DISSERTATION

A HOLISTIC EVALUATION OF HUMAN- ELEPHANT INTERACTIONS IN MULTI-USE LANDSCAPES

Submitted by

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ABSTRACT

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In East Africa, rangelands and savannas are complex social-ecological systems with a history of land sharing among pastoralists, their livestock and wildlife. Today, many are systems of global importance for biodiversity conservation. As in Earth's other biomes, East African rangelands and their inhabitants face growing challenges as the result of global change, namely ecological, climate, political, and socioeconomic changes that are threatening wildlife populations and straining human-wildlife relationships. African savanna elephants (*Loxodonta africana*) are key actors in these systems and the center of many of these challenges. Thus, sophisticated land-use planning that addresses the resource use and needs of both people and elephants that can be integrated into conservation policy at relevant scales of governance is a key need for elephant conservation. However, studies of African elephant spatial ecology rarely examine both ecological and human-elephant relationships in the ecosystems they inhabit, whereas existing studies from human dimensions disciplines, which focus on social aspects of human-elephant relationships, very rarely include landscape-specific analyses. Additionally, detailed, spatially explicit information describing human-elephant interactions is limited, particularly in regions where people interacting with elephants still herd livestock more than they grow crops. This dissertation addresses this research need by applying novel methods with a holistic approach to examine the spatial dynamics of human-elephant interactions in multi-use landscapes with a focus on elephant interactions with pastoral peoples and their livestock.

Most research in this dissertation is specifically focused on the spatial ecology of human-elephant interactions in the Greater Mara Ecosystem of southwest Kenya and combines inference from images captured by remote camera traps, high-resolution GPS tracking data, and social survey data to: 1) Understand how livestock and land management influence spatiotemporal patterns of elephant occurrence, 2) Investigate elephant movement behaviors and understand how people and environmental variation influence elephant movement behaviors, 3) Map core elephant habitat and movement corridors to support conservation planning, 4) Understand how people in mixed-use savannas relate to elephants and how elephants and wildlife conservation impact their lived experiences, and 5) Map and quantify social willingness to coexist with elephants in mixed-use landscapes to support conservation planning that accounts for the needs of both people and elephants.

I found that elephants shifted the quantity and timing of their activity in community conservancies where livestock are present relative to the neighboring protected area where livestock were absent. Elephants were also more likely to occur in the protected area than community conservancies even when controlling for habitat variation. Finally, I found that areas in community conservancies used with higher intensity by sheep and goats, and separately cattle, were somewhat less likely to be used by elephants during the daytime. However, this finding was not consistent across years and the estimated effects had low precision and additional alternative analyses may make this relationship clearer. I then apply network theory to analyze combined information on movement path properties, use intensity, and structural properties of movement networks calculated from

GPS tracking data to delineate the functional landscape of movement for elephants in the wider Mara-Serengeti ecosystem. After identifying movement behaviors, I then investigate the environmental variables driving different movement behaviors with a focus on delineating the habitats that support high elephant use and elephant movement corridors. Finally, I contrast how movement behaviors and the environmental variables driving movement vary between elephants inhabiting the mesic, wet savannas of the wider Mara-Serengeti ecosystem with those previously published and observed in elephants inhabiting the xeric savannas of the Samburu-Laikipia ecosystem. Results showed that human presence strongly influenced elephant movement behavior in the Mara and specifically influenced the location of core areas, whereas in Samburu, water availability and vegetation productivity and predictability strongly were the most important variables explaining core area use for elephants. Although vegetation productivity also influenced elephant core area use in the Mara, predictability did not, and human presence and canopy cover strongly influenced core area use in the Mara more strongly than water availability. Overall, these findings indicate that elephants in the Mara are likely less constrained by water and forage availability than elephants in Samburu and have more flexibility to access these key resources while minimizing the risks posed by people.

I apply cognitive hierarchy theory to understand how elephants impact people in the Greater Mara Ecosystem by investigating values and attitudes associated with African elephants and elephant conservation in communities sharing space with elephants. I use data collected from semi-structured interviewers at 177 households across a mixed-use, agropastoral landscape that also functions as an unprotected elephant corridor and analyzed responses using Bayesian hierarchical models to quantify positive attitudes towards elephants while accounting for self-reporting bias. I interpret quantitative model estimates in the context of qualitative attitude assessments and sociocultural values to gain a deeper understanding of what explains attitudes towards elephants in the region. We found that although a majority of people expressed positive attitudes about elephant conservation in general, most were not also positive about sharing space with elephants on community and private lands at a local scale. Model estimates showed that people who believed that elephants had sociocultural value were the most likely to be positive towards elephant conservation in general, but experiencing conflict with any wildlife lowered the probability of respondents to have a positive attitude towards sharing space with elephants at a local scale. Qualitative data revealed that safety and well-being concerns related to the perceived threats that elephants pose to human life, livestock, and crops, coupled with few social and economic incentives to support elephant conservation in community and private lands contribute to low local positive attitudes. Our results suggest that conservation approaches focused on sustaining existing sociocultural values and relationships with wildlife while also investing in human well-being and safety measures and could improve conservation outcomes in shared landscapes.

Overall, this research develops contributions to the understanding of human-elephant interactions in East African savannas and provides practical applications for elephant conservation. Specifically, this dissertation through the creation of several map products can support conservation planning that accounts for both people and elephants in the Greater Mara Ecosystem. Some of the most important takeaways come from co-interpretation of results with agropastoral communities and can thus provide direct guidance to conservation practitioners on how to better address human well-being in community-based conservation efforts. Though this research was produced in collaboration with non-government organizations, community-based conservation leaders, and government wildlife officials in Kenya, I recommend that future work can improve the collaborative research process by more successfully including local communities as stakeholders at all stages of the collaborative research process.

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CHAPTER 1

INTRODUCTION

This dissertation comprises my study of interactions between people, their livestock and African elephants in multi-use savanna landscapes currently undergoing land-use change. Specifically, my research focuses on how landscape variation, human land-use, people, and livestock tended to by people, influence patterns of space use and movement behaviors of African savanna elephants. I also examine how people sharing landscapes with elephants think about and relate to elephants, and how elephants and wildlife conservation more generally has impacted their lived experiences. African elephants are entangled in a multitude of persistent challenges to the human effort to conserve biodiversity in the context of global change, including harmful legacies of colonialism (Garland 2008), land-use change (Gara *et al.* 2017), climate change (Martínez-Freiría *et al.* 2016), overexploitation of animal populations (Wittemyer *et al.* 2014), human-wildlife conflict, protected area management, and inequality in conservation (Cassidy & Salerno 2020). Despite some success of decades elephant conservation efforts, elephants in Africa remain vulnerable to functional extinction. In 2021, the International Union for Conservation of Nature (IUCN) updated the listing for African savanna elephants to "Endangered" and for African forest elephants (*Loxodonta cyclotis)* as "Critically Endangered", citing habitat loss and human-elephant conflicts (HEC) as rising threats to elephant populations across the continent (Gobush *et al.* 2021).

It is thus clear that a major challenge for the sustainable conservation of heathy elephant populations is securing sufficient space for elephants to persist (Wall *et al.* 2021) in addition to the development and successful application of ethical conservation approaches that can promote coexistence of people and elephants in the context of global change (Madden 2004; Cassidy & Salerno 2020). Elephants thus provide a model case to illuminate the need for interdisciplinary, multidimensional research to inform spatially explicit wildlife conservation planning (van de Water *et al.* 2022) that accounts for the perspectives of both local people and elephants. However, studies of African elephant spatial ecology rarely examine both ecological and human-elephant relationships in the ecosystems they inhabit beyond quantifying human land use, whereas existing studies from human dimensions disciplines, which focus on social aspects of human-elephant relationships, very rarely include landscape-specific analyses (Kioko *et al.* 2022). Thus, detailed, spatially explicit and context specific information describing human-elephant interactions is limited, particularly in regions where people interacting with elephants still herd livestock more than they grow crops (Nyumba *et al.* 2020; Kioko *et al.* 2022). In this dissertation, I use a holistic, interdisciplinary approach to advance understanding of elephant ecology in ways that can meaningfully contribute to the conservation of African elephants by striving to understand the landscape context of human-elephant interactions from the perspective of both people, and by the proxy of high-resolution GPS tracking data and remote wildlife camera data, elephants.

In chapters 2-5, I research underexamined aspects of human-elephant interactions with a specific focus on understanding spatial patterns of elephant space use in mixed-use savanna landscapes and how people and landscape variation influence these patterns. Additionally, I examine how elephant space use impacts pastoralist and agropastoral peoples in shared landscapes, and how interactions, between people and elephants create feedbacks to the social-ecological system of human-elephant interactions that can either enhance coexistence of people and pastoralists or hinder the potential for sustainable coexistence. Overall, this research is focused on drawing inference from empirical data to develop contributions to the understanding of human-elephant interactions in East African savannas with practical applications for elephant conservation. The majority of my research is focused on the Greater Mara Ecosystem in southwest Kenya Chapter 2 is an examination of spatiotemporal patterns of elephant occurrence and uses novel approaches to analyzing remote camera trap data to tests hypotheses about the influence of livestock in influencing these patterns. Chapter 3 uses innovative approaches from movement ecology to gain detailed, spatially explicit understanding of elephant movement behaviors and evaluates how people and environmental variation across ecoregions influence patterns of elephant movement at the landscape scale and at fine spatial scale. Chapter 4 combines conservation psychology theory with a novel application of the models used in Chapter 2 to examine attitudes towards and perceptions about elephants and elephant conservation to understand how people conceptualize their relationships with elephants and to quantify and map social acceptance of elephants in shared landscapes. Finally, in Chapter 5, I synthesize the most important insights from each of the preceding research chapters for ecologists and conservation practitioners, and to reflect on the experience of research co-production and then conducting interdisciplinary, applied research during a global pandemic. Specifically, this dissertation addresses the following research questions:

(1) Are the spatiotemporal patterns of elephant occurrence related to land management and livestock occurrence in the Greater Mara Ecosystem (Chapter 2)?

(2) Does the occurrence of livestock or the number of livestock in shared landscapes influence spatiotemporal patterns of elephant space use, and do elephants respond differently to the presence of different species (cattle vs. shoats, Chapter 2)?

(3) Where in the Greater Mara Ecosystem do elephants go, and what types of movement behaviors do they employ to get where they are going (Chapter 3)?

(4) Where are the most important areas for elephants (e.g., critical habitat and movement corridors) in the Greater Mara Ecosystem and what habitat characteristics are associated with these locations (Chapter 3)?

(5) What is the relative importance of variation in ecosystem productivity and human land use intensity in shaping elephant movement behavior in East African savannas and do people exert more or less influence depending on the ecological context (Chapter 3)?

(6) What explains attitudes towards elephants and elephant conservation in communities living on the margins of protected areas in the Great Mara Ecosystem where elephants are also present (Chapter 4)?

(7) What are the current perceptions about elephants and elephant conservation in these landscapes, and what level of social acceptance for elephants exists, and does social acceptance vary across the landscape (Chapter 4)?

(8) What are the most important takeaways for elephant conservation from this research and how can future collaborative research efforts improve upon the processes from this dissertation (Chapter 5)?

In this introduction, I provide brief background on the theoretical frameworks that guided my approach and the sub-disciplines that each chapter draws on and contributes to. I also outline my approach to answering the research questions above and discuss the organization of this dissertation.

1.1 THEORETICAL FRAMEWORKS

In this dissertation, I consider human-wildlife interactions to be grounded in Social-ecological Systems (SES) theory. SES theory conceptualizes ecosystems as complex, dynamic systems where discrete biophysical and human components, typically organized in a hierarchy across scales (Figure 1.1), interact to shape the structure and function of the system (Berkes & Folke 1998; Ostrom 2009; McGinnis & Ostrom 2014). In other words, SES theory and related frameworks such as coupled-human and natural systems theory (Walker et al. 2004) have been used as conceptual models to describe and research the complex interactions between people and nature (Liu et al. 2008; Bots et al. 2015; Liu et al. 2017). Within this general framing, human-wildlife interactions can be considered to be a specific subset or type of SESs system and defined as defined as human and wildlife activities driven by behavior that overlap in space and time where humans, wildlife, or both are affected by such activities (Dickman 2010; Lischka *et al.* 2018). Figure 1.1 details a conceptual model adapted from (Lischka et al. (2018) and modified to include domestic animals as additional actors (Figure 1.1). In this dissertation, I consider domestic animals to be independent actors whose role, and effects on wildlife, are mediated by human actors. Livestock are typically not discussed in human-wildlife interactions research, yet, over one quarter of Earth's land surface is grazed by livestock, and this replacement of wildlife with domestic animals can put myriad pressures on wildlife populations by increasing direct negative interactions (e.g., competition, disease transmission, persecution) and indirectly through habitat loss, fragmentation, and degradation (Alkemade *et al.* 2013; Schieltz & Rubenstein 2016; Gordon 2018; Filazzola *et al.* 2020). In pastoral systems particularly, people and livestock and thus their interactions with wildlife are closely linked (Ogutu et al. 2005; Reid et al. 2014; Dheer et al. 2021).

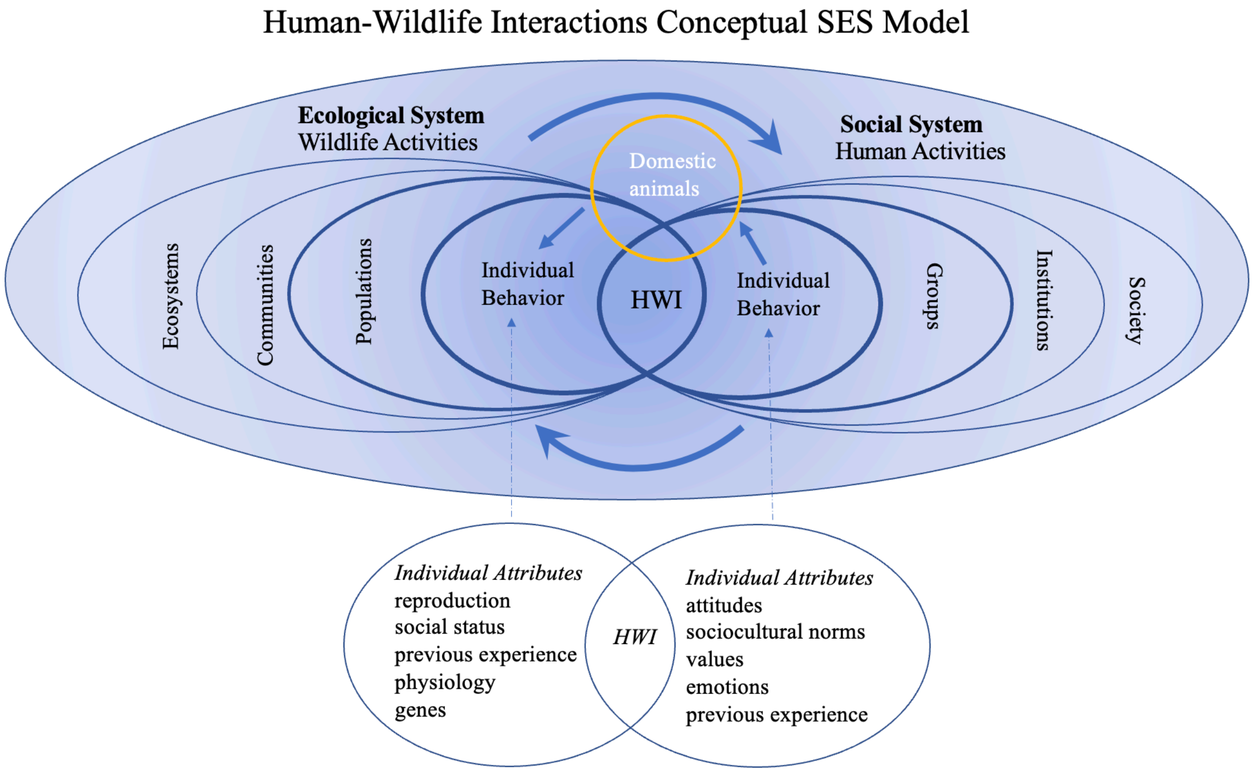

Figure 1.1. Example of a SES-human-wildlife interactions conceptual model adapted from (Lischka *et al.* 2018) and modified to include domestic animals as additional actors. The model allows for bidirectional flows of influence between social and ecological processes that shape human-wildlife interactions and considers how individual-level attributes influence the behavior of both people and wildlife in interactions.

In practice, SESs including human wildlife interactions are incredibly complex, and both social and ecological variables can be difficult to meaningfully measure in a single study, and even more difficult to meaningfully integrate to generate new knowledge because typically, each component of the system is studied with a different discipline and each discipline has a different culture of language and data (Angelstam *et al.* 2013; Bots *et al.* 2015; Niemiec *et al.* 2021). Additionally, although the conceptual model depicted in Figure 1.1 acknowledges the inherent spatiality of human-wildlife interactions and the hierarchal structure of both social and ecological systems, studies describing both ecological and social variables that are spatially and temporally aligned are rare (Ban *et al.* 2013; Guerrero & Wilson 2017). Further, many SES studies often do not integrate ecological variables (e.g., variables that describe ecological relationships and processes like biodiversity) and instead use proxies like land cover (Rissman & Gillon 2017). Thus, spatially explicit research of human-wildlife interactions that matches the scale and geography for both social and ecological data is greatly needed. Furthermore, current conceptual models for the study of human-wildlife interactions such as the model depicted in Figure 1.1 do not provide practical guidance for how to realistically unify and integrate diverse human and wildlife components in the system that are likely studied with disparate methodologies. My approach to address this problem was to frame and conduct my research through the additional lens of spatial ecology. I focus my research in Chapter 2 at the scale of populations to study elephant-livestock interactions at the landscape scale. In Chapters 3 and 4, I focus on describing individual behaviors, with particularly attention to variation in individual attributes and then scale up my inference to the population level to study landscape patterns.

1.1.2 Integrated Spatial Ecology For Conservation

I broadly define spatial ecology as ecological research disciplines that are focused understanding the role of spatial relationships in driving the distributions and dynamics of biological populations (Tilman & Kareiva 1997; Fletcher *et al.* 2018). In particular, much of current spatial ecology seeks to understand how biological populations are responding to anthropogenic land-use and climate change with the goal of developing solutions to conserve biological diversity in this context (Fletcher *et al.* 2018). Spatial ecology thus provides a broad lens with which to apply ecological and social theories to real-world conservation challenges across diverse landscapes. As of today, humans have transformed roughly one-half of Earth's land surface (Sanderson *et al.* 2002; Kennedy *et al.* 2019). The consequences of such broad scale land-use change coupled with the risks of climate change are alarming (Sala *et al.* 2000; Dirzo *et al.* 2014; Di Marco *et al.* 2018). We have changed the content, configuration, and composition of landscapes enough to strongly impact on the functioning and structure of ecosystems and the persistence of biological populations within them by impacting processes such as nutrient fluxes, species dispersal and survival, and disturbance regimes (Lambin *et al.* 2001; Cardinale *et al.* 2012; Di Marco *et al.* 2018).

Land-use change is a leading cause of defaunation, biodiversity loss, and species extinctions across the globe (Ceballos & Ehrlich 2002; Dirzo *et al.* 2014; Haddad *et al.* 2015). For example, 322 species of terrestrial vertebrates have become extinct since 1500, and remaining species show 25% average decline in abundance over the same period (Dirzo *et al.* 2014). Currently, just 15% of earth’s surface is formally protected and many existing protected areas are islands in an ocean of human land use that may not provide sufficient habitat to protect against extinction as global warming continues (Parks *et al.* 2022). Thus, I use the term integrated spatial ecology to indicate the consideration of species distributions, animal movement, human and social landscape variables, and landscape ecology into conservation ecology in this context of global change. My research in this dissertation specifically focuses on the sub-disciplines of movement ecology (Nathan *et al.* 2008), wildlife habitat selection (Morris 2003) and conservation social science (Bennett *et al.* 2017) and applies these disciplines to generate new information about human-elephant interactions that can inform place-based conservation of African elephants.

1.2 ORGANIZATION OF THE DISSERTATION

This dissertation is comprised of this introductory chapter, three research chapters, and a concluding chapter. Chapters 2-4 are intended to be published as stand-alone, peer-reviewed journal articles and thus some information in the Introduction and Methods sections of each of these chapters is somewhat repetitive. Chapter 5 summarizes the findings in Chapters 2-4 and also contains my reflections on collaborative research with local stakeholders and on conducting international, interdisciplinary research as a graduate student during a global pandemic. In Chapters 2-4, I switch from the first person singular to the first-person plural to recognize the contributions of my coauthors.

In Chapter 2, I analyze data from a grid of remote camera traps to improve understanding of elephant-livestock interactions and elucidate the mechanisms by which elephants and livestock coexist at the landscape scale in shared landscapes where land is managed for both livestock grazing and conservation. I address the following research questions: (1) what are the spatiotemporal patterns of co-occurrence of elephants and livestock at the landscape scale? (2) does the occurrence of livestock or the number of livestock present in community conservancies influence spatiotemporal patterns of elephant space use? (3) do elephants respond differently to the presence of different species (cattle vs. shoats vs. wildebeest)? (4) what is the relative importance of species interactions in shaping elephant occurrence among other environmental variables?

We found that African elephants shifted the quantity and timing of their activity in community conservancies where livestock are present relative to the neighboring Mara Triangle protected area where livestock were absent and as expected were more likely to occur in the protected Mara Triangle than community conservancies even when controlling for habitat variation. In addition, we found evidence for a consistent, positive association between elephant occurrence and wildebeest occurrence across the Greater Mara Ecosystem. Finally, we found that areas in community conservancies used with higher intensity by shoats and cattle were less likely to be used by elephants during the daytime. However, this finding was not consistent across years and the estimated effects had low precision. This inconsistency and uncertainty may be related to real interannual variation in patterns of species cooccurrences driven by ecological fluxes, or, as we suspect is more likely, due to the failure of our analyses to detect meaningful spatiotemporal patterns in both years.

