremes of anthropogenic influences.

Space use

Hyena ranges were considerably larger than would be expected given the small size of the two protected areas (Honer et al. 2002, Watts and Holekamp 2008), and the high degree of overlap among home ranges reflected this finding. Other studies have shown that adapting to human-dominated environments may change fundamental social behaviors of certain carnivore species (e.g., Widdows and Downs 2015). The high degree of range overlap for hyenas from different clans in this study may be an indicator of intraspecific social behavior changes which warrant further research.

Hyena home ranges expanded during the dry season, in contrast to studies in ecologically similar regions that show wildlife tend to disperse more widely in the wet season (Koziarski et al. 2016). Previous research has also shown that spotted hyenas in particular have wider ranges in the wet season due to seasonal movement and presence of their wild ungulate prey (Trinkel et al. 2004). Our observed counterintuitive increase in hyena range sizes during the dry season rather than the rainy season could be due to two factors inherent to this fenced ecosystem. First, due to the electric boundary fences, many ungulate species aren't able to disperse during the rainy season (Wilkinson et al. 2021), meaning hyenas have little opportunity or need to expand ranges to seasonally track wild prey. Second, the already small sizes of the protected areas, coupled with an ongoing rise in lake waters, may be driving seasonal resource limitations for spotted hyenas and causing them to expand their ranges during the dry season.

Socio-ecological landscape navigation

Hyenas in this region appear to be selecting for different factors at the landscape scale than they are at the patch level. Differences in resource selection at different scales were particularly apparent for infrastructure and human acceptance covariates, and less apparent for environmental covariates, selection for which largely remained the same across RSF and SSF results. At the patch level, hyena navigation appears to be more influenced by roads, fences, and human experiences and acceptance than by environmental covariates such as NDVI and proximity to water. While there are changes in magnitude of effect, at both broad and fine scales hyenas are selecting for vegetation greenness, lakes, and roads, and against rivers, boundaries, slopes, and high elevation.

Meanwhile, at broader scales hyenas are selecting against participatory mapped livestock predation areas and for areas of participatory mapped risk from spotted hyenas, while the opposite holds true for patch-level selection. The landscape level selection for and against these human acceptance covariates may indicate that hyenas are broadly selecting for areas in which they may face hazing or be poisoned (i.e. perceived risks from/tolerance for hyenas), and against areas that people use for livestock grazing (i.e., perceived livestock predation). Although in densely populated areas where tolerance is high or there are policies against wildlife killing, carnivore populations may thrive (Athreya et al. 2013, Gebresenbet et al. 2018), in areas where tolerance is low (such as in our study site), carnivore populations can be negatively affected by retaliation and other practices (Ripple et al. 2014).

Our results also showed seasonal differences in landscape level and patch-level hyena selection for environmental and anthropogenic variables. On the landscape level, the dry season exhibited an increase in hyena selection for NDVI, boundaries, and participatory mapped livestock predation. The latter two support our findings that hyenas may be expanding their ranges and potentially traveling outside of the protected areas during the dry season. When resources are scarce, animals living alongside people may be more likely to choose anthropogenic food sources (Johnson et al. 2015), and hyena predation on livestock or scavenging of livestock and other anthropogenic food sources may be increasing during dry seasons. The boundary navigation result at the landscape level also supports these hyenas' tendency toward dry season range expansion. Meanwhile, at the patch-level, the dry season showed a minor increase in hyena navigation toward roads, with minimal differences in selection for environmental and human experience covariates. While species in other studies have been known to use roads for easier traversal of the landscape (Abrahms et al. 2015, Hill et al. 2020), hyenas in this study area may use roads in the dry season for dust bathing and for access to artificial water points, particularly in the conservancy.

When looking at variation in movement for hyenas living in different and management types across both seasons, at the landscape level roads in particular were avoided by Soysambu hyenas more than by LNNP hyenas, despite human use of roads being extremely low in the conservancy at night. One reason for this could be that despite being active at night, hyenas in Soysambu associate roads with the abundance of human activities that occur during the day on the roads within the conservancy, while in LNNP, there is only one activity happening on roads: tourism. Vehicle speeds in the national park are also heavily regulated. Hyena avoidance of roads in Soysambu stands in contrast to research that has found that animals may select for human infrastructure at night for resources or ease of movement, while avoiding it during the day when humans are more active (e.g., Toverud 2019). However, hyenas are generally more skittish in the conservancy than in the national park, possibly due to historical hyena bounties (K. Combes, pers. comm.) prior to the conservancy's designation as a wildlife habitat. The anthropogenic activity signature on Soysambu's roads may thus have a strong enough effect on the spotted hyena's human-caused "landscape of fear" (Smith et al. 2017, Suraci et al. 2019) as to cause nighttime avoidance of roads that are devoid of human activity.

SSFs revealed that hyenas with dens in LNNP are also selecting for distance to boundaries to a much stronger degree than hyenas with dens in Soysambu. However, patch-level selection against NDVI and toward verified livestock predation locations, as well as known fence-crossing behaviors by LNNP hyenas (Wilkinson et al. 2021), point to a lack of sufficient resources or space in the national park.

Fence behaviors

The abundance of *quick cross* and *bounce* behaviors captured by the barrier behavior analysis, as opposed to walking along the fence or exhibiting average movements near the fence, implies that hyenas may perceive boundaries as risky in this rapidly developing area, and may approach the fence only out of need. When they reach the fence, if they cannot cross, they appear to immediately move away (i.e., *bounce*), and if the fence is permeable, they cross quickly. While McInturff et al. (2020) concluded that fences create “ecological winners and losers”, the hyena populations in this region may be a combination of both, depending on individual, season, land management type, or other factors.

Though our study was able to assess movements of hyenas representing 5 clans, the sample size for assessing fence navigation was limited. Camera trap analyses of individual hyenas at the fence line revealed hyenas are approaching the fence and possibly crossing in and out of the national park in extraordinary numbers. Previous studies have suggested that social rank, age, and sex influence spotted hyena risk taking behavior (Belton et al. 2018, Green et al. 2018), yet our analysis shows that individuals spanning different demographics and social ranks may be crossing in and out of the national park. While evidence suggests these behaviors may be caused by resource limitations within this relatively small protected area, further research is needed to assess the ecological factors driving these behaviors.

Implications for landscape permeability

At broad scales, hyenas in this developing region appear to be selecting for ecological covariates that reflect their resource selection in other, less developed systems. However, movement choices at the patch level are more nuanced and influenced by anthropogenic factors. Hyena clan sizes in this region are relatively large (with more than 50 animals per group for clans assessed thus far) despite the small size of the protected areas, which could be influencing the apparent movement of hyenas toward people and likely toward anthropogenic resource subsidies.

Despite this suspected reliance on anthropogenic resources, hyenas showed a general aversion to roads, with different selection strengths depending on scale and land management type, which is contrary to what we expected. Fences also present a nuanced and semi-permeable barrier for spotted hyenas, which appear to cross them as quickly as possible. Other studies have found that keeping development and subdivision below a certain threshold may allow for sustained carnivore navigation of the landscape between core habitat areas (Smith et al. 2019). This may also prove true for the spotted hyenas, which appear to have complex relationships with infrastructure within and surrounding the protected areas. Yet, hyena relationships with fences can also provide information that is helpful for management efforts. We can use fence behavior analyses to determine existing permeable fence segments (Xu et al. 2020) and make ecologically-informed decisions about where carnivore corridors in and out of fenced regions will be the most useful and cost-effective.

Overall, our results imply that anthropogenic factors may influence patch-level decision making differently than landscape-level resource selection. Hyenas may be adaptable enough to switch to anthropogenic food sources in regions of depleted natural prey or limited resources, yet their ability to rely on anthropogenic food may be linked to regional tolerance of hyenas (e.g, Yirga et al. 2012). Spatially explicit human acceptance and experience has the potential to predict where wildlife corridors are likely to succeed for certain species or taxa, while also providing insight into how wildlife may be using anthropogenic resources (Behr et al. 2017). Coupled with their context-specific selections for and against infrastructure covariates, these results demonstrate that a multiscale and multidisciplinary understanding of hyena landscape use and navigation can help with determining where and when this species may thrive in human-dominated landscapes. Future research should include incorporation of land cover covariates, as well as testing of hyena collar data across RSF- and SSF-informed socio-ecological least cost corridor models.

CONCLUSION

Spotted hyenas are one of the most behaviorally plastic large carnivores, yet their reputation for adaptability has previously discouraged study on whether and to what extent their movements and behaviors are impacted by people. As a species that is widespread across sub-Saharan Africa, spotted hyenas provide us with a litmus test for understanding carnivore abilities to live alongside people and move through landscapes on coexistence frontiers. Yet, we also know that coexistence requires adaptation by both people and carnivores in order to succeed (Chapron et al. 2014). This study has demonstrated that integrating spatial and contextual information on ecology, infrastructure, and human acceptance can help us to better understand how carnivores may adapt to proliferating human disturbances and learn to navigate human-dominated landscapes at different scales.

FIGURE 1. SPOTTED HYENA HOME RANGES

50% (left panel) and 95% (right panel) kernel utilization distribution home ranges for 7 spotted hyenas representing 5 clans in Lake Nakuru National Park and Soysambu Conservancy. Hyenas 1 and 3 are in the same clan and hyenas 5 and 9 are in the same clan.

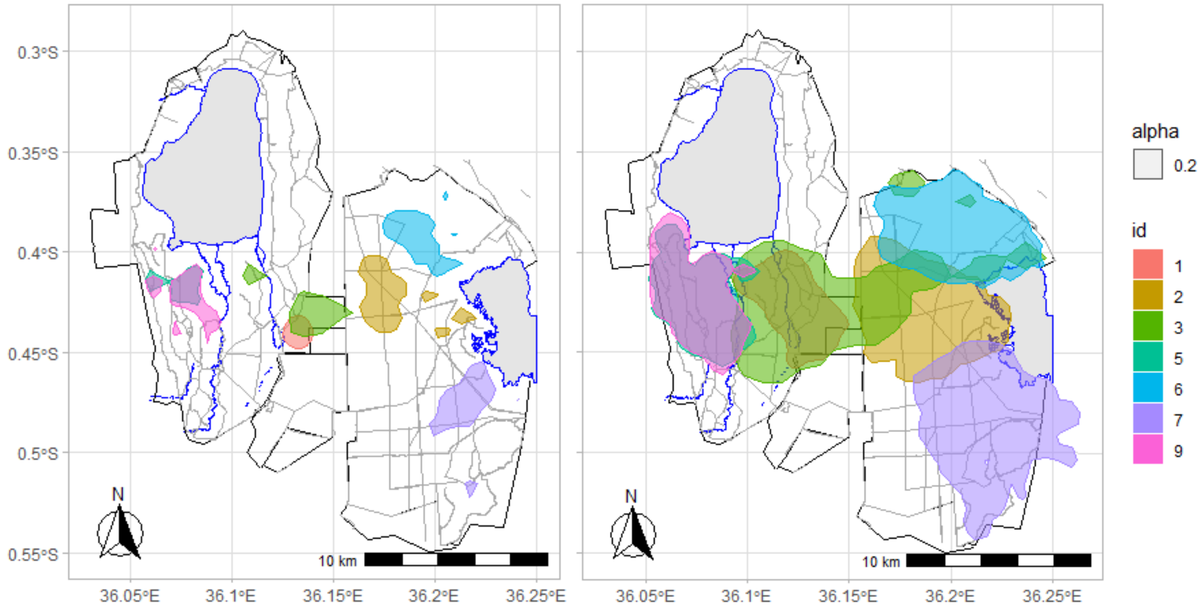


FIGURE 2. SPOTTED HYENA SEASONAL COVARIATE SELECTION

Seasonal results using a) resource selection functions and b) step selection functions. Bounds = protected area boundaries, VC= verified livestock predation, PC = participatory mapped livestock predation, and risk = participatory mapped risk from spotted hyenas.

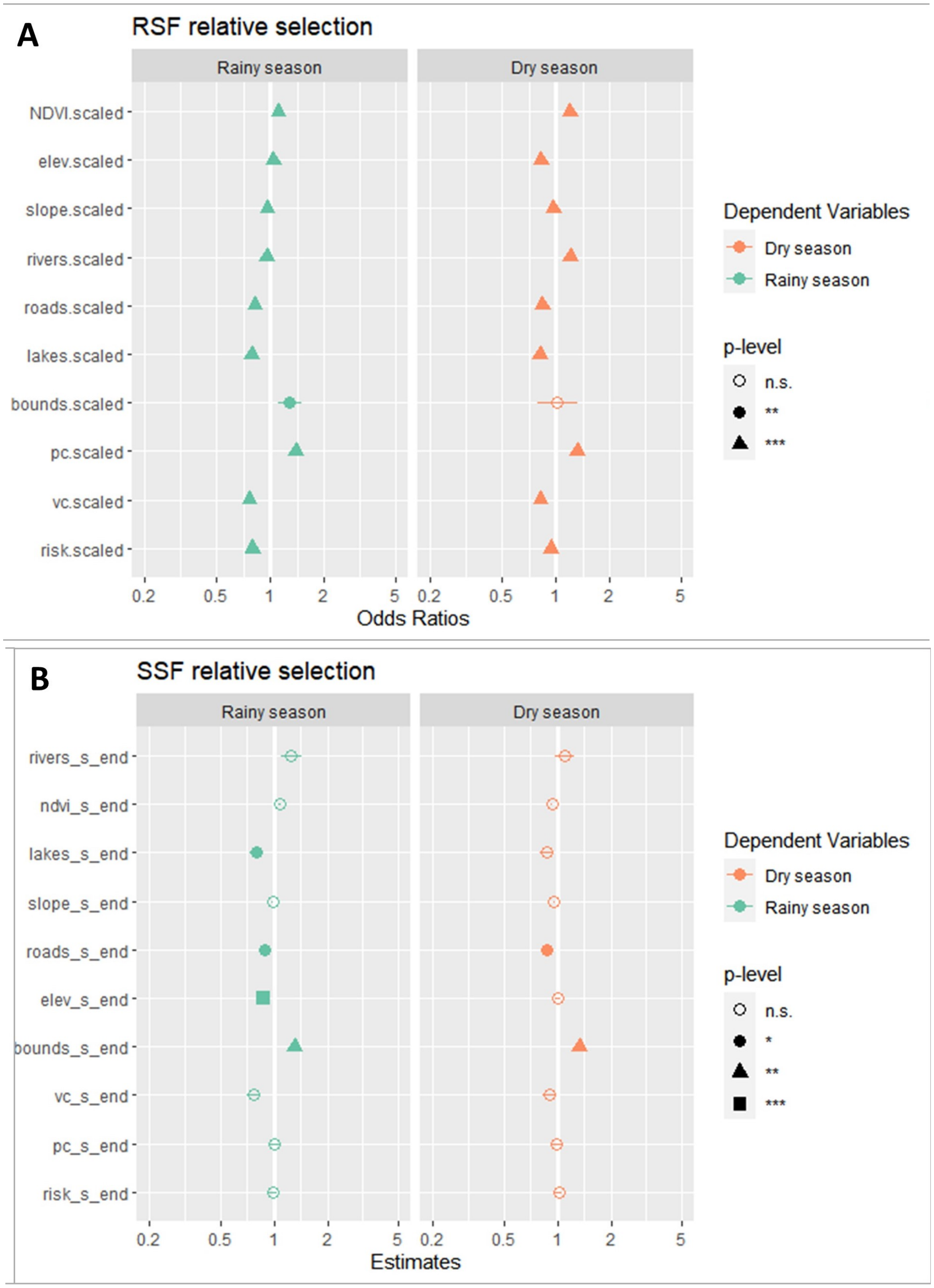


FIGURE 3. SPOTTED HYENA COVARIATE SELECTION ACROSS MANAGEMENT TYPES

A) Resource selection and b) step selection function model outputs across land management types (LNNP: fully protected, or Soysambu: multi-use). Bounds = protected area boundaries, VC= verified livestock predation, PC = participatory mapped livestock predation, and risk = participatory mapped risk from spotted hyenas.

