EXPLORING DRIVERS OF THE RESEARCH-IMPLEMENTATION GAP IN LARGE CARNIVORE CONSERVATION

By

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ABSTRACT

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The number of scientific publications centered on threats to large carnivore populations has increased exponentially over the last two decades. However, this notable growth in research effort has not resulted in a commensurate positive impact on the population status of those carnivore species. My dissertation explores a range of drivers that may be contributing to this evident disconnect between research effort and conservation impact in large carnivore conservation. Each chapter delves into a different step in the processes of research and conservation practice in which this research-implementation gap may be perpetuated. In Chapter 1, I conducted a review to assess whether taxonomic bias was evident among the published literature on carnivore depredation of livestock in sub-Saharan Africa. I used lexical analysis to compare the central large carnivore species in each study to the species identified as the primary livestock depredator. I found that, while the spotted hyena (*Crocuta crocuta*) tended to be the primary livestock depredator, the African lion (*Panthera leo*) was the most common focal species. I argued that this pattern is likely due to the African lion's charisma and its role as a global rallying point for conservation funding. In Chapter 2, I assessed the complexity inherent to human-wildlife coexistence systems through an exploration of emergent themes from semi-structured interviews in Northern Tanzania. I found that the nature of human-elephant interactions amplified the negative impacts of human-carnivore interactions, and decreased human willingness and capacity to participate in interventions designed to promote human-wildlife coexistence. In Chapter 3, I quantified carnivore-livestock encounter rates, attack rates,

and depredation risk at bomas in Laikipia, Kenya. I found that carnivores encountered potential livestock prey far more often than they attacked, and that these encounter rates exhibited notable temporal patterning at multiple resolutions. Furthermore, spotted hyenas (*Crocuta crocuta*) had substantially higher encounter and attack rates than any other carnivore species, and thus posed the greatest depredation risk for livestock. I concluded that better understanding of species-specific encounter rates such as those I explored will aid in the prediction of depredation risk, and therefore the mitigation of carnivore depredation of livestock. In Chapter 4, I applied three geostatistical measures to assess spatial clustering in data describing carnivore depredation of livestock in the Maasai steppe region of Tanzania. My analysis revealed that the spatial patterns of carnivore depredation of livestock tended not to significantly differ from random. I concluded that other drivers of spatial randomness may be obscuring patterns of depredation. Thus, analysis of research to inform depredation interventions must carefully apply diagnostic approaches to ensure accurate interpretation of spatial patterning. I conclude my dissertation with a summary of key findings and recommendations to improve research efforts to better bridge the research-implementation gap moving forward. This dissertation incorporates a diversity of research techniques, which provide a range of valuable contributions to current understanding of the research-implementation gap and large carnivore conservation.

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PREFACE

Each chapter within this dissertation was originally drafted as a standalone manuscript for publication in a peer-reviewed journal. Although I am listed as the sole author and use the pronoun I within this dissertation, each chapter was a collaborative effort and all associated manuscripts include one or more co-authors when submitted for peer-review. However, the methods used in Chapter 2 are inherently team-based. Thus, I use the pronoun we within that chapter. Chapter 1 is currently in press at *Oryx*. Chapter 2 has not yet been submitted. Chapter 3 is currently under review at *Ecological Applications*. Chapter 4 was submitted and accepted for publication in *Frontiers in Ecology and Evolution*. Due to copyright restrictions, Chapter 4 could not be included in this dissertation. The citation for Chapter 4 is as follows.

Hoffmann, C.F., Kissui, B., and Montgomery, R.A. 2019. Spatial pattern analysis reveals randomness among carnivore depredation of livestock. Frontiers in Ecology and Evolution. 7:478. doi: 10.3389/fevo.2019.00478.

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INTRODUCTION

Large carnivores play key roles in maintaining ecosystem functions, and are a source of inspiration for conservation of the natural world across many regions of the globe (Albert et al., 2018; Clucas et al., 2008; Estes et al., 2011; Ripple et al., 2016). Yet, despite this ecological and cultural status, more than three quarters of the remaining species of large carnivores have declining populations (Courchamp et al., 2018; Ripple et al., 2014; Wolf and Ripple, 2017). Drivers of the persistent progress towards extinction exhibited by many of these species has become an increasingly common topic of study among conservation researchers. In fact, the number of publications centered upon threats to large carnivore populations have increased exponentially over the last two decades (Krafte Holland et al., 2018; Lozano et al., 2019; Montgomery et al., 2018; van Eeden et al., 2018a). These research efforts have identified a broad range of factors contributing to large carnivore population declines (Estes et al., 2011; Inskip and Zimmermann, 2009; Ripple et al., 2016; Wolf and Ripple, 2017). While the primary drivers at play vary by region and species, conflict with humans consistently emerges as one of the key threats to carnivore populations globally (Inskip and Zimmermann, 2009; Krafte Holland et al., 2018; Ripple et al., 2014; Torres et al., 2018; van Eeden et al., 2018a). Conflict between humans and carnivores tends to be associated with carnivore depredation of livestock, where the death of livestock often triggers retaliatory killing of carnivores (Krafte Holland et al., 2018; Lozano et al., 2019; Merson et al., 2019).

It is evident from the wealth of scientific publications on threats to large carnivore populations that a large amount of knowledge has been accrued regarding these drivers. However, very little of this knowledge has been translated into effective conservation of the species upon which it centers (Gray et al., 2019; Sunderland et al., 2009; Wright et al., 2020).

Currently, the field of large carnivore conservation is characterized by a pervasive disconnect between the collection of academic knowledge and the development of effective conservation strategies to address the threats identified within that knowledge (Balme et al., 2014; Gray et al., 2019; Montgomery et al., 2018; Tensen, 2018). This vast accumulation of scientific knowledge without commensurate conservation impact has been termed the research-implementation gap (Arlettaz et al., 2010; Knight et al., 2008; Toomey et al., 2017). The research-implementation gap in large carnivore conservation is particularly notable in regards to carnivore depredation of livestock (Eklund et al., 2017; van Eeden et al., 2018b).

Given the imminent threat of extinction facing many carnivore species, effective use of resources, time, and energy is of primary importance (Balmford et al., 2003; Stroud et al., 2014). Thus, the research-implementation gap poses a direct threat to large carnivore conservation (Balme et al., 2014). The critical nature of addressing the research-implementation gap has been widely recognized, resulting in a rapid growth in publications exploring potential social, political, and methodological drivers of this gap. These studies have identified a range of contributing drivers, including a lack of planning for conservation action during the research process (Arlettaz et al., 2010; Knight et al., 2008), taxonomic bias among study species (Di Marco et al., 2017; dos Santos et al., 2020; Trimble and Van Aarde, 2012), minimal interdisciplinarity in research teams (Beck et al., 2019; Holzer et al., 2019; Montgomery et al., 2018), ineffective communication between researchers, practitioners, and local stakeholders (Dubois et al., 2020; Gossa et al., 2014; Gray et al., 2019), and limited assessment of the effectiveness of prescribed management actions (Catalano et al., 2019; Eklund et al., 2017; Knight et al., 2019).

Importantly, however, knowledge is not a concrete entity that can be handed from researchers to conservation practitioners. Rather, knowledge is a process of relating, communicating, and exchanging meaning (Roux et al., 2006; Toomey et al., 2017; Wright et al., 2020). Thus, the progression from research to conservation impact is neither linear nor straightforward (Toomey et al., 2017). Both the accumulation of knowledge via research and the development and implementation of conservation practice based upon that knowledge are processes, each containing a multitude of steps. Any one of those steps can serve as a bridge or a roadblock to effective carnivore conservation (Holzer et al., 2019; Toomey, 2016; Toomey et al., 2017). The aforementioned examples of potential drivers of the research-implementation gap exemplify this series of steps, as they highlight roadblocks within steps spanning from the conceptualization of research programs to the continued assessment and adaptation of conservation impacts. Therefore, it is evident that the research-implementation gap is not a single point of failure, but instead a series of steps within which the effective flow along the processes of research and conservation can be interrupted (Roux et al., 2006; Toomey et al., 2017). Each chapter of my dissertation explores one or more of these steps, assessing how current approaches emerged, the process by which those approaches may be creating a barrier to effective conservation, and identifying strategies to minimize the research-implementation gap moving forward.

In Chapter 1, I assess the potential social and institutional structures that may be contributing to taxonomic bias within the carnivore depredation of livestock literature. In Chapter 2, I conceptualize human-carnivore interactions within a complex system approach to develop stronger theoretical understanding of the systems in which human-wildlife coexistence must occur. In Chapter 3, I advance current understanding of carnivore depredation of livestock risk by quantifying carnivore-livestock encounter rates. In Chapter 4, I assess spatial patterns in carnivore depredation of livestock to determine how common strategies in spatial risk models may be obscuring sources of spatial randomness resulting in inaccurate risk maps. Within each chapter, I draw explicit connections between my findings and the research-implementation gap and provide recommendations for mitigation of that gap based upon those findings. I conclude my dissertation with a summary of these key results and recommendations, and identify productive avenues of future research to continue bridging the research-implementation gap.

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CHAPTER 1: IMPLICATIONS OF TAXONOMIC BIAS FOR HUMAN-CARNIVORE CONFLICT MITIGATION

1.1 Abstract

Carnivore population declines represent a time-sensitive global challenge where conservation success requires alignment of applied practice and research priorities. However, large carnivore conservation is limited by gaps among research, conservation practice, and policy formation. One potential driver of this research-implementation gap is research effort bias towards charismatic species. Using large carnivore depredation of livestock in sub-Saharan Africa as a case study, I examined whether taxonomic bias could be detected and explored the potential effects of such a bias on the research-implementation gap. Via a literature review, I compared the central large carnivore species in research efforts to the species identified as the primary livestock depredator. I detected a substantial misalignment between these factors for two species. Spotted hyenas (*Crocuta crocuta*) were the most common depredator of livestock (58.5% of studies), but were described as a central species among only 20.7% of the studies. In comparison, African lions (*Panthera leo*) were the most common central species (45% of studies) while being the primary depredator among just 24.4% of studies. Such patterns suggest that taxonomic bias is prevalent within this research. Though spotted hyenas may depredate livestock most often, their low charisma in comparison to sympatric species like the African lion and leopard may be limiting the number of research-informed conservation efforts centered around them. Human-carnivore conflict mitigation efforts designed for one species may not be applicable to another co-occurring species. Thus, taxonomic bias can undermine the efficacy of interventions built to reduce carnivore depredation of livestock.

1.2 Introduction

Large carnivores are species of conservation concern the world over. More than three-quarters of the world's remaining large carnivore species have declining population trajectories (Chapron et al., 2014; Eklund et al., 2017; Ripple et al., 2014). Further, the majority of these species are threatened with extinction (i.e. categorized as 'vulnerable' or higher by the International Union for the Conservation of Nature (IUCN)) with some experiencing > 90% range contraction over the last century (Ripple et al., 2016; Wolf and Ripple, 2017). Widespread concerns relating to carnivore conservation are reflected in the literature, where publication of peer-reviewed research has increased exponentially in the last three decades (Montgomery et al., 2018; Krafte Holland et al., 2018; Lozano et al., 2019). This literature has identified a variety of drivers of carnivore population declines including habitat loss, prey depletion, disease, and climate change, among others (Estes et al., 2011; Inskip and Zimmermann, 2009; Ripple et al., 2016; Wolf and Ripple, 2017). However, conflict with humans over livestock depredation is consistently cited as one of the primary threats to carnivore population persistence around the world (Inskip and Zimmermann 2009; Tumenta et al. 2013; Ripple et al. 2014; van Eeden et al. 2018a, b; Krafte Holland et al. 2018).

As funds for conservation work are limited, each conservation project needs to use those resources efficiently to maximize positive on-the-ground impacts (Balmford et al., 2003; Brambilla et al., 2013; Eklund et al., 2017). To do so, research must be interpretable among conservation practitioners and policy makers (Balmford et al., 2003; Bennett et al., 2015; Knight et al., 2008; Ripple et al., 2016). However, even after extensive calls for improvement, important gaps between research and conservation implementation remain (Knight et al., 2008; Eklund et al., 2017; Montgomery et al., 2018; Krafte Holland et al., 2018; Gray et al., 2019). Factors contributing to this research-implementation gap include low interdisciplinarity among research teams, scale discordance, and limited actionability of research (Montgomery et al.a, b, 2018; Gray et al., 2019). Another factor that may be influential in this context is taxonomic bias.

Taxonomic bias is prevalent throughout conservation research, and describes a tendency for research effort, funding, and public interest to focus on a small subset of species (Clark and May, 2002; Di Marco et al., 2017; Donaldson et al., 2017; Lawler et al., 2006; Stroud et al., 2014; Tensen, 2018; Troudet et al., 2017). This bias is primarily driven by human social factors including perceptions of species charisma, as well as the value of those species for society and as subjects of conservation funding (Bonnet et al., 2002; Donaldson et al., 2017; Rosenthal et al., 2017). This uneven distribution of research and funding among taxa can result in mismatches between research effort, the resulting knowledge base, and conservation needs (Bonnet et al., 2002; Fazey et al., 2005; Hortal et al., 2015; Lawler et al., 2006; Linklater, 2003; Rosenthal et al., 2017; Wilson et al., 2007). These biases are not only influential between taxonomic orders but also within them, and may have important consequences for the research-implementation gap (Anonymous, 2007; Fleming and Bateman, 2016; Knight et al., 2008; Martín-López et al., 2009; Trimble and Van Aarde, 2012). To mitigate these effects, regular assessments of taxonomic bias have been recommended (Di Marco et al., 2017; Lawler et al., 2006; Wilson et al., 2007). While previous studies have explored taxonomic bias in other conservation fields, its effect on the research-implementation gap has yet to be evaluated among the carnivore depredation of livestock literature.

Here, I used livestock depredation by large carnivores in sub-Saharan Africa as a case study to assess whether taxonomic bias is evident in human-carnivore conflict research. I conducted a literature review and compared the central carnivore species of each study to those identified as being most responsible for livestock depredation. I then examined the ways in which misalignment among these factors could contribute to the research-implementation gap affecting human-carnivore conflict mitigation. I explore the role of species charisma in catalyzing research effort and conservation funding, and discuss the implications of my study for the creation of conflict interventions and policies that can promote human-carnivore coexistence. Highlighting issues that further the research-implementation gap is necessary to promote more effective alignment between research effort and conservation impacts.

1.3 Methods

The term human-carnivore conflict is increasingly recognized as overly homogenizing, thus obscuring the nuanced experiences inherent to interactions between humans and carnivores (Dickman, 2010; Krafte Holland et al., 2018; Lozano et al., 2019; Redpath, 2015; Redpath et al., 2013). I acknowledge that in assessing carnivore depredation of livestock, my study does not allow for a broader perspective on both positive and negative human-wildlife interactions. However, I focused my review on livestock depredation given that it is often a primary driver of agonistic interactions between humans and carnivores, and thus constitutes a notable threat to carnivore conservation (Inskip and Zimmermann, 2009; Ripple et al., 2014; Tumenta et al., 2013). Further, minimizing depredation is a common strategy among human-carnivore coexistence efforts (van Eeden et al., 2018a, b; Krafte Holland et al., 2018). I chose to highlight sub-Saharan Africa because it is a hotspot for carnivore depredation of livestock and carnivore biodiversity (Krafte Holland et al., 2018; Lozano et al., 2019; Ripple et al., 2014).

I completed my review in June 2019, using four bibliographic databases including Web of Science (WoS) Core Collection, Scopus, Wildlife and Ecology Studies Worldwide (WESW), and Google Scholar search engine. I conducted my review in English, as studies in the carnivore depredation of livestock field are predominately published in that language (van Eeden et al., 2018; Krafte Holland et al., 2018). Using an iterative search process, I mined each database a total of three times. I first included the terms ‘human carnivore livestock,’ adding ‘conflict’ in the secondary search and ‘depredation’ in the tertiary. As Google Scholar operates in a slightly different fashion, I started my search in that engine using ‘human carnivore conflict’ as a bound phrase and added ‘livestock’ and ‘depredation’ in the secondary and tertiary searches, respectively. I excluded any studies that were not published in a peer-reviewed journal, those that were outside the geographic extent of sub-Saharan Africa, and those that were not directly relevant to my assessment (e.g., examined carnivore predation of wild prey, carnivore attacks on people, or human attitudes towards conservation actions). For each study I recorded: *i*) the location of the field site, *ii*) the central carnivore species, and *iii*) the carnivore species responsible for the majority of livestock depredation. For studies that did not provide exact geographic coordinates, I approximated the field site location based on site maps and study area descriptions. I selected the centroid for those that included multiple field sites across a geographic area.

1.3.1 Central species

I identified the central carnivore species of each study using a lexical analysis in the MAXQDA software (MAXQDA Analytics Pro 2020 20.0.8; Kuckartz and Radiker 2019). I conducted the lexical searches among all studies to record the number of times that depredating carnivore species were mentioned. My search terms included ‘African lion’ (*Panthera leo*), ‘spotted hyena’ (*Crocuta crocuta*), ‘African wild dog’ (*Lycaon pictus*), ‘leopard’ (*Panthera pardus*), ‘Ethiopian wolf’ (*Canis simensis*), ‘cheetah’ (*Acinonyx jubatus*), ‘jackal’ (*Canis mesomelas*), ‘brown hyena’ (*Parahyaena brunnea*), ‘African wolf’ (*Canis lupaster*), ‘caracal’ (*Caracal caracal*), and ‘striped hyena' (*Hyaena hyaena*). I used only the common name of each species as a search term, included the alternate spelling of hyena (i.e., hyaena) for all three hyena species, and specified each search term to be a character string instead of a bound phrase. I also included words from lemma list without case sensitivity. With these search settings, the MAXQDA software returned a hit for any combination of the search terms and any word forms (Kuckartz and Radiker, 2019). For example, "lion" returned a hit for the exact match, along with "Lion" and "lions." For each study, I recorded the number of hits for each carnivore species within all sections of the document, excluding the references and running title. I converted the number of hits by carnivore species into a percentage of the total hits in the study. I considered a carnivore species to be central if the number of hits were ≥ 25% of the total hits for that study. Thus, it was possible for one study to have multiple central species. I classified a study as having "none" if no single species exceeded 25% of the total hits.

Lexical analysis is an established tool for assessing text-based media, as high frequency terms are representative of content themes and biases (Bednarek and Caple, 2014; Wodak and Meyer, 2008). Lexical analyses are replicable, easily quantifiable, and taxonomically unbiased, and thus are valuable for studies of taxonomic bias (dos Santos et al., 2020). However, as the application of this method is still emergent in conservation, I used a secondary document analysis to verify my results. I identified the central species based upon references to carnivore species throughout the manuscript. For example, I classified a study to be centered around the spotted hyena if that was the primary species around which the introduction, methods, and results were framed. I performed the document analysis separate from the lexical analysis to minimize the risk of implicit coding bias from the results of the lexical analysis.

1.3.2 Measures of livestock depredation

Next, I determined the carnivore species that was responsible for the majority of livestock depredation in each study. I used the two most prevalent methods for measuring livestock depredation (Krafte Holland et al., 2018). These include quantitative measures of livestock depredated by carnivores (e.g., the number of livestock killed), and perceptions of depredation risk among livestock owners (e.g., the proportion of respondents who considered a carnivore species to be the greatest threat to their livestock; see Marker et al., 2003; Kissui, 2008; Miller et al., 2016). I identified the carnivore species with the greatest contribution to these two conflict measures, depending on which was reported. Thus, my final database consisted of the geographic location, the central carnivore species, and primary depredator for each study. I then mapped the distribution of all studies in ArcMap 10.5 (ESRI, Redlands, CA) and assessed the alignment between central species and primary livestock depredator.