In Chapter 3, I utilize long-term GPS tracking data to increase understanding of African elephant movement behaviors and the ecological drivers of variation in movement behaviors both within and across East African savannas. Specifically, I analyze combined information on movement path properties, use intensity, and structural properties of movement networks derived from GPS tracking data collected in the mesic Maasai Mara and the xeric Samburu ecosystems of Kenya to contrast the landscape structure of elephant movement behaviors (e.g., 'movescapes',(Bastille-Rousseau & Wittemyer 2021). This approach was particularly useful for identifying and mapping critical habitat for elephants across the ecosystem, including movement corridors. We then use spatial regressions with detailed data on landscape dynamics to evaluate how variation in ecosystem productivity, landscape structure, and human-land use intensity influence the spatial patterns of critical elephant habitat and movement corridors.

Also in Chapter 3, we compare the factors that most strongly influenced elephant movement behaviors in the mesic Greater Mara Ecosystem with the factors that most strongly influenced elephant movements in the xeric Samburu-Laikipia ecosystem. We found that water availability and vegetation productivity and predictability strongly influenced core areas for both male and female elephants in Samburu and were more influential than anthropogenic factors. Although vegetation productivity also influenced elephant core area use in the Mara, predictability did not, and human presence and canopy cover strongly influenced core area use in the Mara more strongly than water availability. Overall, these findings indicate that elephants in the Mara are likely less constrained by water and forage availability than elephants in Samburu and have more flexibility to access these key resources while minimizing the risks posed by people.

In Chapter 4, I apply cognitive hierarchy theory and the tools of conservation social science to understand how elephants impact people in the Greater Mara Ecosystem by investigating values and attitudes associated with African elephants and elephant conservation in pastoral communities sharing space with elephants. My objectives were to: (1) understand experiences with and attitudes about elephants, (2) gain insight into what drives positive attitudes towards elephants and elephant conservation, (3) quantify local support for elephant conservation, (4) and map local support for elephant conservation across the landscape to support conservation planning. We analyze 177 household questionnaires from an agropastoral landscape important for African elephants with

Bayesian hierarchical models to quantify positive attitudes towards elephants while accounting for self-reporting bias. Spatially explicit and accurate attitude assessments may be critical for developing more effective conservation plans for wide-ranging species, particularly if assessments also address *why* attitudes may be held. We interpret quantitative model estimates in the context of qualitative attitude assessments and sociocultural values to gain a deeper understanding of what explains attitudes towards elephants in the region and map positive attitudes across the landscape to support conservation planning.

We found that although a majority of people expressed positive attitudes about elephant conservation in general, most were not also positive about sharing space with elephants on community and private lands at a local scale. Model estimates showed that people who believed that elephants had sociocultural value were the most likely to be positive towards elephant conservation in general, but experiencing conflict with any wildlife lowered the probability of respondents to have a positive attitude towards sharing space with elephants at a local scale. Qualitative data revealed that safety and well-being concerns related to the perceived threats that elephants pose to human life, livestock, and crops, coupled with few social and economic incentives to support elephant conservation in community and private lands contribute to low local positive attitudes. Overall, our results suggest that conservation approaches focused on sustaining existing sociocultural values and relationships with wildlife while also investing in human well-being and safety measures and could improve conservation outcomes in shared landscapes.

Finally, in Chapter 5, I summarize key take-aways for elephant conservation based on the findings detailed in Chapters 2-4 and reflect on the research process including the collaborative process, remote research during the pandemic, and experiences with co-interpretation and sharing research back to communities that participated in the research. I discuss the key findings for the practice of elephant conservation and the specific contributions of this dissertation including the map products produced. We identified specific locations on the landscape in the Greater Mara Ecosystem that are crucial for elephants, including highly used areas and corridors, and were able to delineate these areas from those occasionally used by elephants that are not important for connectivity. This work can directly support conservation planning in the Greater Mara Ecosystem. Some of the most important takeaways come from the findings of Chapter 4, which can provide direct guidance to conservation practitioners on how to better address human well-being in community-based conservation efforts. Also in Chapter 4, we provide maps detailing estimated social acceptance of elephants at a local level that can be directly integrated into spatial conservation plans. Finally, the reflections in Chapter 5 provide can guidance to other researchers seeking to conduct collaborative, applied research and for conducting partially remote research and data collection.

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CHAPTER 2

CAMERA TRAP DATA LABELED BY MACHINE LEARNING REVEALS CO-OCCURRENCE PATTERNS OF AFRICAN ELEPHANTS WITH WILDEBEEST AND LIVESTOCK IN MIXED-USE SAVANNA

2.1 INTRODUCTION

Wildlife occurrence patterns are strongly shaped by habitat selection, the behavioral process by which animals use habitats asymmetrically in space and time to fulfill requirements for survival, growth, and reproduction while balancing potential fitness costs and perceived mortality risk (Rosenzweig 1981; Morris 2003). Because habitat selection theory describes the relationship between spatiotemporal patterns in animal occurrence and the environment, it provides a framework to test hypotheses about the abiotic and biotic factors that explain animal occurrence patterns and ultimately constrain the realized niches of species (Rosenzweig 1981; Morris 2003; Kearney 2006). Most studies of wildlife occurrence have focused on the role of abiotic factors in shaping habitat use, for example, identifying variation in population density and species occurrence associated with rainfall patterns (Georgiadis *et al.* 2003; Ogutu & Owen-Smith 2003; Ogutu *et al.* 2008), or wildlife selection and avoidance of specific habitat types (Dickson & Beier 2002; Harju *et al.* 2011; Latham *et al.* 2011). However, species interactions, including inter- or intra-specific competition (Morris 2003; Young *et al.* 2005; Apps *et al.* 2006), predator-prey interactions (Valeix *et al.* 2009; Latham *et al.* 2011), and facultative interactions (Bertness & Callaway 1994; Odadi *et al.* 2011) can also strongly shape habitat selection and spatiotemporal patterns of wildlife occurrence.

Multiple types of species interactions can simultaneously influence patterns of wildlife occurrence (Arsenault & Owen-Smith 2002; Chesson & Kuang 2008; Valeix *et al.* 2009; Riginos 2015). For example, in East African savannas, evidence suggests that mixed-species wild herbivore groups are the result of predator avoidance behavior for some species (Sinclair 1985; Riginos 2015), whereas others are likely balancing the trade-off between increased interspecific competition for forage and lower predation risk in mixed groups (Sinclair 1985; Pays *et al.* 2014). The strength of species interactions in shaping wildlife habitat use patterns can also change with environmental conditions (Odadi *et al.* 2011; Riginos 2015). Riginos (2015) found that wild mesoherbivores generally avoided woody habitat due to perceived higher predation risk, except during drought periods when they instead favored areas with high grass biomass including woody areas over areas with high visibility (Riginos 2015). Predators can thus shape prey-species habitat use by creating a 'landscape of fear' (Brown *et al.* 1999) where prey species perceive different levels of predation risk in different habitat types or across temporal periods and adjust their habitat use in response (Brown *et al.* 1999; Riginos 2015; Gaynor *et al.* 2019). Humans and some domestic animals can also create landscapes of fear for wildlife with strong influences on the habitat selection of species that are harvested or persecuted by humans (Clinchy *et al.* 2016; Suraci *et al.* 2019; Dill & Frid 2020).

Domesticated animals including livestock and pets are increasingly predators and/or competitors of wildlife (Twardek *et al.* 2017; Gordon 2018). Recent global biomass estimates show that the biomass of livestock (mostly cattle and pigs, ≈0.1 Gt C) far surpass that of wild mammals, which is more than a thousand times less than livestock (wild mammals ≈0.007 Gt C, (Bar-On *et al.* 2018). Over one quarter of Earth's land surface is grazed by livestock, and this replacement of wildlife with domestic animals can put myriad pressures on wildlife populations by increasing direct negative interactions (e.g., competition, disease transmission, persecution) and indirectly through habitat loss, fragmentation, and degradation (Alkemade *et al.* 2013; Schieltz & Rubenstein 2016; Gordon 2018; Filazzola *et al.* 2020). A global review of case studies found most cases (55%) reported negative impacts of livestock on wild mammal populations (Schieltz & Rubenstein 2016). For wild ungulates, these impacts were mostly interference competition (e.g., avoidance of livestock), as well as reductions in forage quantity and quality by livestock (Schieltz & Rubenstein 2016). However, as described below, several studies reviewed also reported neutral or positive effects, and positive effects of cattle grazing were mostly reported for small-bodied ruminants (Schieltz & Rubenstein 2016).

Sympatric assemblages of wild herbivore species are hypothesized to coexistence with minimal competition with each other because they partition forage niches through variation in body size, digestive physiology, and mouthpart anatomy, and therefore food choice (Jarman 1974; Arsenault & Owen-Smith 2002). One species can positively impact another (e.g., facilitation) such as a large species facilitating smaller species by lowering grass height and removing lower quality vegetation, or by stimulating new regrowth and thereby enhancing forage quality (Arsenault & Owen-Smith 2002; Augustine *et al.* 2003). Alternatively, competition may occur when one species reduces forage resources enough to lower the intake of forage by another species (Murray & Illius 1996; Augustine & Springer 2013). We could thus expect the greatest potential for competition between wild and domestic species with similar body size, functional traits, and diets, particularly during periods of resource scarcity, and similar potential for facilitation between wild and domestic species with different functional traits and dietary requirements (Western, 1989; du Toit and Cumming, 1999, Fynn et al. 2016). Yet, most studies of interactions between wild and domestic herbivores have been conducted in temperate ecosystems and assessed only the impacts of cattle (Schieltz & Rubenstein 2016; Gordon 2018).

Increased understanding of interactions between wildlife and livestock for wildlife conservation and management is particularly important in rangeland and savanna ecosystems. In East Africa, these landscapes are complex social-ecological systems of global conservation importance where people, wildlife, and livestock have shared space for millennia (Homewood & Rodgers 1984; McCabe 1994; Reid *et al.* 2004; Reid 2012). Traditional pastoral practices in East Africa (e.g., grazing cattle on common land) are generally considered to be compatible with wildlife conservation because pastoral lands are open for wildlife and slow land-use change and habitat loss compared to other land uses (Homewood & Rodgers 1984, 1991). In Kenya, 50-70% of wild herbivore populations occur in pastoral lands outside of and bordering protected areas (Western *et al.* 2009; Ogutu *et al.* 2016). But these systems are increasingly vulnerable due to land-tenure policy favoring private land ownership, political and economic marginalization of pastoralists, land conversion, social conflicts, growing human and livestock populations, habitat loss, fragmentation, persecution of wildlife, and climate change (Reid *et al.* 2004; Homewood *et al.* 2009; Galaty 2013; Ogutu *et al.* 2016). However, livestock remain the primary livelihood source for most people in Kenya's rangelands (Bedelian & Ogutu 2017). Wild herbivore populations in Kenya's rangelands declined by 68% on average from 1977- 2016, while the number of sheep and goats increased by (76%) over the same period (Ogutu *et al.* 2016).

In central Kenya, long-term experiments found that at moderate stocking densities, cattle appear to compete with wild mesoherbivores during dry periods, but during wet periods, wildlife facilitated cattle by enhancing the quality of forage resources (Odadi *et al.* 2011). After 20 years, grazing cattle in plots with or without mesoherbivores strongly impacted soil nutrient pools because cattle effectively exported nutrients from plots to bomas (nighttime livestock corrals), impacting vegetation quality and depleting soil carbon (Sitters *et al.* 2020). However, African savanna elephants (*Loxodonta Africana*) increased nutrient pools across plot replicates and mitigated the negative effects of cattle by up to 43% (Sitters *et al.* 2020). One explanation for this result is that elephants compete with cattle and thus reduce the amount of protein-rich vegetation eaten and exported by cattle, and/or elephants import nutrients from woody vegetation to soil nutrient pools via dung and tree removal and thus compensate for some of the export (Young *et al.* 2005, 2018; Sitters *et al.* 2020). However, it is unclear how these relationships might change at the landscape scale, particularly at higher cattle stocking rates, and in savannas with grazing by livestock other than cattle.

African savanna elephants (*Loxodonta Africana*) are both keystone herbivores and ecosystem engineers in East African savannas because they influence the physical structure and composition of vegetation mostly by suppressing and reducing woody plants and indirectly influencing the distribution of other vertebrates (Dublin *et al.* 1990; Valeix *et al.* 2011; van de Water *et al.* 2022). Because of the keystone role of elephants in structuring savanna ecosystems, significant spatial displacement of elephants by livestock could have cascading ecological impacts (Veldhuis *et al.* 2019; Sitters *et al.* 2020). African elephant avoidance of human-modified landscapes is well documented (Wall *et al.* 2021). But in pastoral landscapes where human habitat modification is moderate, this response is less clear (Bastille-Rousseau *et al.* 2020). Some evidence suggests that elephants likely avoid livestock as a behavioral response linked to fear of herders whom elephants can perceive as a threat (Lee & Graham 2006; Bates *et al.* 2007a; Wittemyer *et al.* 2017; Gaynor *et al.* 2018). Because elephants are both persecuted by people and may compete with livestock, elephant space use in mixed-use savannas could be strongly shaped by livestock presence. However, it remains unclear if elephants adjust their habitat use in response to spatiotemporal variation in the presence or number of livestock, particularly at fine spatiotemporal scales across large landscapes. In addition, very few studies have considered the potential impacts of livestock other than cattle.

In this study, we address these gaps in knowledge by examining spatiotemporal occurrence patterns of African savanna elephants, wildebeest (*Connochaetes taurinus*), cattle, and sheep and goats (hereafter referred to as 'shoats') in several areas of the Greater Mara Ecosystem (GME) in southwest Kenya. The GME has the greatest density of both wildlife and livestock in Kenya, and shoat populations have dramatically increased in recent years (Ogutu *et al.* 2016; Bedelian & Ogutu 2017; Løvschal *et al.* 2019). We compare spatiotemporal patterns of elephant occurrence in the Mara Triangle part of the Maasai Mara National Reserve, a highly protected area where livestock cannot graze legally, with patterns of elephant occurrence in adjacent community conservancies where both livestock grazing and wildlife tourism are allowed, and some small villages exist (MMWCA 2017). We sought to improve understanding of elephant-livestock interactions in mixed use savannas and elucidate the mechanisms by which elephants and livestock coexist at the landscape scale by addressing the following research questions: (1) What are the spatiotemporal patterns of co-occurrence of elephants and livestock at the landscape scale? (2) Does the occurrence of livestock or the number of livestock present in community conservancies influence spatiotemporal patterns of elephant space use? (3) Do elephants respond differently to the presence of different species (cattle vs. shoats vs. wildebeest)? (4) What is the relative importance of species interactions in shaping elephant occurrence among other environmental variables? We expected that elephants would use the protected area more than community conservancies to avoid livestock, and that elephants and livestock in community conservancies would show evidence of spatiotemporal partitioning due to elephant avoidance of livestock. Finally, if elephant avoidance of livestock is primarily driven by competition, then we expected that elephants may also avoid wildebeest, but if avoidance of livestock is more strongly driven by fear of people, then elephants may show little response to wildebeest presence.

2.2 METHODS

Study Area

The Greater Mara Ecosystem (GME) is the northernmost part of the Mara-Serengeti system located in Narok county of southwest Kenya (Figure 2.1). Annual rainfall follows a gradient averaging 650mm in the southeast to 1450mm in the northwest and is typically bimodal with some rains occurring from November–December and more rain from January–June (Ogutu *et al.* 2008; Bartzke *et al.* 2018). Vegetation is comprised of open grassland interspersed with lone *Balanites aegyptiaca* trees and patchy acacia woodlands (*Vachellia drepanolobium*) as well as riverine woodland dominated by *Diospyros abyssinica* and *Vachellia kirkii*, and *Euclea divinorum*, and *Croton dichogamus* bush thickets which dominate hilltops. The region is the ancestral home of the Maasai people who are traditionally semi-nomadic pastoralists. Maasai still herd livestock, but over the last twenty years land tenure has transitioned from mostly common landholdings to mostly individual landholdings as a result of national land policies that favor agriculture over pastoralism (Thompson & Homewood 2002; Homewood *et al.* 2009). As a result, many Maasai in the GME settled near village centers and diversified their livelihoods through leasing of privately owned land parcels for commercial agriculture or wildlife conservation and tourism through community conservancies (Homewood *et al.* 2009). However, Narok also supports the greatest density of wildlife including an estimated 2,595 elephants (Ogutu *et al.* 2016; Waweru *et al.* 2021). The core protected area is the 1,500 km^2 Maasai Mara National Reserve (MMNR) where wildlife photo-tourism is the only permitted land use. However, the western third of the MMNR (510km^2), locally called the 'Mara Triangle' is managed as a separate unit by a non-profit group and has strict protection enforcement, whereas in other parts of the MMNR, livestock grazing inside the reserve sometimes occurs (Butt 2014). To the north and east, the MMNR is buffered by community conservancies (CC) covering about 1,400 km^2 which allow regulated livestock grazing in addition to wildlife tourism (Bedelian & Ogutu 2017; MMWCA 2017). We focused our analysis on the conservancies that directly border the MMNR: Mara North Conservancy, Olare-Motorogi Conservancy, which was previously two separate conservancies but is now managed as one, and Naboisho Conservancy (Figure 2.1).

Remote Camera Trap Survey

Camera trap surveys in the Greater Maasai Mara ecosystem were conducted by the Biome Health Project at the Center for Biodiversity and Environment Research at the University College of London. Researchers and conservancy rangers deployed 180 Browning motion-detection infrared flash cameras with a detection range of ~24 meters (model BTC-6HD-MXP) in a grid with 2km^2 spacing stratified by land management in the Mara Triangle protected area and in Mara North, Olare-Motorogi, and Naboisho Conservancies (Figure 2.1). Cameras were placed at the center of each grid cell or within 50m of the grid center, orientation was randomly assigned, and if possible, cameras were affixed to trees or otherwise to temporary metal posts. Cameras were placed with the bottom of the trap box 50cm from the ground to approximate shoulder height of medium mammals and at minimum 1m distance from where animals were likely to enter the sensor's detection cone (Burton *et al.* 2015). Any vegetation obstructing the field of view was cleared at installation and during monthly checks during the survey period to replace batteries, ensure operation, and fix camera placement as necessary. Surveys occurred during the dry season in 2018 and 2019 and operated from October 5th – November 29th in 2018, and from July 5th – November 30th in 2019.

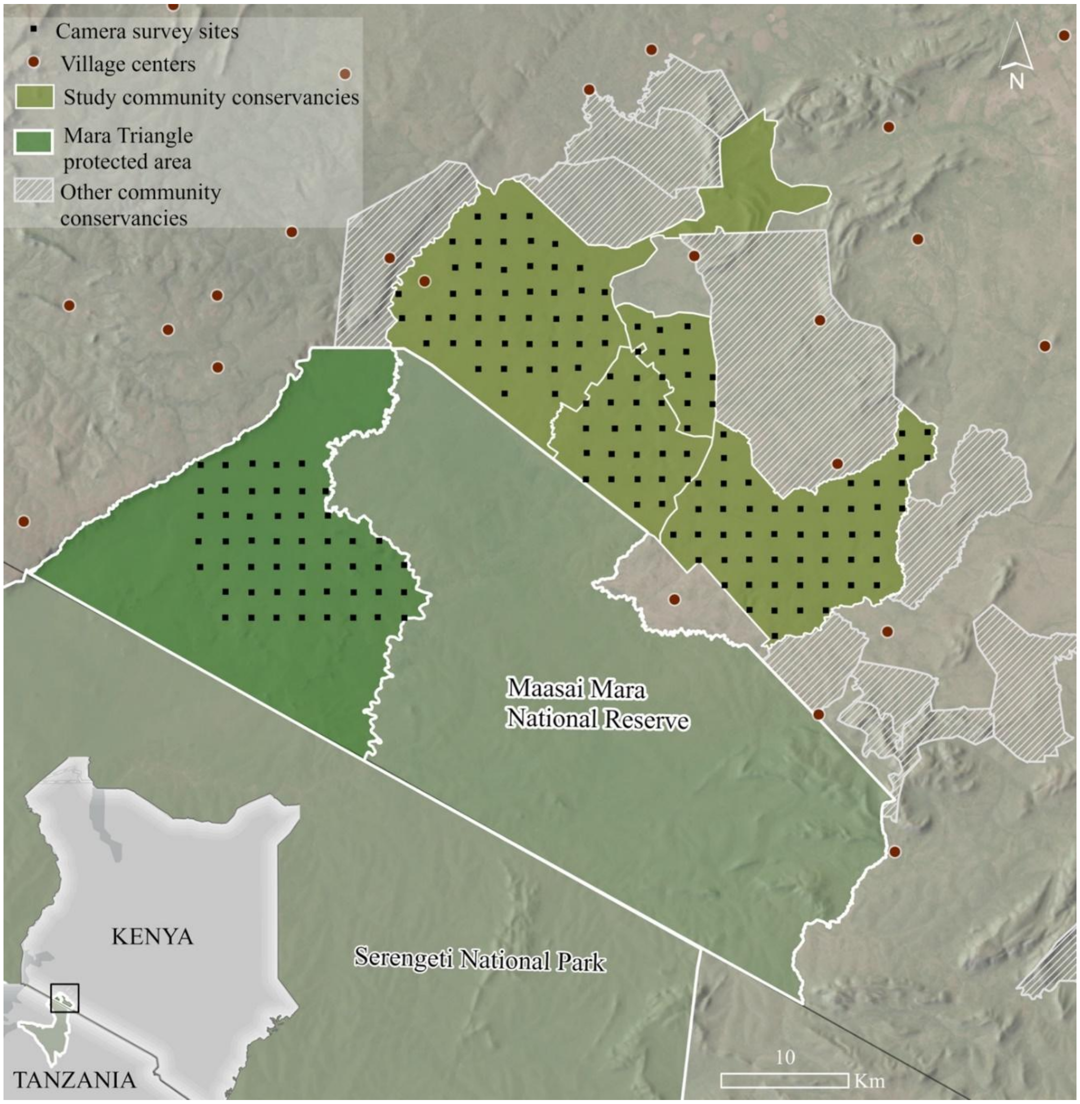

Figure 2.1. Map of study area showing the location of 180 remote camera trap locations surveyed from 2018-2019 in the Mara Triangle (50) and three community conservancies (from west to east: Mara North (46), Olare-Motorogi (34), and Naboisho (50) across the Greater Mara Ecosystem.