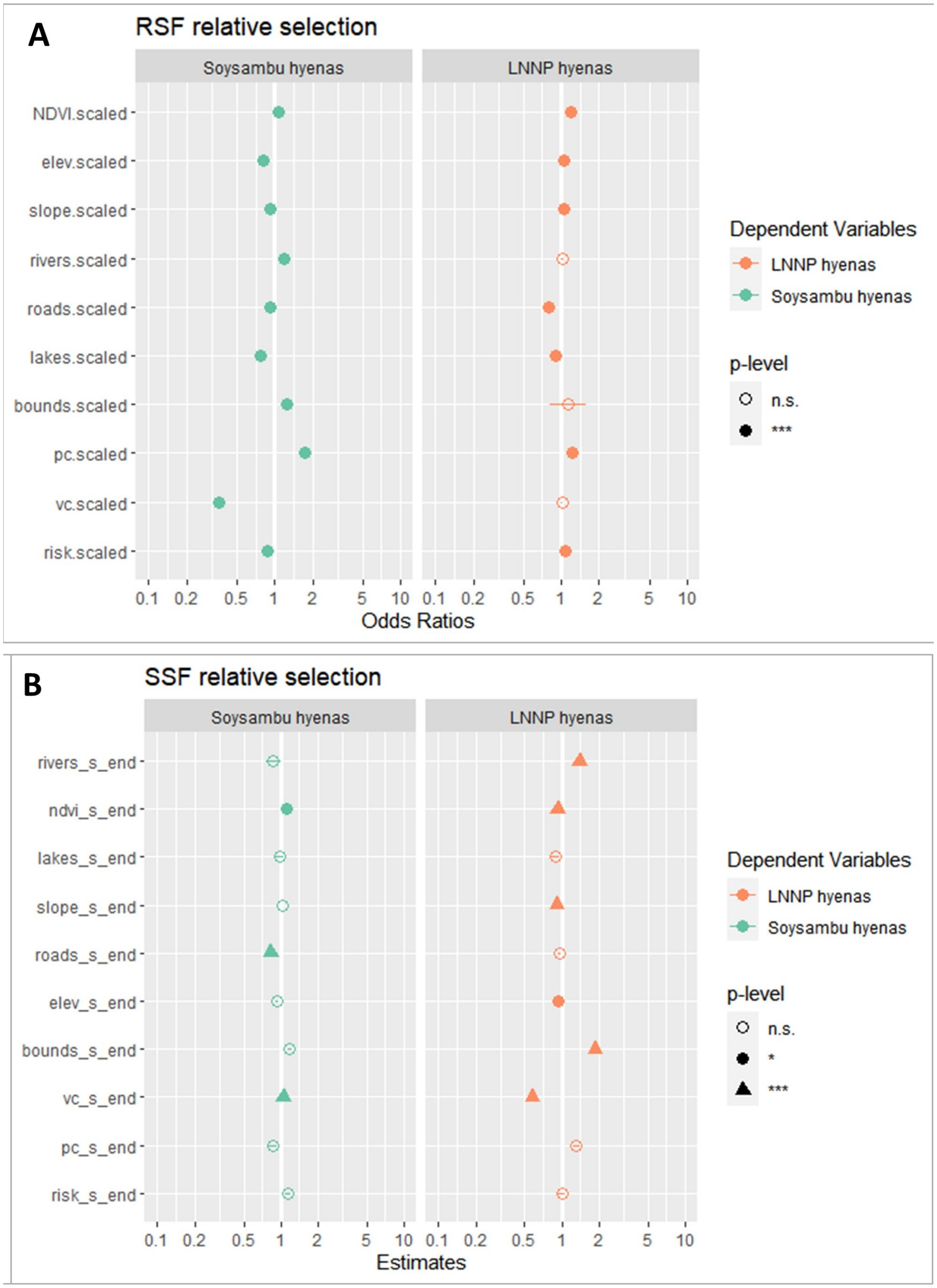


FIGURE 4. INDIVIDUAL RELATIVE COVARIATE SELECTION STRENGTH

Relative covariate selection strength by individual collared hyenas, revealed through step selection functions using conditional logistic regression.

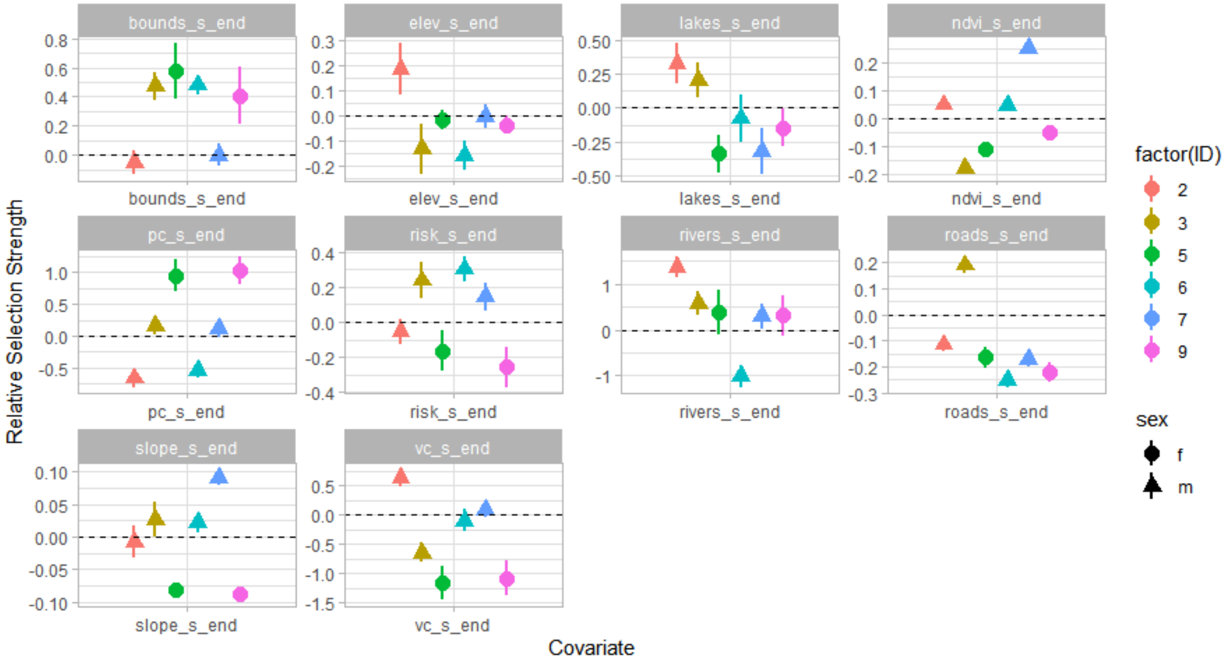


FIGURE 5. BARRIER BEHAVIORS

A) Total frequency of fence behaviors revealed through barrier behavior analysis, and b) seasonal frequency of fence behaviors.

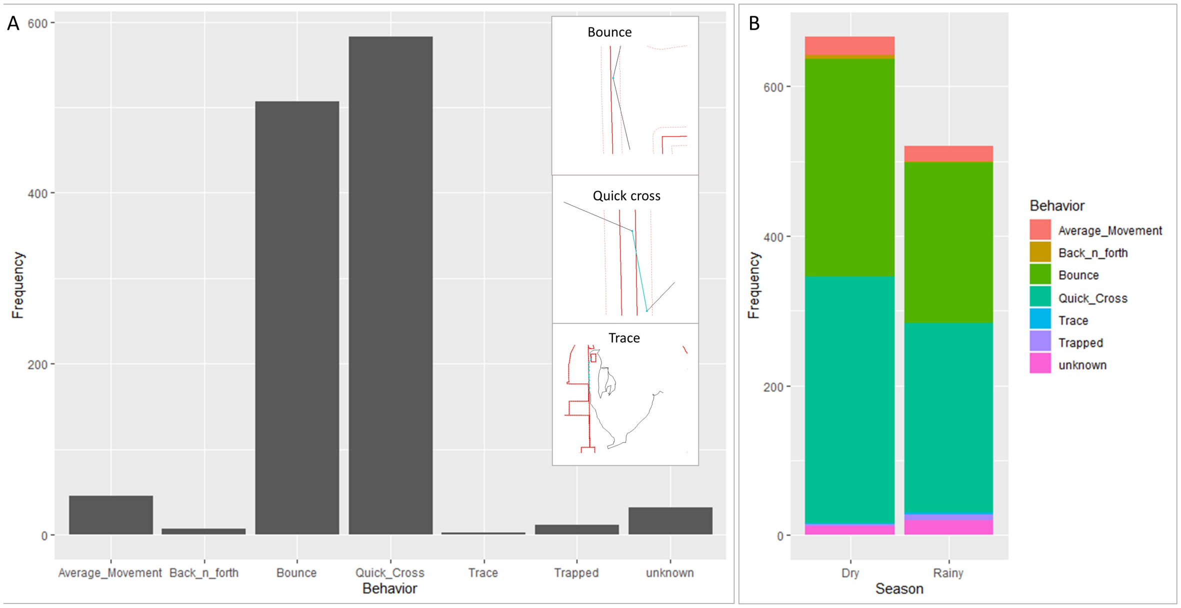


TABLE 1. GLOBAL RESOURCE SELECTION FUNCTION RESULTS

Results from global resource selection function model for spotted hyenas.

Variable	*coeff*	*se*	*z-value*	*p-value*
NDVI.scaled	0.142	0.003	42.738	<0.001
elev.scaled	-0.151	0.004	-36.702	<0.001
slope.scaled	-0.031	0.003	-11.448	<0.001
rivers.scaled	0.111	0.007	16.684	<0.001
roads.scaled	-0.172	0.003	-59.327	<0.001
lakes.scaled	-0.207	0.003	-60.249	<0.001
bounds.scaled	0.148	0.0923	1.609	0.108
pc.scaled	0.271	0.006	47.135	<0.001
vc.scaled	-0.255	0.004	-63.387	<0.001
risk.scaled	-0.16	0.005	-35.14	<0.001

TABLE 2. GLOBAL STEP SELECTION FUNCTION RESULTS

Results from global step selection function model for spotted hyenas.

Variable	*coeff*	*se*	*z-value*	*p-value*
rivers_s_end	0.179	0.047	0.862	0.389
ndvi_s_end	0.026	0.004	0.458	0.647
lakes_s_end	-0.193	0.028	-2.303	<0.05
slope_s_end	-0.027	0.003	-0.835	0.404
roads_s_end	-0.121	0.007	-2.160	<0.05
elev_s_end	-0.08	0.012	-3.346	<0.001
bounds_s_end	0.273	0.017	2.791	<0.01
vc_s_end	-0.163	0.029	-1.193	0.233
pc_s_end	-0.002	0.028	-0.015	0.988
risk_s_end	0.013	0.017	0.163	0.87

TABLE 3. SPOTTED HYENA INDIVIDUALS AT THE FENCE

Number of spotted hyena individuals appearing on camera at the fence line across 8 sites.