1.4 Results

My literature review returned 119 peer-reviewed publications of livestock depredation in sub-Saharan Africa published between 1997 and 2019. I eliminated 19 studies that did not fit the conditions of my review (e.g., did not directly examine livestock depredation or were not published in a peer-reviewed journal), so my final database consisted of a total of 100 studies (Fig. 1.1). The majority of these studies were conducted in Eastern Africa (i.e. Ethiopia, Tanzania, and Kenya; 51.0%, n = 51), and Southern Africa (i.e. Botswana, Namibia, South Africa, and Zimbabwe; 43.0%, n = 43). The remaining six were based in Western and Central Africa (i.e. Niger, Guinea, Chad, Cameroon, and Benin; 6.0%). Seven studies did not have any central species (7.0%), as identified via lexical analysis and confirmed through the document analysis. Among those with a single central species, African lions were the most common

(29.0%, n = 29; Table 1.1; Fig. 1.2; Fig. 1.3a, c, e). Other single central species included spotted hyenas (9.0%, n = 9), African wild dogs (9.0%, n = 9), leopards (6.0%, n = 6), Ethiopian wolves (4.0%, n = 4), cheetahs (7.0%, n = 7), black-backed jackals (5.0%, n = 5), and brown hyenas (1.0%, n = 1). The studies with at least two central species included African lions/spotted hyenas (10.0%, n = 10), African lions/leopards (3.0%, n = 3), African lions/spotted hyenas/leopards (3.0%, n = 3), and spotted hyenas/leopards (2.0%, n = 2). Ethiopian wolves/African wolves, cheetahs/black-backed jackals, black-backed jackals/caracals, spotted hyenas/leopards/black-backed jackals, and leopards/black-backed jackals/caracals each represented 1.0% (n = 1) of the reviewed studies (Table 1.1; Fig. 1.2; Fig. 1.3a, c, e).

There were 41 studies that included measures of livestock depredation. Over three-quarters (85.4%, n = 35) of these studies reported depredation events while the remainder (14.6%, n = 6) reported perceptions of depredation risk (Table 1.2). Spotted hyenas were the primary livestock depredator in the majority of these studies (58.5%, n = 24), followed by African lions (24.4%, n = 10), leopards (7.3%, n = 3), black-backed jackals (4.9%, n = 2), African wild dogs (2.4%, n = 1), and African wolves (2.4%, n = 1; Table 1.2; Fig. 1.3b, d, f). Notably, not all reported measures of livestock depredation were indicative of the magnitude of loss resulting from the depredation (e.g., monetary value of the livestock killed).

Among four of the most common single central species (African lions, spotted hyenas, African wild dogs, and leopards), there was a mismatch between central species and primary depredator for spotted hyenas and leopards (Table 1.3; Fig. 1.3). Spotted hyenas were not a central species in over a third of the studies (37.5%, n = 9 of 24) in which they were the primary livestock depredator. I detected such a mismatch for leopards in one study (Table 1.3; Fig. 1.3).

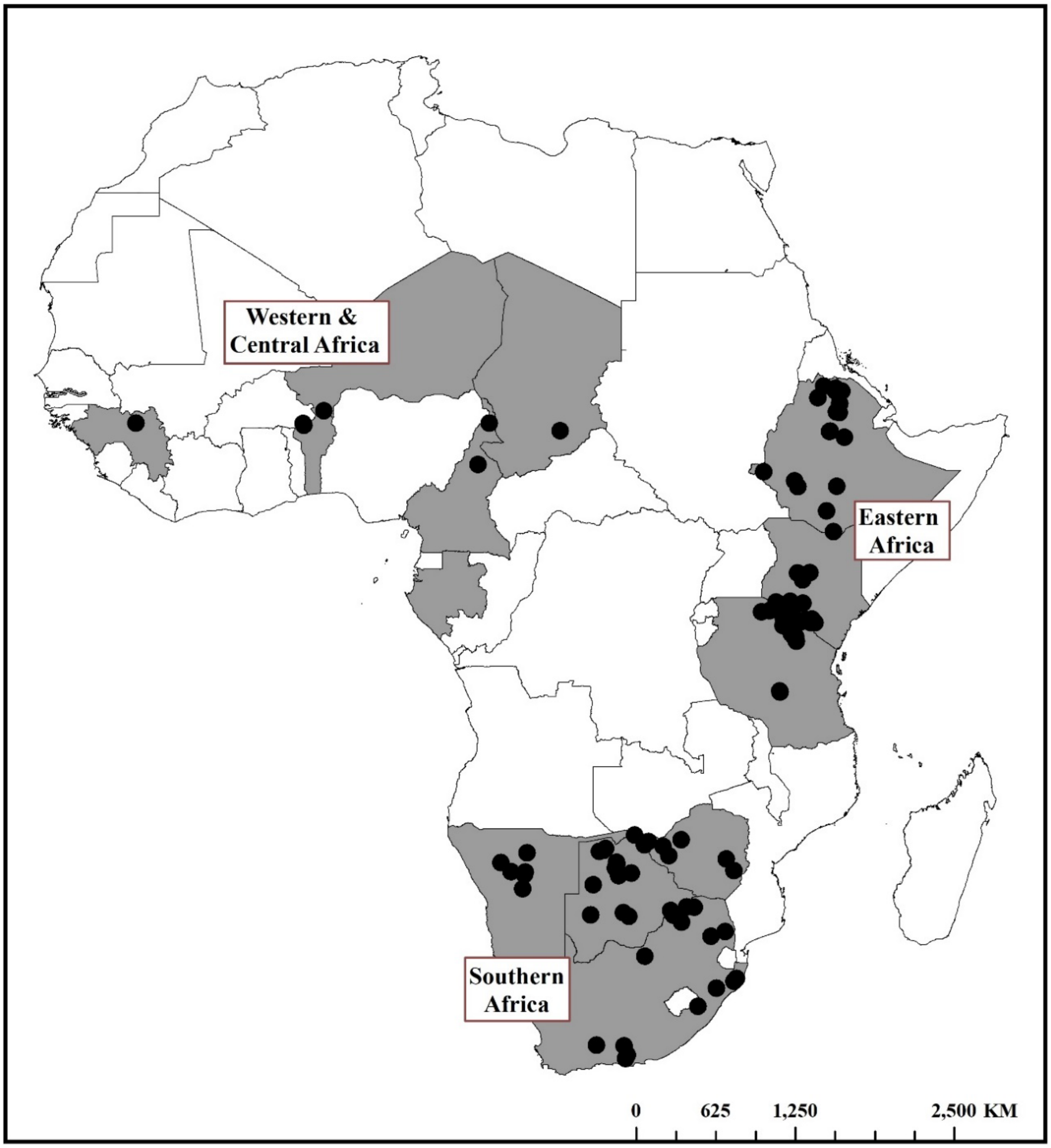

Figure 1.1. The location of field sites featured in 100 studies on livestock depredation in sub-Saharan Africa.

Table 1.1. The central carnivore species among 100 studies, published between 1997 and 2019, evaluating livestock depredation in sub-Saharan Africa. “Single” indicates the number of studies in which the carnivore species was the only central species, and “Multiple” indicates the number of studies in which it was one of two or more central species.

	African lion	Spotted hyena	Wild dog	Ethiopian wolf	Cheetah	African leopard	Black-backed jackal	Brown hyena	African wolf	Caracal
	Panthera leo	*Crocuta crocuta*	*Lycaon pictus*	*Canis simensis*	*Acinonyx jubatus*	*Panthera pardus*	*Canis mesomelas*	*Parahyena brunnea*	*Canis lupaster*	*Caracal caracal*
Single	29	9	9	4	7	6	5	1	0	0
Multiple	16	16	0	1	1	10	4	0	1	2
Total	45	25	9	5	8	16	9	1	1	2

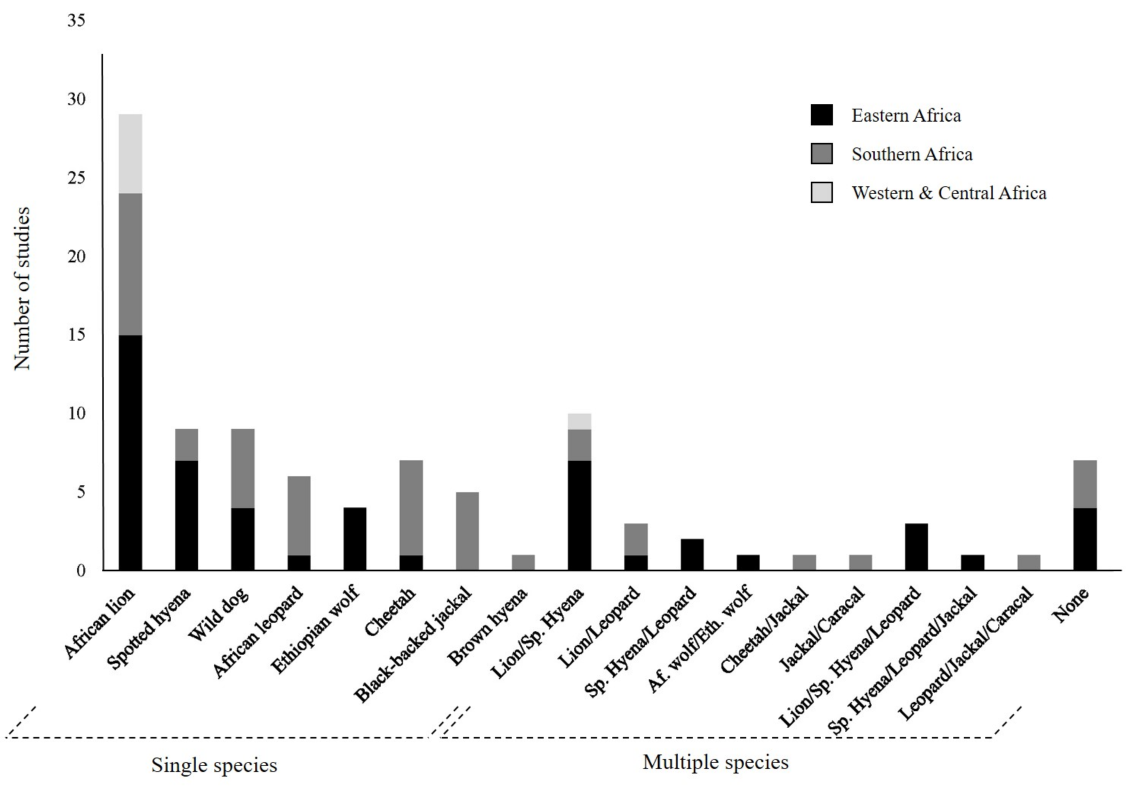

Figure 1.2. The central carnivore species among 100 studies on livestock depredation in sub-Saharan Africa. The results are divided by studies with a single central species, and those with

Figure 1.2. (cont'd) two or more. Coloration within each column indicates the region in which the studies were conducted.

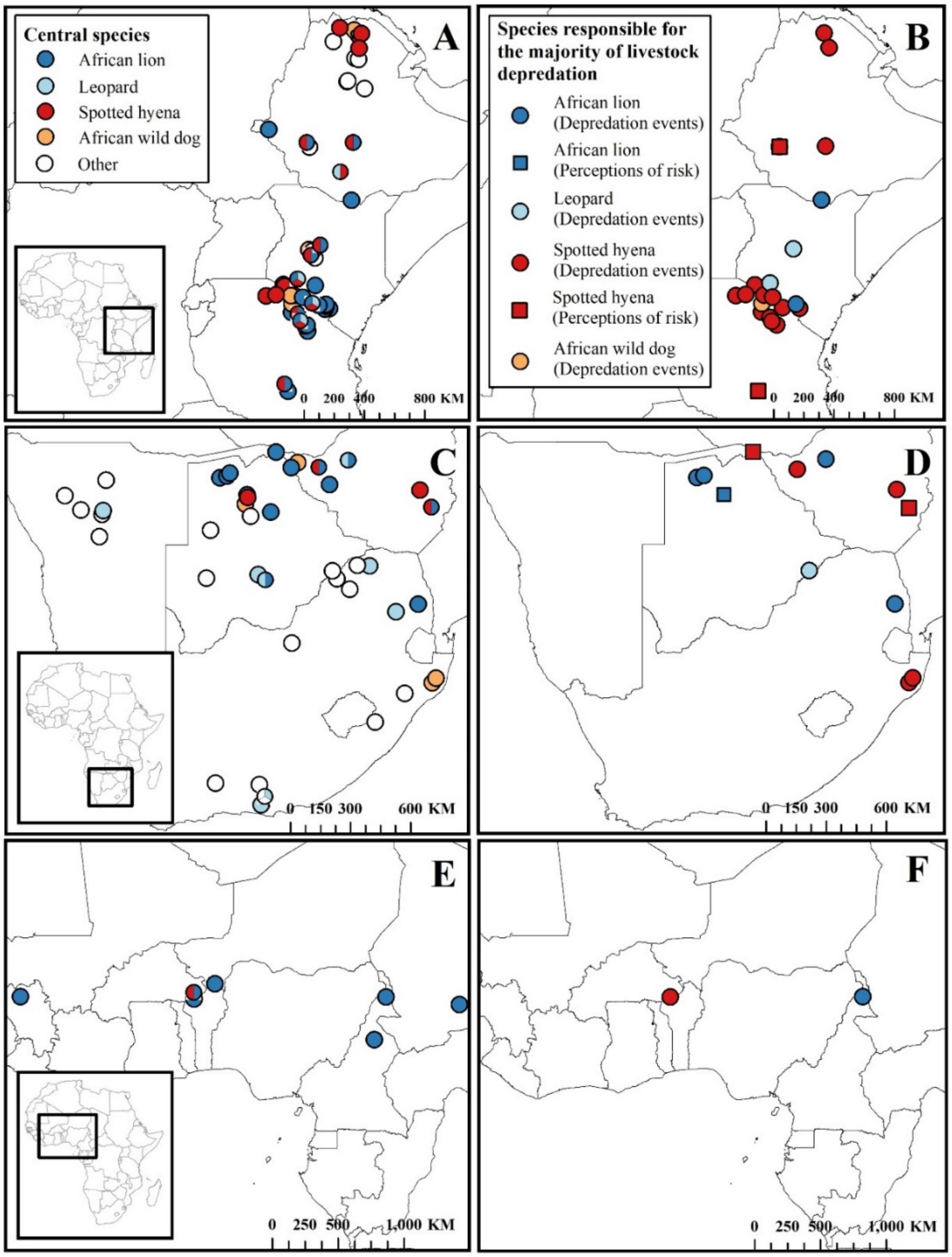

Figure 1.3. The misalignment between central species and species responsible for the majority of livestock depredation. This pattern is highlighted for the four most common single central species: African lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta*

Figure 1.3. (cont'd) *crocuta*), and African wild dogs (*Lycaon pictus*) by geographic region. Panels a) and b) show Eastern Africa, panels c) and d) show Southern Africa, and panels e) and f) show Western and Central Africa. The left-hand panels (a, c, and e) show the central carnivore species, while the right-hand panels show the carnivore species responsible for the majority of livestock depredation.

Table 1.2. The carnivore species responsible for the majority of livestock depredation for 100 studies in sub-Saharan Africa published between 1997 and 2019. The results are divided into two reported measures: depredation events and perceptions of depredation risk.

	African lion	Spotted hyena	Wild dog	Ethiopian wolf	Cheetah	African leopard	Black-backed jackal	Brown hyena	African wolf	Caracal
	Panthera leo	*Crocuta crocuta*	*Lycaon pictus*	*Canis simensis*	*Acinonyx jubatus*	*Panthera pardus*	*Canis mesomelas*	*Parahyena brunnea*	*Canis lupaster*	*Caracal caracal*
Depredation events	7	18	1	0	0	3	2	0	1	0
Perceptions of risk	2	4	0	0	0	0	0	0	0	0
Total	9	22	1	0	0	3	2	0	1	0

Table 1.3. The alignment between central carnivore species and primary livestock depredator for 41 studies in sub-Saharan Africa published between 1997 and 2019. The results show the number of studies in which the carnivore species responsible for the majority of livestock depredation were the only central species ("Single"), one of multiple central species ("Multiple), or not a central species ("Mismatch") in that same study.

	African lion	Spotted hyena	Wild dog	Ethiopian wolf	Cheetah	African leopard	Black-backed jackal	Brown hyena	African wolf	Caracal
	Panthera leo	*Crocuta crocuta*	*Lycaon pictus*	*Canis simensis*	*Acinonyx jubatus*	*Panthera pardus*	*Canis mesomelas*	*Parahyena brunnea*	*Canis lupaster*	*Caracal caracal*
Single	7	4	1	0	0	0	0	0	0	0
Multiple	3	11	0	0	0	2	1	0	1	0
Mismatch	0	9	0	0	0	1	1	0	0	0

1.5 Discussion

The most effective applied conservation research is that which demonstrates proper alignment between research practices and conservation outputs (Balmford et al., 2003; Eklund et al., 2017; Stroud et al., 2014). A discrepancy between these two factors may limit the applicability of research findings for policy and management practices (Balmford et al., 2003; Eklund et al., 2017; Gray et al., 2019; Linklater, 2003). I detected a misalignment of this type within carnivore depredation of livestock research in sub-Saharan Africa. Specifically, I found that spotted hyenas were the most common primary livestock depredator despite being the central species in a much smaller proportion of the studies. Similarly, in over a third of the studies that reported spotted hyenas as the primary livestock depredator, they were not a central species in that same study. In contrast, neither African lions, African wild dogs, nor leopards showed similar rates of mismatch (Fig. 1.3). In fact, all three were more commonly central species than the primary livestock depredator. African lions, in particular, were disproportionately listed as the central species relative to their contributions as livestock depredators. They were central species in 45.0% of the studies while being recorded as the primary livestock depredator among only 24.4% of the studies. Notably, the misalignments identified here emerged in both the lexical and document analysis. These patterns are likely attributable, in part, to differing levels of charisma among large carnivores.

Species charisma is a relational trait, derived not from the inherent attributes of a species, but from the ways in which people respond to those attributes (Albert et al., 2018; Lorimer, 2007). Consequently, charisma is subjective and must be interpreted within the context of culture, experiences, and values (Albert et al., 2018; Ducarme et al., 2013; Smith et al., 2012). Importantly, charisma often refers to a species' ability to rally financial support for a conservation effort (Albert et al., 2018; Courchamp et al., 2006; Lorimer, 2007; Macdonald et al., 2015). As the majority of conservation funding comes from Western societies (Albert et al., 2018), charisma is most often framed in a Western context (Courchamp et al., 2018; Ducarme et al., 2013). Within this Western perspective, African lions and leopards are consistently highly ranked in lists of the world's most charismatic species (Albert et al., 2018; Davies et al., 2018; Macdonald et al., 2015; Smith et al., 2012). African wild dogs are also considered to be charismatic, but their overall cultural appeal is likely reduced due to being comparatively less recognizable outside of their range countries (Di Minin et al., 2013; Monsarrat and Kerley, 2018). Spotted hyenas, in contrast, tend to be negatively perceived across most regions of the world (Dickman, 2010; Macdonald et al., 2015). There are notable examples of local reverence, respect, and tolerance for the species (see Baynes-Rock, 2013). However, spotted hyenas are commonly perceived in Western cultures as ugly, greedy, unintelligent scavengers and are almost exclusively absent from the scientific literature on charisma (De Pinho et al., 2014; Goldman et al., 2010; Mitchell et al., 2019). I infer that these narratives, and comparative lack of charisma, limit the ability of spotted hyenas to draw financial support from Western institutions for sustained research-informed conservation efforts.