Camera trap data processing

Remote cameras across the 180 stations collected more than 2 million images in 2018 and over 3.5 million images in 2019. Given the enormous volume of data, we followed the camera trap image review process described in Beery et al. (2019) to increase efficiency of data processing (Beery *et al.* 2019). We first applied a machine learning model that identified animals (not species-specific) in camera trap images (MegaDetector, Beery et al. 2019) to all images captured in both years. MegaDetector extracts a rectangular cropped image of each individual animal identified in the full image (hereafter referred to as 'crops', Figure 2.2). The model is trained with hundreds of thousands of camera trap images collected across diverse ecosystems, is accurate when applied to novel data (e.g., locations/species not used to train the model), and drastically reduces the time that human observers would otherwise spend filtering blank images (Beery *et al.* 2019). We retained all images with ≥ 65% confidence that animals appeared in the image, resulting in ~3 million unique crops from 2018 and ~6 million unique crops from 2019. Researchers then manually labeled ~ 60,000 images collected in 2018 using open-source software by identifying species and drawing localized crops around each animal appearing in every image. From the human-labeled images, a split of 25,000 animal crops were held out as test data to evaluate and validate model performance (e.g., were not used to train the species classifier). A total of 53,102 human-labeled animal crops from 24,646 images were used to train a convolutional neural network (CNN) deep learning model to classify crops of animals to the species level, and the model was then used to predict species labels for all image crops containing animals captured in 2018 and 2019 (Pantazis *et al.* 2021).

Figure. 2.2. Examples of images collected by camera traps in Mara North conservancy in 2018 and animal image crops used to train machine learning models to classify image crops to species level.

Evaluating the Machine Learning Model's General Performance

We evaluated overall performance of the convolutional neural network model following common approaches used to evaluate similar models in the literature (Norouzzadeh *et al.* 2018; Tabak *et al.* 2019). We calculated the top one accuracy (both overall and balanced accuracy) using the human-labeled test data at a confidence threshold of 0.90 for the machine learning labels. Top one accuracy is the percent of human labels that match the top-ranking label generated by the machine learning model, and balanced accuracy is the average of the true positive classification rate and true negative classification rate (Whytock *et al.* 2021). Top one accuracy for the machine learning model classifying all species groups was 92% overall and the balanced accuracy was 87% (Appendix I). Elephant labels had an overall accuracy of 89.6%, cattle labels 90%, shoat labels 95.2 %, and wildebeest labels 88.9 % (Appendix I).

Validation of Machine Learning Labeled Data for Ecological Inference

A major challenge in the application of high-performance machine learning models to processing camera trap data is the ability of models to generalize predictions to out-of-sample datasets, especially for the purpose of classifying images of animals at the species level (Beery *et al.* 2019; Tuia *et al.* 2022). However, biases in machine learning model labeled data are predictable and quantifiable, and when carefully tested and validated, images labeled with high performance machine learning models can be used for ecological inference (Whytock *et al.* 2021). Prior to using machine learning model species labels in our ecological analyses, we conducted validation tests building on the approach outlined in Whytock et al. (2021) to evaluate accuracy of the machine learning labels for use in ecological modeling. For each species group (elephants, wildebeest, cattle, shoats) we calculated ecological parameters of interest for our study (daily activity patterns, detection probability, and occupancy probability) from human generated labels and compared results to the same metrics calculated using machine learning generated species labels. We used a test subset of 11,508 unique livestock, elephant, and wildebeest image crops for validation tests captured during a 20-day period in 2018 (November 10-29) that were held out from model training (e.g., the classifier had not 'seen' these images prior to making species predictions). We tested machine learning model generated labels at a minimum threshold of 90% confidence in the species label and omitted images below this threshold (Whytock *et al.* 2021). Increasing the confidence threshold is a trade-off between improved accuracy and lower errors of commission (false positive classifications) versus data loss and errors of omission (false negatives). For each species of interest, we evaluated the percentage of data loss at ML confidence thresholds of .90, .95, .970, and .99 for the species label. To validate activity pattern estimates, for each species and threshold combination, we tested for a significant difference in the daily activity estimated by machine learning labels and human labels with the Wald test on a chi-squared distribution with one degree of freedom using the package *activity* in R (Rowcliffe *et al.* 2014).

To validate space use parameters (e.g., detection, occupancy) estimated from machine learning labels, we ran single-species, single-season occupancy models for each species and threshold combination and compared results to models fit with human labeled data (Appendix I). We tested both a null model (no effect of covariates) and variation model with one covariate each on detection and occupancy for each combination to test if ML labels biased covariate relationships. For detection probabilities we inspected estimates and 95% confidence intervals, and we then followed the approach of Guillera-Arroita & Lahoz-Monfort (2012) and used an alternative Wald test (normal distribution, 1 degree of freedom) to test for a significant difference at the $\alpha = 0.05$ level between occupancy estimates based on human labeled data and ML labeled data (Guillera-Arroita & Lahoz-Monfort 2012). Because our primary goal was to assess interactions among common species that are already known to widely occupy the study area rather than to obtain highly precise occupancy estimates, we considered ML labeled data sufficiently accurate for use in our analyses if there was not a statistically significant difference in estimates of occupancy obtained using human generated labels and ML generated labels based on the Wald test.

Analysis of spatiotemporal patterns of co-occurrence

We implemented two analytical methods to evaluate spatiotemporal patterns of co-occurrence among elephants and livestock to test for attraction and/or avoidance because different approaches can provide complimentary information about spatiotemporal co-occurrence patterns (Table 2.1). For example, elephants may use the same locations as livestock but at different hours during a 24-hour period, and therefore potential patterns of avoidance or attraction in time could be missed with a single analysis that requires aggregating data to a daily or multi-day scale (e.g., occupancy modeling). Similarly, assessing only temporal patterns such activity overlap, could miss potential spatial partitioning among species. We give an overview of the ecological inference provided by each approach in Table 2.1.

Table 2.1. Overview of analytical approaches used to evaluate spatiotemporal species interactions.

Method	Description	Inference	References
Daily activity pattern overlap	assessment of daily temporal activity patterns of two species	overall temporal association	Ridout & Linkie 2009; Rowcliffe *et al.* 2014
Single-species false positive occupancy models	assessment of spatiotemporal space use; corrected for imperfect detection and false-positive detection	relative importance of interspecific interactions compared to environmental factors in shaping daily patterns in species space use and intensity of use	MacKenzie *et al.* 2002; Royle & Link 2006; Miller *et al.* 2011

Daily Activity Patterns

We estimated daily activity patterns based on species detections at camera traps by treating the observed detection times in 2018 and 2019 as random samples from a circular, continuous probability distribution and fitting probability density functions to detection times using the R package '*activity*' (Rowcliffe *et al.* 2014). This approach assumes temporal events are independent, so we thinned detection data and retained images captured at least 30 minutes apart at a given trap for this analysis (Ridout & Linkie 2009). Previous studies have found that factors such as rainfall and body size can influence the effective detection (distance, angle) of animals at camera traps and bias detection rates (Marcus Rowcliffe *et al.* 2011). We acknowledge the potential for similar bias in our data, but because the species of interest in our study are abundant, with body mass ≥30 kg, and because surveys occurred in the dry season, we assume that these factors have a negligible influence on activity estimated from detection rates (Marcus Rowcliffe *et al.* 2011).

We expected that elephants and wildebeest may exhibit reduced activity during daylight hours in community conservancies when livestock are active compared to the Mara Triangle protected area where livestock are strictly not permitted. Thus, we calculated two daily activity distributions for elephants and wildebeest: (1) activity in the Mara Triangle and (2) activity in community conservancies. Because livestock are permitted only in community conservancies, we calculated a single distribution for each livestock group (cattle and shoats). We then calculated the coefficient of overlap (Δ) between activity distributions over a 24hr day of elephants and livestock, then wildebeest and livestock in community conservancies, where Δ values near 1.0 indicate perfect overlap and values near 0 indicate no overlap in activity. To test for a difference in elephant and wildebeest activity levels between the Mara Triangle protected area and CC's, we used a Wald test to evaluate whether the difference in activity level between the two land management zones was significantly different from zero (Rowcliffe *et al.* 2014). We then used a randomization test to evaluate if the distribution of activity over a 24hr day for elephants and wildebeest was significantly different between the two land management zones than would be expected by chance because while overall activity levels might not change, there could be differences in the timing of activity. We used bootstrapping with 1,000 replicates to estimate 95% confidence intervals (CI) for activity estimates and 10,000 replicates for the 95% CI of Δ for each species pair (Rowcliffe *et al.* 2014).

False-Positive Occupancy Models

Occupancy models are hierarchical extensions of generalized linear regression models (GLMs) that are useful for understanding patterns of space use. Occupancy models account for the imperfect detection of animals by utilizing the information from repeated surveys to account for the ambiguity of an observation of animal ‘absence’ (e.g., non-detection) which could arise when the animal is truly absent at the survey site or when the animal is present but not detected (MacKenzie *et al.* 2002; Mackenzie *et al.* 2004). Occupancy models therefore jointly estimate the presence (occurrence) of animals and the probability that the animal is detected given it is present at a survey site, allowing for the investigation of relationships between the presence-absence of animals and habitat characteristics. In order to account for detectability, the assumptions of occupancy models are: 1) that sites are closed to changes in the occupancy status of target species between surveys, 2) that sites and repeated surveys are spatially and temporally independent, 3) that any heterogeneity in both occupancy and detection is accounted for in the model and 4) that there are no misidentifications of species (e.g., false positive detections).

These assumptions are typically relaxed for camera trap studies of wide-ranging species in continuous habitat, as is the case in this study because elephants and livestock could be detected at more than one camera site in a single survey (violation of assumption 1). Following previous camera trap studies, we interpret occupancy probability as the probability of use at camera sites for each species during the study period and hereafter use the term ‘occupancy’ to refer to probability of use (Efford & Dawson 2012; Tobler *et al.* 2015). We also acknowledge our choices of survey length are arbitrary given the continuous collection of images at camera traps and could thus result in some temporal dependence in surveys (e.g., assumption 2), and that even with the inclusion of covariates to account for heterogeneity in detection and occupancy, we build and evaluate models based on parsimony which is a trade-of between model complexity and interpretability (assumption 3).

However, to meet assumption 4, we implement false-positive occupancy models that account for the species misidentifications that are present in the ML labeled data (Royle & Link 2006; Miller *et al.* 2011). For the 2018 data, we use the multiple-detection approach of Miller et al. (2011) to account for false positive errors, where a subset of the ML labeled detection data are *certain* detections because they have been verified to be correct via the human-labeled test dataset, and the remaining data are *uncertain* because they many contain false-positives (Miller *et al.* 2011). Using multiple methods of observation reduces bias in parameter estimates when false positives occur (Miller *et al.* 2011; Ferguson *et al.* 2015; Kéry & Royle 2020). We thus model the elephant occupancy state as a Bernoulli process where $z_i = 0$ (unoccupied) or 1 (occupied) is the occupancy state for a single species at i camera sites with ψ probability of occurrence.

To allow for false positives in the observation (detection) process model, we allow detections even when a site is truly unoccupied ($z_i = 0$) and expand observations to three possible states where for $y_{i,j}$ detections at i sites across j survey occasions, $y = (0, 1, 2)$ or where 0 is not detected, 1 is an *uncertain* detection (unverified ML label), and 2 is a *certain* detection (verified ML label) (Miller *et al.* 2011; Kéry & Royle 2020). The multi-state observation model requires the estimation of three distinct detection probabilities: p_{11} is the probability of a true positive detection (Pr ($y = 1 \mid z = 1$), p_{10} is the probability of a false positive detection (Pr ($y = 1 \mid z = 0$), and b is the probability that an observation is a *certain* (verified) true positive detection (Pr (*certain* true positive | $y = 1, z = 1$). For the 2019 data for which we had no verified detections (e.g., $b = 0$), we use the Royle and Link (2006) finite-mixture formula for false positive occupancy and assume that $p_{11} > p_{10}$ ((Royle & Link 2006; Kéry & Royle 2020).

In the context of camera trap studies of wide-ranging, common species, the true detection probability (p_{11}) often varies with animal movements and population density (Rowcliffe *et al.* 2008, 2014). Thus, in our case, (p_{11}) is a parameter of interest because it provides an index of use intensity at each camera site, and when modeled as a function of covariates it can be useful to test hypotheses about what factors influence use intensity. Hereafter, we interpret true detection probability as the intensity of use at camera sites. We fit separate, single-season, false positive occupancy models for each species group for each year to estimate the daily dry season occupancy probability (October 5 – November 29, j = 55). To address our research questions, we fit two models each year for African elephants. We first fit an ecosystem-wide model (e.g., including detections at all camera sites) to assess environmental factors and interactions with wildebeest which are potentially present at all camera sites. Because livestock occur only in conservancies and are largely active only during the day, we then conducted a separate analysis to assess elephant interactions with wildebeest and livestock in community conservancies. We modeled daily elephant occupancy for camera sites in community conservancies only and restricted this analysis to detections of elephants, livestock, and wildebeest captured from 6am – 7pm. Thus, for the conservancies only analysis, estimates strictly represent daytime occupancy and detection probabilities. We used the R package '*unmarked*' and the function 'occuFP' to fit all occupancy models which estimates model parameters using maximum likelihood estimation (Fiske & Chandler 2011).

Covariates Used in Occupancy Modeling

We first used the camera data to develop a suite of covariates representing the presence of target species groups to test for species interactions effects. To test for interspecific interaction effects on elephant occupancy and detection, we used the wildebeest and livestock detection data with .97 confidence in the species label to create covariates indexing the frequency of occurrence for each species group (Table 2.2). For wildebeest, cattle, and shoats, we used the number of unique images of each species group captured at each camera site and survey day as an index of occurrence frequency. To minimize the potential influence of false positives in these covariates, we calculated the number of unique animal image crops for each image, and if the detection was a single animal crop in a single image for that site and survey day, we set it to zero assuming that a single crop in a single image for an entire day was likely to be a false positive for livestock and wildebeest. Finally, we created combined 'livestock' covariates that included both cattle and shoats, hypothesizing that the total amount of livestock regardless of the species could influence elephant occupancy and detection probabilities (Table 2.2).

Table 2.2. Environmental and interspecific interaction covariates tested in single species false-positive occupancy models hypothesized to influence occupancy and detection probability.

Covariates	**Description**	**Data sources**
Interspecific interactions		
Wildebeest	(1) frequency of detections each day at each site (2) median frequency of detections at each site over the study period, index of use intensity	this study
Shoats		〃
Cattle		〃
Environmental	*all spatial covariates were summarized within a 250m and 500m radius at each site*	
local Human Footprint Index (HFI)	quantification of cumulative impacts of human presence and landscape modification (average)	Tyrrell *et al.* 2022
temporal mean NDVI (2009 -2019)	index of predictability of vegetation productivity at each site (average)	MODIS vegetation indices; Didan 2015
current NDVI for each survey day	index of vegetation productivity at each site on each day (average)	〃
open grassland (< 20% canopy cover)	proportion of cover type at each camera site	Wall *et al.* in review, this dissertation
proportion of semi-open canopy (20-70 % cover)	〃	〃
proportion of forest/bush thicket (>70% cover)	〃	〃
distance to waterway	surface distance to nearest river or drainage	Grill *et al.* 2019
land management type	Mara Triangle (MT) vs. community conservancies (CC); each conservancy vs. MT	

We expected human presence and land modification to influence the space use of elephants expecting lower detection and occupancy probabilities areas with greater human influence. To account for the cumulative impacts of human presence and landscape modification in the study area, we created a local "Human Footprint Index" (HFI) at a resolution of 30m on scale from 0−5 where 5 represents the highest human impact. We used ground-mapped and digitized spatial data layers (Tyrrell *et al.* 2022) and based the formulation of our index on existing global human footprint datasets (Sanderson *et al.* 2002; Theobald *et al.* 2020) with modifications based on our knowledge of the ecosystem. We calculated the density of bomas (traditional households and livestock corrals) within a radius of 500m across the landscape and then calculated the Euclidean distance to three other settlement types (village centers, hotels, and tourism lodges at a 30m resolution. We then classified cells on a scale from 0−5 based on their proximity to these three settlement types and combined the classified layers in weighted sum based on the relative impact of the settlement type, for example, locations within 100m of village centers were scored as having the highest HFI value. We followed a similar approach for roads, scoring HFI impact according to road type (primary, secondary, or tertiary) and proximity to roads with cells within 100m of primary roads having the highest HFI score and cells near tertiary roads were assigned a maximum impact score of 1. We used ground-mapped fence data to create a fence line density layer weighted by fence type with electric fences having the highest weight. Finally, we used a weighted sum to combine boma density (weight = .30), proximity to village centers, hotels, and lodges (weight = 0.25), roads (weight = .25), and fences (weight = .10) into a single HFI score on a scale from 0−5.

We expected vegetation structure, specifically the amount of woody canopy cover (tree cover or bush thickets) around camera traps to influence elephant occupancy probability; expecting elephants to be to less likely to occupy open grassland. We quantified canopy cover at camera sites using a high-resolution (10m) land cover map developed with data derived from Sentinel-1 and Sentinel-2 multispectral satellite images collected from 2018-2021. We conducted image analysis and classification using the Google Earth Engine (Gorelick *et al.* 2017) platform with a Random Forest classification model and over 2,000 ground-truth samples (Wall *et al.* in review). Land cover classes included: (1) forest and thicket (> 70% canopy cover), (2) woodland and open bushland (20-70% cover), (3) open savanna and wooded savanna (< 20% cover), and (4) a class for bare ground, rock, and built-up cover. We then calculated the proportion of each cover type in a 250m radius and 500m radius around each camera site. We also expected that elephants, wildebeest, and livestock may favor greener, productive vegetation and so we composited Terra Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day v.006 normalized difference vegetation index (NDVI) images (Didan 2015). We calculated the temporal mean NDVI for each pixel across the study period as an index of productivity predictability from 2009-2019, and then calculated the spatial mean NDVI in both a 250m and 500m radius around each camera site. We also expected that the detection probability of the target species on any given day in the dry season could be related to current productivity conditions which can be strongly heterogenous across the ecosystem. For each sampling day and camera site, we also calculated the 'current' spatial mean NDVI value in a 250m and 500m radius around each camera site by matching the survey day with the temporally closest MODIS 8-day median NDVI image.

To control for potential effects of water availability, we mapped waterways from the global HydroSHEDS Free Flowing Rivers Network and from ground-mapped and digitized waterways (Grill *et al.* 2019; Tyrrell *et al.* 2022). We then calculated the surface distance from waterways to camera sites at a 30m resolution. To test for differences in animal occupancy and detection across conservancies and between conservancies and the Mara Triangle protected area, we created two covariates indexing this variation in land management, one treating each unit as a separate factor, and another grouping community conservancies as one type of land management separate from the Mara Triangle protected area.

Occupancy Model Selection and Inference

We used a multi-stage model selection approach to identify ecologically relevant candidate models because testing all possible combinations of environmental and interspecific interaction covariates on detection and occupancy parameters would have resulted in an unreasonably large number of possible model combinations (Doherty *et al.* 2012; Bromaghin *et al.* 2013). First, we tested each covariate in univariate models for true detection probability (p_{11}) with a plausible model for (ψ) and ranked competing models against the constant (null) model using Akaike's information criterion (AIC) (Anderson & Burnham 2002). At this stage, we eliminated uninformative covariates resulting in models with essentially the same log-likelihood value and equal or lesser Akaike weight than that of the constant model for each parameter (Arnold 2010; Wisdom *et al.* 2020). If any two remaining covariates with some support were colinear, we proceeded with the variable that was more supported based on AIC for inclusion in the global model. We repeated this process for the occupancy (ψ) parameter to eliminate uninformative variables, and then fit a global model with the narrowed set of informative covariates for detection and occupancy. We then used best-subsets selection on the global model to identify the most parsimonious combination of covariates for both parameters based on AIC (Arnold 2010). We used the R package '*AICmodavg'* for model checking and model selection (Mazerolle & Mazerolle 2017). We present results for the best-supported models based on AIC in the Results section and include full model selection results in Appendix I.

2.3 RESULTS

Survey effort

In 2018, cameras captured 284,667 unique images over 5,309 camera trap days (24 hr. periods when cameras were active) labeled by the machine learning model with .90 or greater confidence that the image contained elephants, cattle, shoats, or wildebeest. In 2019, there were 1,019,767 unique images remaining at the .90 threshold for the target species captured over 15,808 camera trap days. Overall, wildebeest were the most frequently detected species, followed by cattle, shoats, and then elephants.