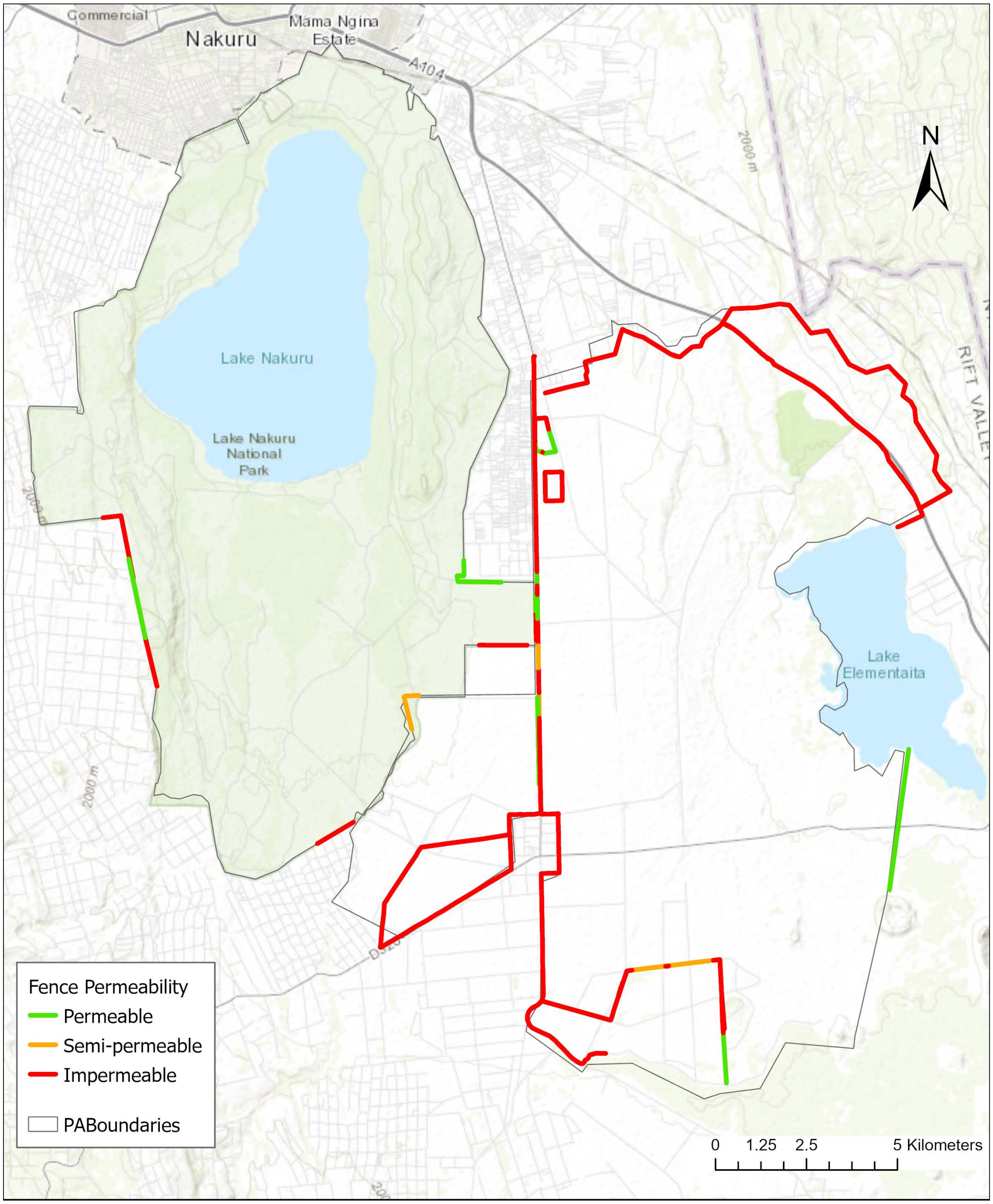
Site	**# Individuals**	**Total frequency of hyena photographs**
C1	24	505
C2	56	301
C3	37	505
C4	22	273
C6	3	10
C7	1	2
C8	47	241
C17	67	3848
Total # Individuals on Camera	199	

SUPPLEMENTARY FIGURE 1. SPOTTED HYENA IDENTIFICATION

Example of left and right side photographs used to identify individual spotted hyenas.

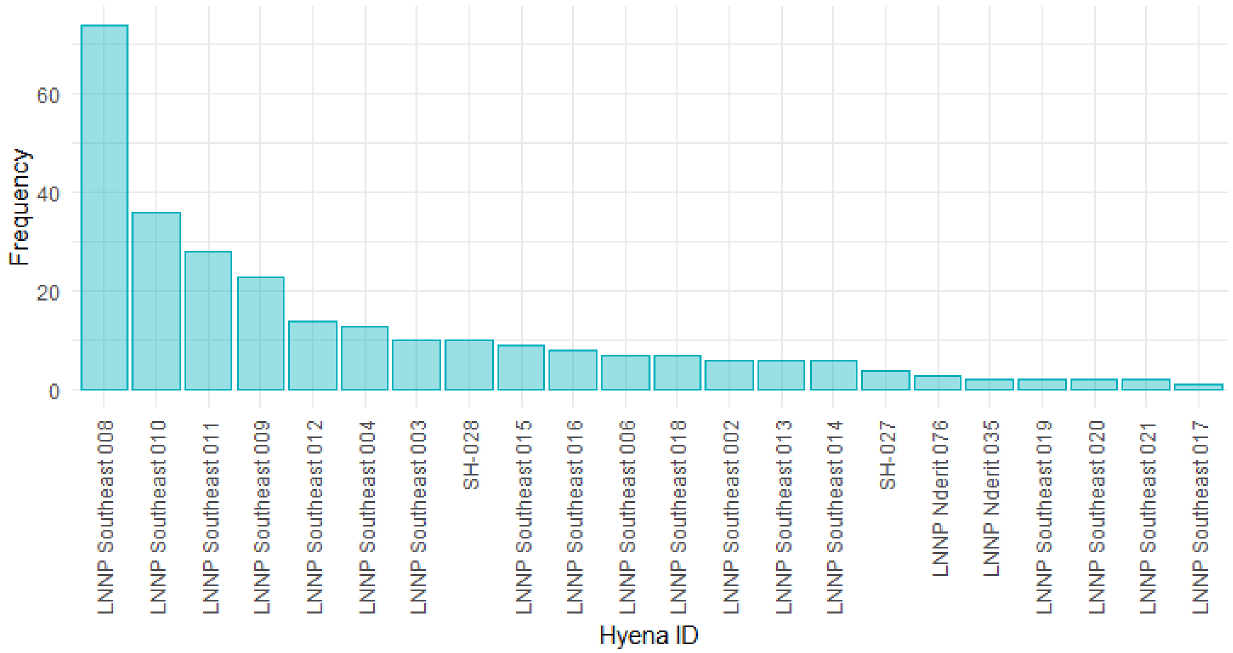
SUPPLEMENTARY FIGURE 2. FENCE PERMEABILITY

Permeable, semi-permeable, and impermeable portions of the protected area fences as revealed by Barrier Behaviour Analysis results. Permeability of other stretches of the boundaries is unknown due to lack of sufficient hyena encounters.



SUPPLEMENTARY FIGURE 3. INDIVIDUAL SPOTTED HYENAS APPEARING AT FENCE

An example showing photo frequency for individual spotted hyenas appearing at the fence at one camera site (Site C4).



SUPPLEMENTARY TABLE 1. INDIVIDUAL CASE STUDY OF COVARIATE SELECTION

Seasonal step selection of environmental and infrastructure covariates for a hyena that frequently travels between Lake Nakuru National Park and Soysambu Conservancy.

Dry season				
Variable	*coeff*	*se*	*z-value*	*p-value*
rivers_s_end	0.147	0.133	1.25	0.21
ndvi_s_end	-0.127	0.013	-11.127	<0.001
lakes_s_end	0.175	0.077	2.644	<0.01
slope_s_end	0.073	0.017	4.82	<0.001
roads_s_end	0.63	0.025	27.179	<0.001
elev_s_end	-0.154	0.043	-4.28	<0.001
bounds_s_end	0.189	0.058	3.694	<0.001
bounds_s_end:log_sl	0.020	0.003	6.165	<0.001
slope_s_end:log_sl	-0.012	0.003	-4.098	<0.001
roads_s_end:log_sl	-0.107	0.003	-33.050	<0.001
Rainy season				
Variable	*coeff*	*se*	*z-value*	*p-value*
rivers_s_end	-0.255	0.157	-1.846	0.065
ndvi_s_end	-0.010	0.015	-0.760	0.447
lakes_s_end	0.160	0.105	1.832	0.067
slope_s_end	-0.150	0.023	-7.417	<0.001
roads_s_end	0.699	0.032	23.945	<0.001
elev_s_end	-0.055	0.060	-1.039	0.299
bounds_s_end	-0.184	0.066	-3.145	<0.05
bounds_s_end:log_sl	0.061	0.005	13.923	<0.001
slope_s_end:log_sl	0.028	0.005	6.952	<0.001
roads_s_end:log_sl	-0.112	0.004	-27.810	<0.001

Chapter 5. Quantifying wildlife responses to conservation fencing in East Africa

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ABSTRACT

The fencing of protected areas is increasing worldwide. However, the implementation of fences for conservation has outpaced scientific assessment of their effectiveness, non-target impacts, and long-term costs. We assessed landscape predictors of fence crossing sites and employed camera traps over a one-year period to investigate wildlife responses to a conservation fence around Lake Nakuru National Park, Kenya. Specifically, we measured the impact of the fence on wild mammal movement, and the temporal impacts of fence maintenance on wildlife crossings and behavior. Cameras captured more than 65,000 detections of animals approaching fences, with 3,626 observed crossings over 2,818 trap nights at 19 sites. Using these data, we developed a guide to classifying fence-specific mammal behaviors. Thirty-eight wild mammal species approached known weak points in the fence, and 27 species were recorded crossing the fence. No single environmental variable predicted detection or fence crossing points for all species, but seasonality, human activity, habitat visibility, and proximity to an adjacent protected area were each correlated with species-specific crossing locations. Additionally, breaches of repaired fence-crossing locations occurred within days of maintenance. We conclude that popular, 'one-size-fits-all', conservation fence designs may be ineffective and costly for restraining movement of many wildlife species. We recommend that those deploying conservation fences start with clearly articulated management goals, that fence maintenance be informed by taxa-specific tendencies to breach fences, and that managers consider the strategic creation of wildlife corridors, overpasses, or ungulate-proof fences to link fenced protected areas with surrounding habitat.

INTRODUCTION

Protected areas are a central component of conservation, and researchers, land managers, local communities, and politicians have advocated for the fencing of these areas to better safeguard their contents and to protect people living on their edges from conflict with wildlife (Hayward and Kerley 2009, Packer et al. 2013). While fencing of protected areas, whether public or private, can be effective for reducing human-wildlife interactions and protecting animals and their habitats from unwanted incursions, these conservation fences come with significant economic and social costs (Ferguson and Hanks, 2012). Moreover, our understanding of the ecological consequences of fencing on wildlife communities is incomplete, with some species potentially benefiting over short or longer time scales (ecological 'winners'), while others may suffer (ecological 'losers'; Jakes et al. 2018, McInturff et al. 2020).

Conservation fences come in various forms but are typically composed of parallel lines of electrified wire that may be accompanied by wire mesh. As reviewed elsewhere (McInturff et al. 2020), these structures will be beneficial to some species, detrimental to others, and easily ignored or breached by many. Ultimately, the effect of a fence on a species will be shaped by a combination of features of the fence and its surrounding environment (i.e., extrinsic factors) and physical and behavioral characteristics of the species in question (i.e., intrinsic factors).

Extrinsic factors affecting fence ecology include fence construction as well as patterns of fence maintenance, surrounding habitat and soil types, human disturbance, hydrology and season. The intrinsic factors that best predict species' response to fences are often as simple as mode of locomotion, body size, agility, strength and adaptations to dig or break through or under fences (Karhu and Anderson 2006, Pirie et al. 2017). Capacity for problem-solving and searching can also be useful predictors. For example, in the case of species that seek and use fence openings created by other species (Stander 1990, Kesch et al. 2014). The interplay of intrinsic and extrinsic drivers of fence interactions is evident, for example, among primate species that exhibit extreme behavioral plasticity, physical dexterity, and a strong attraction to anthropogenic sources of foods that are often available in lands surrounding conservation areas (Fehlmann et al. 2017).

The taxa-specific permeability of fences directly and indirectly affects wildlife distributions and can ultimately lead to shifts in community structure and abundances both inside and outside of fenced areas (Cozzi et al. 2013, Massey et al. 2014). Specifically, by altering wildlife movement patterns at different spatial and temporal scales (Sawyer et al. 2020), fences can profoundly influence community composition and dynamics (Shamoon et al. 2018, Nickel et al., 2020). Fences can also affect population and community-level processes through direct mortality when wildlife become entangled in fences (Rey et al. 2012), or where predators use fences to corner or ambush prey (Dupuis-Desormeaux et al. 2016). Finally, fences may have less obvious impacts on wildlife by requiring energy expenditure to move around or through fenced areas (McInturff et al. 2020), or simply through the stress responses fences induce in wildlife as artificial, anthropogenic structures (Vanak et al. 2010). If wildlife show avoidance of fences similar to the avoidance observed in response to other anthropogenic structures and effects (Wang et al. 2017, Gaynor et al. 2018), the indirect impacts of fenced boundaries may be far reaching. In sum, the responses of wildlife to fences will be taxa-specific and even where fences may be effective in achieving conservation goals for targeted species, they may negatively impact the movement and survival of non-target species.

The fact that fences change in permeability over time as a function of maintenance investment adds yet another layer of complexity in predicting their longer-term effects on wildlife (Woodroffe et al. 2014, Massey et al. 2014). Fences are often exposed to harsh conditions and deteriorate quickly. In other cases, they may be actively sabotaged, broken down for snare wire, or simply not adequately and comprehensively maintained (Hoole and Berkes 2010). Many terrestrial wildlife species patrol fence lines until they find a weakness (Cavalcanti et al. 2012), thus even small breaches may quickly result in major changes in fence permeability (Jori et al. 2011). Even where the structural integrity of fences is maintained, temporary disruptions in electrification can result in increased fence-crossing behavior from wildlife (McKillop and Sibly 1988). In addition, many species exhibit high site fidelity to known fence crossing sites (Dupuis-Desormeaux et al. 2018), and may thus be likely to repeatedly return to dig through repaired holes. Thus, if maintenance budgets are low, as is typically the case for protected areas globally and notably in Africa (Pekor et al. 2019), fence permeability will steadily increase over time.

Assessing the long-term efficacy of conservation fences both for targeted ecological outcomes and economic sustainability is critical, yet, as outlined above, elusive (Hayward and Kerley 2009). Much remains opaque regarding how and when wildlife cross fences, and how fence maintenance alters these behaviors through time. As the call for conservation fences and fenced protected areas increases globally, site-based, quantitative assessments of wildlife responses to fences must guide decisions on when and where it is effective to employ and maintain conservation fences. Here, we summarize our effort to quantify the responses of land mammals to conservation fencing in East Africa with the targeted goals of measuring animal behavior associated with fences broadly and the effects of fence maintenance on fence-crossing behavior. Specifically, we 1) tested for landscape-level predictors of wildlife fence crossing using documented crossing locations, and 2) employed camera traps along a conservation fence to address the following questions: a) How does fence-crossing behavior vary by taxa?, b) How do anthropogenic, ecological, and temporal factors influence fence crossing behavior?, and c) To what degree does fence maintenance alter fence-crossing behavior? Additionally, we provide a practical guide to classifying mammal behaviors around fences from camera trap images with the hope of fostering more uniformity among studies in fence ecology.