Species such as the African lion, that are considered to be charismatic in the West (Albert et al., 2018) also tend to be associated with complex social dynamics within their range countries (Dickman, 2010; Goldman et al., 2013; Inskip and Zimmermann, 2009). These dynamics may be driven by factors such as the role of the species in traditional ceremonies, the relative socio-economic position of the local communities, or the political history of the region (Dickman, 2010; Inskip and Zimmermann, 2009; Pooley et al., 2016). The cultural implications of these factors influence the willingness of local people to participate in conservation actions (Pooley et al., 2017; van Eeden et al., 2018). The social context surrounding depredating carnivores is also linked to the species' life history. The African lion, for instance, tends to select cattle over concurrently available smaller livestock such as sheep and goats (Hemson et al., 2009; Holmern et al., 2007; Kissui, 2008). As cattle carry higher economic and cultural value in many local communities than other livestock types, preventing depredation by African lions is of particular importance in many parts of sub-Saharan Africa (Hemson et al., 2009; Holmern et al., 2007). Combined with high levels of charisma, this cultural context has likely resulted in species such as the African lion being prioritized as central species among human-carnivore conflict research, while less charismatic species, such as the spotted hyena, remain under-emphasized. As previously noted, not all reported measures of livestock depredation in the studies I reviewed were indicative of the financial or emotional impact of the livestock loss. Therefore, I do not contend that the African lion's prevalence in the literature is without merit. Regardless, I did find that taxonomic bias exists within the human-carnivore conflict literature.

I find that this taxonomic bias has two primary consequences for the mitigation of livestock depredation, and therefore for the conservation of large carnivores in sub-Saharan Africa. First, coexistence between humans and large carnivores largely depends upon increasing the tolerance of local people for carnivores (Bruskotter and Wilson, 2014; Pooley et al., 2016; Treves and Bruskotter, 2014). Tolerance is informed by a complex combination of attitudes, behaviors, and perceptions, all of which are informed by socio-cultural norms as well as political and economic trends (Goldman et al., 2013; Bruskotter & Wilson, 2014; Treves & Bruskotter, 2014; Margulies & Karanth, 2018; van Eeden et al., 2018). Importantly, tolerance of large carnivores is also strongly influenced by overall rates of livestock depredation (Bruskotter and Wilson, 2014; Kolowski and Holekamp, 2006; Treves and Bruskotter, 2014). Increased rates of livestock depredation can degrade human attitudes towards carnivores and increase the probability of retaliatory killing, even for unoffending species or individuals (Farhadinia et al., 2017; Miller et al., 2016; Romañach et al., 2007). Spotted hyenas, as the primary depredators of livestock across much of sub-Saharan Africa, may be eroding human tolerance of sympatric carnivore species. Yet, few studies emphasize livestock depredation by spotted hyenas.

The second consequence of this bias is the restriction of the knowledge base upon which conservation efforts are built. Taxonomic biases result in a large amount of knowledge on a very small number of species, which limits the development of broad theoretical insights (Clark and May, 2002; Hortal et al., 2015; Rosenthal et al., 2017). This is not to suggest that research centered on one carnivore species necessarily omits others during fundraising, data collection, and analysis. It is certainly possible that studies within this review had comprehensive research-informed conservation programs that equitably assessed depredation patterns of multiple carnivore species. However, my results suggest that the resultant publications tended to frame the issue of human-carnivore conflict around a small group of highly charismatic species. Again, over a third of the studies that identified spotted hyenas as the primary depredator of livestock did not include them as a central species. It follows that conflict management recommendations derived from these studies are not emphasizing the contributions of spotted hyenas. Additionally, I suspect that conflict management recommendations as a whole are being framed around an understanding of livestock depredation by more charismatic species, such as African lions. As such, recommendations for interventions are derived from knowledge of behavioral patterns of those select species. The limited research on livestock depredation by spotted hyenas indicates that they exhibit vastly different patterns of depredation than African lions and leopards (Kissui, 2008; Ogada et al., 2003; Woodroffe et al., 2007). Therefore, interventions built upon understandings of charismatic species may omit those of more common depredators and consequently be incomplete in their ability to prevent livestock depredation.

The taxonomic bias that I detected in research on carnivore depredation of livestock in sub-Saharan Africa is consistent with other patterns observed in the broader conservation literature (Clark and May, 2002; Lawler et al., 2006; Lozano et al., 2019; Tensen, 2018; Troudet et al., 2017). Conservation research effort tends to be biased towards vertebrates, with mammals and birds receiving a level of research effort disproportionate to their prevalence in nature and, in many cases, to their level of extinction risk (Clark and May, 2002; Davies et al., 2018; Donaldson et al., 2017). These types of biases correlate with species charisma, resulting in the majority of research centering around taxa that contain colorful, large, distinctive species (Bonnet et al., 2002; Clark and May, 2002; Donaldson et al., 2017; Lawler et al., 2006). For example, Brambilla et al. (2013) found that more 'appealing' bird species in Italy received significantly more research attention, and Fleming and Bateman (2016) found that 'ugly' Australian mammals were vastly underrepresented in the published literature. The consequences of such biases have been examined in the fields of climate change mitigation (Feeley et al., 2017), animal behavior (Rosenthal et al., 2017), species reintroductions (Seddon et al., 2005), and conservation more broadly (Clark and May, 2002; Di Marco et al., 2017; Lawler et al., 2006; Stroud et al., 2014). There is clear evidence that these biases limit the development of ecological theory and conservation management practices (Fleming and Bateman, 2016; Lawler et al., 2006). Thus, taxonomic bias is a potential driver of the research-implementation gap in conservation (Amori et al., 2008; Martín-López et al., 2009; Seddon et al., 2005; Troudet et al., 2017).

Another important component of taxonomic bias relates to conservation funding, which tends to disproportionately support charismatic species (Curtin and Papworth, 2020; Davies et al., 2018; Di Marco et al., 2017; Fleming and Bateman, 2016; Stroud et al., 2014). In fact, many of the world's largest conservation non-governmental organizations explicitly focus their funding efforts on charismatic species (Brockington and Scholfield, 2010a, 2010b; Holmes et al., 2012). Prioritization of funding in conservation is determined by a blend of political agendas and social contexts (Martín-López et al., 2009; Stroud et al., 2014). Public interest in charismatic species motivates donations, which support further opportunities to study those same species (Davies et al., 2018). Further, as reviewers and researchers are implicitly biased towards papers that emphasize their own study organisms, the literature increasingly highlights the same subset of charismatic species (Bonnet et al., 2002; Martín-López et al., 2009; Rosenthal et al., 2017; Wilson et al., 2007). This trend is evident within the field of carnivore conservation, where big cats consistently receive more funding and research effort than other species (Curtin and Papworth, 2020; Davies et al., 2018). This bias is particularly notable in Africa (Di Marco et al., 2017). For example, in 2017 the Leonardo DiCaprio Foundation announced a $1 million seed donation to establish the Lion Recovery Fund in collaboration with the Wildlife Conservation Network. This effort was subsequently supported by a variety of additional sponsors, including the Disney Conservation Fund. Within its first year, the fund distributed approximately $2.4 million across 28 different research and conservation projects centered on the African lion (*Lion Recovery Fund Progress Report* 2018). Similarly, National Geographic's Big Cat Initiative is currently requesting proposals for research programs examining lion conservation among 20 lion-specific priority areas. Through this initiative, up to $100,000 of support may be awarded per project. These conservation funds are allocated across a geographic range where less charismatic spotted hyenas co-occur and tend to be more problematic for livestock owners than African lions.

It is possible that the negative effects of taxonomic bias as discussed here could be ameliorated by the ‘flagship species concept’. According to this concept, conservation of many co-occurring species may be simultaneously aided by the focus of conservation attention on large charismatic species (i.e., ‘flagships’; Andelman and Fagan 2000; Roberge and Angelstam 2004; Smith et al. 2012; Albert et al. 2018). These flagships tend to be large-bodied mammals that are often described as ‘beautiful’ or ‘impressive’ (see Albert et al. 2018). Conservation status can also contribute to species charisma (Albert et al., 2018; Martín-López et al., 2009). Species at greater risk of extinction, particularly those that are charismatic, tend to motivate conservation engagement and fundraising (Albert et al., 2018; Brambilla et al., 2013; Courchamp et al., 2006; Smith et al., 2012). Spotted hyenas are considered to be of “least concern” by the IUCN and thus carry little power for motivating conservation engagement from the perspective of species rarity. However, African lions and leopards are listed as ‘vulnerable,’ and African wild dogs as ‘endangered.’ As the populations of these three species continue to decline, their value as a conservation flagship only grows (Martín-López et al., 2009; Ripple et al., 2014; Wolf and Ripple, 2017). However, the extent to which the flagship species concept demonstrably supports the conservation of species below the flagship remains a source of considerable debate (Andelman and Fagan, 2000; Caro et al., 2004).

1.6 Conclusion

Recent studies have indicated the benefits of strategic prioritization of charismatic species to further broad-scale biodiversity conservation (Bennett et al., 2015; McGowan et al., 2020; Smith et al., 2012). However, such an approach may have adverse effects on the development of practices intended to address human-carnivore conflict. While my study may initially contribute to the large number of publications on antagonistic human-carnivore interactions, I hope that this critical assessment may help to maximize the conservation impact of future research efforts in this field. My results indicate that current patterns of research prioritization are resulting in a misalignment between the drivers of human-carnivore conflict and research on that topic. Consequently, conflict intervention practices founded upon that research may be limited in their ability to mitigate the declines in large carnivore populations evident around the world. Solutions for this global conservation challenge may be better served by alternate prioritization schemes that promote species-specific knowledge and more comprehensive understanding of the patterns of livestock depredation. I advocate for increased incentivization of the study of livestock depredation by less charismatic carnivore species including the spotted hyena. Development of this knowledge base will facilitate the explicit examination of the effectiveness of conflict mitigation efforts.

The call for research on less charismatic species is often based upon the conservation status of those species, where their relative omission from the literature may be increasing their risk of extinction (Brambilla et al., 2013; Seddon et al., 2005). Here, I provide evidence for an additional motive for addressing this bias, as the underrepresentation of spotted hyenas is unlikely to put the species itself at risk of extinction. Instead, I show that in the case of livestock depredation, and subsequent human-carnivore conflict, this bias may be negatively impacting the conservation of other depredating species as well. As taxonomic bias is widespread in conservation, further examination is likely to reveal similar trends in other regions and fields of study. My study suggests that increased examination of current patterns of funding and research effort is needed to bridge the existing gap between conservation priorities and conservation research.

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CHAPTER 2: CONCEPTUALIZING HUMAN-WILDLIFE COEXISTENCE IN COMPLEX SYSTEMS: THEORETICAL FOUNDATIONS AND LIVED EXPERIENCES

2.1 Abstract

Human-wildlife coexistence is often impeded by the complexities of the systems in which humans and wildlife regularly interact. These complex systems can be distilled into two primary dimensions, structural and relational, each of which contains a variety of constitutive components. The structural dimension contains components associated with the social and ecological structures of the system, including political histories of the region and trophic structures of the ecological community. The relational dimension contains components associated with the interactions among the human and non-human actors in the system. For the purposes of human-wildlife coexistence, these components can be characterized as human-human (e.g., conflicts between land owners and conservationists) or human-wildlife (e.g., carnivore depredation of livestock). Most often, research on human-wildlife coexistence focuses on just one component of the system at a time. Even when studies bridge components, they tend to focus on a single wildlife species or guild. As a result, the field of human-wildlife coexistence lacks theoretical explanations of the ways in which components of these complex systems interact. We conducted a qualitative assessment of human-wildlife coexistence experiences in Northern Tanzania. We carried out 100 semi-structured interviews of subsistence agro-pastoralists using a grounded theory approach, and examined the intersection of human coexistence with carnivores and African elephants (*Loxodonta africana*). We identified six themes from these interviews: *i*) threat to food security, *ii*) threat to human safety, *iii*) threat to societal well-being, *iv*) need for wildlife education, *v*) need for trust in government, and *vi*) need for resources and solutions. We then explored the ways in which these themes contained

components from multiple dimensions of the complex system, and the implications of those interactive components for human-wildlife coexistence. We found that the nature of human-elephant interactions amplified the negative impacts of human-carnivore interactions, and decreased human willingness and capacity to participate in interventions designed to promote human-wildlife coexistence. All themes co-occurred with at least two others, exemplifying the interconnected nature of all components in this system. Furthermore, the theme need for resources and solutions was the most common (28.4% of all theme occurrences) and was the only theme to co-occur with all others, indicating that addressing this need may have cascading positive effects on human-wildlife coexistence throughout the system. Our study provides a stronger theoretical foundation of human-wildlife coexistence in complex systems, and grounds this understanding in the lived experiences of individuals within those systems.

2.2 Introduction

Complex systems research is increasingly common among the conservation sciences (Ladyman et al., 2013; Liu et al., 2007). Complex systems are those in which a diversity of components interact in often unpredictable patterns of feedback, resulting in constant change and shifting system boundaries (Game et al., 2014; Jochum et al., 2014; Ladyman et al., 2013). Thus, it is difficult to isolate and address the drivers of, and solutions to, challenges within these systems (Game et al., 2014; Ladyman et al., 2013; Mason et al., 2018). As conservation challenges tend to contain a range of both social and ecological components, they are often situated within particularly complex systems (Bennett et al., 2017b; Dunnink et al., 2019; Thondhlana et al., 2020). The expansion in research on such systems is largely attributable to an increased appreciation for the role system complexity plays in maintaining the research-implementation gap inherent to many of these challenges (Game et al., 2014; Holzer et al., 2019). This gap is often defined as the breakdown between the accumulation of scientific information and the development of effective management actions (Knight et al., 2008; Toomey et al., 2017). For challenges enmeshed in complex systems, this gap may be perpetuated by a lack of understanding of the linkages and interactions among system components (White et al., 2009). Therefore, assessments of the system as a whole may help elucidate these patterns and mitigate research-implementation gaps (Knight et al., 2019; Toomey et al., 2017).

Coexistence among humans and wildlife is one such challenge characterized by a research-implementation gap driven in part by the complexity of the systems in which it must occur (Beck et al., 2019; Game et al., 2014; Gray et al., 2019; Mason et al., 2018; R.A. Montgomery et al., 2018). In the case of human-wildlife coexistence, the components of these complex systems can be broadly sorted into two dimensions (Fig. 2.1). The first dimension is structural, and as such contains components that are associated with the social and ecological structures of the system (Game et al., 2014; Lischka et al., 2018). Social components, for instance, may include political histories of colonialism, apartheid, and other forms of institutionalized inequality (Madden and McQuinn, 2014; Rust et al., 2016). Similarly, the dynamics of ecological communities such a species interactions contribute to the ecological structure of the system (Laguna et al., 2015; Thinley et al., 2018; Fig. 2.1). Secondly, the relational dimension contains components of the interactions between various actors in the system (Lozano et al., 2019; Pooley et al., 2016). Here, we define actors to be individuals, both human and non-human, institutions, or entities that have the capacity to influence systems-level values and actions (sensu Jepson et al., 2011, also see Barua, 2013; Evans and Adams, 2018; Lorimer, 2007). Human-human interactions can include conflicts arising from contradictory interests or goals related to wildlife, particularly when one party is perceived to prioritize its interests at the expense of the other's (Mason et al., 2018;

Redpath, 2015; White et al., 2009). Human-wildlife interactions can include processes such as carnivore depredation of livestock and coupled retaliatory killing of carnivores (Lozano et al., 2019; Pozo et al., 2021; Fig. 2.1). These relational components are often framed as conflicts. However, this negative framing is increasingly recognized as overly simplistic and detrimental to coexistence (Bhatia et al., 2020; Pooley et al., 2016; Redpath, 2015; Redpath et al., 2013; Young et al., 2010). Therefore, we refer to these components as relational to avoid limiting our assessment to purely negative interactions among actors.

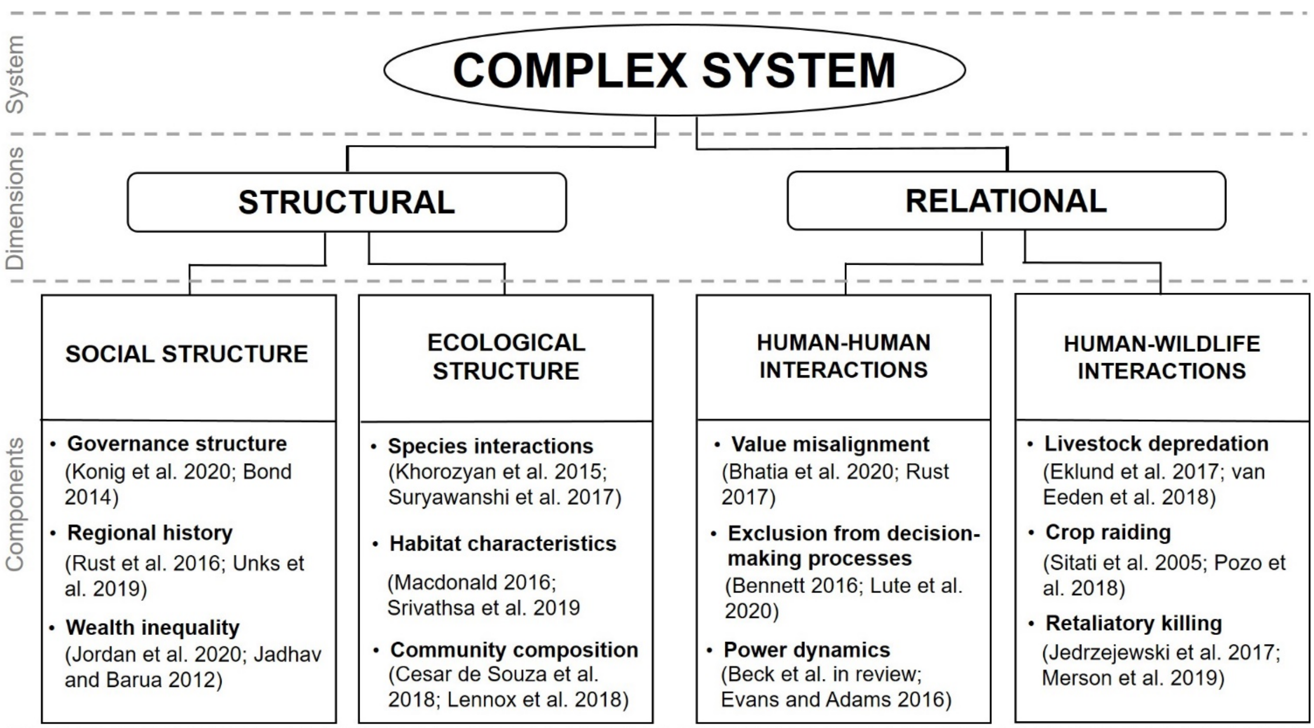

Figure 2.1. A conceptual diagram illustrating some of the potentially interacting components of the complex systems in which human-wildlife coexistence is situated. The systems can be divided into a structural dimension, containing social and ecological components, and a relational dimension containing human-human and human-wildlife components. A non-

Figure 2.1. (cont'd) exhaustive list with representative examples of each type of component are provided, along with supporting citations.

As this is a complex system, it is inherently characterized by interactions among these components (Jochum et al., 2014; Mason et al., 2018). In this case, structural components determine the types of interactions that can occur, and in turn the relational components can influence newly emergent structures. As an example, competition among carnivores can drive rates of livestock depredation (Miller et al., 2016; Rostro-García et al., 2016), and livestock depredation can subsequently trigger retaliatory killing of carnivores (Inskip et al., 2014; Merson et al., 2019). In some cases, this retaliatory killing is extreme enough to result in the functional extinction of carnivore species, thus shifting the trophic structure of the ecosystem (Courchamp et al., 2018; Ripple et al., 2016, 2014). Therefore, consideration of all components together is necessary to develop true understanding of the system (Game et al., 2014; Redpath et al., 2013). Recent publications have presented detailed theoretical and methodological outlines to better blend components of these dimensions in scientific explorations of human-wildlife coexistence (see Beck et al., 2019; Kansky et al., 2016; Lischka et al., 2018; White et al., 2009; Wilkinson et al., 2020). However, empirical research, up to this point, has tended to focus on only one component (Emerson et al., 2003; Germain and Floyd, 1999; White et al., 2009). This trend is not dissimilar from tendencies to simplify complex systems across many types of ecological research (see Montgomery et al., 2019). Furthermore, research commonly explores one component via single-species or single-guild case studies (Hoffmann and Montgomery, 2021; Pozo et al., 2021; White et al., 2009). Therefore, prevailing depictions of the factors impeding human-wildlife coexistence are fragmented, with deep vertical knowledge regarding individual species-specific components but weak understandings of horizontal connections between them

(Lischka et al., 2018; White et al., 2009). Consequently human-wildlife coexistence research typically lacks underlying connections to theory, particularly in regards to the ways the different components of complex systems interact (Emerson et al., 2003; White et al., 2009).