Validation Tests of Machine Learning Species Labels

Validation tests showed that the optimal threshold to minimize data loss and ensure accuracy of ML labels varied by species group and by the ecological parameter of interest (Table 2.3). For African elephants, differences in estimates of elephant activity and occupancy probabilities between human generated labels and ML generated labels at a threshold of .90 were not statistically significant (Table 2.3). We found that a threshold of .90 was sufficiently accurate for activity pattern estimates for wildebeest, cattle, and shoats, but that a threshold of 0.97 was required to achieve reasonable accuracy for occupancy estimates based on Wald tests (Table 2.3). Thus, we report validation results for livestock at a threshold of 0.97, and for brevity, validation results for occupancy estimates from only null (constant) models in (Table 2.3). However, we note that analysis of occupancy models with variation in detection and ψ also resulted in sufficiently accurate estimates at a threshold of 0.90 for elephants and 0.97 for livestock based on Wald tests (Appendix I). Our finding that livestock occupancy models required a higher ML confidence threshold to avoid significant bias in occupancy estimates likely reflects the higher false positive error rate for both cattle and shoats compared to elephants in the ML labeled data (Appendix I). Based on the results of validation tests, we proceeded with activity and occupancy analysis of ML labeled data at a confidence threshold of .90 for African elephant labels and a threshold of 0.97 for livestock (cattle and shoats) labels and wildebeest labels.

Table 2.3. Summary of selected results from validation tests for ecological parameters estimated using machine learning (ML) species labels from the 2018 test dataset. Wald test statistics are based on the Chi-square distribution ($\alpha = 0.05$) for activity estimates and on the normal distribution for occupancy estimates ($\alpha = 0.05$). CI = confidence interval.

Species	Daily activity (95 % CI)	Daily occupancy (ψ) (95% CI)	optimal ML label confidence threshold	% data from the full ML dataset omitted
Elephants			0.90	30%
Human	0.56 (0.44 – 0.64)	ψ_{h} = 0.52 (0.39 – 0.65)		
ML	0.53 (0.38 – 0.59)	ψ_{ML} = 0.42 (0.30 – 0.55)		
Wald statistic	p = 0.724, n.s.	p= 0.141 n.s.		
Wildebeest			0.97	19%
Human	0.59 (0.47 – 0.68)	ψ_{h} = 0.62 (0.53 – 0.70)		
ML	0.52 (0.42 – 0.59)	ψ_{ML}=0.50 (0.41 – 0.58)		
Wald statistic	p = 0.31, n.s.	p= 0.177, n.s.		
Cattle			0.97	26 %
Human	0.35 (0.28 – 0.40)	ψ_{h} = 0.42 (0.33 – 0.52)		
ML	0.39 (0.29 – 0.41)	ψ_{ML} = 0.53 (0.43 – 0.63)		
Wald statistic	p = 0.472, n.s.	p = 0.063, n.s.		
Shoats			0.97	19%
Human	0.29 (0.25 – 0.33)	ψ_{h} =0.30 (0.23 – 0.39)		
ML	0.28 (0.25 – 0.32)	ψ_{ML} = 0.39 (0.30 – 0.49)		
Wald statistic	p = 0.84, n.s.	p =.087, n.s.		

Daily Activity Patterns

During both dry seasons of 2018 and 2019, we found high temporal overlap in cattle and shoat activity in community conservancies within each 24-hour period (Table 2.4). Temporal activity overlap between elephants and cattle and wildebeest and cattle in community conservancies was moderate and considerably lower, ranging from 0.59 to 0.62 (Table 2.3).

Table 2.4 Estimated daily temporal overlap in species activity in community conservancies estimated from independent detections (> 30 minutes apart) of each species at across camera traps in the Greater Mara Ecosystem in 2018 and 2019.

	Coefficient of overlap (Δ) with **cattle** and 95% CI)		Coefficient of overlap (Δ) with **shoats** and (95% CI)	
	Dry season 2018 n = 896 (cattle)	Dry season 2019 n= 2,208 (cattle)	Dry season 2018 n = 1,073 (shoats)	Dry season 2019 n= 3,510 (shoats)
shoats	0.84 (0.79 – 0.87) n= 1,073	0.89 (0.87 – 0.92) n= 3,510		
elephants	.60 (0.54 – 0.66) n= 205	0.59 (0.55 – 0.63) n= 616	0.59 (0.52 – 0.64)	0.55 (0.51 – 0.59)
wildebeest	0.62 (0.59 – 0.64) n= 2,592	0.62 (0.60 – 0.64) n= 12,442	0.57 (0.55-0.59)	0.55 (0.54 – 0.57)

Cattle and shoat activity was concentrated during daylight hours in community conservancies, whereas elephant activity in community conservancies was more evenly distributed across day and night hours, and wildebeest activity was greatest near dawn and dusk (Figure 2.3). However, in the Mara Triangle protected area, elephant and wildebeest activity was highest during midday (Figure 2.3). We found strong evidence that elephant activity level and the temporal distribution of elephant activity were significantly different between the Mara Triangle protected area and community conservancies (Figure 2.3). Elephant activity was 19.5% lower ($p < 0.0001$, Figure 2.3) in community conservancies compared to the Mara Triangle, and the randomization test indicated a significant difference between the distribution of elephant activity in each zone (observed overlap of distributions =0.855, expected overlap = 0.956, $p < 0.001$, Figure 2.3). For wildebeest, we did not find evidence of a significant difference in activity level between land management zones (estimated difference = -0.035, $p = 0.7$) but the randomization test indicated that the temporal distribution of wildebeest activity in community conservancies was significantly different from the temporal distribution of activity in the Mara Triangle (observed overlap = 0.86, expected overlap =0.979, $p < 0.001$).

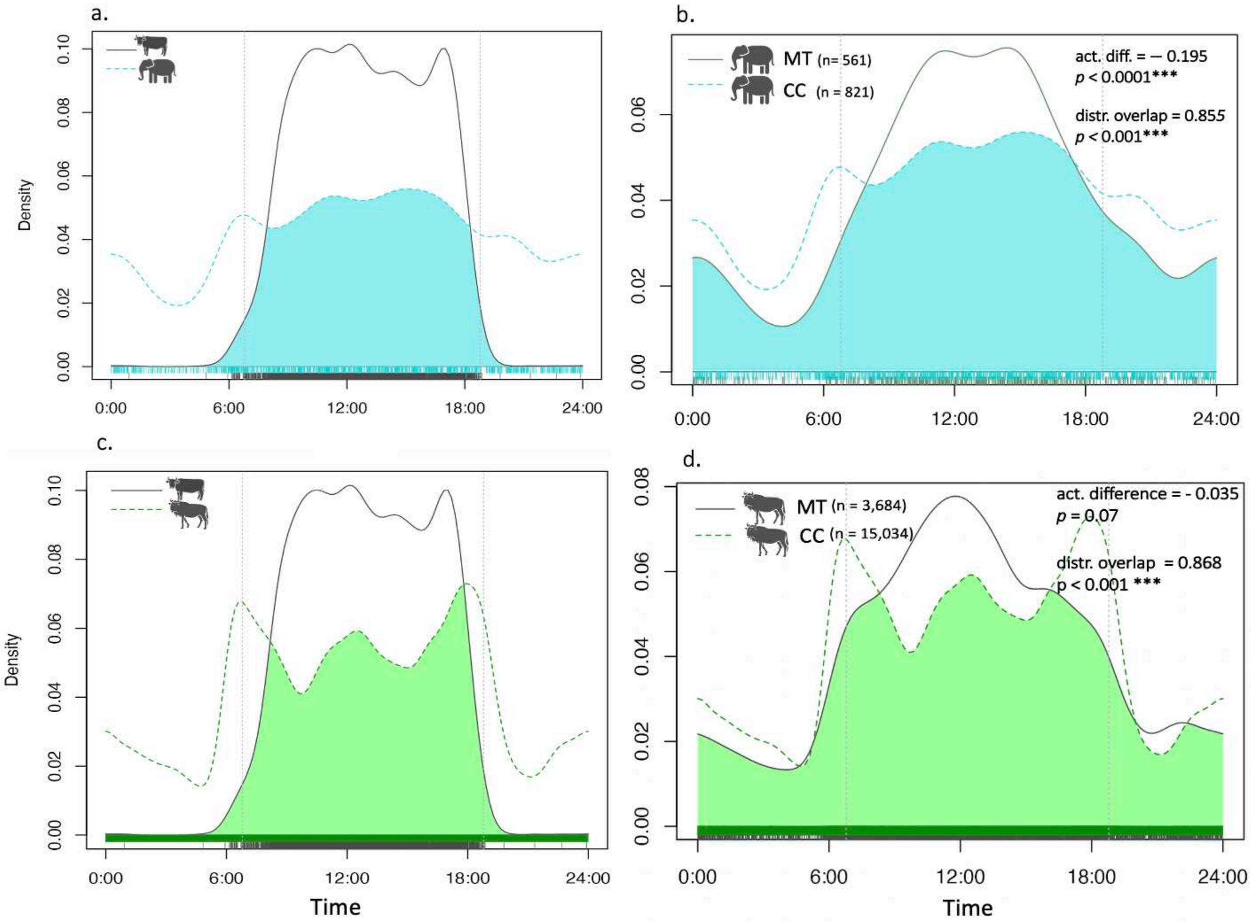

Figure. 2.3. Shaded regions show the estimated overlap in activity distributions over a 24-hour period for: **a)** daily activity and temporal overlap between elephants and cattle in community conservancies, **b)** daily activity of elephants in the Mara Triangle (MT) compared to community conservancies (CCs) with estimated difference in activity level and distribution, **c)** daily activity and temporal overlap between wildebeest and cattle in community conservancies, and **d)** daily activity of wildebeest in the Mara Triangle compared to community conservancies (CCs) with estimated difference in activity level and activity distributions.

Elephants at All Sites, Daily Occupancy

Across dry-seasons, model results indicated that elephant occupancy (i.e., probability of use; ψ) and true detection probability (i.e., intensity of use; p_{11}), varied with land management, vegetation productivity, and the occurrence of wildebeest and livestock (Table 2.5). For 2018, four models had substantial support (3 models with ΔAIC < 2 of the top model), but all three were more complex versions of the top model suggesting that additional covariates had relatively little information value (Grueber *et al.* 2011). For 2019, four additional models were within 2 ΔAIC of the top model, but all except one were more complex versions of the top model. Therefore, we report results only from the top model for each year. In both years, predicted daily elephant occupancy was higher in the Mara Triangle ($\psi_{2018} = 0.72$, 95% CI = [0.33-0.92], $\psi_{2019} = 0.54$, 95% CI = [0.22-0.83]) than in community conservancies ($\psi_{2018} = 0.40$, 95% CI = [0.23-0.59], $\psi_{2019} = 0.20$, 95% CI = [0.05-0.53]; Fig 2.4a) and was positively associated with higher average vegetation productivity at each camera site (Table 2.5, Figure 2.4b). In 2019, the best supported model included a positive effect of wildebeest occurrence on elephant occupancy (Figure 2.4c).

In both years, true detection probability was associated with higher NDVI values on the date of detection (Figure 2.4d) and the best models for both years also indicated variation in detection probability with land management (Table 2.5). In 2018, p_{11} was slightly higher in the Mara Triangle protected area and Naboisho conservancy than in Mara North and Olare-Motorogi conservancies. Additionally, the best model for 2019 indicated higher true detection probability (p_{11}) in the Mara Triangle compared to all conservancies, but not among Mara North, Olare-Motorogi, Naboisho and the Triangle as in 2018 (Table 2.5). In 2018, the best supported model also included a positive effect of wildebeest occurrence frequency on the intensity of elephant use (Table 2.5). Across both years, the probability of false-positive detection was less than 6% (2018 $p_{10} = 0.040$, 95% CI = [0.032 – 0.051]; 2019 $p_{10} = 0.050$ 95% CI = [0.041 – 0.063]).

Table 2.5. Best AIC-ranked false-positive occupancy models for elephants across all camera trap sites in the Mara Triangle (MT) and community conservancies (CC) in 2018 and 2019 with

untransformed (logit-scale) maximum likelihood estimates (MLE) and associated standard errors (SE).

Parameter and coefficient description		**MLE**	**SE**	**MLE**	**SE**
		2018		2019	
ψ (occupancy probability)	β mean NDVI (2000-2019)	1.3	0.47	0.78	0.50
	β mean wildebeest frequency	N/A		1.03	0.36
	β MT	0.92	.83	0.20	0.73
	β CC	-1.33	.97	-1.4	.81
p_{11} (true positive detection probability)	β current NDVI	.172	0.076	0.13	0.09
	β daily wildebeest frequency	.178	0.075	N/A	
	β MT	-1.68	0.12	-1.60	0.11
	β CC	N/A		-1.74	0.21
	β Mara North	-2.17	0.19	N/A	
	β Naboisho	-1.41	.20	N/A	
	β Olare-Motorogi	-1.96	0.23	N/A	
p_{10} (false positive detection probability)		-3.16	0.122	-2.92	0.14
b (probability certain detection)		-1.7	0.151	$b=0$	

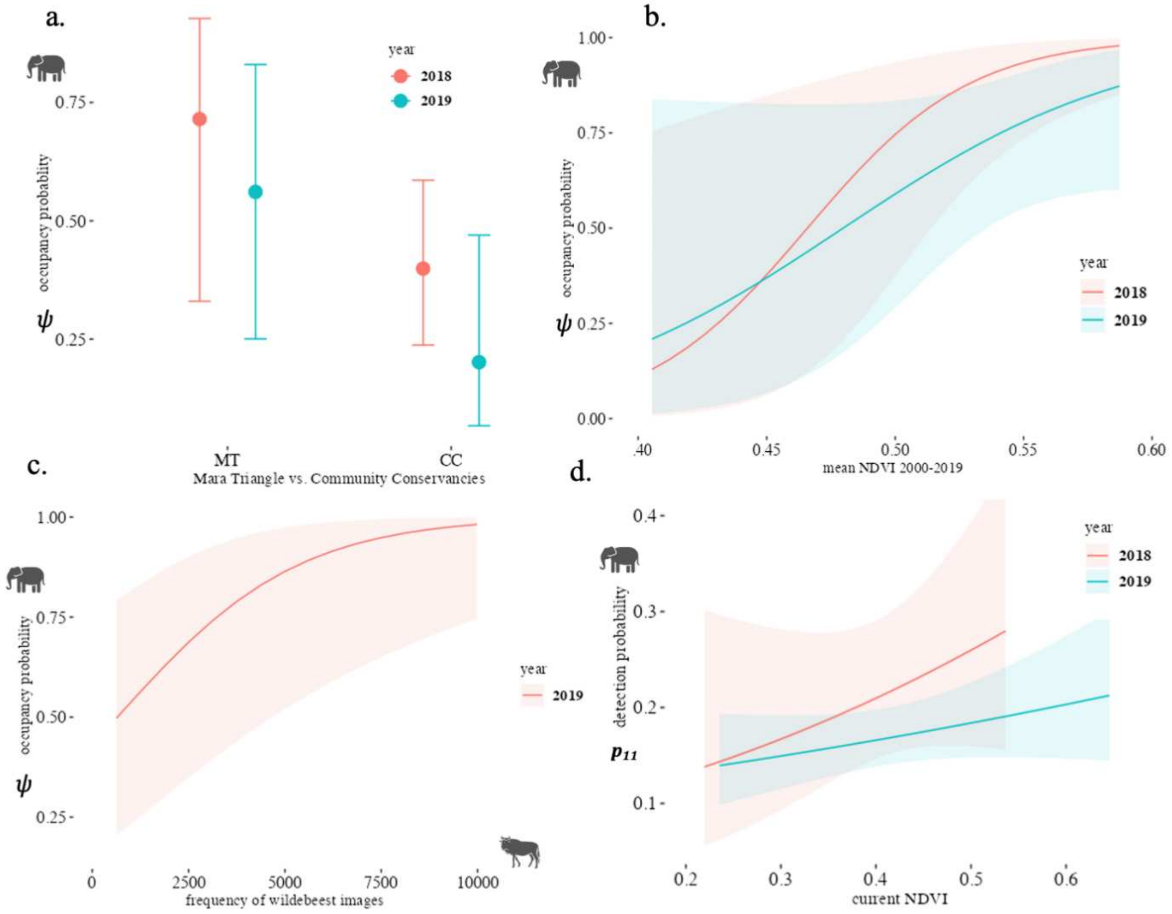

Figure. 2.4. Predicted probabilities of elephant occupancy and true detection probability for selected covariates from the most supported models of elephant occupancy across all sites in 2018 and 2019. These include: **a**) predicted effect of land management on elephant occupancy, **b**) predicted effect of vegetation productivity on elephant occupancy, **c**) predicted effect of frequency of wildebeest presence on elephant occupancy in 2019, and **d**) predicted effect of vegetation productivity on the day of detection at each site on true detection probability for elephants.

Elephant Daytime Occupancy in Community Conservancies

The best-supported model of daytime elephant occupancy in 2018 indicated that livestock presence influenced occupancy probability in addition to vegetation productivity and wildebeest presence (Table 2.6, Figure 2.5 a & b). The best supported model included a negative effect of both cattle and shoat use intensity on elephant occupancy and a positive effect of wildebeest use intensity and vegetation productivity on elephant occupancy (Table 2.6, Figure 2.5). In addition, the best supported models for both 2018 and 2019 included negative effect of distance from rivers and drainages on elephant occupancy indicating elephants were more likely to occupy sites near rivers and drainages (Figure 2.5c). The baseline (e.g., no effect of covariates) daytime occupancy probability for elephants in community conservancies was ψ = 0.42 in 2018 (95% CI = [0.23 – 0.64]) and ψ= 0.20 in 2019 (95% CI = [0.09 – 0.40]).

Table 2.6. Best AIC-ranked false-positive occupancy models for elephants during daylight hours in community conservancies in 2018 and 2019 with untransformed (logit-scale) maximum likelihood estimates (MLE) and associated standard errors (SE).

Parameter and coefficient description		**MLE** 2018	**SE** 2018	**MLE** 2019	**SE** 2019
ψ (occupancy probability)	Intercept	-0.30	0.45	-1.38	0.5
	β mean NDVI (2000-2019)	1.08	0.56		
	β distance to drainage	-0.145	0.37	-0.39	0.38
	β mean wildebeest frequency	0.36	0.29		
	β cattle frequency over survey period	-0.19	0.24		
	β shoat frequency over survey period	-0.92	0.59		
	β proportion open grassland			-0.27	0.353
p_{11} (true positive detection probability)	Intercept	-2.56	0.16	-1.95	0.185
	β current NDVI	0.327	0.12	0.54	0.165
	β wildebeest frequency at each camera + day	0.27	0.09	0.16	0.46
	β cattle frequency at each camera + day	0.142	0.193		

	β shoat frequency at each camera + day	-0.08	0.49		
	β proportion open grassland	-0.49	0.15		
$\boldsymbol{p_{10}}$ **(**false positive detection probability)		-3.45	0.15	-3.19	0.12
b (probability certain detection)		-2.6	0.38	***b**=0*	

Th best supported model for 2018 also indicated some influences of species interactions on true detection probability estimates (Table 2.6). Specifically, true detection probability was positively associated with daily wildebeest use intensity, and weakly positively associated with daily cattle use intensity (Table 2.6, Figure 2.5d). The best supported model also included a negative effect of shoat use intensity on p_{11}, but the coefficient estimate was small with very low precision and was thus unlikely to provide reliable inference. The true detection probability in 2018 also had a negative relationship with the proportion of open grassland within a 250m meter radius around the camera site (Table 2.6). For 2019, we were unable to fit more complex models and obtain reliable estimates for ψ and did not detect effects of livestock on elephant occupancy or true detection probability. However, the best supported model indicated a negative effect of open grassland on elephant occupancy in 2019 (Table 2.6). For 2018, there was low model uncertainty (only 2 models within 2 ΔAIC of the top model, and for 2019, there was slightly higher uncertainty (5 models within 2 ΔAIC), however, all were more complex than the top model and three contained unreliable (boundary) parameter estimates.