METHODS

Study Area

Our research was conducted at Lake Nakuru National Park (hereafter LNNP) in the Rift Valley of southwest Kenya (0.3562° S, 36.1002° E; inset Fig. 1). LNNP (188 km^2) is one of only two fully fenced national parks in Kenya. Lake Nakuru encompasses nearly one third of the park (Elliot et al. 2020), leaving a land area of approximately 135 km^2. The park lies directly adjacent to and west of the Soysambu Conservancy (190 km^2), which is partially fenced and functions simultaneously as a private wildlife reserve and working ranch, housing 10,000 sheep, goats, and cattle. Dense agricultural settlements surround both LNNP and the adjacent conservancy, directly abutting their boundaries in many locations, and the nearby city of Nakuru, directly to the north of LNNP, is the fourth largest city in Kenya with a population of 570,000 in 2019. Lake Nakuru is classified as a UNESCO World Heritage and Ramsar site. This region supports multiple mammal species, including threatened and endangered species such as black rhinoceros (*Diceros bicornis*) and Rothschild's giraffe (*Giraffa c. camelopardalis*), as well as numerous carnivore species whose populations are stable or increasing despite heavy historical persecution (Ogutu et al., 2017). According to data on eight representative large mammal species, wildlife density inside of the national park is at least 20% higher than community lands outside (Ogutu et al. 2017), though Soysambu Conservancy maintains higher populations of most ungulates than LNNP (K. Combes, pers. comm., 5 July 2019). The region is characterized by a combination of savanna, woodland, and dense brush habitats, and experiences two major rainy seasons and two major dry seasons each year. Four rivers enter LNNP, three from the south and one from the northwest, and provide incomplete riparian corridors outside of the park.

The electrified LNNP perimeter fence was erected in 1986 to primarily "deter intruders and to keep rhinos within the sanctuary" (Lever 1990), but it is also maintained to alleviate human-wildlife conflict and demarcate the park boundary (Kenya Wildlife Service, pers.

comm.). The current fence, typical of conservation fences in sub-Saharan Africa, is 2.3m tall and consists of 11 parallel electrified wires, with low tensile barbed wire below the bottom-most wire in select areas. Some portions of the fence, particularly those adjacent to Nakuru city, have a component of woven wire mesh that extends approximately 0.6m above the ground and 1m below ground to reduce wildlife crossing through digging. The perimeter is periodically walked and maintained by park employees. Maintenance includes cutting the grass directly beneath the fence wire, filling in holes with large stones, and replacing, adjusting, or tightening loose wire. The timing of maintenance events varies considerably across the year as a function of staff availability, budgets, and access to materials.

Camera Trap Placement and Image Classification

In June 2018, we used a handheld GPS to map the LNNP perimeter fence on foot and by vehicle. While mapping, we recorded signs of mammal crossings, including holes dug under the fence or signs of digging, hair in barbed wire, loose electric wire, tracks and paths crossing under the fence, signs of crop raiding from nearby farms (e.g., corn husks strewn in paths toward the park), and animals observed crossing the fence. We also relied on the expertise of Kenya Wildlife Service (KWS) rangers to find suspected weak points on the fence and assess whether mammals had recently crossed. We conducted this survey again in October 2018 and March 2019 to assess new weak points. Through these surveys, we identified 175 crossing points in the fence. Because carnivores were of special interest due to nearby human-carnivore conflict, camera traps were placed at 19 sites along the fence (Fig. 1a) that showed recent sign of carnivore crossings (scat, hair, tracks, and size of hole), but all 175 sites appeared similar in other characteristics, including signs of digging under the fence and game trails extending in both directions into and out of the park. We deployed cameras (Bushnell TrophyCam E2, Bushnell, Overland Park, Kansas) at the 19 sites for varying periods from June 2018-June 2019, for a total of 2,818 trap nights, after malfunctioning camera periods (where camera dates automatically reset and were incorrect) were excluded (paring the data from the total 3,043 trap nights). Cameras were placed either directly on a pole of the perimeter fence or on a tree within the park facing the hypothesized crossing point. We configured the cameras for a two-exposure burst with a 15 second interval between bursts.

Photos were manually grouped by wildlife species as well as people, domestic animals, and detections of fence maintenance. Wildlife photos were placed into seven behavioral categories (Table 1): *Cross to LNNP (*2220 total images), *Cross from LNNP* (2073), *Straddle* (individuals from same group moving together on either side of the fence, 2733), *Implied cross* (observed closely approaching or trying to breach a fence opening or weak point- carnivores only, 5185), *Vigilant* (watchful directly across fence line for more than one photo burst, 1942), *Grazing/drinking* (grazing within 2m of the fence, drinking from water gathered in a hole under the fence, 14186), and *Undefined* (no indication of crossing and none of the above behaviors, 45812). If at least one individual in a photo was crossing, the photo was classified as such. Because of limitations in camera sample size and photo capture settings, the ‘straddle’ behavior was recorded only for taxa such as primates, which crossed the fence frequently, quickly, and with ease. Though exhibited by multiple taxa, ‘implied cross’ was particularly important for carnivores, as they were most likely to exhibit fast, perpendicular movements through or under the fence which reduced the likelihood of photos capturing the exact moment of their crossing. *Implied cross* was assigned to images of carnivores that satisfied the following criteria: a) the animal was seen in a perpendicular orientation to the fence actively placing head near a gap, or pushing head through a gap, b) individuals of that species had been previously captured in an ‘observed cross’ at that gap, and c) there had been no fence maintenance since the species had been captured in ‘observed cross’ previously. Thus, recording *implied cross* addressed the limitations in camera settings that prevented detection of every crossing event. Nevertheless, to ensure transparency, we provide combined and separated analyses of confirmed (‘observed cross’) and hypothesized crossings (‘implied cross’).

Data Analyses

Landscape predictors of crossing points

To test for landscape predictors of wildlife crossing locations, we ran a logistic regression using the 175 observed fence crossing points and 700 randomly generated points along the fence line, assuming no additional crossing points were created after the 175 detected during the study period. We considered the following covariates: distance to Lake Nakuru, distance to rivers, road density, cost distance to Soysambu Conservancy boundary, human population density outside the park boundary, soil type, NDVI at the fence (e.g. for foraging or ambush- Dupuis-Desormeaux et al. 2016) the difference in NDVI inside and outside the fence, slope, and elevation (Suppl. Table 1). We scaled all continuous covariate values around zero using the *scale* function in the *base* package in R, and we used the *vif* function in the *car* package in R (R Core Team, 2018) to test for multicollinearity between variables. After eliminating any collinear variables, we used the *dredge* function in the *MuMIN* package in *R* to conduct model selection, retaining model variables within 2 delta AIC of the top model for model averaging (Burnham and Anderson, 2002). We tested the robustness of the top model by bootstrapping a calculation of the area under the receiver operating characteristics curve (AUC; Pearce and Ferrier, 2000). We randomly split the data into 80% training and 20% testing data, and calculated the AUC using the *performance* function in the *ROCR* package in *R* (R Core Team 2018). We repeated this calculation 100 times, generating a range, a mean, and a standard deviation. Following Hosmer and Lemeshow (2000), we define AUC values below 0.7 as poor or unacceptable, values between 0.7 and 0.8 as acceptable, and values greater than 0.8 as good or excellent.

Crossing behaviors

To test for predictors of animal crossing behaviors at the 19 camera sites, each site was classified according to the following categorical variables: human activity (high or low), adjacency to Soysambu Conservancy (adjacent or not adjacent), fence maintenance (maintained or not), and vegetation structure directly inside and outside of the crossing point (open grassland, mixed grassland, and dense shrub/forest). Human activity at each site was classified as a binary by quantifying per trap night detections of people and livestock (which were always accompanied by a herder); sites with per trap detections greater than or equal to 1 (*n*=8), indicating presence of an average of at least one person on camera per day, were classified as high human activity, and other sites (*n*=11) were classified as low human activity (Suppl. Fig. 1). Other independent variables considered were season (rainy or dry), time of day (night: 19:21-5:30, pre-dawn: 5:31-6:40, day: 6:41-18:19, twilight: 18:20-19:20), and body size (small: ≤ 10kg, medium: > 10kg and ≤ 100kg, and large: > 100kg). For the crossing response variable, behaviors were grouped as *No*

Cross, which combined images scored as 'vigilant', 'grazing/drinking', and 'undefined'; and *Cross*, which included images scored as 'cross to LNNP' and 'cross from LNNP'. For carnivores, an additional analysis included images scored as 'implied cross' under the *Cross* designation. Because we were seeking to analyze behaviors, rather than individuals or populations, images were treated as independent regardless of timing; but if an animal's confirmed or observed crossing occurred over two photos within the same burst, the two photos were only counted as a single crossing event. This allowed for a more accurate estimate of crossing behavior. For this behavioral analysis, we used the same methods outlined in section *2.3.1* to test for multicollinearity, perform logistic regressions, determine best models (within 2 delta AIC), and retain variables for model averaging. We determined model strength by splitting data into 70% training and 30% testing data, and calculating AUC using the *predict* and *ROC* functions in the *pROC* package (R Core Team 2018).

Temporal behavior

To determine influence of temporality on crossing behavior, we combined data combining data from all camera sites and ran logistic regressions across pre-dawn, day, dusk, and night. Further, to determine temporal behavior and the temporal overlap coefficient (Dhat4 or Dhat1 depending on available behavior sample size for a particular species) for fence crossings by all species and by broad taxa across variables, we used the 'overlap' package in *R* (Meredith and Ridout 2014). The effects of season, human activity, and adjacency on temporal fence approaches and crossings of carnivores, primates, and ungulates (Suppl. Table 3) were determined by comparing the smoothed bootstrapped mean overlap coefficient (10,000 resamples) and 95% confidence intervals between variables.

Fence maintenance and crossing behavior

The effects of fence maintenance were analyzed by subsetting the data from the 19 camera sites to equivalent periods before and after each maintenance event (these periods varied from 2-14 days before and after, dependent on camera and battery functionality), measuring daily confirmed and implied fence crossing behavior before and after maintenance, and conducting non-parametric χ^2 and Mann-Whitney U tests to determine differences in overall and site-level detections and crossings in the periods before and after maintenance.

RESULTS

Landscape predictors of fence-crossing

Following model selection, we identified three candidate models within 2 delta AIC of the top model, which included the following variables: NDVI at the fence, distance to rivers, distance to Lake Nakuru, slope, elevation, soil type, cost distance to the neighboring Soysambu Conservancy, and human population density (Suppl. Table 2). Soil type, NDVI, and distance to water were the strongest predictors. The weighted top model had a mean bootstrapped AUC of 0.73, indicating an acceptable, but not good or outstanding, diagnostic of the model.

Assessment of crossing behavior

The 19 camera traps placed along the conservation fence recorded 65,560 photos of terrestrial mammals, with an average of 22.33 ($\sigma = 12.8$) non-independent detections per trap night for all sites combined. Thirty-eight non-domestic mammal species (Suppl. Table 3) were detected (classified into ungulates: 12.9 detections/trap night on average; primates: 5.1 detections/trap night on average; carnivores: 5.2 detections/trap night on average; and aardvarks, hares, and rodents: 0.48 detections/trap night on average; Fig. 1b), and 27 of these species were recorded crossing the fence. Cameras at 17 of the 19 sites detected human-associated activity, such as people, fence maintenance, and livestock (1.5 detections per trap night on average) near the fence. Of the 11 species that did not cross the fence, most were ungulates (Suppl. Table 3). When including *implied cross*, the highest cross-to-detection ratio was seen in bat-eared fox (*Otocyon megalotis*) and spotted hyena, followed by all carnivore species except genet (*Genetta genetta*), mongoose (*Ichneumia albicauda* and *Herpestes ichneumon*), and caracal (*Caracal caracal*; Fig. 2). The average ratio of crossing to total detections (Suppl. Table 4) across all species was 0.06 for confirmed crossings (*Cross*), and 0.14 when implied crossing behavior (*Implied cross*) was included for carnivores.

Models based on the camera data revealed that adjacency to the Soysambu Conservancy, body size, and vegetation inside the fence at the camera site were the strongest predictors of fence crossing in binomial logistic regressions (Fig. 3a, Suppl. Table 4). After testing for multicollinearity, the best model for all taxa combined (AUC = 0.834, Cross:No Cross = 3626:59365) retained all variables except fence maintenance. The strongest model for carnivores (AUC = 0.66, Cross:No Cross = 1232:13070) retained adjacency to Soysambu, body size, time of day, season, fence maintenance, and vegetation outside the fence at the camera site. The strongest carnivore model that included the *implied cross* detections retained human activity, body size, time of day, season, fence maintenance, and vegetation outside the fence at the camera site, and showed an improved model fit (AUC = 0683, Cross:No Cross = 6130:8172). When including the *implied cross* behavior for carnivores, the effect of season flipped from negative to positive, the effects of maintenance increased, the effects of body size and vegetation outside the fence crossing point were weaker, and the positive effect of adjacency nearly halved (Fig. 3b, Suppl. Table. 4). The strongest model for ungulates (AUC = 0.902, Cross:No Cross = 225:34850) retained body size, time of day, adjacency to Soysambu, and season. The strongest model for primates (AUC = 0.676, Cross:No Cross = 2112:9955) retained human activity, season, and vegetation inside and outside the fence at the crossing point. When combining all taxa, mammals were significantly less likely (OR = .749, $p < .001$) to engage in crossing behavior at sites of low human activity than at sites of high human activity (Fig 3, Suppl. Table 4).

Temporal behavior

From our logistic regression result, primates and ungulates were more likely to cross during the day, while carnivores were more likely to cross during the pre-dawn (Suppl. Table 4). Yet, at four sites that were directly adjacent to the conservancy with no road between the two protected areas (C2, C3, C4, C19), carnivores were less likely to cross at night (proportion of crossings = .6) than animals seen crossing at the adjacent sites (prop. of crossings at night = .87). Overlap analyses were pooled across the full study period after no seasonal differences in temporal behavior were found for any taxa. Overall, overlap analyses suggested that fence crossing behaviors coincided with other behaviors near fences for most species, yet there were notable exceptions for several species (Suppl. Fig. 2; Appendix S1). At sites of low human activity, carnivores showed more overall diurnal crossing behaviors than non-crossing behaviors (which were largely crepuscular and nocturnal); primates, meanwhile, exhibited marked noon-centered behaviors at sites of high human activity (Suppl. Fig. 3). Additionally, carnivores showed a trend of crossing out of LNNP in the evening, and crossing into LNNP in the morning (Suppl. Fig 4).

Fence maintenance and crossing behavior

Camera data showed that 5 of the 19 sites experienced instances of fence maintenance (repair of wildlife crossing holes), for a total of 14 fence maintenance events. Fence maintenance events had no consistent impact on wildlife crossing ($W = 115$, $p = 0.43$) or overall detections ($W = 102.5$, $p = 0.84$) when combining all taxa. Both mammal detections and crossings increased in about half of post-maintenance events (Suppl. Fig. 5). Carnivores were the only group with a cumulative decrease in detections post-maintenance (before: 1,162 detections, after: 614 detections), yet the decrease was not significant at the site level ($W = 116$, $p = 0.42$). Primates, rodents, and lagomorphs were cumulatively more likely to cross after fence maintenance events, while carnivores and ungulates were less likely to cross immediately post-maintenance (Pearson's $\chi^2 = 26.67$, $p < 0.001$).