Here we explored the interactions among components via a qualitative assessment of the experiences of individuals inhabiting a system that experiences intense human-wildlife interactions in Northern Tanzania. This system is particularly complex given the colonial history of the country, largely intact carnivore and herbivore guilds, and high spatial overlap between human and wildlife populations (Bluwstein, 2018; Mkonyi et al., 2017a; Ripple et al., 2014; Sachedina, 2006; Torres et al., 2018). We conducted semi-structured interviews to assess both the nature of these human-wildlife interactions and how they are situated within the complex system. Following analysis of the interview data via constant comparative analysis to detect emergent themes, we explored how those themes embody the linkages among the components of the complex systems in which human-wildlife coexistence must occur. Throughout, we considered how system components related to traditionally isolated study species may be linked. Specifically, we explored components related to African elephants (*Loxodonta africana*; hereafter 'elephants') and carnivores, as our interview participants repeatedly expressed the intrinsic connection between the two. We discuss the implications of our assessment for human-wildlife coexistence given the need for better theoretical understanding of the linkages among the components and dimensions of complex systems. We provide empirical evidence of these connections in our study system, and highlight the importance of developing foundational understanding of the complexity that may impede human-wildlife coexistence globally.

2.3 Methods

2.3.1 Study site

We positioned our case study in a region of Northern Tanzania that is comprised of a matrix of protected areas and human community lands (Nelson, 2005). The study area contains four primary protected areas including Lake Manyara National Park, Tarangire National Park, Manyara Ranch Conservancy, and Ngorongoro Conservation Area (Fig. 2.2). The region supports a population of approximately 640,000 people, growing at an average rate of 3.4% per year (Mponzi et al., 2014; Msoffe et al., 2011a). Local people primarily maintain subsistence agro-pastoralist lifestyles with small scale agricultural crops and livestock including cows, sheep, and goats (Kissui, 2008; Nelson, 2005). The region includes populations of carnivores such as African lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas *(Crocuta crocuta*), and black-backed jackals (*Canis mesomelas*; Kissui, 2008; Mponzi et al., 2014). It also supports diverse guilds of browsing and grazing herbivores such as elephants, plains zebras (*Equus quagga*), and common wildebeest (*Connochaetes taurinus*; Kioko et al., 2013; Mkonyi et al., 2017a). The population densities of these species vary substantially by season, generally increasing during the wet season (November to May; Kissui, 2008; Morrison and Bolger, 2014; Msoffe et al., 2011b). Together, these human and wildlife populations, along with the high rates of interactions among them (Kissui, 2008; Mkonyi et al., 2017b; Pittiglio et al., 2013), constitute many of the social and ecological components of the complex system.

This system is further complicated by the country's governmental structure. While the formal structures of the Tanzanian government have experienced profound changes over time, it has maintained a hierarchical arrangement since its independence from the United Kingdom in 1963 (Bluwstein, 2018; Torell, 2002). As a result, the Tanzanian government is generally characterized by a hierarchy of administrations, with nested government systems including national, regional, district, ward, and village offices (Venugopal and Yilmaz, 2010). There is a decentralized local government system, which gives officials at smaller local offices substantial power of decision (Slocum and Backman, 2011; Venugopal and Yilmaz, 2010). However, much of the administrative functions remain centralized, so fiscal power is primarily held at the national and regional levels (Slocum and Backman, 2011; Torell, 2002; Venugopal and Yilmaz, 2010). Wildlife management is similarly centralized, and is almost exclusively the purview of national institutions (Bluwstein, 2018; Caro and Davenport, 2016; Nelson et al., 2007).

2.3.2 Semi-structured interviews

We centered our examination on ten focal villages across our study region (Mbuyuni, Esilalei, Losirwa, Makuyuni, Minjingu, Mswakini Chini, Mswakini Juu, Naiti, Naitolia, Olasiti, and Oltukai; Fig. 2.2). We selected households (i.e., bomas) for inclusion in our study via a stratified random sample designed to ensure geographic distribution across the extent of our study area (Fig. 2.2). We then chose ten bomas per village, with at least one in each of the spatially distinct areas (i.e., sub-villages) that compose the villages. The field team for this study consisted of CH, a Tanzanian doctoral student in the Department of Social Work at Michigan State University, and a Tanzanian master's student from Sokoine University of Agriculture. Both of these latter students were fluent in English and Swahili, commonly spoken in the rural communities within our study area. In each village, we also hired a local guide to help us locate bomas, introduce us to the head of each household, and provide additional translation assistance if the participant preferred to conduct the interview in Maa. Upon arriving at a potential boma, we waited while the local guide approached the head of the household to introduce us and our research. We then received verbal consent to conduct the interviews and captured each interview with notations and audio recordings. Consistent with the cultural practice of the region, if the male head of the household was not present, we conducted our interview with the female head of the household, as long as she was comfortable doing so. In instances in which the interview was conducted in Maa, we translated the participants' responses to Swahili in real time to ensure the notations and recordings were interpretable at a later date.

Prior to conducting the study, all procedures were approved by Michigan State University's Institutional Review Board on the Use of Human Subjects (IRB # i053842) and were fully permitted and approved both by the Tanzanian National Parks Authority (TANAPA) and the Tanzanian Wildlife Research Institute (TAWIRI). We also received written permission from the Tanzanian government at the regional, district, ward, and village levels prior to carrying out interviews. We followed a semi-structured protocol and initiated our interviews with general queries related to daily life and community (e.g., "*What do you like about this community?*"). We differentiate communities from villages, in that we considered communities to be social groups with no institutionalized boundaries. Villages, in contrast, referred to the administrative locality derived from the hierarchical Tanzanian government structure. In doing so, we allowed participants to determine which individuals were relevant for inclusion in their responses, regardless of which village they lived in. We then transitioned to human-carnivore interactions (e.g., "*Which carnivore species do you think poses the greatest risk to your livestock or livelihood?*") and finished with broader explorations of complexity in the system (e.g., "*Do community members participate in decisions regarding wildlife?*"; see Appendix 2.1 for full interview protocol). Participants could introduce new topics of conversation, via open-ended questions but we did not expand on those avenues of inquiry beyond the information that was volunteered. After completion of all interviews, we translated the audio recordings into English.

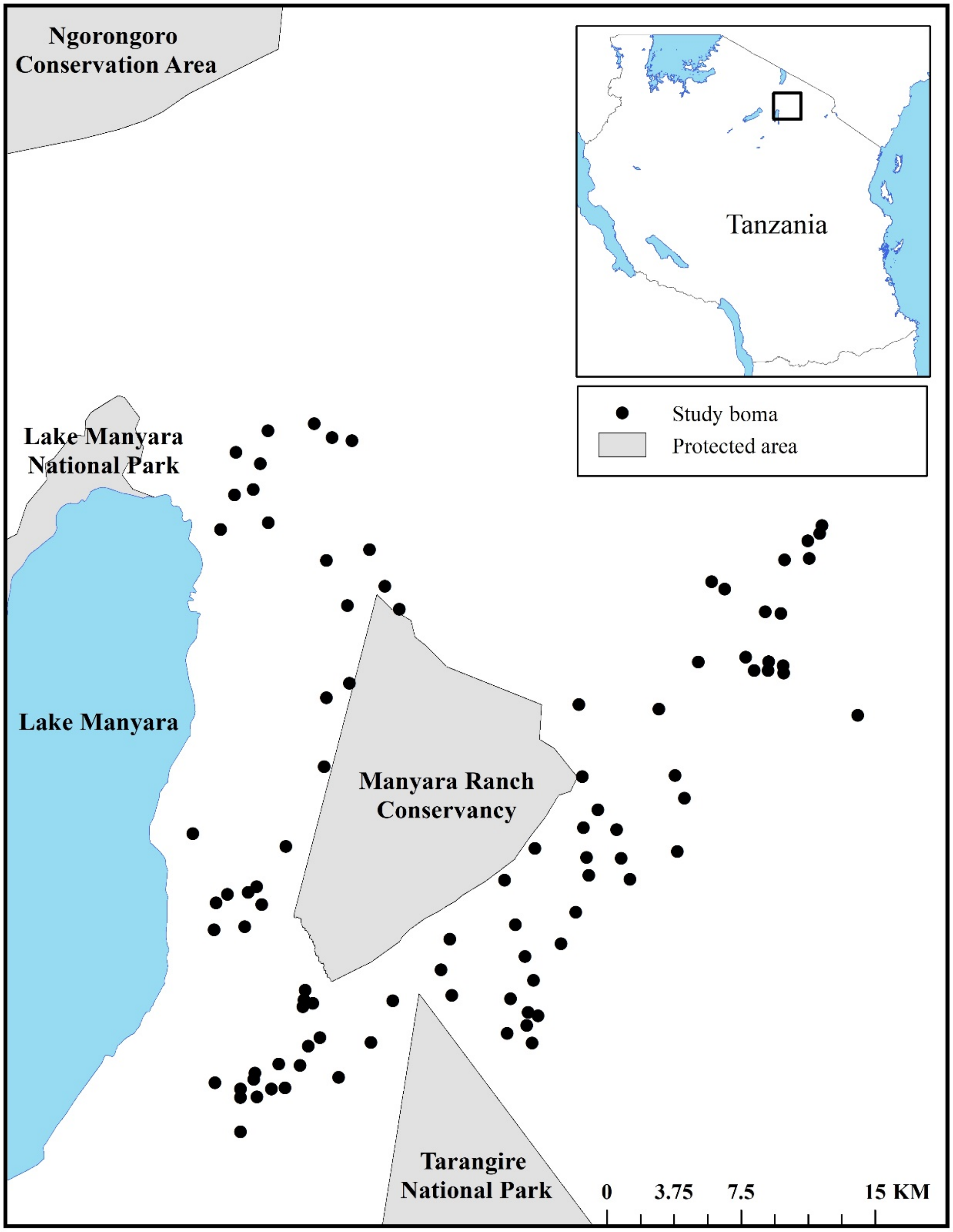

Figure 2.2. The location of the 100 bomas included in interviews about human-wildlife coexistence in Northern Tanzania from May to August 2018.

2.3.3 Interview analysis

The interview analysis was also conducted using a three-person team, consisting of CH, a doctoral student from the Department of Social Work, and a third doctoral student specializing in the social aspects of human-wildlife coexistence. We used a grounded theory approach to analyze the interview transcripts (Charmaz, 2006; Glaser and Strauss, 1967), which allows for interpretive theories to be derived from the content under study, rather than pre-existing hypotheses. While conducting the interviews, it became evident that human coexistence with carnivores and elephants were intrinsically linked. Participants commonly discussed their interactions with both carnivores and elephants in the same response, even though we only mentioned carnivores in the interview questions. Thus, we centered our analysis on the intersection between elephant and carnivore-related system components. Specifically, we assessed system components related to elephants, within the carnivore-centric interview structure. Within this grounded theory approach, we analyzed the interview transcripts using the constant comparative analysis method (Anfara et al., 2002; Glaser and Strauss, 1967). Through this process, we conducted two rounds of coding, the first to identify initial codes and the second to identify patterns and themes among those codes (Anfara et al., 2002). We conducted this analysis in triplicate, with each member of the team independently coding the transcripts. We then discussed our codes and rationales until we came to an agreement on the final emergent themes. Each team member then independently re-analyzed the interviews to quantify the frequency of the six emergent themes. Here, the emergent themes are representative of multiple system components, and how they may be linked in the lived experiences of our participants. Next, we assessed theme co-occurrence via a multi-step process. First, by working on an interview-by-interview basis, we determined which themes were present and created a pairwise list of co-occurring themes. Second, we calculated the total number of co-occurrences for each pair of themes, across all interviews. Finally, we assessed whether this number was > 50% of the total number of occurrences for either theme within a given pair. This value represents intersections of themes within each interview, and thus is again indicative of the relationships between system components in the personal experiences of our participants.

We also explicitly assessed how each theme may contain components of multiple dimensions of the complex system (i.e., social structure, ecological structure, human-human interactions, human-wildlife interactions), based upon the content of the interview excerpts that comprised that theme. As an example, many excerpts within the theme threat to food security centered around the prevalence of elephant crop raiding. Crop raiding is a human-wildlife interaction strongly influenced by the ecological structures of the system (e.g., competition for food resources) and thus represents the intersection of those two types of components. We also mapped out the patterns of theme co-occurrence across the different dimensions.

2.4 Results

We conducted 100 interviews across 43 sub-villages, 71 of which included comments related to elephants although no interview questions specifically addressed that species. Further, the participants in 76% (n = 54) of those interviews mentioned threats to both human-carnivore and human-elephant coexistence together, without any separation between them (e.g., "We lose our livestock and the animals destroy our crops"). Among the 71 interviews, 52 participants (73.2%) were male, and the remaining 19 (26.8%) were female. We identified 74 initial codes in the first iteration of analysis, and six emergent themes in the second (Table 2.1; Table 2.2). The themes were *i*) threat to food security, *ii*) threat to human safety, *iii*) threat to societal well-being, *iv*) need for wildlife education, *v*) need for trust in government, and *vi*) need for resources and solutions (Table 2.2). We identified a total of 409 occurrences of these six themes. The most common theme was need for resources and solutions (*n* = 116, 28.4%), followed by threat to food security (*n* = 94, 23.0%), need for trust in government (*n* = 82, 20.0%), need for wildlife education (*n* = 49, 12.0%), threat to societal well-being (*n* = 49, 12.0%), and threat to human safety (*n* = 19, 4.6%; Table 2.3).

Table 2.1. The codes and themes identified via constant comparative analysis of 71 interviews on human-wildlife coexistence in Northern Tanzania. The codes and themes are specific to elephants, but framed within interview questions centered around carnivores or wildlife more broadly. The codes shown here are representative examples of those subsequently consolidated into emergent themes.

First iteration: Initial codes		
1A. Crop loss	1B. Threat to human safety	1C. Hunger
1A. Farm destruction	1B. Elephants kill people	1C. Poverty
1A. Wildlife attack (farms)	1B. Wildlife attack (people)	1C. Societal impact
2A. Education	2B. Elephants more important than people	2C. Farm protection strategies
2A. Lack of solutions	2B. Compensation	2C. No solutions/help
2A. Community meetings about problems	2B. No follow through on promised help	2C. Human-elephant conflict mitigation
Second iteration: Emergent themes		
1A. Threat to food security	1B. Threat to human safety	1C. Threat to societal well-being
2A. Need for wildlife education	2B. Need for trust in government	2C. Need for resources and solutions

Table 2.2. The emergent themes identified among 71 interviews on human-wildlife coexistence in northern Tanzania. The themes are specific to elephants, but emerged from interview questions centered around carnivores or wildlife more broadly. Each theme is presented with a detailed description and a representative quotation.

Emergent theme	**Description**	**Example quotation**
Threat to food security	Elephants pose a direct threat to the production, harvesting, or availability of food in farms.	"Now our main resource is livestock because elephants have destroyed the farms, we can't rely on the farms. If we are lucky we have rains, we can grow enough crops, but elephants destroy the farms"
Threat to human safety	Elephants pose a direct threat to the safety of humans.	"We have several people who have died during elephant attacks. We also have a couple people who have been injured by elephants as well."
Threat to societal well-being	Elephants contribute to the undercurrent of challenges that the community members face. They increase the difficulty of life in this landscape, sometimes to the point of threatening lives and lifestyles.	"There has been an increase in animals. Yesterday I was talking to someone about how in the next three years I don't think that we will be able to do agriculture anymore because of them."
Need for wildlife education	Community members need opportunities to learn how to help themselves. They want access to the knowledge that has been gathered regarding negative human-wildlife interactions, and best practices to mitigate the resultant impacts.	"We told you we want meetings, workshops, and seminars in our village [about wildlife], is that going to happen? Are we going to get that education and collaboration?"
Need for trust in government	Community members cannot rely on the support of the government (or its associated agencies) to prevent negative interactions with elephants or to recover afterward. They feel the government values animals above them.	"Sometimes people get hurt, these wild animals destroy our farms and livestock, and still no one is paying any attention. We don't get any support from the government."
Need for resources and solutions	Community members need assistance obtaining resources to protect themselves and their crops from elephants. They know what tools would be helpful, but they do not have a way to access them on their own.	"Our youth don't sleep at night- they just stay awake to chase elephants away. Sometimes we try traditional methods like burning manure."

Table 2.3. The frequency of occurrence for each of the six emergent themes identified among 71 interviews on human-wildlife coexistence in Northern Tanzania. Themes are also presented as a percentage of all theme occurrences.

Emergent theme	No. of codes	% of all codes
Threat to food security	94	23.0%
Threat to human safety	19	4.6%
Threat to societal well-being	49	12.0%
Need for wildlife education	49	12.0%
Need for trust in government	82	20.0%
Need for resources and solutions	116	28.4%

The theme threat to food security contained components that represent the intersection between Ecological structure x Human-wildlife interactions (Fig. 2.3A), while threat to societal well-being represented Social structure X Human-wildlife interactions (Fig. 2.3B). The threat to human physical safety represented the intersection of components from both Human-wildlife interactions X Ecological structures and Human-wildlife interactions X Social structures (Fig. 2.3A, B). The themes need for resources and solutions, need for wildlife education, and need for trust in government all contained components representative of the intersection of Social structure X Human-human interactions (Fig. 2.3C). No themes contained components representing the intersection between Ecological structure X Human-human interactions (Fig. 2.3D). All themes co-occurred with at least two others, but the need for resources and solutions was the only theme that co-occurred with all five additional themes (Fig. 2.3).

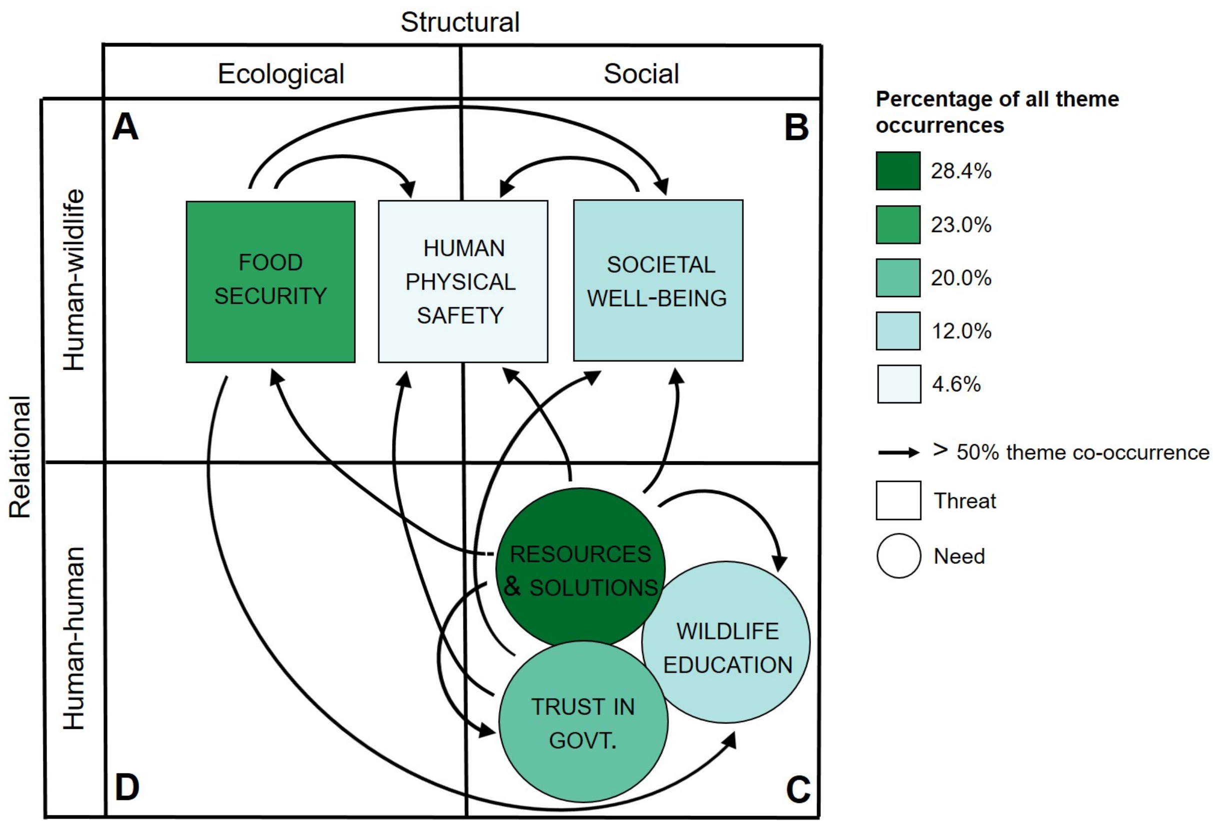

Figure 2.3**.** The six emergent themes, representing intersecting components within the two dimensions of complex systems in which human-wildlife coexistence must occur. Each theme is colored according to its frequency of occurrence, and the patterns of co-occurrence among the themes are represented by arrows. The theme at the origination of each arrow exhibits > 50% co-occurrence with the theme at the terminus of the arrow.