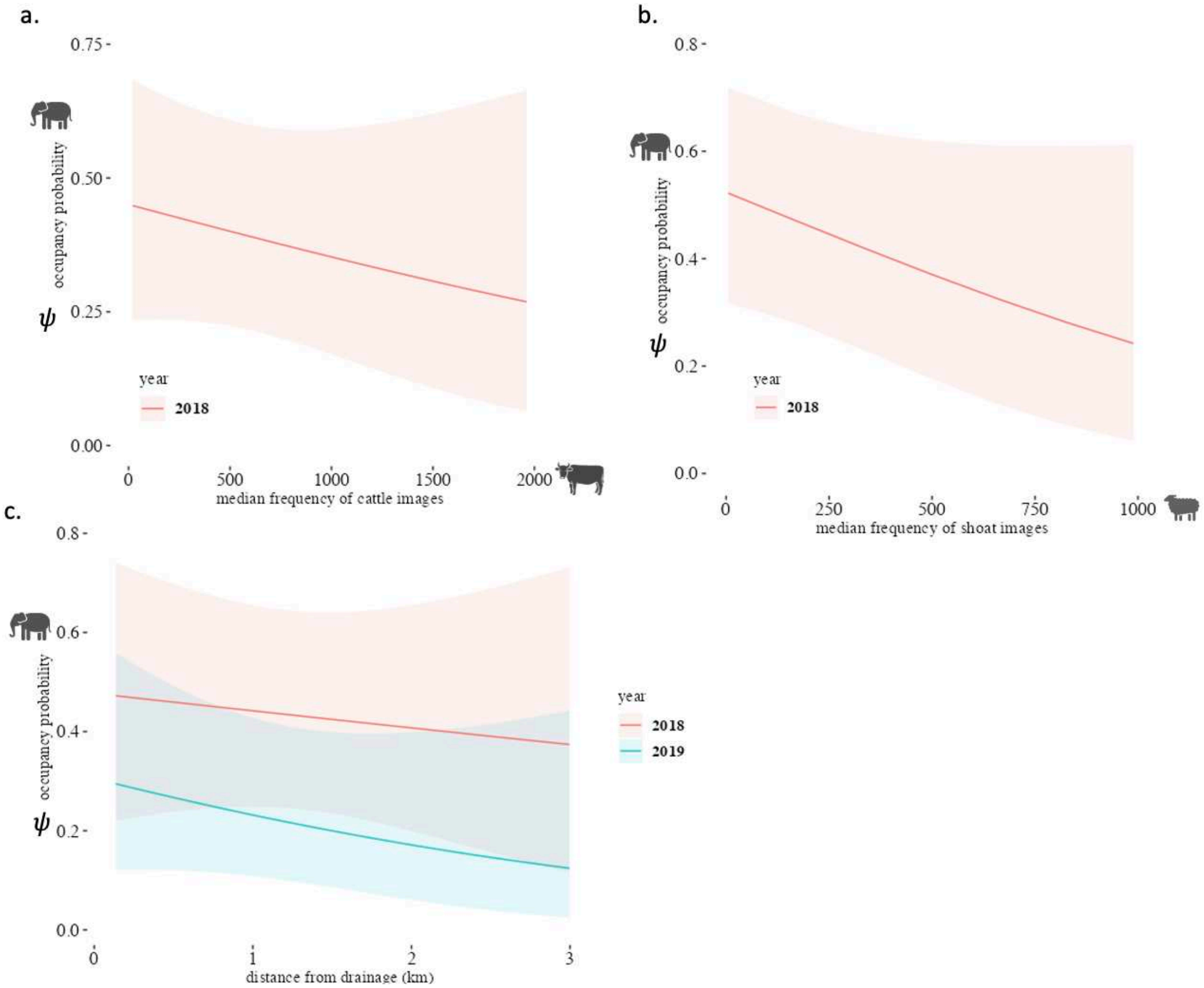

Figure 2.6. Predicted probabilities of elephant occupancy for selected covariates from the most supported models of daytime elephant occupancy in community conservancies in 2018 and 2019. These include **a**) predicted effect of median cattle use intensity at a site over the study period, **b**) predicted effect of median shoat use intensity at a site over the study period, and **c**) predicted effect of distance from drainage on elephant occupancy in 2018 and 2019.

2.4 DISCUSSION

In both dry seasons of 2018 and 2019, we found evidence that African elephants shifted the quantity and timing of their activity in community conservancies where livestock are present relative to the neighboring Mara Triangle protected area where livestock were absent. As expected, elephants were more likely to occur in the protected Mara Triangle than community conservancies even when controlling for habitat variation. In addition, we found evidence for a consistent, positive association between elephant occurrence and wildebeest occurrence across the Greater Mara Ecosystem. Finally, we found some evidence that daily variation in elephant space use in community conservancies was negatively related to spatial variation in the intensity of livestock use. Specifically, we found that areas in community conservancies used with higher intensity by shoats and cattle were less likely to be used by elephants during the daytime. However, this finding was not consistent across the two dry seasons considered and the estimated effects had low precision. This inconsistency and uncertainty may be related to real interannual variation in patterns of species cooccurrences, or, as we suspect is more likely, due to the failure of our analyses to detect meaningful spatiotemporal patterns in both years at the temporal resolution (13-hour day) of our models.

Overall, we found more evidence of spatial partitioning between elephants and livestock than temporal partitioning. Elephant activity was estimated to be 19% lower in community conservancies than in the Mara Triangle over both years. Similarly, occupancy analyses showed that on a daily basis elephants were likely to occur at 20 – 40% of camera sites in conservancies compared to 54 – 72 % of camera sites in the Mara Triangle. For the 2018 dry season, the most supported model of daily occupancy indicated that elephants were less likely to use sites in conservancies with higher median shoat and cattle use intensity; a finding that suggests clear spatial avoidance of high livestock use areas. Moreover, we did not find support for the combined total livestock covariate, which suggests that high shoat use areas and high cattle use areas may have limited spatial overlap in Mara North, Olare-Motorogi, and Naboisho. This is a plausible explanation because shoats are not officially included in conservancy grazing plans, and shoat grazing may happen more opportunistically near the conservancy borders and not in official cattle grazing blocks (MMWCA 2017; Løvschal *et al.* 2019). However, the estimated coefficients for these livestock effects had low precision, possibly due to the temporal resolution (13-hour day) of our models. Occupancy analysis also indicated that elephants were less likely to use open grassland sites in conservancies during the day where cattle are typically grazed and were more likely to use sites near rivers and drainages in both years. In the Mara, drainages are riverine, riparian habitats that are relatively rare on the landscape and tend to have higher canopy cover and elephants may use these areas more to avoid livestock (and their herders). Overall, livestock effects were less influential than vegetation productivity.

Our finding that both elephants and wildebeest showed evidence of temporal shifts in activity related to land management aligns with other studies and meta-analyses that have identified increases in crepuscular (dawn/dusk) and nocturnal activity among wild mammals where there is more human disturbance (Gaynor *et al.* 2018; Cox *et al.* 2022; Gallo *et al.* 2022). For example, increased nocturnal movement activity in female elephants in the Samburu-Laikipia ecosystem outside of protected areas was related to poaching risk (Ihwagi *et al.* 2015). Elephants, particularly non-breeding adults, are free from predation concerns and are known to regularly forage at night as well as during the day (Owen-Smith 1988). Thus, the potential fitness costs of increasing night activity are unclear. However, for breeding females with calves, increased nighttime activity could require increased vigilance because predator species have also been found to avoid diel human activity and young elephants are more vulnerable to predation (Wang *et al.* 2015; Gaynor *et al.* 2018; Cox *et al.* 2022). Wildebeest may be more vulnerable to increased nighttime predation pressure than elephants (Hopcraft *et al.* 2005). Alternatively, wildebeest may be more active at dawn and dusk in conservancies relative to the reserve as a predation avoidance strategy because grass height in the community conservancies is typically short because of livestock grazing, and thus predator visibility can be better than in the national reserve (Ogutu *et al.* 2005; Bhola *et al.* 2012; Reid 2012).

We found a surprisingly strong and consistent positive association between elephant space use and wildebeest occurrence even after accounting for vegetation productivity. In a similar study of multispecies associations in the Serengeti, Anderson et al. (2016) also reported a positive association between elephant and wildebeest occurrence though the estimated effect size was small (Anderson *et al.* 2016). It is unclear if this association is primarily driven by both elephants and wildebeest tracking vegetation productivity and thus favoring higher biomass areas (Fryxell *et al.* 2004; Holdo *et al.* 2011; Bohrer *et al.* 2014). Previous research found that wildebeest in the Serengeti typically favor multispecies foraging groups though not necessarily with elephants (Kiffner *et al.* 2014). It is also possible that this association is partially the result of very high wildebeest detections across the study period and thus it was unlikely that we would detect an elephant on a given day but not several wildebeest.

A secondary objective of our study was to assess whether camera trap data labeled with a machine learning model could be used to characterize the spatiotemporal occurrence patterns of African elephants and other wild and domestic herbivores. Overall, we found that images collected from remote camera traps labeled with a machine learning model could be effectively used for ecological inference about African elephant occurrence patterns, with some limitations. We found that temporal activity analyses were particularly amenable to machine learning labeled data, whereas occupancy modeling proved more challenging. We used false positive occupancy models to account for the known presence of species misidentifications in the dataset, however, model estimated false positive rates were very low for elephants (less than 6%), and the additional parameters required for these models may have limited our ability to fit more complex models of the study system, particularly in 2019. We had reasonable success building complex models for the 2018 season for which we had verified detections to reduce uncertainty in our parameter estimates, but the 2019 data had no verified detections and thus required that we fit the finite-mixture model, which was more challenging to fit to daily occurrence data (Kéry & Royle 2020).

In the future, additional verifications of some machine learning species labels from the 2019 may improve models or alternatively, future work could instead fit these data with a full, dynamic false-positive occupancy model in which year to year differences are accounted for in the same model (Kéry & Royle 2020). A dynamic model may also be more useful for detecting species interactions, but because additional parameters are included, this approach requires a large dataset. It is also possible that elephant temporal avoidance of livestock in conservancies occurs at the scale of minutes or hours, and thus were not possible to model adequately using survey occasions of 13 hours in length. However, reducing the survey length to a shorter period (e.g., 3-4 hours) may also result in data that are difficult to fit, because reducing the survey length in occupancy analysis typically results in sparser encounter histories. Analysis focused on the temporal spacing of elephant and livestock detections may help to evaluate if elephants and livestock exhibit spatiotemporal avoidance or attraction at fine temporal scales at camera sites where they co-occurred (Cusack *et al.* 2017).

Despite these limitations, our study provides some of the first direct evidence that livestock presence may influence elephant space use in the community conservancies neighboring the GME. However, the relative importance of livestock compared to other variables remains unclear given the uncertainty in our estimates and our inability to detect any effects of livestock on elephant space use for the 2019 season. It is possible that annual variations in resource availability or other fluxes in the ecosystem such as those associated with the wildebeest migration may have also contributed to this result (Holdo *et al.* 2007; McNaughton 2016). Overall, our results suggest that elephant-livestock coexistence in the Greater Mara Ecosystem is largely facilitated by spatial partitioning and to a lesser degree, temporal partitioning. African savanna elephants are intelligent and cognitively complex (Bates 2020). For example, they have demonstrated advanced spatial memory (Polansky *et al.* 2015) and complex communication and social interactions including recognizing relatives and the location of these relatives through olfactory cues in urine (Bates *et al.* 2007b) as well as recognizing contact calls of dozens of other elephants that they are familiar with (McComb *et al.* 2000). Bates et al (2007) found that African savanna elephants classified different human ethnic groups in the Amboseli ecosystem of southwest Kenya by odor and garment color, and elephants showed a higher fear response when they detected the scent of garments previously worn by Maasai men, who have a tradition of spearing elephants, than Kamba men who are traditionally agriculturalists and typically pose little threat to elephants (Bates *et al.* 2007a). Thus, it is possible that elephants in the GME have assessed that in the context of community conservancies adjacent to the National Reserve, livestock with Maasai herders are not a threat (Bates *et al.* 2007a; van de Water *et al.* 2022). However, further research is needed to elucidate the potential impacts of livestock on elephant space use, particularly if livestock and specifically shoat numbers continue to increase dramatically in the Mara (Løvschal *et al.* 2019).

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CHAPTER 3

VARIATION IN AFRICAN ELEPHANT MOVESCAPES ACROSS ECOSYSTEMS: THE ROLE OF PEOPLE AND PRODUCTIVITY IN SHAPING ELEPHANT MOEMVENT IN EAST AFRICAN SAVANNAS

3.1. INTRODUCTION

Animal movement is a fundamental driver of individual fitness and profoundly effects ecological processes across scales from survival and gene flow to the distribution and abundance of populations (Fahrig 2003; Ovaskainen & Hanski 2004). Because movement behavior mediates interactions between individuals and their environment across space, movement provides a framework to evaluate how environmental variation including the impacts of global change influences these interactions by elucidating the factors that drive space use and ultimately shape population distributions (Nathan *et al.* 2008; Morales *et al.* 2010; Sih *et al.* 2011; Tucker *et al.* 2018). For example, animal movements are influenced by trade-offs between resource access and perceived mortality risk because both increase with activity such as foraging (Schoener 1971; Werner & Anholttt 1993; Morris 2003; Hebblewhite & Merrill 2009). For species that are sensitive to human disturbance or are directly persecuted by humans, perceived mortality risk (e.g., 'the landscape of fear'; Brown *et al.* 1999) and subsequently movement behavior can be strongly structured by human presence and infrastructure (Clinchy *et al.* 2016; Christie *et al.* 2017; Moleón & Sánchez-Zapata 2022), noise (Suraci *et al.* 2019), and activities such as agriculture and hunting (Cleveland *et al.* 2012; Branco *et al.* 2019).

Concurrent advances in tracking technology and analytical methods have led to new understanding of where and when animals move (Kays *et al.* 2015). For example, high resolution tracking has facilitated the identification of movement strategies across taxa on a spectrum from residency (e.g., high site fidelity) to nomadism (low site fidelity and high inter-patch movement rates), and migration where persistent movement to predictable locations occurs with predictable timing (Douglas-Hamilton *et al.* 2005; Bunnefeld *et al.* 2011; Holdo *et al.* 2011; Bastille-Rousseau *et al.* 2016; Abrahms *et al.* 2017b). Many studies have applied resource selection models to examine movement-habitat relationships by comparing habitats where movement was observed to locations where movement was not observed (Boyce & McDonald 1999; Manly *et al.* 2002). Selection models have advanced understanding of variation in animal space use across seasons (Zeller *et al.* 2019) and environmental gradients (Roever *et al.* 2012; Stabach *et al.* 2016), but most do not differentiate among movement behaviors (e.g., resource use vs. resting vs. transiting) when evaluating selection (Abrahms *et al.* 2017a; Wittemyer *et al.* 2019).

When the behavioral context of movement is ignored, the selection framework assumes that used habitat is representative of the habitat used for all movement behaviors (e.g., assumes that the same habitat type is used for resource use, resting, and transiting). When this assumption is false as is often the case, it can influence the accuracy of inference about movement such as the identification of movement corridors (Wilson *et al.* 2012; Zeller *et al.* 2014; Gastón *et al.* 2016). For example, animals may move through corridors without stopping to rest or forage or may use different habitats for hunting than for dispersal (Abrahms *et al.* 2017a). Recent studies have used machine learning to characterize variation in behavioral tactics among individuals (Bastille-Rousseau & Wittemyer 2019), or hidden Markov or state-space models to identify discrete behavioral states in populations (e.g., ‘encamped’ vs. ‘exploratory’ (Morales *et al.* 2004; McClintock *et al.* 2020) to better quantify the behavioral ecology of movement. Yet, most approaches utilize only one or two components of movement data such as temporal segmentation or speed to delineate behaviors, and while informative, these approaches can be sensitive to sampling frequency and other concerns like missing data.

Network analysis has recently emerged as an alternative approach to analysis of animal movement data (Jacoby & Freeman 2016). In mathematical graph theory, a graph or network is a collection of elements (nodes) connected or related by edges for which various metrics can be calculated to describe the structure and function of the network such as network connectivity (Minor & Urban 2007, 2008; Rayfield *et al.* 2011). Spatially explicit networks provide an intuitive approach to delineate animal movement behaviors in complex datasets and to quantify variation in animal movement across space. For example, Bastille-Rousseau et al. used simulations and movement data to identify network metrics that capture movement strategies (e.g., nomadism) and local properties of space use such as core areas and movement corridors across taxa (Bastille-Rousseau *et al.* 2018). Others have applied network analysis to identify locations important for specific behaviors like resting (Wittemyer *et al.* 2017) or to identify movement corridors and critical habitat to guide conservation (Bastille-Rousseau & Wittemyer 2021; Kot *et al.* 2022).

However, few studies have assessed intraspecific variation in specific movement behaviors across environmental and ecological contexts at the scale of large landscapes (Lubitz *et al.* 2022). Context dependent movement behavior in animals is generally more complex and adaptive and can directly impact individual fitness (Eggeman *et al.* 2016; Byrne *et al.* 2019). For example, elk (*Cervus elaphus*) movement behavior varies from residency to migratory depending on local elk density and abundance, local predator abundance, and winter severity (Eggeman *et al.* 2016). Thus, when animals move to meet life history requirements, movement patterns are determined by behavioral traits and the environmental, ecological, and individual context (Shaw 2020; Lubitz *et al.* 2022). Comparing movement patterns and the drivers of movement across study systems (e.g., ecosystem or sex) provides a framework to improve understanding of context-dependent movement behavior and to identify factors that shape intraspecific variation in movement. Developing this knowledge is particularly crucial to inform conservation of generalist species inhabiting different ecoregions such as African savanna elephants (*Loxodonta Africana*), because different populations may respond differently to anthropogenic change across their geographic range and may thus require context-specific conservation measures that account for variability (Brennan *et al.* 2022; Lubitz *et al.* 2022).

Previous research has identified vegetation productivity and structure, water availability, and social hierarchy dynamics as ecological and behavioral factors that strongly influence elephant movement patterns (Wittemyer *et al.* 2007; Young *et al.* 2009; Knegt *et al.* 2011; Roever *et al.* 2012; Bastille-Rousseau *et al.* 2020). For example, in southern Africa, Young et al. found that within protected areas, female elephants inhabiting wet savannas had smaller home ranges and showed higher site fidelity across seasons and years than those inhabiting dry savannas (Young *et al.* 2009). Increasingly, elephant space use is also strongly shaped by human presence and activities (Wall *et al.* 2021). Multiple studies across Africa have reported that elephants avoid areas with higher human population density and human infrastructure (Douglas-Hamilton *et al.* 2005; Graham *et al.* 2009; Gara *et al.* 2017; Wittemyer *et al.* 2017). Other studies have found increasing elephant activity during nighttime and crepuscular periods compared to daytime in areas with more human activity, potentially as a response to lower the risk of encountering people (Jachowski *et al.* 2013; Ihwagi *et al.* 2015, 2018; Gaynor *et al.* 2018; Hahn *et al.* 2021).

Yet, it remains unclear how elephants may adjust their movement behaviors in response to environmental variation in different ecological contexts, particularly in mixed-use landscapes where people and elephants overlap. For example, if resources are limited, elephants may be more likely to incur the risks posed by people to access key resources (Bastille-Rousseau *et al.* 2020), whereas in regions with higher habitat quality (e.g., water and forage availability), elephants may be able to exploit key resources while avoiding people. Though research has identified vegetation productivity, water availability, and human presence as having strong influences on elephant movement behavior, it is unclear how the relative importance of these factors in shaping movement may change and what variation in movement behaviors may emerge depending on the context.

In this study, we build on recent applications of network analysis to animal movement data (Bastille-Rousseau *et al.* 2018; Bastille-Rousseau & Wittemyer 2021) to investigate intraspecific variation in movement behavior of African savanna elephants across two savanna ecosystems dominated by mixed-use (human and wildlife) land uses. Specifically, we analyze combined information on movement path properties, use intensity, and structural properties of movement networks derived from long-term GPS tracking data collected in the mesic Mara-Serengeti and the xeric Samburu-Laikipia ecosystems of Kenya to contrast the landscape structure of elephant movement behaviors (e.g., movescapes; Bastille-Rousseau & Wittemyer 2021). In both ecosystems, wildlife conservation and pastoralism are the dominant land uses and elephants are persecuted by people due to human-elephant conflict (HEC) (Hahn *et al.* 2021) and some illegal ivory hunting (Wittemyer *et al.* 2014).

We first delineate the functional landscape of movement for elephants in the Mara-Serengeti ecosystem (similar to the ways this was delineated previously in Samburu-Laikipia in Bastille-Rousseau & Wittemyer 2021) and then identify the environmental variables (i.e., human presence, vegetation productivity, water) associated with different movement behaviors with a focus on delineating the habitats that support high elephant use and elephant movement corridors (Bastille-Rousseau & Wittemyer 2021). We then investigate how movement behaviors and the environmental variables driving movement vary between elephants inhabiting the mesic, wet savannas of the Mara-Serengeti with those observed in elephants inhabiting the xeric savannas in Samburu (as previously published). Because the mesic savanna has more high quality habitat than then xeric savanna, we expected that: (1) elephant movement in the mesic savanna would reflect shorter distance, more frequent movement (akin to central place foraging) compared to the xeric savanna, (2) that elephants in the mesic savanna would use more of the landscape with high-use intensity, and that (3) that human presence would more strongly influence elephant movements in the mesic savanna relative to water availability and productivity because in high quality habitat we expected the risks of encountering people may be more limiting than resource availability.

3.2 METHODS

Study areas and African elephant GPS tracking data

Mara-Serengeti

The transboundary Mara-Serengeti ecosystem extends from northern Tanzania into southwest Kenya from approximately 3.2°S to 1°S, 34.6°E to 35.6°E. Currently, the Mara-Serengeti ecosystem supports an elephant population of 7,535 individuals with about 2,595 on the Kenya side of the border (Waweru *et al.* 2021).We focused our analysis on 9,167 km^2 in the north-central portion of the ecosystem covering northern Serengeti National Park, the Maasai Mara National Reserve (MMNR) and surrounding landscape in Narok county. Vegetation is comprised of open grassland interspersed with lone *Balanites aegyptiaca* trees and patchy acacia woodlands (*Vachellia drepanolobium*) as well as riverine woodland dominated by *Diospyros abyssinica* and *Vachellia kirkii*, and *Euclea divinorum*, and *Croton dichogamus* bush thickets which dominate hilltops. Annual rainfall follows a gradient averaging 650mm in the southeast up to 1450mm in the northwest and is typically bimodal with rains occurring from November–December (short) and January–June (long) (Ogutu *et al.* 2008b). However, the frequency of severe droughts and severe floods may be increasing with changing rainfall patterns (Bartzke *et al.* 2018). The western border of the contiguous Serengeti-MMNR protected area is a 'hard edge' that transitions rapidly from savanna and forest to a landscape dominated by agriculture. To the north and east, the MMNR is buffered by community conservancies (CC) covering about 1,394 km^2. Most CCs in Narok are comprised of individual land holdings leased in aggregate by local landowners for wildlife conservation where livestock grazing, and tourism operations are permitted. Unprotected areas in the landscape are dominated by agropastoral land-use (livestock grazing and small-holder agriculture).