DISCUSSION

Our results revealed that the majority of mammal species detected by camera traps in Lake Nakuru National Park regularly crossed the park's boundary fence to and from the surrounding human-dominated landscapes. This suggests that many animals occurring within the park are subsidized by resources they acquire outside of its boundaries, or vice versa. Our methods offer a novel approach for quantifying wildlife responses to fencing, and our findings are consistent with surveys and frequent observations that report wildlife regularly passing in and out of the park (Kassilly et al. 2008, but see also Elliot et al. 2020). Our findings also echo indirect assessments that have shown fences are permeable to many wildlife species elsewhere in Africa (e.g., Pirie et al. 2017).

Of the 27 mammal species we recorded crossing the fence, carnivores and primates crossed most frequently, and crossing behaviors were strongly predicted by microhabitat at the crossing point, body size, and adjacency to the nearby Soysambu Conservancy. This result supports other studies that have shown primates and carnivores frequently move over, under, and through fence lines (Pirie et al. 2017). Most ungulates, on the other hand, faced difficulties crossing. To our surprise, crossing frequency was unaffected by temporal patterns of fence maintenance. Below, we discuss the importance of these findings for animal behavior, conflict, connectivity, and conservation planning around fences.

Landscape predictors of fence crossing

In our landscape-scale study of predictors of fence-crossing locations, our analysis yielded only a moderately strong model, with soil type and water proximity among the strongest predictors. Having a model with only a moderately strong fit suggests that the factors affecting wildlife crossing sites varied sufficiently by species, space, and time to inhibit strong overarching predictions. Nevertheless, we conclude from this model that fences placed in soil types that are amenable to digging will require constant investment in maintenance (Kesch et al. 2014). Even if managers install and bury mesh or other specialized material to inhibit digging, maintenance will still be required (Hoare 1992, Gusset et al. 2008). Finally, due to their topography, rivers and smaller waterways provide easy crossing points under fences for animals, even for very large-bodied species such as Cape buffalo (*Syncerus caffer*). In our study area, as for many others (e.g., Jori et al. 2011), fences placed along or crossing waterways were prone to degradation due to the physical disturbance and erosion caused by running water in the rainy season, which gave way in the dry season to sunken riverbeds or small rivulet-caused dips that served as wildlife highways beneath fences. Soil type was our variable most associated with erosion-potential, and was one of the strongest predictors of fence gaps in our model. NDVI, meanwhile, may have factored strongly in our model due to certain species using the fence for foraging or ambush (Dupuis-Desormeaux et al. 2016). Future studies may have more success in identifying landscape correlates of crossing points by focusing on crossings observed in a single season or by a targeted subset of species rather than combining all points that showed evidence of crossing by any species.

The vegetative cover at crossing point factored strongly in the best models for primates, carnivores, and all taxa combined, indicating that microhabitat was an important component of whether and where an animal chose to cross the fence. Carnivores and all taxa combined preferred crossing points with dense vegetation outside of the park (as opposed to open or mixed), and primates preferred crossing points with mixed vegetation inside of the park (as opposed to open or dense). This could be because wildlife prefer predictable cover when crossing out of the park into a risky landscape, while they may prefer not to cross into dense cover within the park where there is more risk of ambush by wild predators (see Boinski et al. 2003, Stears and Shrader 2015). The act of crossing underneath the fence wire inherently requires at a minimum a brief moment of vulnerability, including the hazard of being stuck in the wire, and wildlife may be choosing microhabitat to mediate their risks during the crossing moment. Due to the likely importance of immediate cover, managers seeking to maximize connectivity by opening up portions of the fence may consider locating several small but safe microhabitat crossings rather than focusing money and effort on a few longer stretches of fence that aim toward broader landscape variables.

Wildlife crossing by taxa

Detections from our 19 camera traps revealed that nearly all of the larger (i.e., > 1kg) mammal species known to occur in the national park were seen at the fence line, and most of the species that approached the fence also crossed. Species that did not cross the fence nonetheless exhibited marked interest in gaps and holes (i.e., were recorded pointedly approaching gaps), but apparently could not easily pass through them. This hypothesis is supported by other studies that have shown wildlife may spend considerable time seeking to breach fences (Connolly et al. 2009) even if they are likely to be unsuccessful due to body size and lack of agility (Mbaiwa and Mbaiwa 2006).

Our use of cameras and a precise classification scheme for fence-specific behaviors allowed us to build an understanding of detailed movements and behavioral patterns of select species around the fence line. For example, many carnivores recorded in our study appeared to exit the park during the evening and returned in the morning. The change in model results when including *implied cross* for carnivores also suggests that fine-scale timing of fence crossings (i.e. hesitancy) may be influenced by ecological and anthropogenic variables. Though carnivores may be able to adapt to and even thrive in human-dominated areas (Chapron et al. 2014), they may need nearby protected areas to serve as a population source (Lamb et al. 2020) or as a temporal refuge from human influences and persecution (Gaynor et al. 2018). The fact that carnivores appear to regularly utilize areas shared by local human communities emphasizes the necessity of community engagement, education, and interventions aside from fences to ensure their persistence, as has also been noted in areas surrounding unfenced protected areas (Dickman et al. 2014, van Eeden et al. 2018). Finally, the ease with which primates crossed the electrified fence, particularly baboons (*Papio anubis)* and vervet monkeys (*Chlorocebus pygerythrus*), both by digging underneath and climbing over and through, raises the question of whether restricting their movements is ever a realistic goal of conservation fencing. Our study is far from alone in reporting such a result; in fact, in their survey of the relevant literature, Junker et al. (2019), could find no evidence of fences containing baboons (*Papio* sp.) or other cercopithecine monkeys.

Anthropogenic and ecological factors influencing crossing behavior

Within the 19 camera trap sites, mammals showed more likelihood of exhibiting crossing behavior at sites that were adjacent to Soysambu Conservancy, but also preferred to cross (rather than exhibiting other behaviors) at sites with high human activity. Adjacency to Soysambu appeared to be one of the strongest drivers of crossing behavior within the 19 sites, yet the pattern of crossing preference at sites of high human activity held true even for camera trap sites that were not adjacent to the conservancy. Analysis of the camera data revealed no strong overall predictors of crossing behavior at specific sites for all primates or all carnivores. Ungulates, however, showed a strong relative increase in crossing behavior at camera trap sites adjacent to the neighboring Soysambu Conservancy, and this appeared to drive the all-taxa model. This pattern matches our prediction because the conservancy is a large tract of protected habitat that might also serve as a corridor to other protected lands to the southeast. Furthermore, while most carnivores and primates in LNNP are capable of tolerating and utilizing adjacent human-dominated areas (Fehlmann et al. 2017, Pirie et al. 2017), attractive surrounding habitat for ungulate species may be limited to the conservancy. Future studies in this region and elsewhere should further assess ecological and anthropogenic drivers of fence crossing through deployment of additional cameras for a longer study period.

Temporality of wildlife crossing

Our results showed contrasting temporal trends in fence crossing behavior. At a seasonal scale, primates and carnivores were less likely to cross in and out of the park in the rainy season than in the dry season, contrary to what we expected given that animals in arid landscapes tend to move farther in the rainy season when they are less restricted by access to water (Kesch et al. 2014, Koziarski et al. 2016). It is possible that better foraging opportunities in the park during the rainy season make staying in the park a more attractive option at this time, but additional research is required to test this idea.

Surprisingly, primates and ungulates appeared to be most active in the middle of the day at sites with high human activity, for crossing and other behavior. This is in contrast to carnivores in this study, as well as other studies that have found human activity pushes wildlife to be more nocturnal (Gaynor et al. 2018). It is likely that human activity, which was highest in the early morning and early evening at these camera sites, was pushing primate and ungulate activity into the heat of the day. This might have negative consequences for energetics of the affected species, since crossing a fence is inherently risky, but crossing at noon on the equator is likely much more energetically costly than doing so at other times of the day (see McFarland et al. 2019). Additionally, many primate and ungulate species appeared to rely on a thin line of habitat along the inner boundary of the park for grazing and other needs, and human activity outside of the fence impacted the temporality of their non-crossing behaviors even within the park. Human activity thus seemed to attract crossings spatially but altered crossings and other behaviors temporally. Designated buffer zones of wildlife habitat and vegetation around fenced protected areas, rather than allowing human development to directly abut the fence, may allow wildlife to maintain their normal temporal activity without being impacted or influenced by people.

Fence Maintenance

We found little evidence for the effectiveness of fence maintenance in stopping or even slowing wildlife crossings. After maintenance occurred, wildlife tended to resume crossing at the same site within 24 hours, and in some places, crossings increased in the period following maintenance. The small number of maintenance events and maintained sites in our study likely contributed to the absence of clear patterns in our results. Maintenance events were intermittent and without predictability, and there were relatively few maintenance events (14) over the course of the study, leading to a limited dataset from which to draw conclusions about maintenance effects. However, it is clear from our camera detections that wildlife exhibited strong fidelity for crossing points, as shown at another site in Kenya (Dupuis-Desormeaux et al. 2018). In our study, digging species, such as spotted hyena, were commonly seen undoing maintenance efforts (typically by moving stones placed in fence gaps) within hours of their execution. This suggests that at least some species would rather exert energy breaking through or digging in a well-used crossing site than creating a new hole elsewhere, a concern that has been raised in the past (Hoare 1992) but not quantified until now. The tenacity of wildlife seeking to cross a given fence segment, the well-noted challenges of supporting regular fence maintenance efforts (Pekor et al. 2019), and the lack of a clear effect of maintenance in reducing wildlife crossing suggest protected area managers should carefully consider the opportunity costs of erecting new fences (Durant et al. 2015). As has been argued elsewhere (e.g., Creel et al. 2013), conservation funding targeted for fencing may have greater positive impact when applied instead to manage buffer areas and engage local communities to foster human-wildlife coexistence (Dickman et al. 2014)

Measuring the Effectiveness of Conservation Fencing

Any rigorous study of conservation fencing will likely show a mix of successes (e.g., containment of focal species, reduction of human activity) and failures (e.g., unabated crop raiding, negative impacts on non-focal species); thus, perhaps the fairest assessment of a fence’s efficacy is a comparison of outcomes in relation to the stated goals of fence construction

(McInturff et al. 2020). However, identifying the exact goals of fencing is often difficult, particularly when fences have been in place for decades. Several justifications have been put forth for the construction and maintenance of the perimeter fence at LNNP. One original goal of the fence was to prevent rhinoceros and Cape buffalo from entering community lands, which it appears to have largely achieved, with the exception of one consistent buffalo crossing point. Our findings suggest other large ungulates, such as eland (*Taurotragus oryx)* and zebra, are also mostly contained within the park's fence, though they too were recorded crossing on several occasions. A second stated purpose of the fence was to prevent carnivore-livestock and primate-crop interactions (Kassilly et al. 2008). Our results suggest the fence is not effectively performing this function. Baboons and vervet monkeys cross the fence each day and baboons were regularly reported crop-raiding in nearby farms (Kenya Wildlife Service, pers. comm.). Furthermore, we documented that every large carnivore species in LNNP crossed the perimeter fence. Regardless of the biological realities, nearby human communities perceive the fence as being effective at containing wildlife (C. Wilkinson, unpub. data), and perceptions can be a key component to alleviating human-wildlife conflict (Dickman et al. 2014, Ohrens et al. 2019). The efficacy of the fence in achieving the goal that most directly inspired its original creation at LNNP, to prevent poaching of rhinoceros (Lever 1990), was not analyzed in this study and would be difficult to decouple from the effects of other anti-poaching activities of the Kenya Wildlife Service.

CONCLUSIONS

Contrary to previous assertions (Kassilly et al. 2008, Elliot et al. 2020), we found that a diverse array of wildlife readily found their way in and out of Lake Nakuru National Park. Some may interpret this finding as suggesting fences have fewer ecological impacts than is often claimed, however, it may also undermine justifications for investment in fences in the first place. Ultimately, measures of success and failure with regard to conservation fencing will be context-dependent and only relevant where the intended goals of fencing are clearly articulated (e.g., written into management plans) and regularly revisited over time. The outlined goals for a particular conservation fence should identify and differentiate between species and processes within an ecosystem the fence is intended to contain from those for which ongoing permeability or connectivity is desired. Such forward-thinking and inclusive planning will require a detailed understanding of the responses of a diversity of species to different types of conservation fences over space and time. Ideally, an integration of ecological and economic costs and benefits of conservation fences, as well as analyses of potential alternatives to fences such as community outreach or the creation of buffer areas, will prevent short-sighted, short-lived, and ineffective fencing efforts.

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FIGURE 1. STUDY AREA MAP

A map of Lake Nakuru National Park (188 km^2) in western Kenya showing: A) sites of year-long camera trapping efforts and recorded weak points in the park's barrier fence, and B) per trap night detections and crossings of wild mammal taxa at camera sites over the study period.