2.5 Discussion

Human-wildlife coexistence research must mirror the complexity of the systems in which it is situated. The importance of broadened systems approaches became readily apparent during the process of conducting our interviews. We did not introduce the topic of elephants, crop raiding, or any specific aspect of human-wildlife coexistence beyond that associated with carnivores.

Despite that reality, almost three quarters of our participants voluntarily described threats to coexistence with elephants, most of the time in the same phrase as they discussed those related to carnivores. Thus, it became evident that human-carnivore and human-elephant coexistence are fundamentally linked in this system. In recognition of this complexity, we explored the ways in which these themes contained elements from multiple dimensions of the complex system and the implications of these interactions for human-wildlife coexistence.

2.5.1 Ecological structure X Human-wildlife interactions

We detected an important interaction between the threat that elephants and carnivores pose to food security (Fig. 2.3A). Specifically, we found that elephant threats to food security amplify threats from carnivores. Our participants consistently identified both livestock and crops as important resources in their communities, but more commonly noted the threat elephants posed to the availability of those resources. For instance, one participant explained "we all use these resources, so if we are lucky enough to have rain throughout the year we have enough crops. But elephants are always the big problem, they come and destroy our crops." In some locations, elephant destruction of food crops makes up 90% of the damage caused by large mammals, which may equate to a loss of an entire year's food supply (Lamarque et al., 2009). Elephants also commonly raid food stores, which cannot be replaced until the next growing season, leaving families without supplies to subsist on during the drier months (Hoare, 1999; Lamarque et al., 2009). Importantly, however, this threat is not distinct from that associated with carnivores. Carnivore depredation of livestock also presents a profound threat to food security (Jordan et al., 2020; Mwakatobe et al., 2013). Additionally, it can cause substantial financial stress that limits abilities of livestock owners to purchase the supplementary food resources necessary for survival after elephant crop raiding (Jordan et al., 2020; Manoa and Mwaura, 2016; Mwakatobe et al., 2013). Consequently, the coupled threats of crop raiding and livestock depredation can erode both daily resources and emergency fallbacks in agro-pastoral food supplies (Jordan et al., 2020; Mackenzie and Ahabyona, 2012). Our participants noted this intersection, describing the substantial decrease in food security they experience when elephants destroy their crops and carnivores eat their livestock. One man from Mbuyuni summarized the double threat, stating "wild animals destroy crops, and carnivores such as lions, hyenas, and leopards eat our livestock. Especially in our area, elephants are destroying our crops which is why we depend on the livestock."

The threat that elephants pose to human safety continues to build upon these layers of impacts. We did not ask any participants to discuss the threats that elephants posed to their physical safety. Yet, they offered up stories of community fears and personal traumas on multiple occasions. This pattern clearly indicates that they viewed the physical threats posed by elephants to be implicitly intertwined with the questions we presented about carnivores. One male participant from Minjingu was especially transparent about the impact elephants have had on his family, telling us

> "My son was killed by an elephant almost four years ago...The government came to see the situation. The district commissioner came and they came to see the area, but I never got any response or feedback from the government. So I also went to report to Monduli District. I took all the documentation, but never got any response. Other government officials came and took some photos but nothing happened. You know, we love animals. But they hurt us. He was our firstborn."

This example is representative of a common trend within our interviews. In every story told about elephant-related deaths or injuries, the victim was male. This pattern was not unexpected, as in many cultures in sub-Saharan Africa, male members of households are primarily responsible for guarding crops and thus are most likely to come into contact with elephants (Barua et al., 2013; Hoare, 2000; Thondhlana et al., 2020). These individuals are also the most likely to be working to earn additional income from outside sources (Barua et al., 2013; Hoare, 2000; Thondhlana et al., 2020). Consequently, death or injury often results in an increased household reliance on farming and pastoralism (Thondhlana et al., 2020).

2.5.2 Social structure X Human-wildlife interactions

Threats to human safety can also have psychological and social effects, resulting in a reduced capacity for individuals to respond to negative human-wildlife interactions (Barua et al., 2013; Lamarque et al., 2009; Nyumba et al., 2020; Ogra, 2008; Fig. 2.3B). We found that this impact was also amplified through the intersection of carnivore and elephant interactions. For instance, when a male member of a family is injured or killed by an elephant, as was commonly described by our participants, the rest of the family must undergo rapid shifts in responsibility and workloads (Lamarque et al., 2009; Ogra, 2008). These individuals have to maintain their other household responsibilities, and are therefore often working under conditions of stress and sleep deprivation (Barua et al., 2013; Thondhlana et al., 2020). The death or injury of a family member also brings additional emotional trauma, including grief, loneliness, and fear (Evans and Adams, 2018; Jadhav and Barua, 2012; Sitati et al., 2005; Thondhlana et al., 2020). These outcomes must be considered for human-wildlife coexistence as a whole, as they can erode overall tolerance for wildlife and individual capacity to respond to the impacts of all species (Kansky et al., 2021, 2016; Kansky and Knight, 2014).

Furthermore, these implications are exemplified by the theme of threat to societal well-being. Well-being is subjective and contextual, and can encompass factors ranging from access to clean water to cultural identity and happiness (Dower, 2015; Milner-Gulland et al., 2014; Thondhlana et al., 2020). Our participants referenced a breadth of threats to their well-being. One of the most notable was fear that increasing rates of crop destruction by elephants might threaten the persistence of their way of life. For example, one participant told us "There has been an increase in elephants. Yesterday, I was talking to someone about how in the next three years I don't think that we will be able to do agriculture anymore because of them." While elephants may be under threat in other regions of sub-Saharan Africa, the elephant population in our study area has remained stable over the past few decades (Kioko et al., 2013; Pittiglio et al., 2014). However, human populations have grown exponentially in the same time period, resulting in an increase in overlap between human agricultural lands and elephant ranges (Msoffe et al., 2011a; Pittiglio et al., 2014). Additionally, changing climates are shortening growing seasons and driving stochasticity in the availability of water (Macdonald, 2016; Msoffe et al., 2011a; Mukeka et al., 2019). Together, these factors have resulted in increased rates of crop raiding during shorter growing seasons, thus limiting agricultural outputs and disrupting traditional livelihood practices (Barua et al., 2013; Thondhlana et al., 2020). The psychological effects of these stressors can substantially reduce both individual capacity for participation in human-wildlife coexistence interventions, and willingness to do so, regardless of the species involved (Kansky et al., 2021; Kansky and Knight, 2014; Milner-Gulland et al., 2014; Thondhlana et al., 2020).

2.5.3 Social structure X Human-human interactions

We found that need for wildlife education, trust in government, and resources and solutions were further eroding capacity and willingness for individuals to participate in coexistence interventions. Many participants expressed frustration that they had been communicating these needs consistently without seeing any changes. One man from Naitolia explained "now we are tired because when you talk about something without any action, it is meaningless. It is supposed to be when you talk about something that an action should be taken." This result was not unexpected as, in many cases, negative human-human interactions regarding wildlife are driven by unmet psychological needs (Dower, 2015; Madden, 2004; Madden and McQuinn, 2014; Redpath et al., 2013). Our participants expressed a desire to share in the wildlife knowledge they helped produce, to be valued by their government, and to have access to the resources they know exist. As these needs remain unmet, their patience for participating in continued human-wildlife coexistence research and interventions was quickly declining.

This reduced willingness to participate in interventions was largely due to frustration with being used to collect information that they were rarely privy to. One participant from Esilalei clearly laid out his thoughts on academic studies in his community, and the sharing of knowledge produced from that research,

> "Really there are three types of research. There's the research that has negative consequences. The second one is the research that will bring positive outcomes later, maybe for example there are things were hidden and you come to do research so we can find out about them. The other kind is where people do research but we don't get to see the purpose of the research or its outcomes. What is the type research you are doing?"

Our participants also identified an uneven distribution of knowledge, in cases where the research findings were shared. They described how the government, wildlife authorities, and leaders in their communities were getting access to wildlife education and knowledge, but they were excluded from those learning opportunities. "The government has all the knowledge, and they're supposed to bring this knowledge to the community. It's very rare to see the government officials bringing it to us though," explained another man from Esilalei. This hierarchical barrier in knowledge distribution is a source of concern in the pursuit of sustainable solutions for human-wildlife coexistence (Jordan et al., 2020). Leaving individuals in a cycle of threats to their well-being along with unmet needs can reinforce the antagonism they feel towards individuals who are perceived to be withholding that knowledge (Blaikie, 2006; Madden, 2004; Thondhlana et al., 2020).

A persistent need for wildlife education rendered our participants reliant upon government support. However, they felt that they could not trust that their government would provide help either. "Wild animals destroy our farms, we don't sleep at night because we have to protect our farms. I wish the government would provide a solution to this problem," one man from Oltukai stated. Our participants expressed, in no uncertain terms, that this pattern was due to the government valuing animals more than people. Some individuals stated this outright, telling us "animals are more important than me," and "it seems like the government cares more about animals than people." Another explained the reasoning behind this perspective, stating "if an animal gets killed, you will see at least 12 cars here, but if a human gets killed, you will just see maybe one." The implications of this lack of valuation by their government were just as apparent. "We've been participating and giving our feedback and recommendations, but no actions have been taken. So for us it doesn't make sense to keep participating," explained one individual. This sentiment was echoed by many others. Exclusion from the spheres of knowledge and distrust in the reliability of wildlife authorities both contribute to decreases in tolerance for wildlife and willingness to participate in future coexistence interventions (Jordan et al., 2020; Kansky et al., 2021; Redpath et al., 2017; Young et al., 2016, 2010). In addition, the types of knowledge and value inequities identified by our participants threaten the long-term sustainability of any interventions that are put in place (Madden, 2004; Madden and McQuinn, 2014)

The need for resources and solutions continues to build upon this erosion of willingness to participate in interventions. Even in instances in which the government offerend support and showed intent to follow through on that promise, these efforts were limited by a lack of resources. “There are way more attacks than rangers, so there aren’t enough resources to help support the communities” one participant explained. At an individual level, the implications of limited resources were even more apparent. When asked what strategies they use to deal with the challenges posed by wildlife, over half of our participants said that they did not have any at all. Many of these individuals mentioned trying “traditional methods” to deter animals. This typically consisted of staying awake at night so they could burn manure, use the bottom of buckets as drums, and yell at the animals. They emphasized an understanding of the ineffectiveness of that approach, particularly over long time periods as “the elephants get used to it so they know that it’s nothing and come and destroy your crops.” Importantly, night is the time period in which both the risk of livestock depredation and crop raiding are highest (Kissui, 2008; Mamo et al., 2014; Nelson et al., 2003; Ogada et al., 2003). Therefore, they must simultaneously attempt to protect their crops from elephants and be prepared to chase off a potentially depredating carnivore. The consistent lack of sleep resulting from this dual threat has been linked to increased rates of alcoholism (Ellis, 2010; Thondhlana et al., 2020), exposure to malaria (Dixon et al., 2009; SARPO, 2005), mental health morbidity (Barua, 2013; Hoare, 2000), and reduced school performance for students (Mackenzie and Ahabyona, 2012; Sitati et al., 2012). Therefore, the persistent need for resources and solutions may increasingly reduce community members’ physical, emotional, and psychological capacity to participate in coexistence interventions. This limited capacity on top of similarly eroded willingness to participate may severely impede human-wildlife coexistence.

2.5.4 Ecological structure X Human-human interactions

No themes contained components from both ecological structures and human-human interactions (Fig. 2.3D). This result indicates that the human-human interactions which constitute a substantial impediment to human-wildlife coexistence are unlikely to be addressed via research that centers on ecological structures. Ecological research tends to focus on the development of technical solutions to the impacts of wildlife (Redpath, 2015; White et al., 2009). While such efforts have value in and of themselves, they cannot provide insights on the interactions that arise from misalignment between the goals, values, and needs of groups of people (Peterson et al., 2010; Redpath, 2015; Redpath et al., 2013). Importantly, ecological research rarely considers the social consequences of findings or of the management recommendations derived from those findings (White et al., 2009). Thus, the prevalence of research that focuses solely on ecological structures is likely a contributing factor to the intractability of human-wildlife coexistence (Knight et al., 2006; Redpath, 2015). Knowledge drawn from the social sciences will be necessary to develop effective solutions to the human-human impediments to human-wildlife coexistence (Beck et al., 2019; Bennett et al., 2017a; Young et al., 2010). Moreover, this knowledge must be applied in explicit consideration of the social components inherent to the complex system (Knight et al., 2006; Madden, 2004; Young et al., 2010).

2.5.5 System perspective

We identified two key patterns from the intersections of themes across the system as a whole. The first is that the need for resources and solutions appears to be foundational in this system. This need was not only the most common theme, but also was the only one that exhibited > 50%

co-occurrence with all five other themes (Fig. 2.3). This result indicates that addressing this particular need may have cascading effects across the system. The importance of reliable resources and solutions has been consistently documented in research on human-wildlife coexistence (Kansky et al., 2014; Kansky and Knight, 2014; Mkonyi et al., 2017b; Pozo et al., 2021; Redpath, 2015). In fact, technical interventions designed to provide such solutions are among the most commonly recommended approaches to promote coexistence (Baynham-Herd et al., 2018). However, the effects of structured resource provision on the social components of coexistence remain in need of further exploration (Baynham-Herd et al., 2018; Madden and McQuinn, 2014; Redpath et al., 2013).

The second notable pattern that emerged from the broad perspective is that no single theme existed in isolation. Each theme was connected via co-occurrence with at least two others (Fig. 2.3). This interconnectedness emphasizes the complexity of this system. Further, it reveals the importance of research that can provide theoretical understanding of the ways in which components interact within such complex systems. We recognize that focused research programs intended to reveal depth and nuance within a single component of the system have value. However, the goal of such research programs is most often purported to be the provision of knowledge that can inform coexistence interventions (Arlettaz et al., 2010). These interventions must consider interactions among the diverse components of the complex system to be successful (Game et al., 2014; Jochum et al., 2014; Madden and McQuinn, 2014). Therefore, basing interventions on human-wildlife coexistence research that only considers one component of the system is unlikely to produce solutions that are effective over the long-term (Bennett et al., 2017a; Jordan et al., 2020; Madden and McQuinn, 2014; Redpath et al., 2013; Thorn et al., 2015). Research that can assess all components of complex systems of interacting dimensions and components is challenging logistically, financially, and conceptually (Game et al., 2014; Mason et al., 2018). To do so effectively requires interdisciplinary research teams that can design, carry out, analyze, and interpret data that bridges traditionally siloed disciplines (Beck et al., 2019; Bennett et al., 2017a; Robert A. Montgomery et al., 2018; White et al., 2009). Furthermore, such research is often difficult to publish in a system that rewards focused research on single species and components (Arlettaz et al., 2010; Linklater, 2003; Martín-López et al., 2009). However, the effort to overcome these obstacles is necessary to effectively advance human-wildlife coexistence.

2.6 Conclusion

The field of human-wildlife coexistence presently lacks underlying theoretical foundations explaining the ways in which components of these inherently complex systems may interact (Lischka et al., 2018; White et al., 2009). As coexistence must occur within complex systems, this knowledge gap serves as a notable impediment to the development of effective interventions (Game et al., 2014; Madden, 2004; Mason et al., 2018). By exploring linkages among social and ecological components of these systems, we contribute to a stronger theoretical foundation for human-wildlife coexistence. We further ground this understanding in the lived experiences of individuals within those systems. Doing so provides empirical evidence of the implications of linkages among system components for the success of human-wildlife coexistence interventions. Through this effort, we found that human-carnivore interactions are intrinsically tied to human-elephant interactions, as are individuals' willingness and capacity to engage with human-wildlife coexistence interventions. We also found that all components of this complex system are intertwined, which emphasizes the importance of developing research that can bridge traditional species or component siloes. We encourage future research to continue to expand the theoretical understanding of human-wildlife coexistence in complex systems.

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APPENDIX

APPENDIX

Appendix 2.1. Interview questions

Introduction

We are students from the Michigan State University Schools of Social Work and Fisheries and Wildlife. We are trying to learn about community participation and interaction with wildlife conservation in Monduli district. In this study, we hope to understand more about your perception of community and wildlife conservation in your area. Most importantly, we hope to understand what you believe to be important or poorly understood about this topic. We have a few specific questions to start off, but then we would like to give you an opportunity to tell us what we missed.

Interviewees must be at least 18 years old in order to participate. The information gathered during the interviews will be used to propose action plans that will help communities interact with wildlife conservation. This discussion will take between 30 and 45 minutes and please feel free not to answer any questions you are not comfortable with. All interviews will be completely anonymous – is it ok if we record our conversation so we can double check that we have correctly noted your answers?

<u>Participant information</u>

Date:

Ward:

Village:

Sub-Village:

Boma #:

Sex of Participant:

GPS:

Background

Can you describe what is your daily life is like?

What do you like about this community? (What is important to you in your community)

Resources

What resources are available in this area?

Do community members use these resources?

How do these resources help community members to improve their well-being?

Are these resources distributed equally among community members?

If YES, how?

If NO, why not?

Livestock predation

How often do are following carnivore species at your boma *i*) trying to kill livestock (Mara ngapi anakuja na kula mifugo) and *ii*) not trying to kill livestock (Mara ngapi anakuja na hali mifugo). All responses to be listed on a five point scale including *i*) Very often (Mara nyingi sana), *i*) Often (Mara nyingi), *iii*) Sometimes (Mara chache),*iv*) Rarely (Mara chache sana), and *v*) Never (kamwe). How many times per week or month, and the perceived reason for not trying to kill livestock?

Species: *Lions (simba), Hyenas (fisi), Leopards (chui), Jackal (mbweha), Other*

In the past year (2017-2018), how many livestock have you lost to carnivore depredation?

Which carnivore species do you think poses the greatest risk to your livestock or livelihood?

<u>Wildlife Conservation</u>

Do you understand the term wildlife conservation?

What are the biggest challenges for wildlife conservation this area?

How has wildlife conservation changed in the past 10 years?

Do community members participate in decisions regarding wildlife?

If so, who participates and how?

What do you think are the benefits that wildlife conservation has for the community?

Have you benefited financially from wildlife conservation?

What are the difficulties wildlife conservation causes for the community?

How do you overcome those difficulties?

Who in your community faces the most difficulties?

<u>Additional Comments</u>

Is there anything else you think we should discuss that was not covered? Do you have any other thoughts or recommendations that you would like to share?