We analyzed GPS tracking data collected from 37 individual elephants (19 females and 18 males) from June 2012 - April 30, 2022, in the central Mara-Serengeti ecosystem. Deployment of GPS collars targeted individuals across the ecosystem to cover the overall distribution of elephants as well as individuals with a high risk of human-elephant conflict and higher poaching risk (large tusked). The sex of each elephant was recorded during collaring and females represent the movements of a distinct family group whereas all males were dispersed from natal groups when collared and so were typically solitary. Some individuals were recollared and so tracking duration ranged from 1 to 9 years across individuals. All immobilization and collaring operations were carried out by Kenya Wildlife Service established procedures approved by Colorado State University's IACUC under protocol no. 1458 (19-9431A). Collars were programmed to collect GPS locations every hour. Raw relocation data were filtered using a maximum speed of 9 km/hr. between consecutive relocations to remove erroneous fixes. In addition, individuals tracked for fewer than six months and those with home ranges that did not sufficiently coincide with available covariate data were omitted resulting in a total of 967, 889 GPS relocations from 37 individual elephants averaging 26,159 (range 5,591- 67,994) locations per elephant used in analyses.

Samburu-Laikipia

The Samburu-Laikipia ecosystem is located from approximately 0.4°S to 2°N, 36.2°E to 38.3°E in north-central Kenya. The study area of 33,817 km^2 centered on the Samburu and Buffalo Springs National Reserves and surrounding landscapes in Samburu, Laikipia, and Isiolo counties. The region ranges from arid to semi-arid remaining hot and dry for most of the year; average annual rainfall is about 360mm (SD = 170mm), and rain is bimodal with rain typically falling from March to May (long rains) and slightly less rain from October to December (Table 1). The Ewaso Ngiro river is the only permanent natural water source and forms the border between the national reserves and vegetation is strongly shaped by water availability. Lowlands include arid savanna and bushland dominated by salt bush, and riparian woodland along the river dominated by *Vachellia elatior*, *Vachellia tortili,* and duom palm (Wittemyer 2001; Kimiti *et al.* 2017). Other dominant communities are *Vachellia-Commiphora* spp. scrub and woodland, and bushland and forest at high elevations (Kimiti *et al.* 2017). Outside formally protected areas, land use is dominated by livestock grazing and includes a large area of community conservancies as well as communal grazing land, private land holdings, and government managed forest reserves (Ihwagi *et al.* 2015).

GPS tracking data were collected from 138 elephants (69 females and 69 males) from 2001 to 2019 as part of a long-term monitoring study (Wittemyer *et al.* 2007). All collaring and animal handling procedures were approved by Colorado State University's IACUC under protocol 18-7741A. Raw relocation data were filtered using a maximum speed of 9 km/hr. to remove erroneous locations and all individual trajectories were resampled to a 2-hour fix rate to accommodate different fix schedules among collars. After resampling, the total sample was 1,627,598 locations from 138 elephants averaging 11,794 (range 53-58,031) locations per elephant (Bastille-Rousseau & Wittemyer 2021).

Table 3.1. Comparison of biophysical and land-use characteristics of the Mara-Serengeti and Samburu-Laikipia ecosystems in Kenya where African elephants were tracked.

	Mara-Serengeti	**Samburu - Laikipia**	References
Area analyzed	9,267 km^2	33,817 km^2	
Formally protected (%)	42.9 %	5.36 %	
Community conservation (%)	15.2 %	59.2 %	
Annual rainfall	mean = 985 mm SD = 165 mm	mean= 360 mm SD= 170 mm	Bartzke *et al.* 2018; Pas 2018
Mean Gross Primary Production (GPP) (2001 -2021)	.019 (low) –.077 (high) kg C/ m^2	.0038 (low) – .071 (high) kg C/ m^2	Didan 2015
Mean annual daytime temperature (°C)	25 °C	32 °C	
Dominant vegetation communities	*Themeda triandra* and *Pennisetum* spp. grassland, Acacia woodland, riparian woodlands, bush thickets	grassland, bushland, Acacia-Commiphora scrubland and woodland, Acacia woodland, riverine woodland	Dublin *et al.* 1990; Ogutu *et al.* 2008a; Kimiti *et al.* 2017

Calculating Individual Network and Movement Metrics

We applied network theory to analyze individual elephant movement trajectories following the approach of Bastille-Rousseau et al. (2018) to capture structural aspects of elephant movements. To analyze animal tracking data with a network approach, relocations were rasterized by overlaying relocations with a grid. Each pixel in the grid was treated as a separate node and movements between pixels as network edges, which are directional and weighted by the number of times movement between any two pixels occurred (Bastille-Rousseau *et al.* 2018). The sum of connections to and from each pixel is tallied in a weighted adjacency matrix which is used to calculate network metrics of interest (Minor & Urban 2008). We calculated graph-level network metrics that can be useful for identifying broad-scale movement patterns (migration, nomadism, central place foraging), and node-level metrics that are useful for describing properties of local space-use by animals and specifically useful for identifying core areas and areas important for connectivity between nodes (Rayfield *et al.* 2011; Bastille-Rousseau *et al.* 2018; Table 3.2).

For each individual elephant movement network, we calculated network density which is related to the efficiency and resilience of the network, and the global clustering coefficient which can indicate robustness of the network if pixels were randomly lost (Minor & Urban 2008). For example, if a new electric fence blocked movement in some pixels of a network that tended to be denser with higher clustering, the impacts to network function may be minimal because the newly blocked pixels would likely be well connected to other interconnected adjacent pixels (clusters). We also calculated network diameter as a measure of size or the total geographic distance covered by each elephant network, Table 3.2). For all nodes (pixels) within each individual's network, we calculated node weight (count of relocations in a given pixel) as a measure of use intensity, degree centrality (the number of unique connections (edges) to a pixel) as a measure of local connectivity, and betweenness centrality (count of shortest paths that cross a pixel relative to the total number of shortest paths) as measure of overall importance of that pixel for network connectivity (Rayfield *et al.* 2011; Bastille-Rousseau *et al.* 2018). We characterized movement paths by calculating two additional movement metrics: (1) the average speed of movement in each pixel and (2) the dot-product index of movement step turning-angles as an indicator of path directionality, where higher values indicate more parallel, unidirectional movement within a pixel (hereafter referred to as ‘directionality’ of movement; Wall *et al.* 2013; Bastille-Rousseau & Wittemyer 2021). We set the resolution of the grid at 200m based on the median step length (median distance between successive GPS fixes; 173m) following the guidance in Bastille-Rousseau et al. (2018). Network size ranged from 391–17,486 (mean=3,319.9, IQR=2,599) 200m^2 pixels across individuals. In Samburu, network and movement metrics were calculated with a 100m resolution grid based on the median step length of the sample. The average network size across all individuals in the Samburu-Laikipia study system was composed of 7,507 100m^2 pixels (range 40–25,293). We used the R packages *adehabitatLT* (Calenge 2006) and *MoveNT* (Bastille-Rousseau 2023) for this part of the analysis.

Table 3.2. Network metrics calculated from African elephant GPS tracking datasets used in Gaussian mixture models to identify different types of elephant movement behaviors.

Metric	Description and ecological inference	References
Network-level: summarized across all pixels for each network	*Broad-scale movement patterns*	
network density	ratio of observed movements between pixels to possible links; indication of efficiency and resilience of network	Csardi & Nepusz 2006; Rayfield *et al.* 2011; Bastille-Rousseau *et al.* 2018
global clustering coefficient	the average probability that adjacent pixels are connected by movement; tendency of distinct clusters of use to be present in the network; robustness	〃
network diameter	maximum length between pixels in the graph; measure of total distance (size) of network	〃
Node-level: summarized at each pixel within a network	*Local-scale movement patterns*	

weight	count of relocations in a pixel; intensity of use in each pixel	Csardi & Nepusz 2006; Bastille-Rousseau *et al.* 2018; Bastille-Rousseau & Wittemyer 2021
betweenness centrality	count of shortest paths that cross a pixel relative to the total number of shortest paths; importance of pixel for overall network connectivity	″
degree centrality	the number of unique movements to and from a pixel; local connectivity and clustering of use	″

Classifying Functional Movement Types with Gaussian Mixture Modeling

We used Gaussian mixture models to identify clusters of functional movement types in the Mara-Serengeti based on the values of the node-level network and movement metrics described above following the approach of Bastille-Rousseau et al. (2021). We first applied clustering to metrics for each individual separately, and then applied a second clustering to the mean (center) of each cluster identified at the individual level to estimate population-level functional movement types. All metrics were standardized prior to clustering. Clustering at the individual level ensures equal weighting among individual elephants in the subsequent population level clustering step. We used the Bayesian Information Criterion (BIC) to identify the optimal number of clusters and set the maximum number to 8 because we did not expect more than 8 functionally meaningful clusters of movement types (Bastille-Rousseau & Wittemyer 2021). Mixture models were applied using the packages *Mclust* (Scrucca *et al.* 2016) and *moveNT*. We then qualitatively classified functional movement types at the population level based on relative differences in the mean value of each metric in the population-level clusters. We extracted the functional movement type classification for each pixel in an individual's network as a raster and overlaid all rasters to map population-level use types across the study area. Thus, because multiple elephants used the same locations, any pixel can be associated with more than one functional movement type, for example, a pixel may be used as core area by one individual while being used as a fast-movement corridor by other individuals.

Modeling Functional Movement Type –Environment Relationships

We used mixed-effects logistic regression models to assess the influence of environmental and social variables on the probability of observing different functional movement types across the landscape. To ensure accuracy, we retained only pixels with > 95% certainty in the population cluster assignment for this analysis resulting in 75,024 observations of use at 58,140 unique 200m^2 pixels (Bastille-Rousseau & Wittemyer 2021). We created environmental variables indexing vegetation cover and vegetation productivity and predictability, topographic variation, water availability, and a set of variables indexing human presence and land-use expecting that each of these variables could influence elephant movement in different ways based on the literature (Wittemyer *et al.* 2007; Young *et al.* 2009; Roever *et al.* 2012; Bastille-Rousseau & Wittemyer 2021; Wall *et al.* 2021).

We mapped land cover with 10m resolution data derived from Sentinel-1 and Sentinel-2 multispectral satellite images collected from 2019-2021 to account for vegetation cover (Wall *et al*. in review). We used Google Earth Engine for image analysis and classification of images with a Random Forest model based on ground-truth land cover data collected in the field. Land cover classes included: (1) forest and thicket (> 70% canopy cover), (2) woodland and open bushland (20-70% cover), (3) open savanna and wooded savanna (< 20% cover), and (4) a class for bare ground, rock, and built-up cover. We used majority filter tools to reduce noise in the land cover classes and then used focal statistics to calculate the proportion of each cover type in a moving window based on our grid size of 200m^2. To characterize vegetation productivity, we composited Terra Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day v.006 normalized difference vegetation index (NDVI) images (Didian 2015)at a 250m resolution across the landscape and calculated the temporal mean and standard deviation in NDVI for each pixel across the study period and then calculated the coefficient of variation (CV) of NDVI as an index of productivity predictability from 2011-2022.

We mapped waterways for the study region from the global HydroSHEDS Free Flowing Rivers Network (Grill *et al.* 2019) and from ground-mapped and digitized waterways. We calculated the surface distance from permanent rivers (Mara and Talek rivers) and seasonally flowing waterways to all other cells in the landscape at a 30m resolution to index water availability. We composited sink-filled elevation data (30m) from NASA's Shuttle Radar Topography Mission Digital Elevation Model (DEM; (Farr *et al.* 2007) and we used focal statistics to calculate the mean elevation and slope for each pixel used by elephants. All analysis of satellite imagery was conducted on the Google Earth Engine Code Editor platform (Gorelick *et al.* 2017).

We characterized human presence using a combination of ground-mapped and digitized households and livestock corrals (known as bomas), village centers, and primary and secondary roads (Tyrrell *et al.* 2022). We calculated the surface distance from each pixel to primary and secondary roads and village centers at a 30m resolution and calculated the density of bomas across the landscape for each pixel used by elephants using focal statistics within a radius of 500m. We accounted for differences in elephant protection and human land-use intensity across the region with a land-management covariate separating national parks and reserves (protected areas i.e., PA), community conservancies (CC), and unprotected land (UP).

Elephants are a highly social species with complex, matriarchal fission-fusion societies within which there are dominance hierarchies among groups (Wittemyer *et al.* 2007; Archie *et al.* 2008). Previous research indicates that social structure can influence space use, for example, dominant groups may use preferred foraging habitats more than subordinate groups when resource availability is limited (Wittemyer *et al.* 2007). We accounted for social (conspecific) influences on the probability of observing functional movement types by extracting observed use by other elephants for each pixel in an individual's network. In the Samburu-Laikipia ecosystem among elephants with overlapping networks, high-use and corridor use by other elephants affected the probability of observing different functional movement types. To test if similar patterns applied in the Mara-Serengeti, we extracted high-use and corridor use by other individuals in the Mara dataset for each pixel used by more than one individual. We created sex-specific social covariates indicating whether the pixel was used only by other females, only other males, or was a high-use area or corridor used by other elephants of both sexes.

We ran separate logistic regression analyses for eight contrasts of movement types to test for differences in the environmental and social context between movement types (Table 3.3). We used a multi-stage model selection approach to identify the most supported model for each contrast because fitting all possible models would have resulted in an unfeasible number of candidate models. Thus, we first composed a global model of environmental variables and used best-subsets selection to identify the most parsimonious combination of variables based on BIC. We repeated this process to identify the most parsimonious combination of social variables, and we then compared the most supported environmental model and the most supported social model with a full model containing both sets of variables (environmental and social) and a null model (no effect of covariates) to identify the final models based on BIC (presented in Table 3.4 for movement types of interest; additional results in Appendix II). We fit separate models for males and females given they likely use space differently (Stokke & Du Toit 2002; Smit *et al.* 2007). Because different individuals may have used the same pixel in different ways, any pixel could appear multiple times in the same regression coded as either a zero or a one.

All models included a random intercept for each individual and a spatial autocovariate at the individual level to account for spatial autocorrelation calculated using a using a symmetrical neighborhood weighting scheme (Bardos *et al.* 2015). We inspected pairwise Spearman correlation coefficients among environmental variables and for any two variables with a correlation coefficient >|.55| we ran univariate models to identify the more supported covariate based on BIC and then included only the more supported variable in the global model. We tested final models for remaining multicollinearity using the variance inflation factor (VIF) and ensured all variables in final models had VIF factors < 3.0 (Bolker *et al.* 2009). Models were estimated using the Adaptive Gauss-Hermite Quadrature maximum likelihood approximation (Bolker *et al.* 2009) with the package *lme4* (Bates *et al.* 2014) and all continuous covariates were scaled prior to modeling. We evaluated model performance with the area under the curve (AUC) of the receiver operating characteristic. We first report results the results of all analyses for the Greater Mara Ecosystem and then report results of comparative analysis of our findings in the Greater Mara Ecosystem with the previously published results for elephants in the Samburu-Laikipia ecosystem.

Table 3.3. Contrasts used in mixed-effects logistic regression models to evaluate the effects of environmental variation and conspecific space use on the probability of observing functional movement types among African elephants in the Mara-Serengeti and Samburu-Laikipia ecosystems.

Regression	variables coded as 1	variables coded as 0	variables excluded	Results in
1	high-use	low and medium use	corridor	Table 3.4
2	corridor (fast)	high, medium, low-use	corridor (fast)	Table 3.4
3	corridor (directed)	high, medium, low-use	corridor (fast)	Table 3.4
6	corridor (fast)	corridor (directed)	high, medium, low-use	Appendix II
7	medium use	low-use	corridors, high-use	Appendix II
8	low-use (fast)	low-use (slow)	corridors, medium use	Appendix II

Comparative Analysis of the Two Ecosystems

To understand differences in movement behaviors of African elephants between the Mara-Serengeti and the Samburu-Laikipia ecosystems we compared our results in the Mara-Serengeti with the previously published results of co-authors in the Samburu-Laikipia ecosystem (Bastille-Rousseau & Wittemyer 2021). We thus compared: (1) graph-level and node-level network and movement metrics, (2) observed functional movement types based on clustering results, and (3) regression model results to identify environmental drivers of observed functional movement types across ecosystems. To test whether graph-level and node-level network metrics differed between ecosystems we normalized metrics to network size and then used non-parametric multivariate analysis of variance tests (MANOVA) implemented in R with the package *npmv* (Burchett *et al.* 2017). We conducted separate tests for graph-level and node-level metrics with the *F* statistic approximation and used a multiple testing procedure that controlled the overall type I error rate at α= 0.001 for all tests (Burchett *et al.* 2017).We report the global test statistic and the relative effects which describe the probability that a given metric will be greater in the Mara-Serengeti given the full range of values across both ecosystems, where relative effect values further from 0.5 (e.g., approaching 0 or 1) indicate a greater ability of a metric to distinguish elephant movement in one ecosystem from the other (Burchett *et al.* 2017). We tested if correlations in node-level metrics differed between study sites with a significance test for the difference between Spearman correlation coefficients with a Bonferroni correction based on a random sample of 1,000 nodes from each ecosystem implemented in R with the package *cocor* (Diedenhofen & Musch 2015).

We compared differences in observed functional movement types between the two ecosystems based on clustering results. For movement types observed in both ecosystems, we used Z-tests of equal proportions with a Bonferroni correction implemented in R to test whether the relative proportion of movement networks assigned to each use type differed between ecosystems. We compared model selection results and partial regression coefficients from the best-ranked logistic regression models (based on BIC) to identify the variables that were most predictive of core habitat use (high-use) and corridor use in each ecosystem based on the relative magnitude of the coefficients (and 95% confidence intervals) and report whether a variable had a positive or negative effect on the log-odds of observing high-use areas and corridors.

3.3 RESULTS

Individual and Population Clustering of Movement Properties in the Mara-Serengeti

At the population level, 8 clusters were identified related to 8 different observed functional movement types on the landscape in the Mara-Serengeti. Most individual elephants (86.4%) displayed 6 or 7 different movement types and no individual displayed all 8 population level movement types. All elephants were assigned to the high-use movement type (colloquially termed core areas), which was with associated with highly used and locally connected areas based on high node weight and degree values (Table 3.6). We observed two movement types characterized by medium-use intensity and locally connected, slower speed movements, and two low-use movement types characterized by infrequent use that was not important for connectivity (Table 3.6). However, the low-use movement types differed from each other with respect to average speed and directionality of movement with slower meandering movements in one, and fast, directional movement in the other (Table 3.6). Medium-use areas were the most prevalent functional movement types observed on the landscape and were assigned to the greatest number of individuals (86.5 % of elephants) following the high-use (core area) movement type.

Three movement types were associated with connectivity (i.e., corridors) based on betweenness values but were distinct from one another with respect to the average speed and directionality of movements, as well as use-intensity (Table 3.6). Corridor hubs were characterized by very high connectivity and fast movements (highest average betweenness and speed; Table 3.6) but were also very intensely used (high weight), indicating that these locations were traversed frequently at fast speeds and were important for network wide connectivity. However, corridor hubs were rare on the landscape (2.7 % of pixels) and assigned to only 21.6 % of individuals (3 females and 5 males) in the Mara. Fast, low-use corridors were also associated with high betweenness and faster speeds but were characterized by more parallel movement than corridor hubs, equivalent to the classic definition of a corridor. Fast, low-use corridors comprised 16% of individual networks on average and were observed in 86.5% of elephants. Finally, directed movement corridors were characterized areas important for connectivity with more parallel, directional movement and slightly slower speeds compared to fast corridors were the most uncommon on landscape after corridor hubs but were relatively common among individuals (assigned to 73% of elephants).

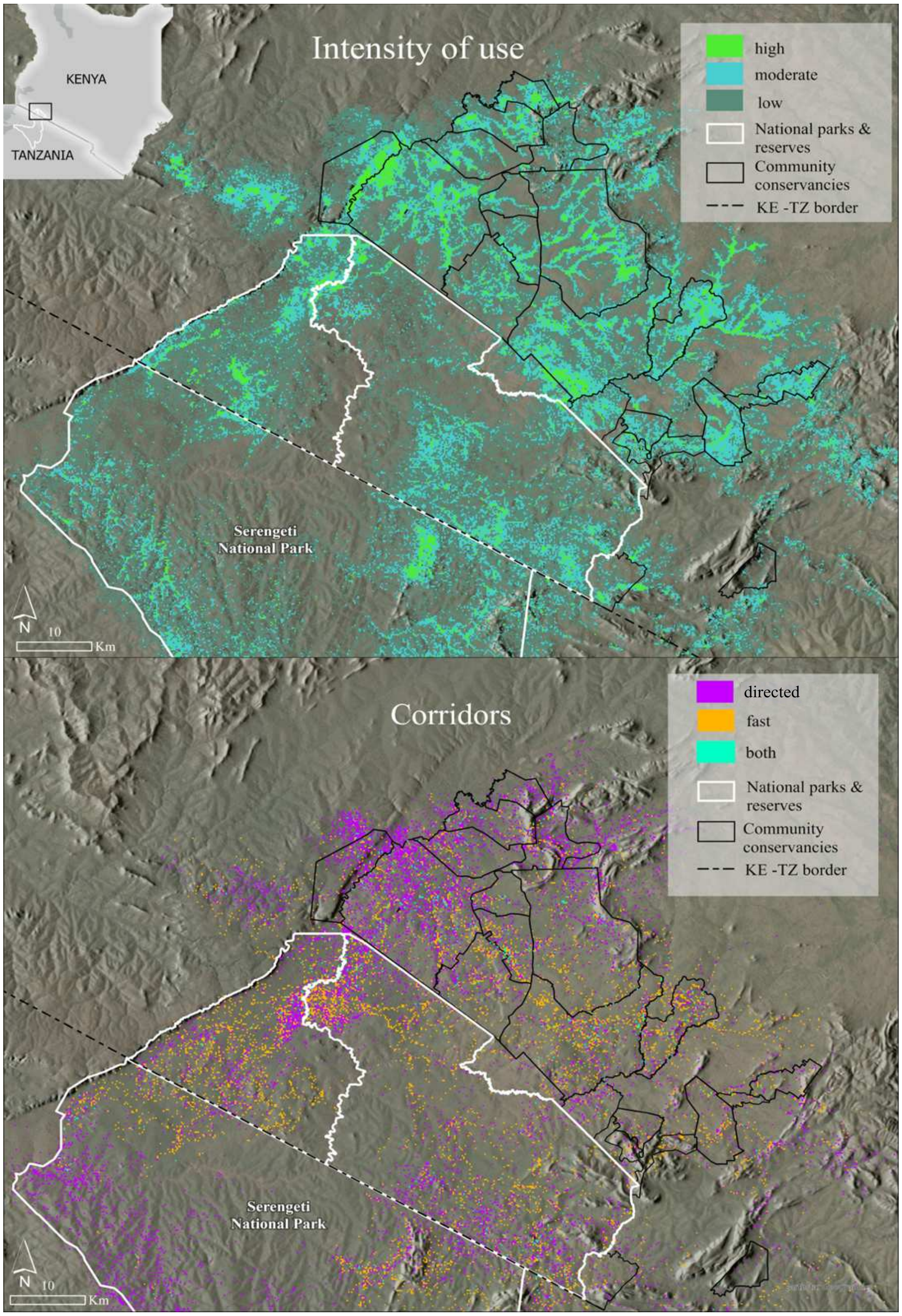

Figure 3.1. **a)** High, moderate, and low-use areas for African elephants in the Mara-Serengeti ecosystem based on tracking data collected from 37 individuals from 2011-2022. Higher use categories are prioritized in the overlay if a pixel belonged to multiple use types at the population level. **b)** Mapped corridors identified at the population level associated with directed (purple) and fast (orange) movements, and pixels used as both directed and fast corridors in aqua; corridor hubs are not shown on map because they were too rare to be visible.