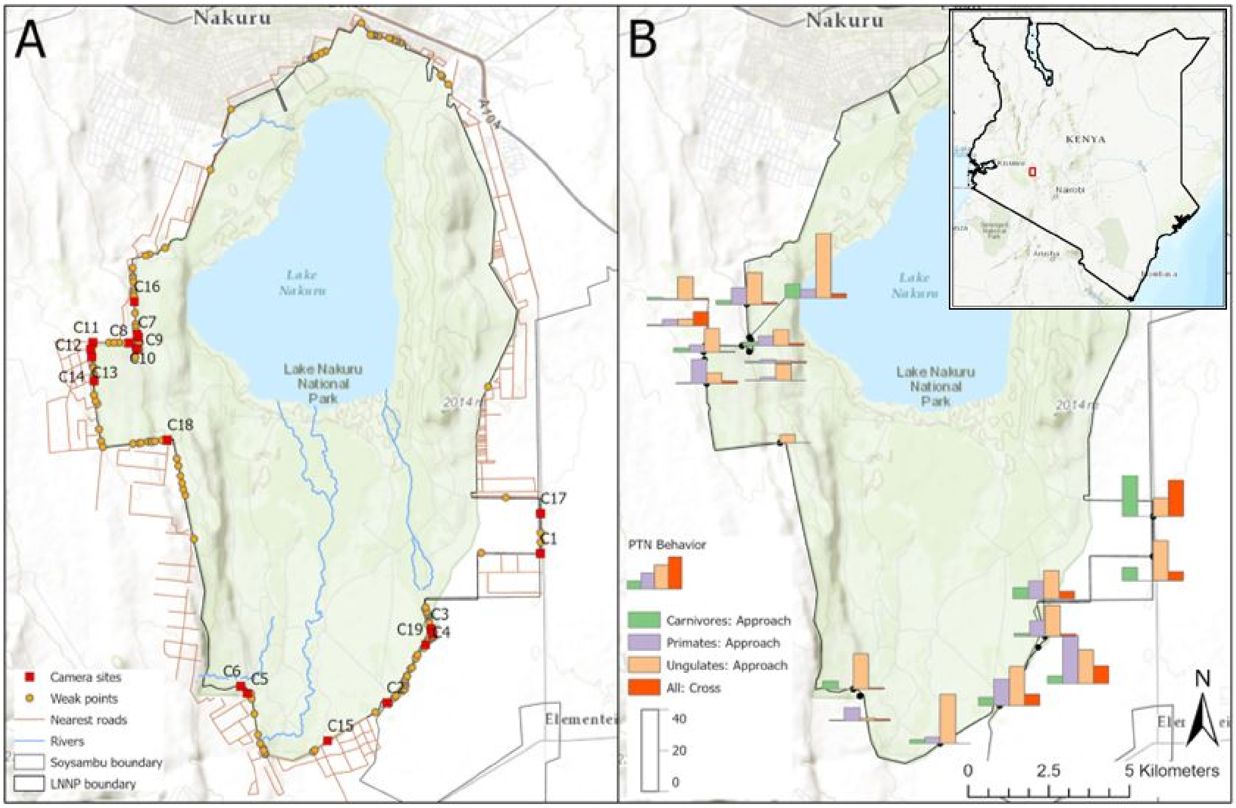


TABLE 1. MAMMALIAN FENCE-SPECIFIC BEHAVIORS

Classification of fence-specific mammal behaviors.

Behavior	Description	Applicable Taxa	Example
Undefined	Animal does not cross or exhibit any of the other classified behaviors	All taxa	
Cross into protected area	- Animal is seen on camera crossing into the national park OR - In 2-photo burst, animal is first outside of the park and then inside, with dust, etc. indicating motion through the fence	All taxa	
Cross out of protected area	- Animal is seen on camera crossing out of the national park OR - In 2-photo burst, animal is first inside of the park and then outside, with dust, etc. indicating motion through the fence	All taxa	

Straddle	- Animals of the same species are captured in one photo moving in parallel along opposite sides of the fence	All taxa, though more likely for social species	
Implied cross	- Animal actively tries to breach the weak point by sniffing, putting nose or other parts of body into gap AND - The same species was previously recorded crossing at this point and fence maintenance has not occurred	Carnivores	
Grazing/Drinking	- Animals graze within 2m of the fence OR - Animals drink from water pooled or flowing through the weak point hole	Grazing: Ungulates Drinking: All taxa	
Vigilant	- Animal spends two or more consecutive 2-photo bursts standing and looking perpendicularly across the fence line with no other movement or behaviors	All taxa, though most visible and classifiable in species with medium to large body sizes.	

FIGURE 2. FENCE CROSSINGS BY MAMMALS

The ratio of observed and implied fence crossings to the total number of camera detections, in ranked order, labeled with total detections for each species. Light blue bars (shown for carnivores only) indicate cross:detection ratio where confirmed and implied cross behaviors have been combined, for carnivores only. Darker blue bars (shown for all species) indicate cross:detection ratio that includes only confirmed cross behaviors. Species with detection sample sizes lower than 60 have been excluded.

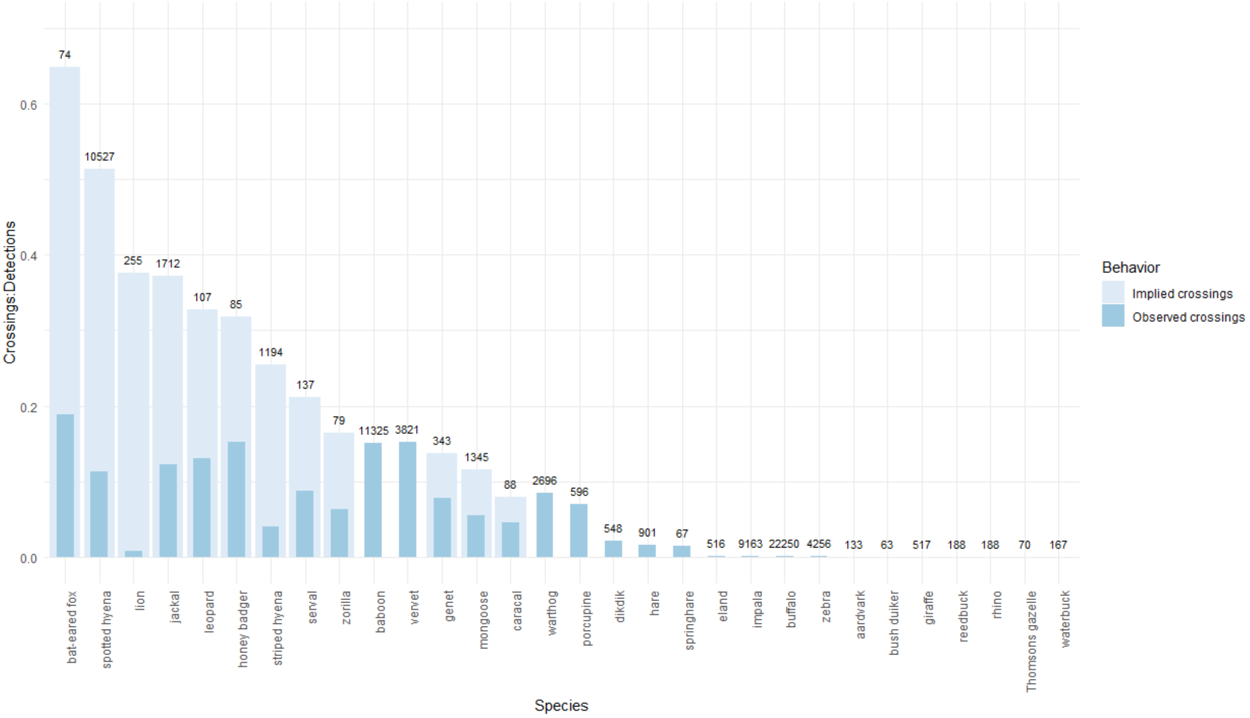
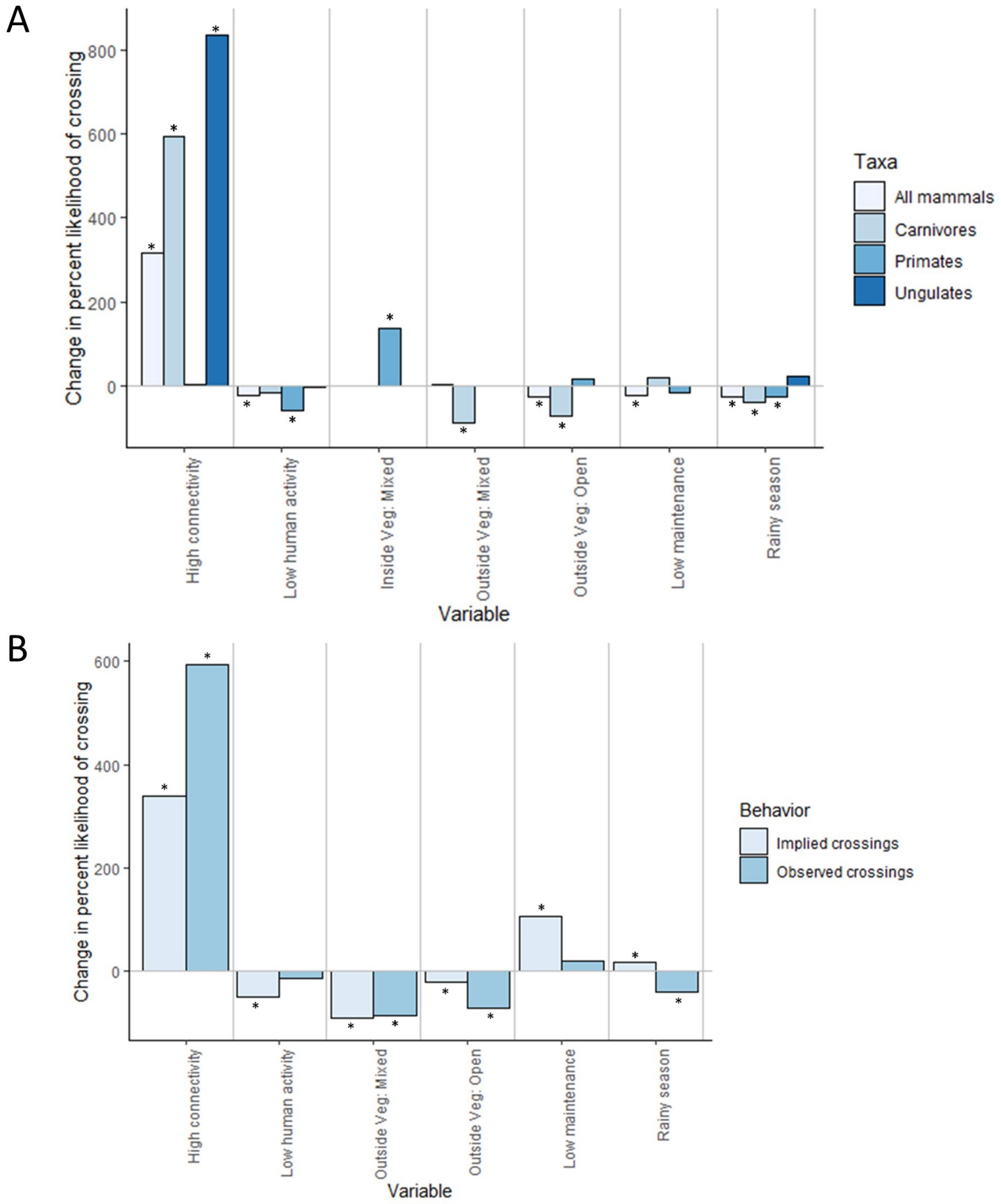


FIGURE 3. FENCE CROSSING ACROSS COVARIATES

(A) Percent likelihood ((odds ratio-1)*100) of crossing after model averaging for each modeled group with binomial response variables *Cross Only* ("Cross to LNNP" and "Cross from LNNP" combined) and *No Cross* ("Vigilant", "Grazing/Drinking", and "Undefined") and (b) percent likelihood of crossing for carnivores showing results where implied crossing behavior is also included in *Cross Only*. * indicates variable significance ($p < 0.001$). Inside and outside microhabitat vegetation both have a reference category of "dense". Other reference categories, in order, are "high connectivity", "high human activity", "high maintenance", "dry season".



SUPPLEMENTARY TABLE 1. PREDICTOR VARIABLES TESTED FOR FENCE WEAK POINTS

Variables tested as predictors of fence crossing points.

Variable	**Calculation**	**Hypothesized effect on crossing point likelihood**	**Resolution**
Distance to Lake Nakuru	Euclidean distance from Lake Nakuru	Positive. We expected greater likelihood of crossing further from the resource abundant lake shores	10m
Distance to rivers	Euclidean distance to major rivers	Positive. We expected resource scarcity further from rivers that would drive fence crossing	10m
Cost distance to Soysambu Conservancy	Cost distance, with fenced cells receiving a cost of 10 and all other cells a cost of 1	Negative. We expected a higher crossing likelihood near Soysambu Conservancy, whose resources might attract animals	10m
Human population density outside the park	Mean population density within 1km of each cell	Negative. We expected animals to avoid crossing points near dense human populations	100m
Road density	We calculated a kernel density of roads within 1km of each cell	Negative. We expected road traffic to deter crossings	30m
Soil type	Raw soil classification data	Categorical. We expected clayey and very clayey soils to be more difficult to cross than sandy and loamy soils	225m
NDVI at the fence	Mean NDVI value within 1km of each cell	Positive. We expected higher NDVI to motivate fence crossings	30m
Difference in NDVI inside and outside the fence	For each cell, we calculated the mean NDVI within 1km inside and outside the fence, and	Negative. When NDVI was higher inside than outside the fence, we expected fewer crossings	30m

	then subtracted the values outside from those inside		
Slope	Raw values	Negative. We expected steeper slopes to create more difficult crossings	30m
Elevation	Raw values	Positive. We expected higher elevations and their associated forested vegetation structure along the inside and outside of the fence to facilitate crossings	30m

SUPPLEMENTARY TABLE 2. VARIABLES ASSOCIATED WITH FENCE CROSSING POINTS

Model average values of variables retained after model selection of fence crossing points

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	Z-value	p-value
Intercept	-0.758	0.469	0.219	1.004	0.389	-1.949	0.051
NDVI at the fence	1.867	6.469	2.895	14.454	0.410	4.551	<0.001
Distance to river	1.835	6.264	3.554	11.038	0.289	6.347	<0.001
Elevation	-1.429	0.240	0.119	0.482	0.356	-4.010	<0.001

Distance to lake	1.334	3.795	2.354	6.117	0.244	5.476	<0.001
Cost distance to Soysambu	<0.001	1.000	0.999	1.001	<0.001	1.824	0.068
Road density	-0.465	0.628	0.464	0.851	0.154	-3.008	0.003
Slope	0.337	1.401	1.076	1.824	0.135	2.506	0.012
Human population density outside the park	0.133	1.113	0.805	1.621	0.178	0.748	0.455
Sandy soil (very clayey soil as reference)	1.933	6.907	1.884	25.324	0.663	2.915	0.004
Clayey soil (very clayey soil as reference)	-0.946	0.388	0.125	1.204	0.577	-1.638	0.101

Loamy soil (very clayey soil as reference)	0.862	2.367	1.220	4.593	0.338	2.547	0.011

SUPPLEMENTARY TABLE 3. MAMMAL FENCE CROSSINGS AND DETECTIONS

Total fence crossings and overall detections of mammals along the Lake Nakuru National Park barrier fence during the study period (including photos with incorrect dates). Carnivore fence crossings include a range from observed crossing behavior only ("Cross to LNNP" and "Cross from LNNP") to implied and observed crossing behavior combined. Both mongoose species and both rhinoceros species were grouped as "mongoose" and "rhinoceros", respectively, for crossing analyses. * indicates species were observed crossing the fence at least once during the study period (see Methods). [ ] indicates values from images with correct dates only.