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CHAPTER 3: THE IMPORTANCE OF ENCOUNTER RATE FOR PREDICTING CARNIVORE DEPREDATION OF LIVESTOCK RISK

3.1 Abstract

Carnivore depredation of livestock is one of the primary drivers of human-carnivore conflict globally, threatening the well-being of livestock owners and fueling large carnivore population declines. Interventions designed to reduce carnivore depredation of livestock typically center around predictions of depredation risk. However, these spatial risk models tend to be informed by data depicting the number of livestock attacked by carnivores. Importantly, such models omit key stages in the predation sequence which are required to predict predation risk, or in this case depredation risk. Applying the classic predation risk model defined by Lima and Dill (1990) demonstrates that depredation risk is dependent upon quantifying the rates at which carnivores encounter livestock before attacking. However, encounter rate is challenging to estimate, necessitating novel data collection systems. I developed and applied such a system to quantify carnivore-livestock encounters at livestock corrals (i.e., bomas) across a 9-month period in Central Kenya. Concurrently, I monitored the number of livestock attacked by carnivores at these bomas. While I detected 1,383 instances in which carnivores encountered livestock at the bomas, I only recorded seven attacks. I found that the encounter rate and attack rate for spotted hyenas were almost six and three times higher than that for any other species, respectively. Consequently, spotted hyenas posed the greatest depredation risk for livestock at the boma. I argue that better understanding of carnivore-livestock encounter rates is necessary for effective prediction and mitigation of carnivore depredation of livestock.

3.2 Introduction

Biodiversity loss is a wicked problem yielding a number of negative impacts on coupled human and natural systems around the world (Beck et al., 2019; Chapin et al., 2000; Pimm et al., 2014, 1995). In the dynamic and increasingly-globalized 21st century, drivers of biodiversity loss are varied, ranging from coarse processes such as climate change and land conversion, to fine-scale ones including the effects of invasive species and poaching (Chapin et al., 2000; Pimm et al., 2014). Loss of biodiversity in the order Carnivora is of particular concern given the influential role that these species tend to play in the apex and meso-predator positions of global ecosystems (Dorresteijn et al., 2015; Estes et al., 2011; Ripple et al., 2014). As these roles are often near the top of trophic systems, large carnivores can be key ecological regulators facilitating the maintenance of ecosystem health (Estes et al., 2011; Ripple et al., 2014). Despite the ecological importance of carnivore conservation, > 75% of the world's remaining large carnivore populations have declining trajectories (Ripple et al., 2016, 2014; Wolf and Ripple, 2017) principally driven by habitat loss and fragmentation, overhunting, prey depletion, and conflict with humans (Dickman, 2010; Eklund et al., 2017; Krafte Holland et al., 2018; Ripple et al., 2014; Wolf and Ripple, 2017). Conflict between humans and carnivores tends to be associated with threats to human security and private property (Ripple et al. 2014; van Eeden et al. 2018a, 2018b). Most common among these threats is depredation of livestock, where retaliatory killing of carnivores by affected livestock owners is a common response (Krafte Holland et al., 2018; van Eeden et al., 2018a). Consequently, carnivore depredation of livestock is an important challenge facing both biodiversity conservation and human well-being (Barua et al., 2013).

Carnivore depredation of livestock persists globally and has expanded with increasing human population growth (Wolf and Ripple, 2017). To date, most applied solutions to this conflict have only proved to be marginally effective (Eklund et al., 2017; Miller, 2015; van Eeden et al., 2018b). This limited efficacy is attributable, in part, to evident disconnects between research effort and the implementation of conservation strategies (Born et al., 2009; Sunderland et al., 2009; Montgomery et al., 2018; Beck et al., 2019; Gray et al., 2019). There are a number of factors contributing to this research-implementation gap including taxonomic bias, minimal interdisciplinarity among research teams, and a misalignment in communication strategies between researchers, practitioners, and local stakeholders (see Sunderland et al. 2009, Montgomery et al. 2018a, Beck et al. 2019, Gray et al. 2019, Hoffmann and Montgomery 2021). Another potential driver of the research-implementation gap involves the misalignment of research practice and conservation need (Di Marco et al., 2017; Lawler et al., 2006; Linklater, 2003; Stroud et al., 2014). This facet of the research-implementation gap is influenced by a range of factors including positive feedbacks in patterns of conservation funding (Stroud et al., 2014; Troudet et al., 2017) and taxonomic biases in publication review and editing decisions (Bonnet et al., 2002; Linklater, 2003; Martín-López et al., 2009). Further, research on carnivore depredation of livestock is often restricted to well established methodologies because of the logistical constraints associated with remote study locations and dynamic animal behaviors (Prugh et al., 2019; Van der Weyde et al., 2018). Consequently, in many cases research practices have been slow in adapting to meet changing conservation needs (Lawler et al., 2006; Stroud et al., 2014). As a result, critical subjects remain unexplored in the human-carnivore conflict literature, one of which is the rate at which carnivores encounter potential livestock prey.

Predator-prey encounters are a fundamental stage of the predation sequence (Creel and Creel, 1995; Lima and Dill, 1990; MacNulty et al., 2007; Mech, 1970) and encounter rate is an integral parameter necessary to predict predation risk (see Holling 1959; Lima and Dill 1990;

Abrams 2000). In the predator-prey model originally presented by Holling (1959) and adapted by Lima and Dill (1990), predation risk can be predicted as a function of:

$$P(\text{death}) = 1 - \exp(-\alpha d T) \quad (1)$$

Where the probability of prey being killed *P*(death) is derived from the rate of encounter between predator and prey (α), the probability of death given an encounter (*d*), and the time spent vulnerable to an encounter (*T*; Lima & Dill, 1990). The probability of death given an encounter (*d*) is calculated by the conditional probabilities of various possible interactions between predator and prey (Fig. 3.1). Specifically, d is defined as:

$$d = [p(1-a)(1-i_1)(1-e_1) + q(1-i_2)(1-e_2)](1-e_3) \quad (2)$$

Importantly, this model predicting predation risk cannot be fit without an understanding of the rates at which predators encounter prey (Abrams, 2000; Curio, 1976; Holling, 1959; Lima and Dill, 1990; Prugh et al., 2019). Despite the importance of encounter rate, depredation risk is typically calculated without this integral parameter.

Depredation risk models are most often informed solely by data on carnivore attacks of livestock (Hoffmann et al., 2019; Miller, 2015; Treves et al., 2004). These models, often termed 'spatial risk models,' typically use the count of these attacks to associate abiotic and biotic conditions with depredation (Baruch-Mordo et al., 2008; Behdarvand et al., 2014; Broekhuis et al., 2017; Hebblewhite et al., 2005; Miller et al., 2015). Here, carnivore depredation data are collated across space and time to map spatial, and sometimes temporal, variation in depredation risk. The accuracy of these models is paramount given that the spatio-temporal predictions regularly inform interventions designed to reduce human-carnivore conflict (Hoffmann et al., 2019; Miller, 2015; Mpakairi et al., 2018). As described by Miller (2015), "spatial risk models quantify the realized predation risk…rather than the overall fundamental predation risk."

Therefore, these models do not quantify depredation risk (sensu the predation risk equation of Lima and Dill 1990), but instead use only the final step in the predation sequence of potential interactions and outcomes (Fig. 3.1) as a proxy for depredation risk. Hereafter, I refer to depredation risk as defined by Lima and Dill (1990), not as this realized predation proxy.

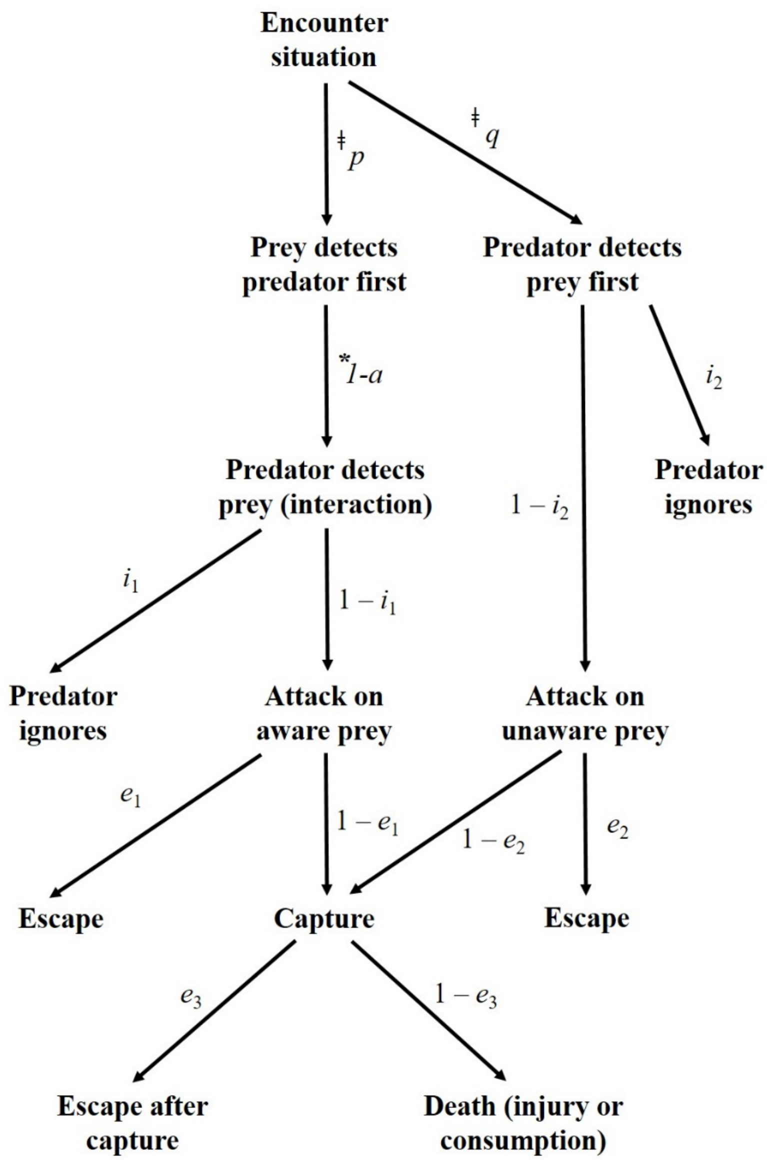

Figure 3.1. Flow chart of the potential outcomes of carnivore-livestock encounters at the boma, adapted from Lima and Dill (1990). The text next to the arrows indicates the conditional probabilities associated with each pathway. ǂ I defined all instances in which carnivores were

Figure 3.1. (cont'd) detected on a camera to be encounters, thus $p + q = 1$. * Bomas restrict livestock movement, removing the possibility of avoidance prior to detection by a carnivore. Therefore, $1 - a = 1$.

Carnivore-livestock encounters have likely not been widely estimated because of the challenges inherent to collecting these types of data. Efforts to collect encounter data are often hampered by the cryptic and wide-ranging nature of carnivores as well as the technological limitations in mapping contact points between carnivores and livestock (Breck, 2004; Gray, 2012; Krafte Holland et al., 2018; Lima, 2002). Consequently, novel means of data collection are required to overcome these constraints. I developed and deployed such a system to detect carnivore-livestock encounters. I applied this system to a region of Central Kenya that experiences high rates of carnivore depredation of livestock (Frank, 2010; Ogada et al., 2003). Concurrently, I also collected data on carnivore attacks on livestock, in the same manner as is traditionally used in the aforementioned spatial risk modeling. I estimated species-specific carnivore encounter rates, attack rates, and calculated depredation risk using the Lima and Dill (1990) equation. As rates of livestock depredation, and the resultant impacts on both humans and carnivores, are likely to continue to intensify, targeted examinations of the applicability of research practice to conservation needs are increasingly necessary. My contribution to this effort here provides valuable insights into carnivore movement and habitat selection, mitigation efforts informed by those behaviors, and recommendations for future studies to better elucidate the stochasticity that remains unexplored in patterns of carnivore depredation of livestock.

3.3 Methods

3.3.1 Study area and data collection

I positioned my study in Central Kenya, along the borders of Samburu, Isiolo, and Laikipia Counties (Fig. 3.2). This landscape is predominantly semi-arid bushland divided among a matrix of privately-owned conservancies, commercial ranches, and agro-pastoralist community-owned conservancies (Bond, 2014; Frank, 2010; Frank et al., 2005; Yurco, 2017). Livestock-owners in this landscape keep cattle, sheep and goats (collectively referred to as shoats), donkeys, and camels (Frank, 2010; Frank et al., 2005; Ogada et al., 2003; Unks et al., 2019). There are two rainfall seasons, with heavier rains from April-June and lighter rains from October-December. Total annual rainfall is highly variable, but often ranges from 500-750mm (Georgiadis et al., 2007; Mizutani, 1999a). The landscape supports a carnivore guild of African lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), striped hyenas *(Hyaena hyaena*), black-backed jackals (*Canis mesomelas*), aardwolves (*Proteles cristata*), caracals (*Caracal caracal*), and African wild dogs (*Lycaon pictus*; Mizutani 1999, Ogada et al. 2003, Frank et al. 2005). Most of these carnivore species depredate livestock in this region (Frank, 2010; Frank et al., 2005).

The 650 km^2 study area included the western units of Oldonyiro Community Conservancy, the southern units of Kirimon Community Conservancy, and the Koija and Il Motiok units within Naibunga Community Conservancy, which are subject to considerable levels of carnivore depredation of livestock (Fig. 3.2). For instance, between March, 2018 and October, 2020, livestock-owners in these communities reported 2,390 livestock injured or killed by large carnivores, 67% percent of which were attacked at night while held in livestock corrals, otherwise known as bomas (Pilfold and Ruppert, unpublished data). Therefore, I focused data collection on detecting carnivores encountering and attacking livestock at the boma. I selected 12 bomas among the four communities in my study site via a stratified random sample (Fig. 3.2). Upon identifying these bomas, I consulted the chairman of each community and met with the heads of all households to gain permission for their participation in my study. I equipped each boma with a suite of motion-activated cameras (Bushnell Trophy Cam HD Aggressor – No Glow, Model 119776C) attached to fence posts, and positioned them to be outward-facing. I placed all cameras 0.5 m off of the ground and evenly distributed around the outer wall of the boma so as to best detect approaching carnivores. Each boma had 6-7 cameras depending on the circumference of the perimeter wall, separated by an average distance of 27.1 m (Fig. 3.3). I programmed the cameras to record videos (15-second duration) with no delay period between triggers. The cameras were active between dusk and dawn, consistent with the time period in which livestock are vulnerable to carnivore depredation at the boma (Frank et al., 2005; Kissui, 2008; Ogada et al., 2003). I maintained these cameras across the duration of my study, between September, 2018 and May, 2019.

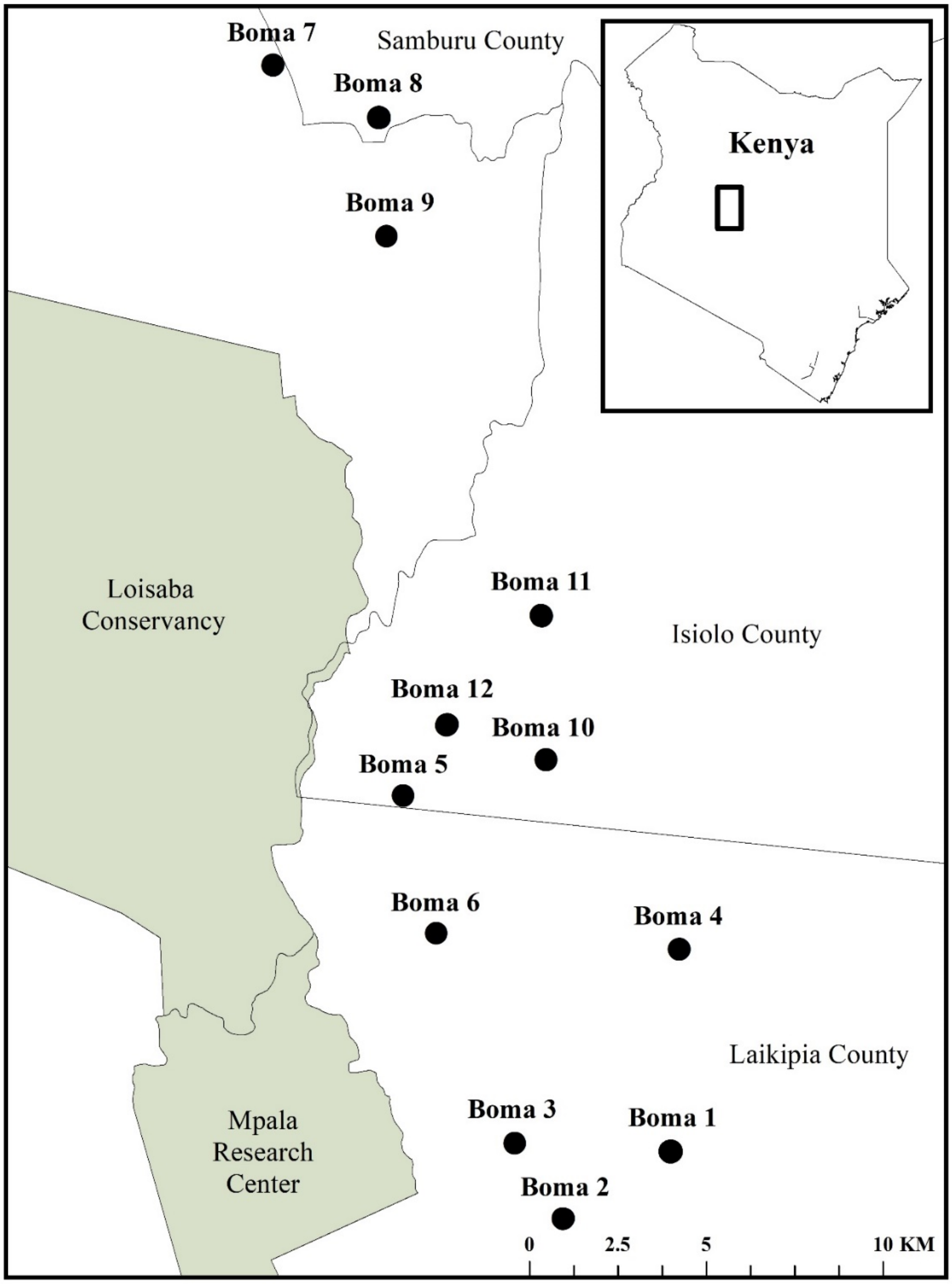

Figure 3.2. The location of 12 bomas equipped with the motion-activated cameras in Central Kenya to detect carnivore species encountering livestock from September, 2018 to May, 2019.