Environmental and social influences on core areas and corridors in the Mara-Serengeti

Model results indicated that the probability of observing different functional movement types was influenced by environmental variation, land management, and social dynamics (Table 3.4). For both female and male elephants, core areas (high-use) were associated with higher mean vegetation productivity compared to medium and low-use areas, but high productivity was more influential on core area use for male elephants (Table 3.4). Core areas for both sexes were strongly influenced by human presence and were more likely to be in areas with low human settlement densities and farther from villages compared to medium and low-use (Figure 3.2a). In addition, core areas were negatively associated with open savanna (<20% canopy cover) and positively associated with high-use by other elephants for both sexes (Figure 3.2b). Core area selection differed between the sexes for forest and bush thickets (> 70% canopy cover correlated with core use for by females; Figure 3.2c), average slope (correlated with core area use by females; Table 3.4). Core areas for males were likely to be near seasonal rivers and drainages but farther away from permanently flowing rivers compared to medium and low-use areas. For both sexes, the probability of observing directed corridors had a small, positive association with crop cover, and for males, a positive association with higher vegetation productivity. For both sexes, directed corridor use was likely to be near rivers or drainages and for females was negatively associated with higher average slope. Fast corridor use by female elephants was negatively associated with higher canopy cover and was likely to be in areas with lower average slopes and nearer to villages. Fast corridors for males were positively associated with open savanna (< 20% canopy cover), were likely to be nearer to permanent rivers, and were negatively associated with crop cover (Table 3.4). Fast corridor use by males was positively associated with high-use by other elephants of both sexes, whereas for female elephants, fast corridor use was negatively associated with fast corridors use by other females.

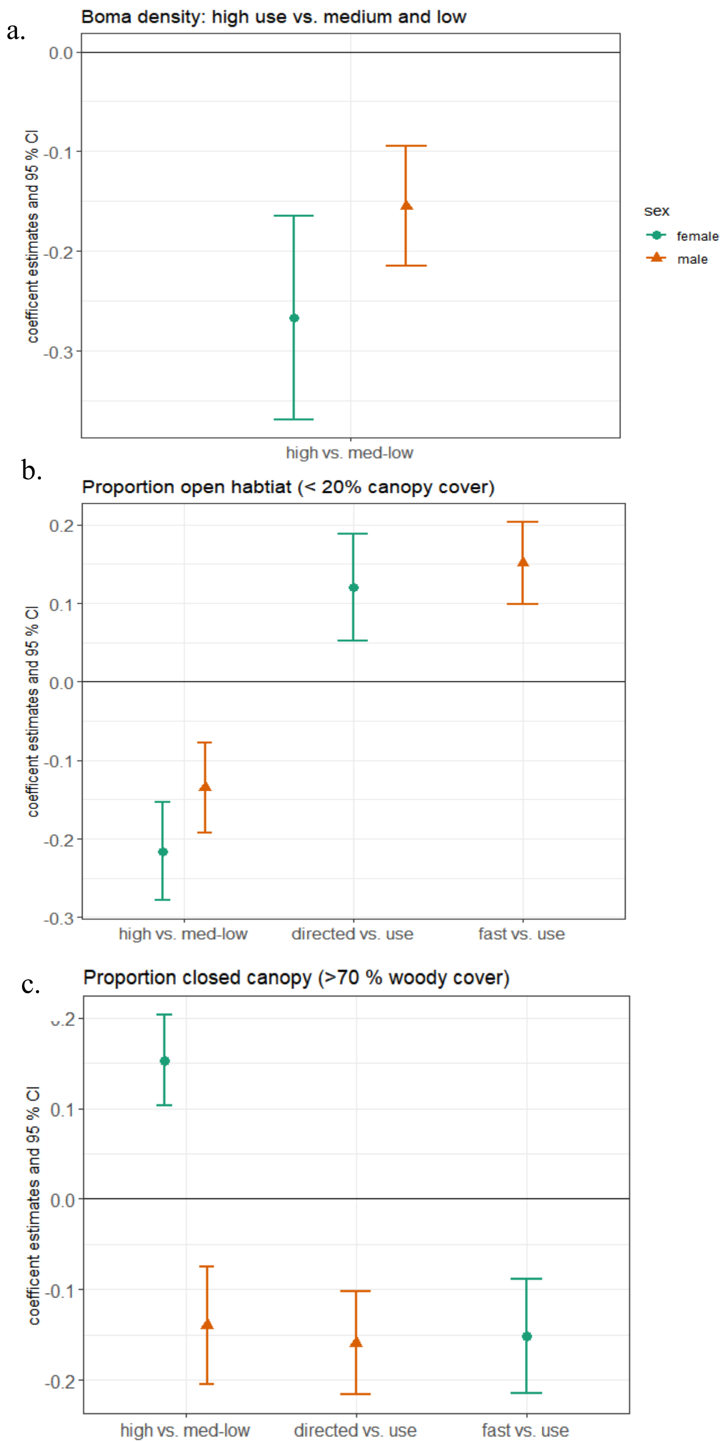

Figure 3.2 Selected coefficient estimates and 95% confidence intervals (log-odds scale) for male (n= 18) and female (n=19) African elephants from the most supported mixed-effects logistic regression models evaluating the effects landscape variation on the probability of observing functional movement types in the Mara-Serengeti.**(a)** Effect of boma density on observing high vs. medium and low-use areas, **(b)** effect of open grassland on observing high vs. medium and low-use, directed corridors vs. all use, and fast corridors vs. all use.**(c)** Effect of forest and bush thickets (closed canopy cover) on observing high vs medium and low-use, directed corridors vs. all use, and fast corridors vs. all use.

Table 3.4.Coefficient estimates and 95% confidence intervals (log-odds scale) for male (n= 18) and female (n=19) African elephants from the most supported mixed-effects logistic regression models evaluating the effects of landscape variation and conspecific use on the probability of observing different functional movement types in the Mara-Serengeti. Land management is abbreviated as UP (unprotected), PA (Protected Area), and CC (Community Conservancy).

	Females			**Males**		
	high vs. medium & low-use	*directed corridor vs. use*	*fast corridor vs. use*	*high vs. medium & low-use*	*directed corridor vs. use*	*fast corridor vs. use*
(Intercept) UP	-2.57 (-3.16 to -1.99)	-5.17 (-7.03 to -3.32)	-3.70 (-4.87 to -2.53)	-3.06 (-3.47 to -2.65)	-4.70 (-6.44 to -2.96)	-4.11 (-5.19 to -3.03)
CC	0.33 (0.19 to 0.47)	0.08 (-0.10 to 0.26)	0.53 (0.36 to 0.70)	-0.11 (-0.24 to -0.01)	-0.19 (-0.32 to -0.06)	0.58 (0.44 – 0.71)
PA	-0.23 (-0.43 to -0.03)	0.23 (0.01 to 0.45)	0.59 (0.41 to 0.77)	-0.68 (-0.86 to -0.50)	-0.15 (-0.29 to -0.01)	0.93 (0.77 – 1.08)
mean NDVI	0.06 (-0.02 to 0.14)			0.90 (0.76 – 1.05)	0.25 (0.14 to 0.36)	
boma density	-0.27 (-0.37 to -0.16)	0.06 (0.01 – 0.12)		-0.15 (-0.20 to -0.09)		
distance to village	0.04 (-0.02 to 0.10)	-0.15 (-0.21 to -0.9)	-0.08 (-0.14 to -0.03)	0.32 (0.26 to 0.38)		
distance to seasonal water		-0.10 (-0.13 to -0.06)	0.14 (0.11 to 0.17)	-0.09 (-0.16 to -0.02)		
distance to permanent water				0.20 (0.13 to 0.27)	-0.10 (-0.17 to -0.03)	-0.15 (-0.23 to -0.08)
closed canopy (>70% cover)	0.15 (0.10 to 0.20)		-0.15 (-0.21 to -0.09)	-0.14 (-0.20 to -0.07)	-0.16 (-0.22 to -0.10)	
semi-closed canopy			-0.17 (-0.22 to -0.11)		-0.16 (-0.21 to -0.11)	

(20-70% cover)						
open canopy savanna (<20 % cover)	-0.22 (-0.28 to -0.15)	0.12 (0.05 – 0.19)		-0.13 (-0.19 to -0.08)		0.15 (0.10 to 0.20)
crop		0.10 (0.06 to 0.14)			0.06 (0.03 to 0.09)	-0.13 (-0.21 to -0.06)
slope	0.14 (0.11 to 0.18)	-0.22 (-0.28 to -0.17)	-0.24 (-0.30 to -0.19)	-0.10 (-0.16 to -0.04)		
distance to roads						
high-use	1.50 (1.05 to 1.95)			2.17 (1.97 to 2.37)		
high-use females only	1.16 (0.97 to 1.35)			0.99 (0.82 to 1.16)		
high-use males only	1.37 (1.20 to 1.54)			1.66 (1.54 to 1.78)		-0.50 (-0.73 to -0.28)
corridor males only	0.35 (0.16 to 0.54)					
corridor females only			-0.86 (-1.29 to -0.43)			
spatial autocovariate	1.45 (1.39 to 1.51)	-0.33 (-0.41 to -0.26)	-0.78 (-0.85 to -0.71)	1.15 (1.11 to 1.20)	0.08 (0.04 to 0.13)	-0.74 (-0.80 to -0.68)
individual variance	1.621	15.46	6.49	0.74	13.33	5.20
AUC	**0.838**	**0.836**	**0.804**	**0.823**	**0.759**	**0.814**
n=1	3,566	2,236	2,728	3,972	2,658	2,323
n=0	25,735	29,301	29,301	31,521	35,493	35,493

Comparative Analysis

Network and movement metrics

The global inference test indicated significant differences in graph-level network metrics between the Mara and Samburu elephants (*F*=87.392, df 1 = 1.987, df 2 =226.572, $p < 0.0001$) and relative effects and post-hoc tests indicated differences in all graph-level metrics ($p < 0.001$). The probability that a randomly chosen elephant movement network in the Mara had a higher clustering coefficient than a randomly chosen network was 0.987, and Mara networks were also likely to have higher density with probability 0.789 (Figure 3.3). Mara elephants had a low probability of having a larger network diameter (0.273, Figure 3.3). There were also significant different at the node-level (*F* =17640.78, df 1= 3.142, df 2 =1,290,766, $p < 0.0001$) and post-hoc tests indicated significant differences in all node-level metrics between movement networks in the Mara and in Samburu ($p < 0.001$). However, relative effects suggest that most differences were small (e.g., relative effects near 0.50) apart from node degree (Figure 3.3). A randomly selected node in an elephant movement network in the Mara was likely to have higher degree with probability 0.723 but was less likely to have faster average speed with probability 0.40, and less likely to have higher betweenness with probability 0.42 (Figure 3.3). Relative effects for average directionality and average weight indicate that nodes could not be well-distinguished between ecosystems by these metrics (Figure 3.3).

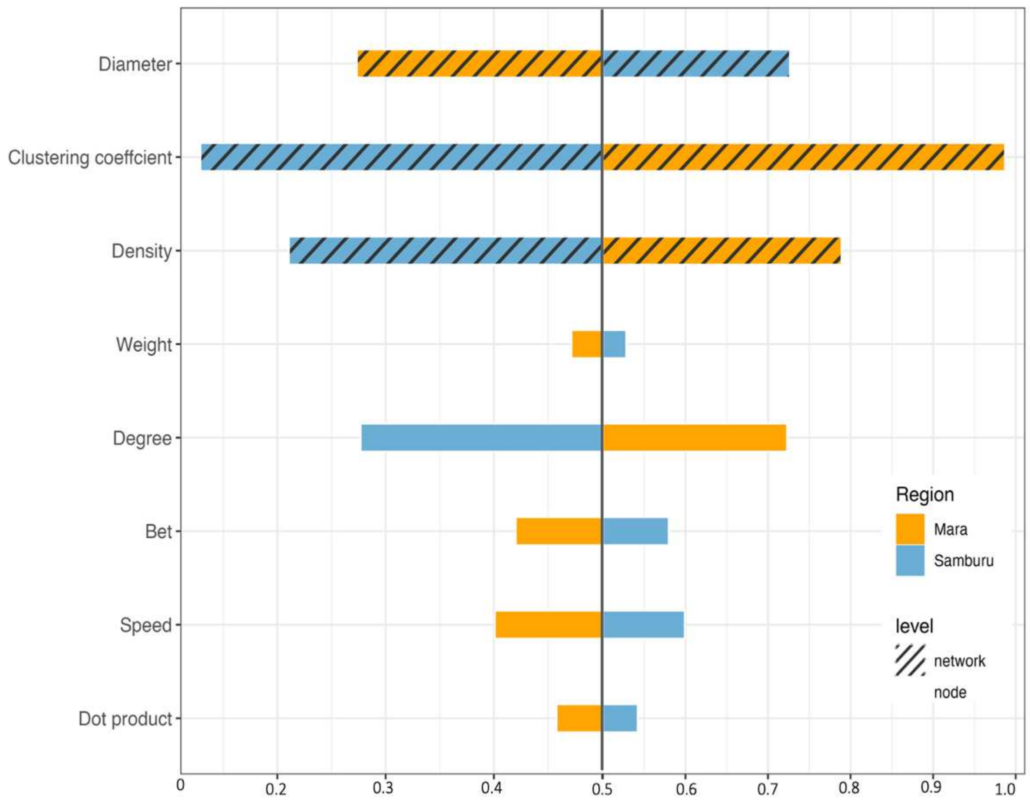

Figure 3.3. Relative effects of elephant movement and network metrics in a nonparametric MANOVA comparing the Mara-Serengeti and Samburu-Laikipia ecosystems at the graph level and node level. Values further from 0.5 (i.e., closer to 0 or 1) indicate a stronger ability of a given metric to discriminate elephant movements between ecosystems here values > 0.5 indicate that a given metric is likely to have a higher value.

Overall, the direction of correlations between node-level metrics from both ecosystems were similar (Table 3.5), with the exception of betweenness and weight which were positively correlated in the Mara and negatively correlated in Samburu. This finding suggests that in the Mara, highly connective areas including corridors were also highly used. However, the strength of correlations differed to some degree. For instance, weight and degree were more strongly positively correlated in the Mara than in Samburu, suggesting that highly used areas in the Mara tend to be more connected to adjacent areas (local connectivity) than in Samburu, and weight and speed had a stronger negative correlation in the Mara, indicating slower movements in high and medium use areas the Mara compared to Samburu. Similarly, degree and speed were more strongly negatively correlated in the Mara suggesting that movements between adjacent, locally connected pixels were slower in the Mara than in Samburu. Finally, speed and directionality were more positively correlated in the Mara than in Samburu, indicating that directional, parallel movements were generally faster in the Mara than in Samburu.

Table 3.5. Correlation matrix for node-level metrics across a random sample of 1,000 nodes from each ecosystem. For significant differences at the α= 0.01 level, we report the 95% confidence interval for the difference in Spearman coefficients between the Mara-Serengeti (M) and Samburu (S) ecosystems, or otherwise "n.s" denotes the difference was not statistically significant.

	M	S	M	S	M	S	M	S
Directionality	-0.19	-0.08	-0.21	-0.12	0.01	0.07	0.24	0.09
	n.s.		n.s.		n.s.		**0.16 (0.075 to 0.25)**	
Speed	-0.29	-0.14	-0.30	-0.15	0.21	0.18		
	-0.15 (-0.23 to -0.07)		**-0.15 (-0.23 to 0.07)**		n.s.			
Betweenness	0.08	-0.09	0.14	0.14				
	0.17 (0.083 to 0.25)		n.s.					
Degree	0.77	0.48						
	0.29 (0.23 to 0.35)							
	Weight		Degree		Betweenness		Speed	

Observed Functional Movement Types and Space Use

In both ecosystems, the maximum number (8) of population clusters of functional movement types were identified based on BIC and no individual elephant displayed all 8 types. However, individuals in the Mara tended to display more variation in movement types compared to Samburu. All elephants in the Mara displayed at least five functional movement types at the population level with 86% of individuals displaying to 6 or 7 types whereas in Samburu, 77.5% of individuals displayed to 5 – 7 clusters and 28.7 % displayed to 2 – 4 different movement types. We found that 5 of 8 movement types were functionally similar and 3 of 8 were functionally distinct between ecosystems (Table 3.6). High, medium, and low-use categories as well as movement corridors were observed in both populations (Table 3.6). However, movement corridors differed between the populations. While both had corridors with high connectivity value and fast movement speed, the Mara elephants also displayed directed corridors characterized by higher directionality and speed, whereas Samburu elephants displayed slow corridors characterized by slow, meandering movements (Table 3.6). We observed two medium-use movement types characterized by high local connectivity, and meandering movements in the Mara, but in Samburu, a high-use cluster characterized by fast movement and a separate high-use cluster characterized by slow movement was observed. Additionally, corridor hubs, which were observed in the Mara were not observed in Samburu.

Table 3.6 Different functional movement types observed based on clustering of network and movement metrics across 37 African elephants in the Serengeti-Mara ecosystem compared to 138 African elephants in the Samburu-Laikipia ecosystem. Metric values are the standardized mean for the cluster where positive values indicate a higher mean and negative values indicate a lower mean, and highlighted columns show functional movement type clusters that were distinct between ecosystems.

Mara -Serengeti

Functional Movement type	**highest use**	**corridor hub**	**medium use**	**directed corridor**	**medium use**	**low-use (slow)**	**fast corridor (low-use)**	**low-use (fast)**
Weight	3.034	3.023	0.428	-0.016	0.637	-0.337	-0.335	-0.443
Degree	2.406	1.93	0.653	0.221	1.067	-0.384	-0.38	-0.622
Betweenness	0.535	4.637	-0.248	1.097	0.503	-0.288	2.349	-0.019
Speed	-0.633	1.547	-0.48	0.54	-0.472	-0.117	0.775	0.891
Directionality	-0.173	-0.187	-0.051	0.326	-0.143	-0.218	-0.255	0.691
Proportion of pixels*	0.134	0.027	0.144	0.138	0.161	0.133	0.16	0.102
Proportion of individuals	1	0.216	0.84	0.73	0.865	0.973	0.865	0.784

Samburu -Laikipia

Functional Movement type	**highest use**	**high-use**	**medium use**	**slow corridor**	**high-use fast**	**low-use (slow)**	**fast corridor (low-use)**	**low-use (fast)**
Weight	2.915	1.203	0.394	0.625	1.604	-0.380	−0.337	-0.383
Degree	2.603	1.393	0.510	0.718	1.580	-0.412	−0.357	-0.411
Betweenness	0.550	0.009	0.019	1.353	0.817	-0.266	1.602	-0.112
Speed	-0.548	-0.364	-0.223	0.144	0.374	-0.230	0.531	0.765
Directionality	-0.143	-0.059	-0.021	0.094	-0.337	-0.258	0.006	0.605
Proportion of pixels*	0.048	0.047	0.122	0.068	0.007	0.478	0.090	0.140
Proportion of individuals	0.993	0.572	0.551	0.616	0.196	0.775	0.804	0.725
Cluster	6	5	1	2	3	4	7	8

** Proportions are calculated with respect to all pixels used across all individual networks.*

We compared the relative spatial proportions of high, medium, and low-use areas, as well as corridors, to understand how prevalent each of these functional movement types were on the landscape in each ecosystem. Across individual networks, high-use areas comprised a greater proportion of elephant space use in the Mara compared to Samburu (χ=1873.6, df = 1, p < 0.001) though only by about 3% (Figure 3.4). However, medium use areas and corridors were approximately twice as prevalent in Mara elephant networks compared to Samburu (medium use χ=45253, df=1, p < 0.001; corridors: χ=32241, df = 1, p < 0.001), whereas low-use areas comprised a much greater proportion of elephant networks in Samburu than in Mara (χ=104131, df = 1, p < 0.001).