Species	**Taxonomic Group for Analysis**	**Crossing Detections**	**Total Detections**
Aardvark (*Orycteropus afer*)	Afrotheria	0	134 [123]
Bat-eared fox (*Otocyon megalotis*)*	Carnivore	8-33	67
Black-backed jackal (*Canis mesomelas*)*	Carnivore	210-641 [200-623]	1735 [1639]
Caracal (*Caracal caracal*)*	Carnivore	4-7	88
Common genet (*Genetta genetta*)*	Carnivore	27-47	348
Egyptian mongoose (*Herpestes ichneumon*)*	Carnivore	75-160 [74-149]	1357 [1266]
White-tailed mongoose (*Ichneumia albicauda*)*	Carnivore		
Honey badger (*Mellivora capensis*)*	Carnivore	13-28	85
Leopard (*Panthera pardus pardus*)*	Carnivore	14-35 [13-33]	107 [85]
Lion (*Panthera leo*)*	Carnivore	2-96 [1-86]	255 [232]
Serval (*Leptailurus serval*)*	Carnivore	12-29 [12-27]	137 [135]

Spotted hyena (*Crocuta crocuta*)*	Carnivore	1190-5510 [835-4826]	10521 [9390]
Striped hyena (*Hyaena hyaena*)*	Carnivore	49-305 [40-258]	1191 [1004]
Side-striped jackal (*Canus adustus*)*	Carnivore	0-1	2
Zorilla (*Ictonyx striatus*)*	Carnivore	5-13	79
African hare (*Lepus victoriae*)*	Lagomorph	15	895 [781]
Baboon (*Papio anubis*)*	Primate	1703 [1575]	11309 [8897]
Blue monkey (*Cercopithecus mitis*)*	Primate	1	3
Mantled colobus (*Colobus guereza*)*	Primate	2 [0]	4 [0]
Vervet (*Chlorocebus pygerythrus*)*	Primate	584 [536]	3811 [3580]
Porcupine (*Hystrix cristata*)*	Rodent	42 [41]	596 [587]
Springhare (*Pedetes surdaster*)*	Rodent	1	67
Black rhinoceros (*Diceros bicornis*)	Ungulate	0	88 [87]
White rhinoceros (*Ceratotherium simum*)	Ungulate		
Bohor reedbuck (*Redunca redunca*)	Ungulate	0	188
Bushbuck (*Tragelaphus sylvaticus*)	Ungulate	0	31
Bushpig (*Potamochoerus larvatus*)	Ungulate	0	13
Cape buffalo (*Syncerus caffer*)*	Ungulate	29 [22]	22181 [19465]
Common duiker (*Sylvicapra grimmia*)	Ungulate	0	63 [59]
Common zebra (*Equus quagga*)*	Ungulate	5 [3]	4234 [3927]
Eland (*Taurotragus oryx*)*	Ungulate	1 [1]	506 [448]
Hippopotamus (*Hippopotamus amphibius*)	Ungulate	0	4
Impala (*Aepyceros melampus*)*	Ungulate	13 [11]	9232 [7827]
Kirk's dikdik (*Madoqua kirkii*)*	Ungulate	12 [10]	552 [485]

Rothschild's giraffe (*Giraffa camelopardalis rothschildi*)	Ungulate	0	511 [480]
Thomson's gazelle (*Eudorcas thomsonii*)	Ungulate	0	70 [68]
Warthog (*Phacochoerus africanus*)*	Ungulate	229 [178]	2727 [2377]
Waterbuck (*Kobus ellipsiprymnus*)	Ungulate	0	172 [88]

SUPPLEMENTARY TABLE 4. VARIABLES ASSOCIATED WITH CROSSING BEHAVIORS

Model average values of variables retained after model selection of crossing behaviors (Cross/No Cross) for each taxonomic group analyzed. A = all mammals, B = ungulates, C = primates, D = carnivores (observed cross), and E = carnivores (observed and implied cross). Reference categories = "high human activity", "dry season", "time of day: day", "low connectivity", "Inside veg: dense", "Outside veg: dense", "body mass: large", and "fence maintained".

A.

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	z-value	p-value
Intercept	-1.96	0.14	0.126	0.156	0.05	-37.12	<.001
Low human activity	-0.29	0.749	0.683	0.82	0.05	-6.2	<.001
Rainy season	-0.29	0.746	0.695	0.801	0.04	-8.03	<.001
Time of day: night	-0.81	0.443	0.408	0.48	0.04	-19.63	<.001
Time of day: predawn	-0.45	0.638	0.52	0.773	0.1	-4.47	<.001
Time of day: twilight	-0.42	0.658	0.528	0.813	0.11	-3.79	<.001
High connectivity	1.42	4.146	3.777	4.556	0.05	29.72	0.05
Outside vegetation: mixed	0.01	1.011	0.852	1.194	0.09	.12	0.9
Outside vegetation: open	-0.29	0.747	0.687	0.813	0.04	-6.77	<.001
Avg. body size: kg	-0.01	0.99	0.9896	0.991	0	-20.8	<.001

B.

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	z-value	p-value
Intercept	-5.067	0.006	0.004	0.01	0.241	21.04	<.001
Low human activity	-.006	.963	.716	1.293	0.063	0.1	.921
Rainy season	0.121	1.225	.933	1.61	0.147	0.825	0.409
Time of day: night	-3.065	0.047	.031	0.069	0.201	15.273	<.001
Time of day: predawn	-2.24	0.106	.034	0.335	0.584	0.584	<.001
Time of day: twilight	-1.173	0.31	.178	0.538	0.282	4.162	<.001
High connectivity	2.235	9.347	5.909	14.786	0.147	9.553	<.001
Body mass: medium	-1.911	0.148	.078	0.279	0.323	5.911	<.001
Body mass: small	1.575	4.831	2.263	10.316	0.387	4.07	<.001

C.

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	z-value	p-value
Intercept	-1.606	0.201	0.173	0.233	0.077	20.874	<.001
Low human activity	-0.918	0.399	0.281	0.567	0.179	5.126	<.001
Rainy season	-0.323	0.724	0.654	0.802	0.052	6.218	<.001
High connectivity	0.006	1.029	0.833	1.271	0.05	0.119	0.906
Outside vegetation: mixed	-0.016	0.985	0.684	1.417	0.186	0.084	0.933
Outside vegetation: open	0.143	1.154	1.024	1.301	0.061	2.346	0.019
Inside vegetation: mixed	0.855	2.351	2.015	2.741	0.078	10.891	<.001
Body mass: small	-0.358	0.699	0.606	0.806	0.073	4.924	<.001

Fence not maintained	-0.05	0.817	0.446	1.494	0.176	0.284	0.777

D.

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	z-value	p-value
Intercept	-5.552	0.004	0.001	0.028	1.014	5.475	0.028
Low human activity	-0.171	0.842	0.647	1.098	0.135	1.27	0.204
Rainy season	-0.524	0.592	0.522	0.671	0.064	8.184	<.001
Time of day: night	-0.474	1.623	0.478	0.811	0.135	3.519	<.001
Time of day: predawn	0.013	1.013	0.731	1.405	0.167	0.08	0.936
Time of day: twilight	-0.415	0.661	0.452	0.964	0.193	2.148	0.032
High connectivity	1.936	6.93	5.33	9.009	0.134	14.458	<.001
Outside vegetation: mixed	-2.102	0.122	0.044	0.338	0.52	4.045	<.001
Outside vegetation: open	-1.286	0.276	0.227	0.337	0.101	12.718	<.001
Body mass: medium	3.25	25.97	3.615	184.08	1.003	3.242	0.001
Body mass: small	3.667	39.116	5.412	282.686	1.009	3.633	<.001
Fence not maintained	0.131	1.191	0.977	1.45	0.115	1.136	0.256

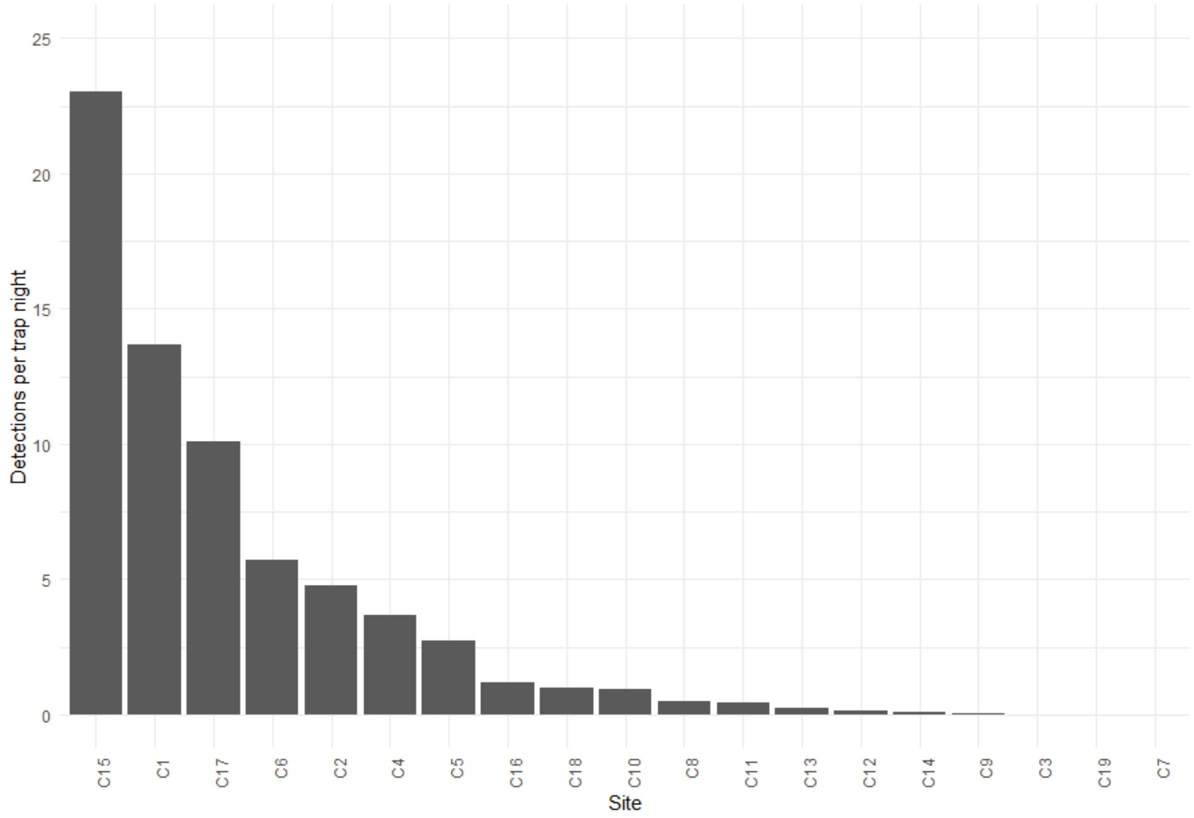
E.

Variable	Estimate	Odds ratio	Odds ratio lower CI (2.5%)	Odds ratio upper CI (97.5%)	Standard error	z-value	p-value
Intercept	-1.81	0.163	0.115	0.23	0.18	-10.31	<.001
Low human activity	-0.69	0.499	0.427	0.584	0.08	-8.66	<.001
Rainy season	0.15	1.158	1.086	1.245	0.04	3.99	<.001

Time of day: night	-0.31	0.734	0.615	0.876	0.09	-3.43	<.001
Time of day: predawn	0.12	0.891	0.711	1.116	0.11	-1.01	0.31
Time of day: twilight	-0.43	0.648	0.507	0.826	0.12	-3.49	<.001
High connectivity	1.48	4.39	3.753	5.143	0.08	18.4	<.001
Outside vegetation: mixed	-2.51	0.081	0.041	0.144	0.32	-7.92	<.001
Outside vegetation: open	-0.24	0.787	0.686	0.902	0.07	-3.43	<.001
Body mass: medium	0.81	2.24	1.703	2.965	0.14	5.71	<.001
Body mass: small	0.03	1.029	0.752	1.415	0.16	0.18	0.86
Fence not maintained	0.72	2.051	1.811	3.326	0.06	11.25	<.001

SUPPLEMENTARY FIGURE 1. DETECTIONS AT FENCE LINE

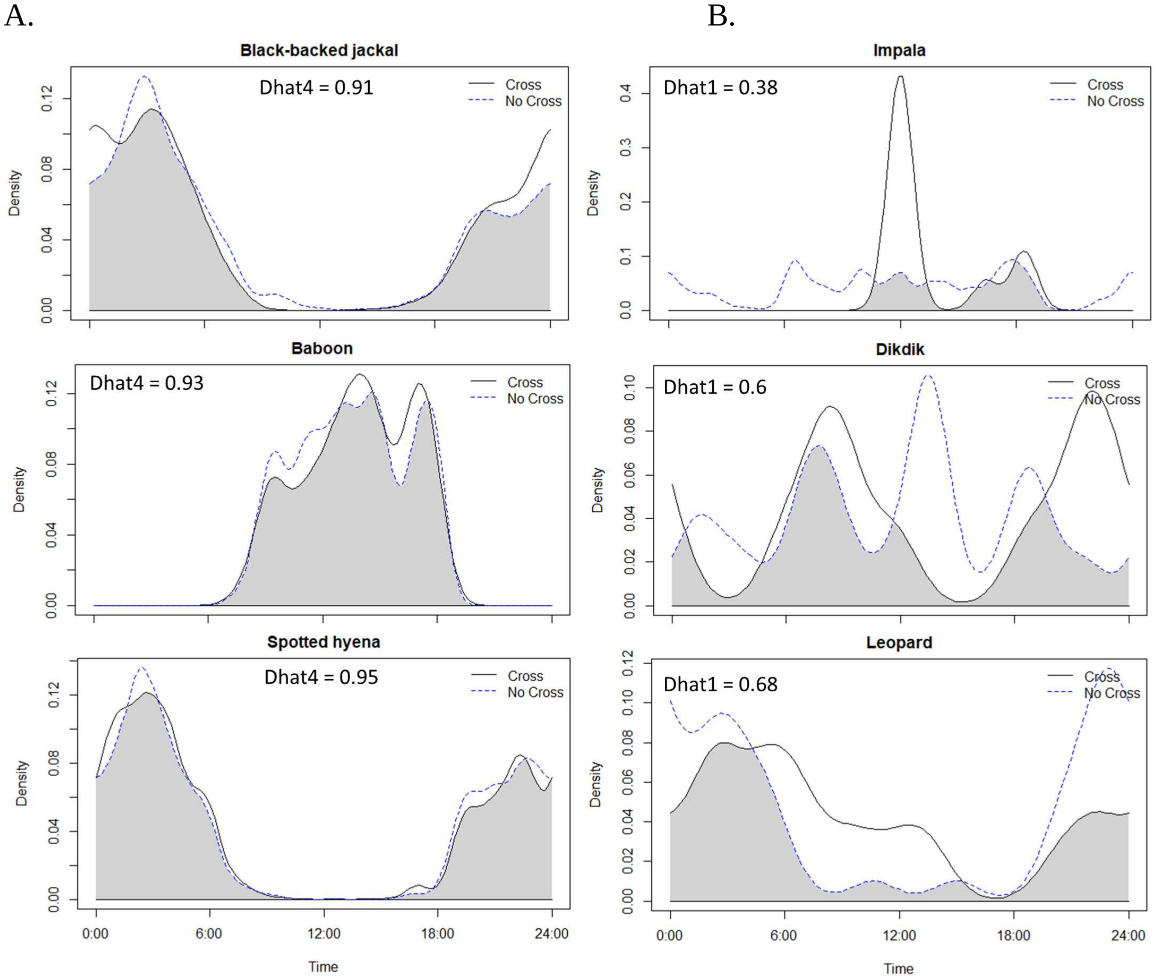
Detections of people and livestock per trap night at each of 19 camera sites.