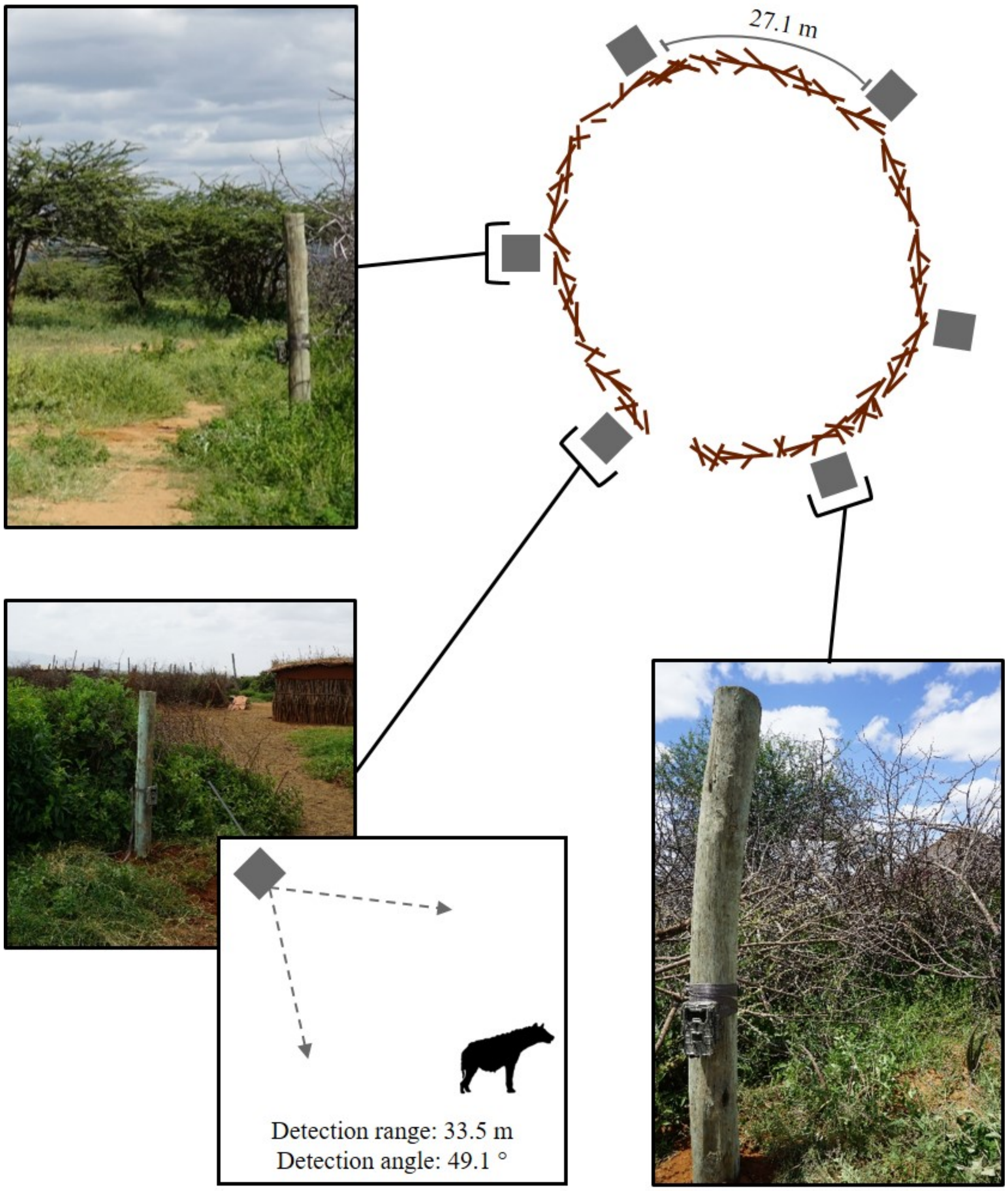

Figure 3.3. The location of the motion-activated cameras around the perimeter of a boma in Central Kenya. The diagram indicates the position of the cameras in relation to the boma wall, the average distance between cameras, and the camera detection range and angle. The photographs show the placement of the cameras on the fence posts.

Over the same time period, I followed established protocols (see Ogada et al. 2003; Woodroffe et al. 2005; Kissui 2008; Leflore et al. 2019) to map the frequency of carnivore attacks on livestock at these bomas. These attack records were documented via a conflict reporting network composed of 19 community representatives selected by local leadership (Ruppert et al. in review). Livestock owners were asked to call their representative immediately following each conflict event involving carnivores. At the incident site, representatives used a structured questionnaire to gather data from the livestock owner and, when available, a witness. Representatives were initially trained to administer the standardized form in March 2018, and guidance on the process and use of equipment were reinforced during monthly field visits. All reports were recorded on Samsung Galaxy J1 phones outfitted with Survey 123 software. I considered attack events to be those in which a carnivore entered the boma and interacted with the livestock, indicating a depredation attempt. Thus, I determined events to be attacks even if they did not result in the death of livestock. At each of these events, a network representative recorded the; *i*) date and approximate time of the attack, *ii*) type and number of livestock injured or killed, *iii*) carnivore species responsible, and *iv*) GPS location of the attack. All representatives entered the data directly into the Survey 123 program while at the location of the attack. Ethical approvals for human subjects research were reviewed and approved by the Institutional Review Board (IRB #02555e) of Miami University, Ohio. Permission was granted by the Kenya National Commission for Science, Technology, and Innovation under Research License #690384, and Kenya Wildlife Services. Methods were also reviewed and approved by the Institutional Animal Care and Use Committee at San Diego Zoo Global (Protocol #18-017).

3.3.2 Data analysis

I analyzed the video files returned from the motion-activated cameras positioned at each of the 12 bomas. I recorded the: *i*) carnivore species detected, *ii*) number of individuals of that species, *iii*) date, and *iv*) time the camera was triggered. I defined a carnivore-livestock encounter to be when a carnivore was detected in the viewshed of the cameras (i.e., within 33.5 m of the boma wall, Fig. 3.3). This detection extent is consistent with the chase initiation distance of the carnivore species (Elliot et al., 1977; Hayward et al., 2006; Kruuk, 1972) and thus, representative of an encounter (sensu Lima and Dill 1990). However, carnivore-livestock interactions are unique in comparison to free-ranging prey encounters due to the structural interference of the boma wall, which can influence attack dynamics. Regardless, the walls of the 12 bomas were all constructed with acacia thorn bush with highly variable structural integrity, often resulting in openings large enough to allow for visibility through the physical barrier (Chaka et al., 2020; Lichtenfeld et al., 2015). Further, carnivores regularly break into bomas to attack livestock, demonstrating they are aware of the presence of livestock within (Kissui, 2008; Kolowski and Holekamp, 2006; Ogada et al., 2003). Livestock also often stampede in an attempt to flee the boma when carnivores are near, indicating they are similarly aware of the presence of carnivores on the other side of the wall (Frank, 2010; Ogada et al., 2003; William et al., 2017). To limit pseudo replication, I consolidated all videos of one carnivore species triggered within 10 minutes of each other at the same boma into a single encounter.

I quantified the number of encounters and attacks per night (defined as 18:00 to 06:00) consistent with the temporal resolution in which livestock are vulnerable to carnivore depredation at the boma (Kissui, 2008; Lesilau et al., 2018; Ogada et al., 2003). I examined variation in carnivore-livestock encounters by date, time, boma location, and carnivore species. I then calculated the species-specific depredation risk for livestock in the boma using Equations 1 and 2. I based these calculations upon the rate of encounter, and the number of attacks by each carnivore species resulting in livestock escape (i.e., no injury), escape after capture (i.e., injury), and death. As noted above, I defined all instances in which a carnivore was detected on a camera to be an encounter. Consequently, I assumed $p + q = 1$, as all encounters progressed to the next stage of the predation sequence (see Lima and Dill 1990; Fig. 3.1). Similarly, I assumed $1 - a = 1$ because bomas constrain the movement of livestock (Chaka et al., 2020; Frank, 2010; Frank et al., 2006). When encounters occur with livestock corralled within a boma, they do not have the freedom of movement to avoid carnivores prior to detection. By the same logic, whether the livestock or carnivore detect the other first is likely to have little effect on subsequent progression through the stages of predation. Therefore, I made the following further assumptions: *i*) depredation risk was equal for both orders of detection ($p = q$), *ii*) risk of attack was equal regardless of whether or not the livestock are aware of carnivore presence ($1 - i_1 = 1 - i_2$), and *iii*) risk of capture was equal regardless of whether or not the livestock were aware of carnivore presence ($1 - e_1 = 1 - e_2$; Fig. 3.1).

3.4 Results

Between September, 2018 and May, 2019 the motion-activated cameras recorded a total of 2,347 videos of carnivores detected at 12 livestock bomas, of which there were a total of 1,383 independent carnivore-livestock encounters. The five species identified among these carnivore-livestock encounters were spotted hyenas, striped hyenas, black-backed jackals, leopards, and African lions (Fig. 3.4; Fig. 3.5D). I also identified one encounter with an aardwolf, but as that species has not been identified as a depredator of livestock in this region, I omitted this detection from further analyses. The most common carnivore species that I detected was the spotted hyena, which encountered livestock at the bomas in 76.1% (n = 1,052) of the detections. The next most detected species was the striped hyena (13.2%, n = 183), followed by black-backed jackals (10.1%, n = 139), leopards (0.5%, n = 7), and African lions (0.1%, n = 1; Table 3.1; Fig. 3.5D; Fig. 3.6). The number of carnivore-livestock encounters increased throughout the evening hours, peaking between 23:00 and 03:00 before declining to 06:00 (Fig. 3.5B). Carnivore-livestock encounters also fluctuated throughout the study period, with peaks in November, 2018 and May, 2019 corresponding to the light and heavy rainy seasons, respectively (Fig. 3.5A). The number of carnivore-livestock encounters also varied by boma, ranging from 26 to 472 (Fig. 3.C; Fig. 3.6).

Across the same time period, I recorded a total of seven carnivore attacks on livestock at the study bomas. Only two carnivores, spotted hyenas (71.4%, n = 5) and leopards (28.6%, n = 2), were responsible for these livestock attacks (Table 3.1; Table 3.2). The attacks resulted in the deaths of one dog and 21 shoats, and the injury of two additional shoats (Table 3.2). I recorded the highest encounter rate for spotted hyenas, with an average of 3.79 encounters/night (Table 3.3). Striped hyenas had the next highest rate (0.66 encounters/night), followed by black-backed jackals (0.51 encounters/night), leopards (0.03 encounters/night), and African lions (0.004 encounters/night; Table 3.3). As only spotted hyenas and leopards attacked livestock at these bomas during my study period, they were the only species with non-zero attack rates and calculated depredation risk. Spotted hyenas averaged 0.02 attacks/night, while leopards averaged 0.007 attacks/night. Depredation risk from spotted hyenas per boma was 0.01, and 0.007 for leopards (Table 3.3).

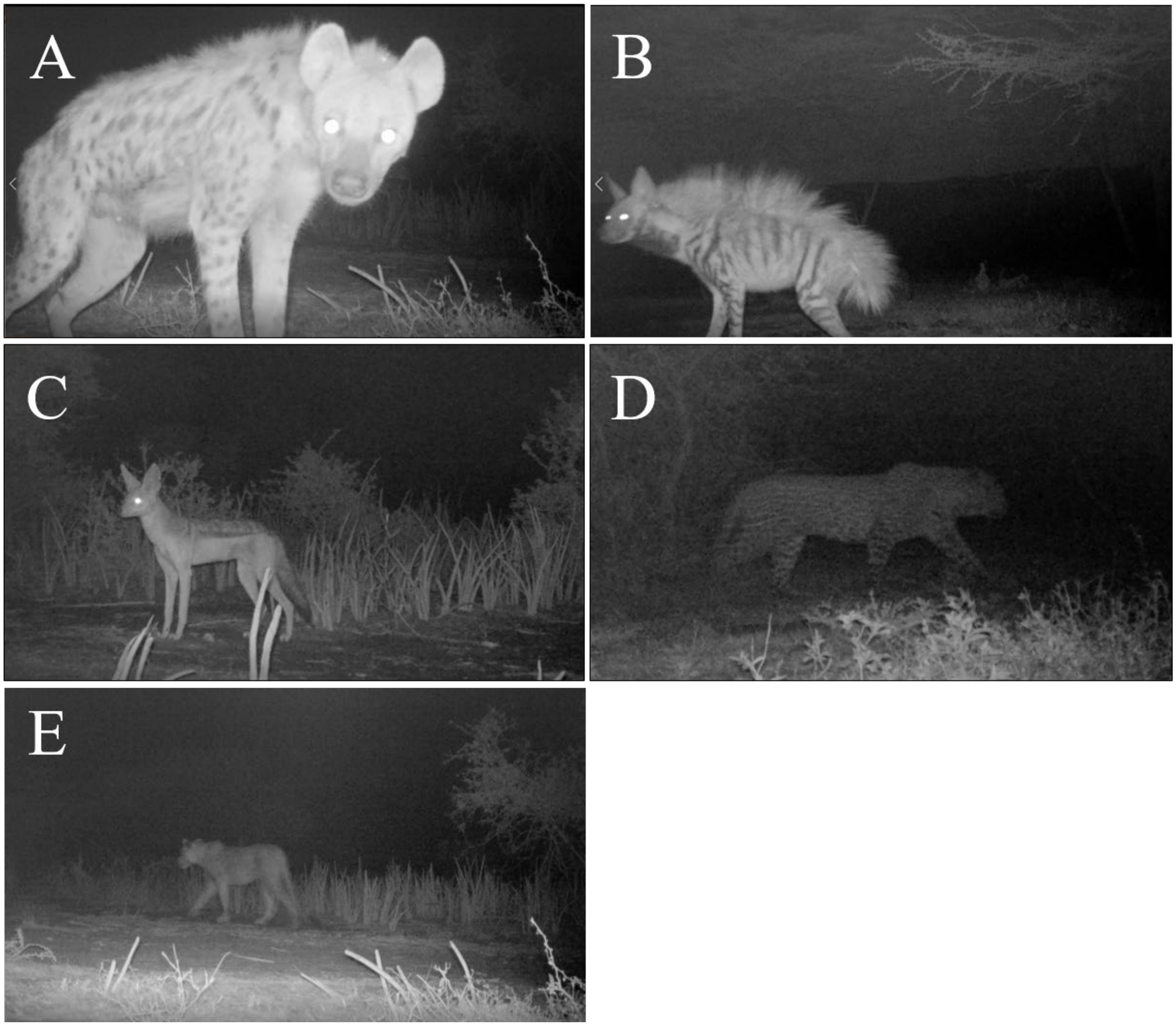

Figure 3.4. The carnivore species detected on motion-activated cameras at 12 bomas in Central Kenya from September, 2018 to May, 2019. The five potentially depredating species recorded to encounter livestock were: A) Spotted hyena (*Crocuta crocuta*), B) Striped hyena (*Hyaena hyaena*), C) Black-backed jackal (*Canis mesomelas*), D) Leopard (*Panthera pardus*), and E) African lion (*Panthera leo*).

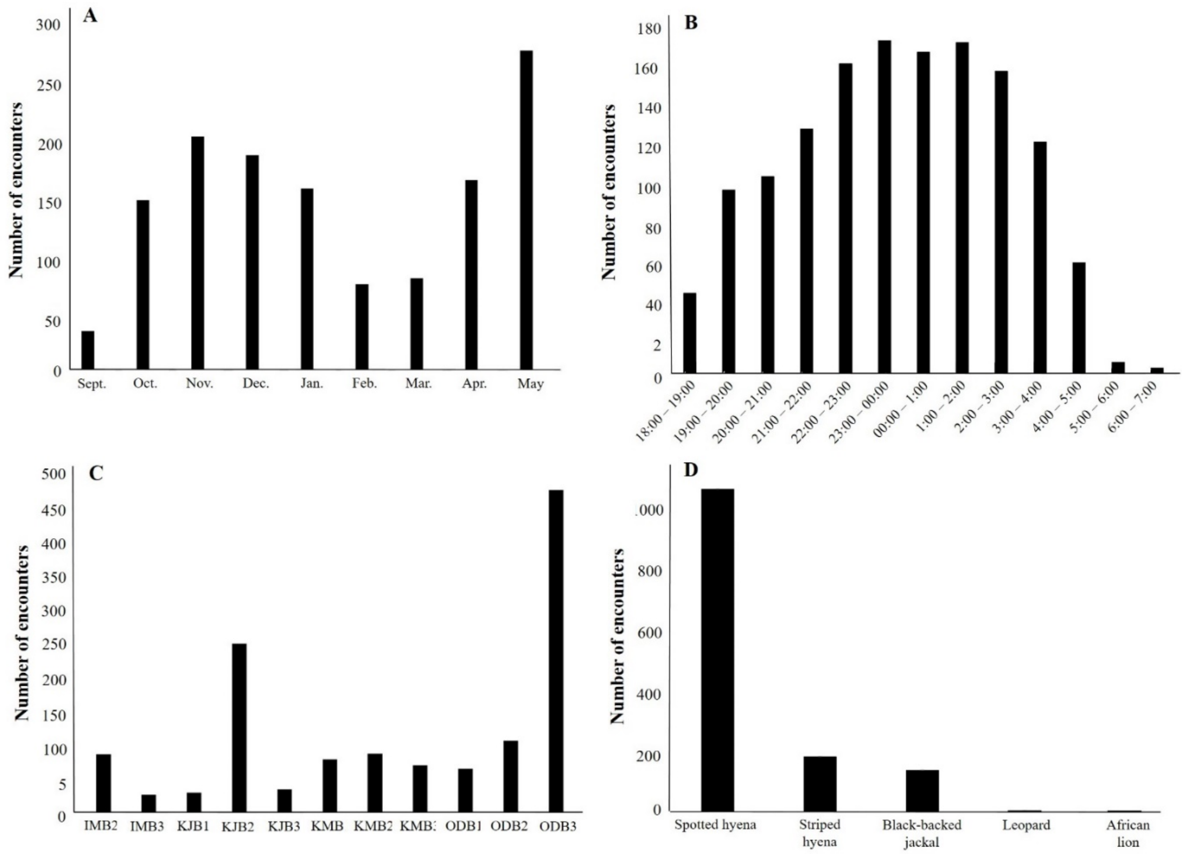

Figure 3.5. The patterns of carnivore-livestock encounters at 12 bomas in Central Kenya from September, 2018 to May, 2019. The panels show the number of carnivore-livestock encounters by: A) month, B) time, C) boma, and D) species.

Table 3.1. The number of carnivore-livestock encounters and carnivore attacks on livestock at 12 bomas in Central Kenya from September, 2018 to May, 2019. The results are shown by boma for the five depredating carnivore species recorded.

	Spotted hyena *Crocuta crocuta*		**Striped hyena** *Hyaena hyaena*		**Black-backed jackal** *Canis mesomelas*		**Leopard** *Pathera pardus*		**African lion** *Panthera leo*	
Boma #	Encounter	Attack	Encounter	Attack	Encounter	Attack	Encounter	Attack	Encounter	Attack
1	52	0	15	0	30	0	1	0	0	0
2	51	0	25	0	6	0	2	1	1	0
3	9	0	12	0	5	0	0	0	0	0
4	15	0	5	0	6	0	0	0	0	0
5	201	2	21	0	18	0	0	0	0	0
6	20	0	6	0	8	0	0	0	0	0
7	69	1	2	0	6	0	0	0	0	0
8	73	1	10	0	1	0	2	0	0	0
9	54	0	9	0	5	0	1	0	0	0
10	25	0	32	0	7	0	0	0	0	0
11	97	1	4	0	3	0	1	0	0	0
12	386	0	42	0	44	0	0	1	0	0
Total	1052	5	183	0	139	0	7	2	1	0

Figure 3.6. The proportion of carnivore-livestock encounters attributed to each of the five recorded carnivore species at 12 bomas in Central Kenya from September, 2018 to May, 2019. Each chart also indicates the total number of carnivore-livestock encounters at the boma.