SUPPLEMENTARY FIGURE 2. TEMPORAL OVERLAP OF CROSSING BEHAVIORS

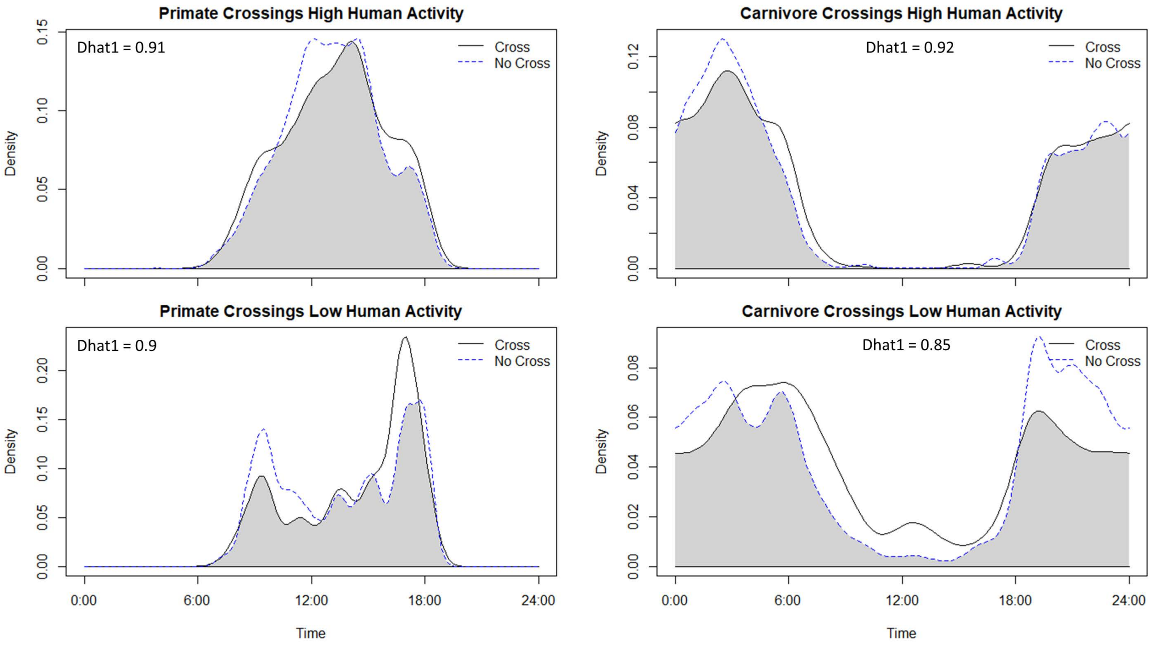
Temporal overlap (Dhat4) between *Cross* and *No Cross* behaviors for a subset of species that crossed the park fence*. Column A indicates examples of species with a high temporal overlap between *Cross* and *No Cross* behaviors, while column B indicates examples of species with a lower temporal overlap between *Cross* and *No Cross* behaviors. Implied crossing behavior is included for carnivores.

**See Suppl. Table 4 for more details*



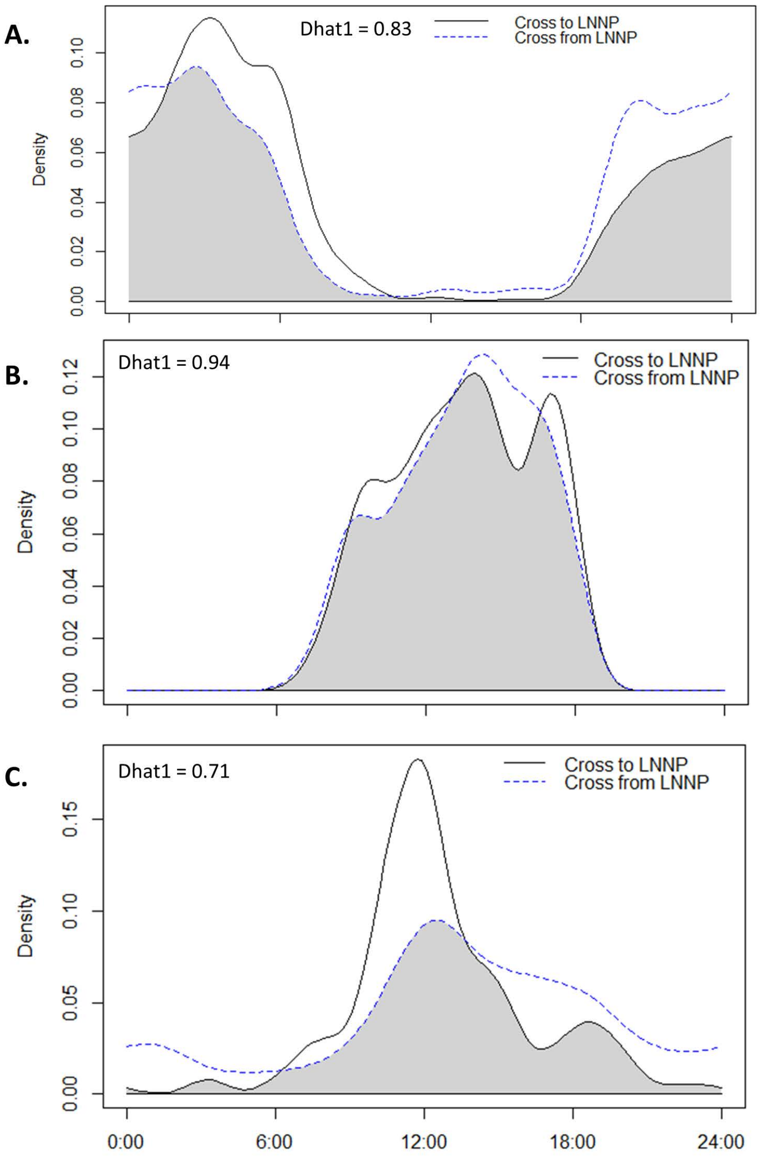
SUPPLEMENTARY FIGURE 3. EFFECTS OF HUMAN ACTIVITY ON CROSSING BEHAVIOR TEMPORAL OVERLAP

Temporal overlap for *Cross* and *No Cross* behaviors of primates and carnivores at camera sites with high human activity and sites with low human activity.



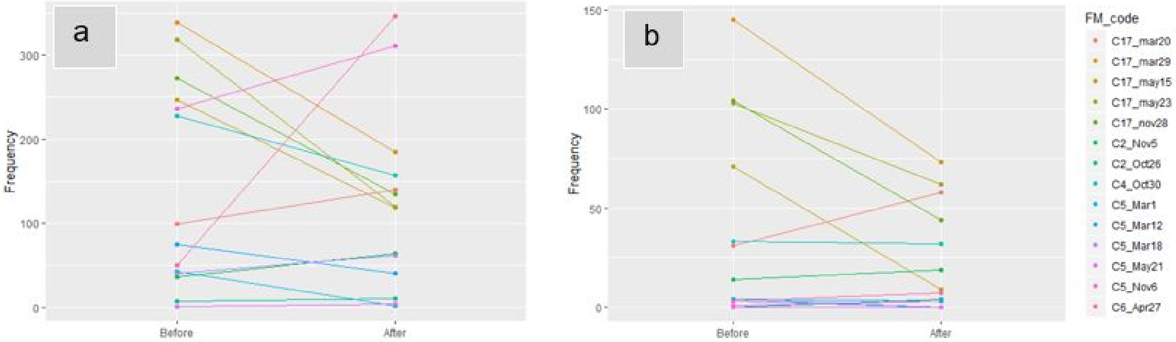
SUPPLEMENTARY FIGURE 4. TEMPORAL OVERLAP OF CROSSING DIRECTIONALITY

Temporal overlap of fence crossings into and out of Lake Nakuru National Park among carnivores (A), ungulates (B), and primates (C).



SUPPLEMENTARY FIGURE 5. FENCE MAINTENANCE EFFECTS

Detections of (panel A) and fence crossings by (panel B) mammals during equivalent periods before and after fence maintenance events. Each fence maintenance event is indicated by a uniquely colored line.



APPENDICES

Appendix S1. Fine-scale temporality of crossing behaviors

At a finer scale, the temporal overlap of crossing and non-crossing activities, i.e., the degree to which crossing occurred at distinctly different times from other behavior, was highly variable across species. Primate species exhibited the highest temporal overlap of crossing and non-crossing behaviors; easily moving back and forth across the fence during foraging or other activities. We interpreted this high temporal overlap of crossing and non-crossing behaviors (also seen in spotted hyena, black-backed jackal (*Canis mesomelas*), mongoose, hare (*Lepus victoriae*), and warthog (*Phacochoerus africanus*); Suppl. Fig. 2) to suggest that the act of crossing was often opportunistic or easily combined with other activities. In contrast, other species, most notably impala, dik-dik, porcupine (*Hystrix cristata*), zebra (*Equus quagga*), and leopard, crossed at times of the day that differed strikingly from when they were otherwise observed to be active (Suppl. Fig. 2). One could interpret this as suggesting that crossing fences among these species is a more deliberate act, but additional study is needed.

Chapter 6. Concluding remarks

This dissertation spans disciplines to explore socioecological connections and interactions that shape human relationships with wildlife and the environment in an era of unprecedented anthropogenic change. The interdisciplinarity of the theories guiding this dissertation is no accident. By designating the Anthropocene epoch, humans have finally begun to come to terms with their role as part of the ecological processes that shape our planet. People have cascading effects on wildlife behavior, while also being influenced by the increasingly close and more frequent proximity of wildlife to humans. Interdisciplinary and participatory methodologies are a requirement for understanding issues as complex as these, and for sorting out our role in shaping and being shaped by novel environmental processes.

While environmental challenges in the 21st century are inherently complex, context-specific, and transdisciplinary, Chapter 2 of this dissertation serves as a reminder of the importance of considering the ecological roots of all environmental challenges. By applying well-known ecological theories to carnivore interactions with people and their livestock, we can begin to disentangle the context-dependency of human-carnivore conflict and operationalize our ecology fundamentals in impactful ways. It is increasingly clear that the world needs ecologically sound interventions that promote coexistence by reducing risks to livestock and people. Using ecological theory to guide conservation action provides a foundation upon which to build our understanding of how socioeconomic and political elements both drive and are influenced by these essentially ecological coexistence challenges.

Chapter 3 explicitly combines ecological and social methodologies and frameworks to explore the role of people's perceptions and histories in human-carnivore conflicts. Visible manifestations of human-wildlife conflict are often rooted in less visible and more complex social conflicts. These sociopolitical and cultural contexts and histories play a heavy hand in shaping people's perceptions and attitudes toward wildlife with which they share landscapes. People's perceptions of human-carnivore conflict may differ from and be as influential for conservation as actual instances of livestock predation or carnivore attacks. These factors highlight the importance of disentangling the conservation influence of perceptions in contrast to verified reports and ecological data. Efforts that thoughtfully employ participatory methodologies to explore these questions have the additional notable benefit of elevating community voices and concerns in regions dealing with conflict.

In parallel to human perceptions and abilities to adapt to coexistence with carnivores in these shared landscapes, understanding the adaptability of carnivores to anthropogenic factors and human acceptance may be equally important. With human development proliferating globally, wide ranging species of all taxa must adapt to novel environments in which anthropogenic structures, activity, and tolerance constitute features on the landscape that hold equal importance to the ecological features that wildlife are accustomed to navigating. Chapter 4 explores the landscape traversal of a highly adaptable large carnivore, the spotted hyena, as a case study examining carnivore navigation of ecological and anthropogenic geographies in a rapidly developing landscape. We can use knowledge about the movements of the most behaviorally plastic species to predict what challenges wildlife may face in their effort to survive and thrive in newly human-dominated landscapes.

As physical barriers separating wildlife from people in shared landscapes, conservation fences embody the philosophy of coexistence in which humans remain set apart from nature. Yet, these structures are imperfect, temporally ephemeral, and can have varying levels of permeability. As a result, their ecological and metaphorical impacts can follow similar patterns, and gathering evidence on the effectiveness of conservation fences is hampered by the tendency to have too few, too broad, or conflicting conservation goals guiding their initial construction. Chapter 5 provides evidence on the ecological and behavioral impacts of fences, as well as the potential effects of fence degradation over time, while providing a framework for future research that adds to this evidence base.

This dissertation explored human-wildlife coexistence in the Anthropocene through many lenses, reflecting the complexity and context-dependency of our current coexistence challenges. While scientists may be accustomed or tempted to view conservation issues as primarily ecological in nature, we cannot decouple the sociocultural influences and feedbacks that are woven throughout every environmental challenge. In using multidisciplinary and participatory methods to confront this complexity head on, conservation scientists can discover ways to apply known theories to new problems while prioritizing socially just solutions to conservation issues. I hope that the research included in this dissertation can contribute to these efforts.

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