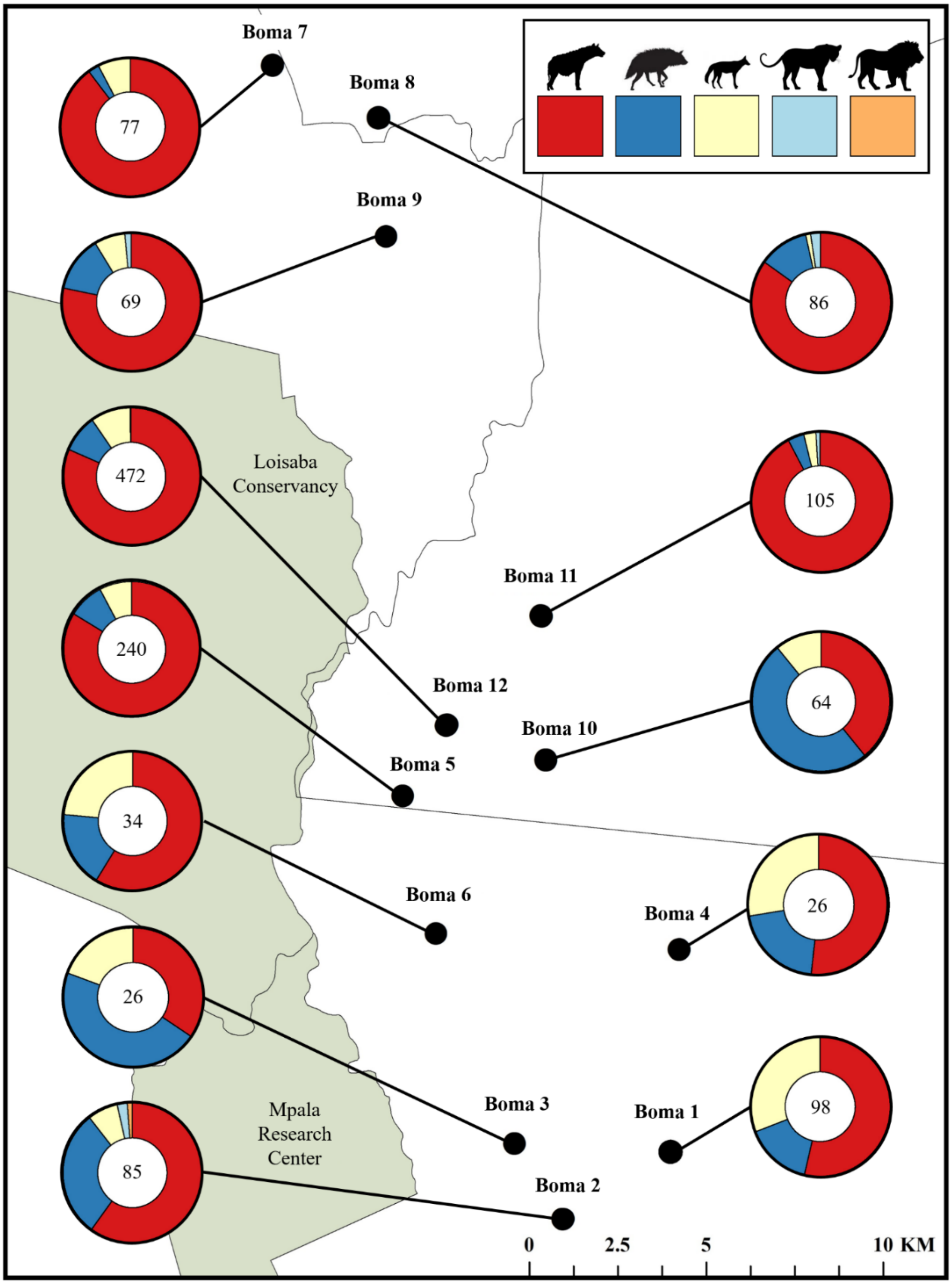

Table 3.2. The seven carnivore attacks on livestock reported at 12 bomas in Central Kenya from September, 2018 to May, 2019.

Attack	Month	Boma #	Carnivore responsible	Type of livestock attacked	Number of livestock killed	Notes
1	Sept. 18	7	Spotted hyena	N/A	0	One dog killed
2	Nov. 18	11	Spotted hyena	Shoat	0	One shoat injured
3	Dec. 18	5	Spotted hyena	Shoat	9	
4	Jan. 19	12	Leopard	Shoat	2	One shoat injured
5	Feb. 19	5	Spotted hyena	Shoat	1	
6	Apr. 19	8	Spotted hyena	Shoat	7	
7	May 19	2	Leopard	Shoat	2	

Table 3.3. The average encounter rate, attack rate, and depredation risk at 12 bomas in Central Kenya from September, 2018 to May, 2019. The results are shown for each carnivore species, and rates are calculated over the time period of a single night (dusk to dawn).

Species	Encounter rate	Attack rate	Depredation risk
Spotted hyena *Crocuta crocuta*	3.79	0.02	0.01
Striped hyena *Hyaena hyaena*	0.65	0.00	0.00
Black-backed jackal *Canis mesomelas*	0.50	0.00	0.00
Leopard *Pathera pardus*	0.03	0.007	0.007
African lion *Panthera leo*	0.004	0.00	0.00

3.5 Discussion

Assessments of the research-implementation gap regularly identify factors that diminish the impact of applied conservation practice (Born et al., 2009; Knight et al., 2008; Miller et al., 2016). Within the context of human-carnivore conflict, effective alignment between data collection and conservation need is of particular importance (Montgomery et al. 2018; Beck et al. 2019; Gray et al. 2019; Hoffmann and Montgomery 2021). My study supports this broader research effort by demonstrating the important nature of encounters in predicting carnivore depredation of livestock risk. I found that spotted hyenas had the highest encounter rate among all carnivores identified, with the average number of encounters per night almost six times higher than any other species. However, the depredation risk associated with spotted hyenas was only marginally higher than that of leopards, which were the next most common depredator. Therefore, my results indicate that carnivore species exhibit vastly different depredatory behaviors at the boma. Furthermore, I found that carnivores encountered livestock at the boma far more often than they attacked (Table 3.1; Table 3.3).

While the number of carnivore attacks of livestock was low overall, I recorded carnivore-livestock encounters at all study bomas, with some experiencing hundreds of encounters during the study period (Fig. 3.5C; Fig. 3.6). However, the fact that the direct effects of carnivore depredation were low does not mean that the indirect effects of carnivore presence were inconsequential. Carnivore presence may have substantial effects on both the livestock and the overall conflict driven by livestock depredation. For instance, carnivore presence influences the behavior of cattle in Eastern African grazing landscapes, which may result in reduced foraging (Beck et al., 2020). Impacts such as these, often termed non-consumptive effects or risk effects, have been well studied in both wild prey systems and grazing livestock herds (Basille et al., 2015; Beck et al., 2020; Fortin et al., 2004; Moll et al., 2017). Additionally, interactions with predators may increase livestock stress levels and modify vigilance behavior, resulting in a range of impacts including reduction of body condition and decreased reproductive output (Creel et al., 2007; Creel and Christianson, 2008; Laporte et al., 2010; Lima, 1998). While I am not aware of any study that has examined these types of impacts at the scale of bomas, it is likely that carnivore presence is similarly impacting the livestock corralled within these structures. As my study presents a limited sample of 12 bomas across one year, I offer the non-consumptive effects of carnivore-livestock encounters at the boma as a rich area of future inquiry.

I also detected substantial differences in encounter rates among the carnivore species recorded. Spotted hyenas accounted for over three quarters (76.1%) of recorded encounters (Table 3.1; Fig. 3.5D; Fig. 3.6). Similarly, they were responsible for 71.4% of attacks on livestock, resulting in the injury or death of 18 shoats, and had the highest calculated depredation risk (Table 3.1; Table 3.2; Table 3.3). This finding aligns with those in other examinations of livestock depredation in both Laikipia County and sub-Saharan Africa more broadly, in which spotted hyenas are commonly reported to be the primary cause of livestock depredation (Hoffmann & Montgomery, in review; Ogada et al., 2003; Kissui, 2008; Frank, 2010; Mponzi et al., 2014; Kissui et al., 2019). When I considered both spotted hyenas and striped hyenas, these Hyaenidae species were responsible for almost 90% of the encounters. Relative carnivore population densities often provide a logical explanation for species-specific variation in livestock depredation (Kolowski and Holekamp, 2006). However, best estimates indicate that there is no significant difference in population density among the species I recorded encountering livestock at the boma (Bauer et al., 2016; Frank et al., 2005; Frank, 1998; Kinnaird and O ’Brien, 2012;

Prager et al., 2012; Wagner, 2006). Thus, the variation I identified among the rates of attack and encounter by carnivore species are more likely due alternative drivers.

One potential explanation for this species-specific variation comes from the foraging and movement behavior of each species. I found that leopards attacked livestock once out of every four encounters at the boma, whereas spotted hyenas attacked only once out of every 211 encounters. Additionally, while I only recorded two leopard attacks, both resulted in the death of livestock. In contrast, livestock were killed in only slightly over half of the recorded spotted hyena attacks. Importantly, this small sample size precludes drawing concrete conclusions related to these depredatory behaviors. However, my results provide a preliminary indication that the risk of death, given encounter (d in Equation 1), may vary substantially by carnivore species. Spotted hyenas are widely recognized as opportunistic feeders, and are commonly recorded scavenging from human landscapes (Abay et al., 2011; Kolowski and Holekamp, 2007, 2006). They may approach bomas in search of refuse, subsequently attacking nearby livestock as those opportunities arise (Chaka et al., 2020; Kolowski and Holekamp, 2007; Yirga et al., 2015). It is therefore likely that spotted hyena-livestock encounters are driven not only by depredatory behaviors, but also by scavenging opportunities (Yirga et al., 2014). As spotted hyenas were the most common depredator of livestock in my study and many others, those scavenging opportunities are likely a key contributing factor to the depredation risk associated with that species. Consequently, the effectiveness of livestock depredation interventions for spotted hyenas may be improved via increased emphasis on reducing encounter rates. For example, efforts to minimize scavenging attractants for spotted hyenas at the boma (e.g., secure off-site butchering locations, better waste management infrastructure) may reduce encounter rates and thus depredation risk (Chaka et al., 2020).

Examination of temporal variation in carnivore-livestock encounters also revealed patterns relevant to the mitigation of depredation risk. I identified a peak in the frequency of carnivore-livestock encounters between the hours of 23:00 and 03:00, with a steep drop-off in the frequency of encounters in the early morning hours (Fig. 3.5B). This result corresponds to trends in carnivore behaviors identified in other studies. For example, Cozzi et al. (2012) recorded a similar reduction in spotted hyena movement between midnight and sunrise. They identified nighttime light availability as the driving force of this trend, with the carnivores maximizing their activity during the darkest part of the night. The carnivores recorded in my encounters also are primarily nocturnal hunters (Hayward et al., 2006; Hopcraft et al., 2005; Van Cleave et al., 2018), and therefore are likely to exhibit similar activity patterns. Depredation risk is generally considered to be high between dusk and dawn, as most livestock are killed at night (Ogada et al., 2003; Yirga et al., 2012). The temporal variation I identified in carnivore-livestock encounters, however, shows that there may be fluctuations in depredation risk across that high-risk time period. The conditions associated with when a carnivore chooses to approach the boma may also correlate with prevailing biotic and abiotic conditions, including stochasticity in human behavior. Few households in this region have access to consistent electrical power, so human activity tends to closely align with natural light availability. Consequently, factors that have been shown to act as carnivore deterrents, such as human voices and dog vigilance (Frank, 2010; Ogada et al., 2003), are likely to be minimal between 23:00 and 03:00. However, the role of these fine-scale factors in deterring carnivore encounters, and subsequent attacks on livestock, requires further investigation.

I also identified variation in carnivore-livestock encounters by season. For instance, there was one peak in carnivore-livestock encounters in November and another in June (Fig. 3.5A).

These peaks closely correlate with the timing of the two wet seasons in my study area. Specifically, the highest numbers of carnivore-livestock encounters aligned with periods of greatest mean rainfall (Mizutani, 1999a; Ulrich et al., 2012). The influence of seasonality on carnivore depredation of livestock has been examined extensively across sub-Saharan Africa (Kolowski and Holekamp, 2006; Mukeka et al., 2019; Patterson et al., 2004; Robertson et al., 2019; Valeix et al., 2009; Woodroffe and Frank, 2005). Consistently, rates of carnivore depredation of livestock increase during rainy seasons (but see Pozo et al. 2020). This seasonality is attributed to many potential drivers, including herding practices, wild prey migration, and prey switching driven by reduced predation success on wild prey (Kissui et al., 2019; Kolowski and Holekamp, 2006; Kuiper et al., 2015; Loveridge et al., 2017; Mponzi et al., 2014; Mukeka et al., 2019; Patterson et al., 2004; Valeix et al., 2012). As far as I am aware, however, this study provides the first evidence of seasonal variation in the frequency of carnivore-livestock encounters. This distinction is important, as it indicates that the well-established seasonal trends in rates of carnivore depredation of livestock are not just associated with the probability of death, given an encounter (d; Equation 1) or increased time spent vulnerable to an encounter (T), but are in fact likely associated with an increase in the rate of encounter itself (α).

I also identified variation in carnivore-livestock encounters across my study region, with the number of carnivore-livestock encounters per boma ranging from 26 to 472 (Table 3.1; Fig 3.4C. Fig. 3.6). There are multiple possible explanations for this uneven distribution, including proximity to protected areas, characteristics of the boma or community, and features of the livestock herds (Kolowski and Holekamp, 2006; Miller et al., 2016). Proximity to protected areas increases risk of livestock depredation in many locations across sub-Saharan Africa (Holmern et al., 2007; Kushnir et al., 2014; Miller et al., 2016; Thorn et al., 2012). The two bomas in my study that experienced the highest number of carnivore-livestock encounters (Bomas 5 and 12) were closest to the border of Loisaba Conservancy (Fig. 3.5A; Fig. 3.6). These two bomas also suffered at least one carnivore attack on livestock (Table 3.1; Table 3.2). Although the conservancies in this region are not considered formal protected areas, they do tend to have a higher density of large carnivores than the surrounding community lands (Frank et al., 2005; Oriol-Cotterill et al., 2015; Suraci et al., 2019; Woodroffe and Frank, 2005). However, as bomas farther away from the conservancies also recorded similar numbers of carnivore attacks on livestock, and relatively high frequencies of carnivore-livestock encounters, other factors are likely also at play.

Isolation (i.e., distance to the nearest neighbor) and size of the boma correlate with rates of attack by spotted hyenas and leopards, with attacks by spotted hyenas significantly more likely at less-isolated bomas (Kolowski and Holekamp, 2006). The composition of individual boma walls may also affect the rate of carnivore attacks on livestock. Wall characteristics such as height, thickness, visibility, and material have all been reported to correlate with rates of livestock depredation (Chaka et al., 2020; Kolowski and Holekamp, 2006; Loveridge et al., 2017; Mkonyi et al., 2017; Ogada et al., 2003; Weise et al., 2018). The size of the livestock herd within the boma may also be driving carnivore depredation of livestock. Prey group size has been shown to significantly affect predator-prey interactions in wild systems (Fryxell et al., 2007; Funston et al., 2001). However, there are few studies of such patterns on carnivore depredation of livestock at the boma (but see Chaka et al., 2021; Kolowski and Holekamp, 2006). Further, no published research has examined the effect of these factors on the frequency of carnivore-livestock encounters. Thus, there is much stochasticity in this system that remains unexplored (Hoffmann et al., 2019). Without examinations of the influence of such characteristics on carnivore-livestock encounter rates, understanding of their effects on depredation risk is incomplete and the development of boma-based interventions may be hampered.

3.6 Conclusion

Prediction of depredation risk is a fundamental strategy among studies seeking to mitigate carnivore depredation of livestock. Yet, logistical and ecological constraints have largely narrowed such approaches to the application of a proxy that cannot capture all aspects of depredation risk. My effort to address this limitation highlights the important role of encounters in this predator-prey system. Encounter rate is an essential component of the prediction of depredation risk, and the subsequent development of interventions to minimize carnivore depredation of livestock. The evident variation in carnivore-livestock encounter rates and depredation risk by species further indicates the value of carnivore-livestock encounters in informing depredation mitigation efforts. However, there are many avenues of research that remain to be fully explored in relation to carnivore-livestock encounters. I advocate for further examination of these encounters to develop more effective livestock protection efforts and continue to narrow the research-implementation gap.

3.7 Acknowledgements

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CHAPTER 4: SPATIAL PATTERN ANALYSIS REVEALS RANDOMNESS AMONG CARNIVORE DEPREDATION OF LIVESTOCK

I assessed spatial clustering in data describing carnivore depredation of livestock in the Maasai steppe of Tanzania using three geostatistical measures. I found that the spatial patterns tended not to statistically differ from random, indicating that other processes, potentially ecological or methodological in form, may be influencing or obscuring the spatial patterns of carnivore depredation of livestock in this region. For the full text of this chapter please see https://doi.org/10.3389/fevo.2019.00478

CONCLUSION

In this dissertation, I explored multiple steps in the process from research to conservation impact within which the development of effective large carnivore conservation efforts may be interrupted. Specifically, I investigated potential drivers of this research-implementation gap within research conceptualization, theoretical explanations of complex systems, data collection, and data analysis. To do so, I applied a diversity of methodological techniques and conceptual frameworks, representing the breadth of approaches within the field of large carnivore conservation. Within each of these varied approaches I centered my examination on carnivore depredation of livestock, as it poses one of the greatest threats to carnivore populations globally. My efforts herein are founded upon the objective of identifying drivers of the research-implementation gap, elucidating the processes by which the drivers may be creating a barrier to effective conservation, and identifying strategies to minimize effects of those drivers moving forward. Thus, the key findings and recommendations within each chapter of my dissertation are in pursuit of this goal.

In Chapter 1, I found evidence of a misalignment between the central large carnivore species under study, and the species responsible for the majority of livestock depredation. This result indicates that carnivore depredation of livestock research may be influenced more by charisma than conflict drivers. I conclude that the efficacy of interventions built to reduce this depredation of livestock are likely to be improved by a realignment of research practice and conservation need. As taxonomic bias is widespread throughout conservation fields, I advocate for similar consideration of the potential conservation implications of those biases in systems and regions outside livestock depredation in sub-Saharan Africa. In Chapter 2, we developed a framework through which to identify linkages among the components of complex systems in which human-wildlife coexistence must occur. Through this framework, we found that human coexistence with carnivores in our study region of Northern Tanzania is intrinsically connected to that with elephants. Based upon these findings, we advocate for increased development of theoretical explanations of how of human-wildlife coexistence is situated within complex systems. This study contributes to a stronger theoretical foundation of human-wildlife coexistence in complex systems, both through the development of a novel framework and through application of that framework to a a system characterized by some of the highest rates of human-wildlife conflict in the world. In Chapter 3, I quantified carnivore-livestock encounter rates and attack rates, as well as depredation risk at bomas in Laikipia, Kenya. I found that the encounter rate and attack rate for spotted hyenas were almost six and three times higher than for any other carnivore species, respectively. As a result, the risk of livestock depredation was highest for spotted hyenas. Encounter rate is integral in the calculation of depredation risk, and the subsequent development of interventions based upon that risk. Therefore, I concluded that better understanding of carnivore-livestock encounter rates is necessary to increase the effectiveness of interventions designed to mitigate carnivore depredation of livestock. More broadly, this study highlights the important role of encounters in carnivore-livestock depredation, and I advocate for further examination of carnivore-livestock encounter rates as a whole. Finally, in Chapter 4, I assessed spatial clustering of carnivore depredation of livestock data in Northern Tanzania. Upon applying three geostatistical measures, I found that the spatial patterns in these data tended not to significantly differ from random. Spatial analyses such as those applied in this chapter are often used to develop models that predict spatial patterns in carnivore depredation of livestock, and thus inform the location of interventions to minimize depredation risk. The predictive ability of such models may be limited where spatial patterns of carnivore depredation of livestock do not statistically differ from random. Therefore, in this chapter I advocate for explicit assessment of such patterns to minimize the threat of misapplication of intervention efforts.

Throughout this dissertation, I also highlight productive avenues of future research and key additional drivers of the research-implementation gap that remain to be addressed. These topics can be broadly consolidated into three overall recommendations. First, I recommend examinations of species-specific depredatory behaviors at the boma, along with empirical tests of depredation interventions targeted at those same species. Current understanding of these behaviors primarily rely on extrapolation of knowledge from wild prey studies, which may not accurately represent the depredatory behaviors of carnivores for livestock, particularly at the boma. This lack of knowledge is especially notable for less charismatic species such as the spotted hyena. Second, I echo the calls for re-evaluation of the rationales behind research prioritization that have become increasingly common in the conservation literature. Plainly stated, there is a need for recognition that the status quos of research in the carnivore conservation field are not meeting the conservation needs of the species under study. I advocate for a critical look at the common approaches and rationales within this research and how they may be adapted to better address urgent conservation needs. Finally, I also recommend explicit consideration of how research findings will be applied during the preliminary steps of the research planning process. This consideration should be based upon a broader understanding of the system in which the research subjects and potential interventions are situated. Doing so may help to reduce the risk of deriving management recommendations that are not sustainable for the system.

While each of my chapters examines such factors in relation to large carnivores within sub-Saharan Africa, these findings and recommendations are broadly relevant and applicable to studies of large carnivores across many other regions. Overall, my research highlights the importance of careful consideration of potential drivers of the research-implementation gap throughout the research and conservation processes. Adoption of the strategies and recommendations included in this dissertation may help to maximize the impact of future research efforts and promote the conservation of large carnivores globally.