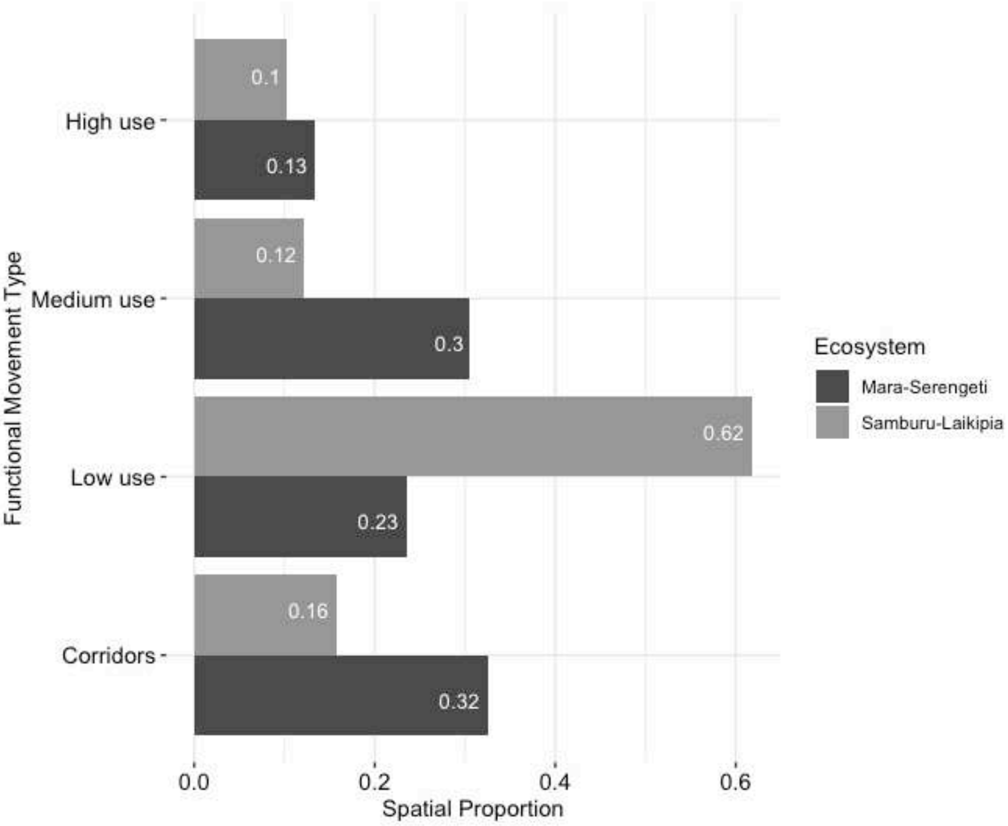

Figure 3.4 Relative spatial proportion of individual elephant movement networks comprised of high-use areas, medium use areas, low-use areas, and corridors in both the Mara-Serengeti and Samburu-Laikipia ecosystems based on clustering results of functional movement types.

Environmental influences on core area and fast corridor use

Model selection results indicate the relative importance of environmental variables associated with core areas differed between Mara and Samburu ecosystems. The dominant variables influencing core area use by females in the Mara were a negative association with boma density, a negative association with open savanna (< 20% canopy cover), a positive association with closed canopy habitat, and a positive association with higher average slopes. Core area use by males was strongly positively associated with higher vegetation productivity, likely to be farther away from villages, farther away from permanent rivers, and in areas with lower boma density. However, in Samburu for both male and female elephants, core areas were most strongly associated with vegetation productivity and predictability, followed by proximity to water ,with female core areas likely to be near permanent water, and male core areas likely to be near seasonal water.

In the Mara, fast corridor use by female elephants was most strongly associated with relatively lower average slopes, open canopy grassland, and areas further away from seasonal rivers and drainages. However, fast corridor use by females in Samburu was associated with locations nearer permanent water, nearer to villages, and in areas with lower average slope. Fast corridors for male elephants in the Mara were most strongly associated with open savanna, permanent water, and crop cover with higher probability in open savanna, near permanent water, and in areas with less crop cover. In Samburu, fast corridor use for males was most strongly associated with relatively lower vegetation productivity and areas with low predictability of productivity but were likely to be closer to permanent and seasonal water sources.

3.4 DISCUSSION

Our results indicate marked differences in structural movement patterns and nuanced, context-dependent differences in African elephant movement behaviors reflected in properties of local space use across ecosystems. As expected, movement networks across individuals in the Mara-Serengeti reflected more short-distance, repeated movements whereas in Samburu, movement networks reflected longer distance, more dispersed movements (e.g., nomadic movements; (Bastille-Rousseau *et al.* 2018) Within networks, elephants in the mesic Mara ecosystem used more of the landscape with medium intensity and for connectivity (corridors) compared to that in the xeric Samburu ecosystem where most locations were used with low intensity and corridors were spatially confined to certain areas. Water availability and vegetation productivity and predictability strongly influenced core areas for both male and female elephants in Samburu and were more influential than anthropogenic factors. Although vegetation productivity also influenced elephant core area use in the Mara, predictability did not, and human presence and canopy cover strongly influenced core area use in the Mara more strongly than water availability. Overall, our results indicate that elephants in the Mara are likely less constrained by water and forage availability than elephants in Samburu and have more flexibility to access these key resources while minimizing the risks posed by people.

Elephant movement networks in the Mara-Serengeti tended to be more clustered, smaller, and denser, whereas in Samburu, networks generally had larger diameters and were less clustered and less dense, reflecting relatively more nomadic to migratory movement structure (Bastille-Rousseau *et al.* 2018). Specifically, movement networks between ecosystems were strongly differentiated by clustering coefficient at the network level and node degree at the local level. The relatively stronger clustering of elephant movement networks in the Mara indicates spatial structuring, where for a given pixel used by elephants, elephants also used most neighboring pixels (i.e., neighborhoods of use), and higher degree reflects that elephants were frequently moving to and from these pixels. Additionally, weight and degree were strongly positively correlated in Mara movement networks and were negatively correlated with speed and directionality, resulting in highly locally connected core areas characterized by frequent, meandering, slow movements. Correlation patterns were similar in Samburu, but the positive association between local connectivity and use intensity was weaker, as were the negative associations between speed and use intensity, and directionality and use intensity.

These differences across spatial scales likely reflect foraging behavior (Owen-Smith *et al.* 2010). Foraging theory predicts that if foraging optimally (e.g., maximizing energy gain), animals should forage more intensely in patches with high forage availability and move to nearby high-resource patches frequently when the cost of traveling is low (Schoener 1971; Charnov 1976; Senft *et al.* 1987). Our results suggest that optimal foraging behavior in the Mara for elephants may be akin to area-restricted search, where elephants generally remain in areas of high resource abundance and make shorter, frequent movements among high quality patches (Focardi *et al.* 1996; Fryxell *et al.* 2008; Mueller & Fagan 2008). However, in environments with high seasonal variability in vegetation productivity that is less predictable at broad spatial scales, more long-distance movements to access high quality resources that are seasonally available (e.g., nomadic and migratory movement) may optimize energy gain (Mueller & Fagan 2008; Mueller *et al.* 2011; Polansky *et al.* 2013, 2015). The latter is likely the case in Samburu, where daily distances moved decline in the dry season when vegetation quality is consistently low across space compared to the wet season (Wittemyer *et al.* 2007; Polansky *et al.* 2013).

Previous studies on elephant movements in both ecosystems conducted in a resource selection framework found that seasonality strongly impacts elephant movement behavior in the Samburu-Laikipia system (Bastille-Rousseau *et al.* 2020), whereas in the Mara-Serengeti, only minor differences in habitat selection between wet and dry periods were observed (Wall *et al*., in review). Our findings at both the network-wide and local scales support the indication that seasonality more strongly structures elephant movement behavior in Samburu compared to the Mara. For example, we found that low-use areas comprised most elephant space use in Samburu, whereas medium use areas and corridors covered a greater portion of elephant movement networks in the Mara. Some low-use areas in Samburu are likely seasonally productive areas used only during wet periods. Additionally, previous studies found strong shifts in space use between wet and dry periods in Samburu where elephants moved further away from permanent water during wet periods to access seasonally productive vegetation (Wittemyer *et al.* 2007; Bastille-Rousseau *et al.* 2020). During dry periods, elephants in Samburu showed strong selection for productive areas and areas near permanent water and these resources are dominated by people and livestock, suggesting that elephants in Samburu incur the risks posed by people to access vital resources (Bastille-Rousseau *et al.* 2020). Several studies have reported that elephants prefer locations with greener vegetation, particularly in arid ecosystems (Loarie *et al.* 2009; Bohrer *et al.* 2014; Bastille-Rousseau *et al.* 2020) and our findings add support for this relationship. We found core areas were likely to be more productive areas in both ecosystems, but in Samburu core areas also showed a strong negative relationship with unpredictable productivity. In contrast, vegetation predictability was not a strong predictor of core area use in the Mara. In addition, Wall et al. (in review) show that dry and wet period elephant home ranges significantly overlap (mean: 56%, IQR: 47% - 66%) in the Mara. Overall, these findings suggest that savanna elephant movement behavior spans a flexible spectrum from residency, characterized by area-restricted search foraging behavior, to largely nomadic and migratory movement strategies, and that the environmental context and conditions likely structure the dominant movement behaviors.

For both male and female elephants in the Mara, core areas were influenced by the human footprint and were likely to be in areas of lower boma density and further away from villages, and for females, boma density was more influential than vegetation productivity. These findings support the growing recognition that humans can influence the landscape of fear for elephants and elephants adjust their activity and space use patterns to minimize risks (Graham *et al.* 2009; Wittemyer *et al.* 2017; Gaynor *et al.* 2018; Wall *et al.* 2021). Core area use was also strongly differentiated by avoidance of open canopy savanna (< 20% canopy cover), particularly for females. In the Mara, open canopy savanna in community conservancies and unprotected areas are dominated by grazing livestock and large populations of other grazing ungulates such as zebra and wildebeest in protected areas. In nutrient-rich savannas like the Mara-Serengeti, elephants may face competition with other herbivores including cattle (Fritz *et al.* 2002; Young *et al.* 2005; Schuette *et al.* 2016). Elephants may also avoid cattle because of the presence of herders whom elephants can perceive as a threat (Bates *et al.* 2007). For female elephants in the Mara, core area use was positively related to higher average slope whereas movement corridors were associated with lower average slope. This finding contradicts previous studies which found elephants avoid steeper terrain (Wall *et al.* 2006; Roever *et al.* 2012). However, most previous studies assessing how elephants respond to terrain have done so in the context of directed movements or general selection/avoidance with no behavioral specificity. In community conservancies and unprotected areas in the Mara, higher average slopes are associated with hillsides that tend to have higher density of woody vegetation and typically lower levels of human activity and females may use these locations for foraging or rest because they may be perceived as having relatively lower risk.

Directed corridors in the Mara appeared to be largely flexible, for example, used to transit within home ranges, to access cropland, or to augment core habitats. Additionally, corridors were diffuse and relatively abundant in the Mara but were spatially limited in Samburu. Yet, node betweenness values (the higher the value, the more important the pixel for network-wide connectivity) tended to be higher in Samburu, indicating that though fewer locations are used as corridors, existing corridors have little redundancy and are important for facilitating elephant movement across greater distances to access seasonally available resources. Corridor hubs in the Mara, defined by high betweenness, high-use, and fast, multidirectional movement paths were not observed in Samburu. Regression analyses indicated that hubs were distinct from high-use areas because they were not associated with vegetation productivity and were distinct from fast corridors because they were more likely to be in locations with higher canopy cover. While corridors hubs were rare on the landscape, they appear to be crucial for network-wide connectivity for the individuals assigned to this cluster and may be indicative of ‘pinch points’ where movement is funneled through a particular location on the landscape due to habitat factors (McRae et al. 2008).

We observed fast corridors and an association of fast corridor use with human presence for female elephants in both ecosystems, a finding consistent with previous studies reporting that elephants move at faster speeds in human dominated landscapes and unprotected areas where elephants likely perceive higher risk (Douglas-Hamilton *et al.* 2005; Graham *et al.* 2009; Wittemyer *et al.* 2017; Ihwagi *et al.* 2018). In the Mara, fast corridors were associated with open canopy savanna for both sexes, but in Samburu were strongly associated with lower vegetation productivity and predictability for female elephants. Our results suggest that fast movement corridors are potentially associated with transit across riskier habitats (more exposed or nearer to people) in both ecosystems and lower quality habitat (lower productivity and predictability) in Samburu. Additionally, our analysis identified low-use movement clusters in both ecosystems characterized by fast, directional movements that were not important for connectivity (e.g., low betweenness). These findings suggest that connectivity models based solely on fast, linear movement within large tracking datasets (e.g., LaPoint et al. 2013) may be insufficient to distinguish key corridors from other behaviors, for example, evading a threat with a burst of movement. By incorporating a structural measure of connectivity in addition to movement path properties we were able to separate corridors from fast, linear movements that did not influence connectivity.

Although the Mara-Serengeti is known for vast protected areas, the region is facing declining wildlife populations, land privatization, growing human populations, land development and expansion of mechanized agriculture, growing livestock populations, and increasing fencing and deforestation (Serneels & Lambin 2001; Reid *et al.* 2004; Ogutu *et al.* 2016; Løvschal *et al.* 2017, 2022; Veldhuis *et al.* 2019). Our results suggest that land use planning should prioritize the protection of riparian woodlands, rivers and drainages, and forests and bush thickets on hillsides to protect critical elephant habitat and movement connectivity. Our results suggest that core areas are mostly well connected in the central Mara-Serengeti, but we did not address changes in land use that occurred during the study period and have the potential to impact connectivity such as fencing (Løvschal *et al.* 2022). Future work could focus on how networks change over time in response to land use changes. We found directed corridors appeared to be in preferred habitats compared to fast corridors, but directed corridors were also associated with crop cover and permanent water, likely reflecting the individuals in the dataset that regularly cross the Mara River to access cropland to the west (Hahn *et al.* 2021). In these unprotected areas on the western edge of the ecosystem, habitats used for directed movements that support connectivity to conservancies and protected areas may also be associated with hotspots of crop-raiding and human-elephant conflict. Our map of directed elephant corridors could be applied by conservation practitioners and wildlife managers to target conflict prevention and mitigation efforts in the region.

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CHAPTER 4
MAPPING WILDLIFE ATTITUDES SHOWS THE IMPORTANCE OF BUILDING ON EXISTING SOCIOCULTURAL VALUES AND ADDRESSING WILDLIFE IMPACTS ON WELL-BEING TO SUPPORT COEXISTENCE

4.1 INTRODUCTION

Where people and at-risk wildlife share space, developing and implementing conservation plans that are both effective and socially supported is necessary (Ban *et al.* 2013; Bennett *et al.* 2017; Niemiec *et al.* 2021). The implicit goal of conservation efforts in such shared landscapes is to achieve coexistence (Carter & Linnell 2016). Crucially, achieving coexistence does not mean the elimination of risk, but instead requires the effective management of risks at a level that is acceptable and sustainable for human communities and wildlife populations (Carter & Linnell 2016; Pooley *et al.* 2021). While coexistence has been an implicit goal of conservation for decades, the explicit focus of most human-wildlife interactions research has been on human-wildlife conflicts (Redpath *et al.* 2015; Bhatia *et al.* 2020). The governance of human-wildlife conflicts is a critical component of coexistence, but the overwhelming focus on conflict in research has hindered understanding of complex human-wildlife relationships and obscured potentially neutral and/or positive aspects that may be important for understanding and promoting coexistence (Redpath *et al.* 2015; Bhatia *et al.* 2020; Pooley *et al.* 2021).

Conservation social science tools can support coexistence through informing the development of conservation practices that are appropriate for local sociocultural and political contexts and promote inclusivity (Ban *et al.* 2013; Bennett *et al.* 2017). Conservation psychology provides a framework to gain insight into human-wildlife relationships by assessing individual values, attitudes, and behaviors in conservation contexts (Vaske & Donnelly 2002; Manfredo 2008; St John *et al.* 2010). Most studies apply a version of cognitive hierarchy theory which posits that cognition is oriented as a hierarchy from general to specific in which values and beliefs give rise to attitudes which, in addition to social pressures and individual perceptions of the relative difficulty or ease of performing a specific behavior, can influence behavioral intent and behavior (Fishbein & Ajzen 1977; Homer & Kahle 1988). Attitudes can be defined as an individual's feelings towards and overall evaluation of an object which may be mostly positive or negative and are frequently measured because they can be antecedents of behavioral intent (Fishbein & Ajzen 1977). While measuring general attitudes towards a broad subject (e.g., conservation) is unlikely to be effective for identifying predictors of specific behaviors, attitudes can be useful indicators when measured with sufficient context and when the measured attitude explicitly corresponds to a specific behavior (St John *et al.* 2010; Liu *et al.* 2011; Ajzen & Fishbein 2014). For example, in Tanzania, Hazzah et al. found that attitudes held about lions and sociocultural norms around lion killing were predictive of the behavior of lion killing (Hazzah *et al.* 2017). Attitudes can be useful indicators of human-wildlife relationships because they are translatable, measurable, and provide a baseline from which to advance understanding of how people evaluate and interact with wildlife, and thus can be used to inform conservation efforts particularly in contexts when behaviors cannot be measured (Manfredo 2008; Fernandez-Llamazares *et al.* 2020).

However, conservation social science remains underutilized in conservation planning (Manfredo *et al.* 2019; Niemiec *et al.* 2021). One difficulty is that social data are frequently treated as aspatial and so cannot be mapped, making them difficult to include in spatial conservation plans or assessments (Ban *et al.* 2013). Additionally, data are collected using surveys or interviews but are rarely analyzed with methods that account for biases that are inherent in self-reported data and thus can propagate error when integrated with biophysical data for spatial planning (Lechner *et al.*

2014). For example, ‘social desirability’ bias is a common source of systematic error in survey data that is introduced when people (consciously or subconsciously) misreport their answers in order to convey a more socially desirable response (Tourangeau & Yan 2007; Blair *et al.* 2020). Such bias can be pervasive when research topics are sensitive such as attitudes and behaviors regarding illegal wildlife hunting or endangered species (Nuno & John 2015). Advanced methods such as anonymous or randomized response techniques (i.e., specialized questioning or SQTs) are increasingly applied to address such bias (Cerri *et al.* 2021; Ibbett *et al.* 2021). But these methods can be challenging to implement and may not work as intended in all cultural contexts (Höglinger & Jann 2018; Ibbett *et al.* 2022).

Rangelands in East Africa are complex landscapes with a history of thousands of years of land sharing among pastoralist peoples and wildlife (Homewood & Rodgers 1984; McCabe 1994; Reid 2012). Many are landscapes of global conservation importance where diverse assemblages of wildlife remain where there are pastoralist societies who have chosen to live with rather than eliminate wildlife (Reid 2012). Today this relationship is vulnerable, largely as a result of colonial policies of forced removal and exclusion of pastoralist peoples from their lands for the creation of parks as well as continued political and economic marginalization (Homewood *et al.* 2009; Galaty 2013). This context coupled with the pressures of land conversion, social conflicts, food insecurity, and climate change have increased the likelihood of conservation conflicts, particularly around species like elephants (Reid *et al.* 2004; Homewood *et al.* 2009; Ogutu *et al.* 2016; Mukeka *et al.* 2018). In 2021, the International Union for Conservation of Nature (IUCN) listed African savanna elephants as “Endangered” and African forest elephants (*Loxodonta cyclotis)* as “Critically

Endangered", citing habitat loss and human-elephant conflicts (HEC) as rising threats to elephant populations across the continent (Gobush *et al.* 2021).

Several studies have assessed attitudes towards wildlife among the traditionally pastoralist Maasai people who are indigenous to the Kenya-Tanzania borderlands (Broekhuis *et al.* 2018; Fernandez-Llamazares *et al.* 2020). Some have explicitly addressed interactions with elephants (Kaelo 2007; Browne-Nunez *et al.* 2013; Kioko *et al.* 2015; Nyumba *et al.* 2020). However, most have focused on documenting HEC alone or on crop use by elephants, precluding holistic understanding of human-elephant interactions, particularly in landscapes where pastoralism is the dominant land use (see (de Pinho *et al.* 2014; Kioko *et al.* 2015). Furthermore, few studies have examined how attitudes towards wildlife might vary across landscapes particularly in Africa (Bowman, Jaconb *et al.* 2004; Carter *et al.* 2014; Piédallu *et al.* 2016). Yet, spatially explicit attitude assessments may be critical for developing more effective conservation plans for wide-ranging species such as elephants, particularly if assessments also address *why* attitudes may be held. This information is crucial to inform elephant conservation efforts in mixed-use landscapes because elephants rely on habitat outside of protected areas across the continent (Wall *et al.* 2021). For example, mapping attitudes could reveal regions of high coexistence potential in unprotected dispersal areas to prioritize for conservation (Bontrager *et al.* 2017), and/or the opposite, exposing where conflict mitigation or other management interventions are most needed.

In this study, we address these gaps in knowledge by quantifying the willingness of people to share space with elephants at a local scale, i.e., in their community grazing lands, village, or privately owned land in an agropastoral landscape in the Kenya-Tanzania borderlands. We apply novel hierarchical modeling techniques to account for response bias in self-reported attitudes about sharing space with elephants to and investigate what explains attitudes towards elephants and elephant conservation (Vasudev & Goswami 2020). We consider willingness to share space with elephants at a local scale to be a locally positive attitude towards elephants and their conservation, which builds on the concepts of wildlife 'tolerance' (Kansky *et al.* 2016) and 'acceptance' (Glikman *et al.* 2021) but differs in that we do not assume an intrinsic cost associated with the presence of elephants. Instead, we measure the propensity of an individual to be positive about elephants and elephant conservation (Vasudev & Goswami 2020; Pooley *et al.* 2021). Our objectives were to: (1) understand experiences with and attitudes about elephants, (2) gain insight into what drives positive attitudes towards elephants and elephant conservation, (3) quantify local support for elephant conservation, (4) and map local support for elephant conservation across the landscape to support conservation planning.

4.2 METHODS

Ethics Statement

This research protocol was reviewed and approved by the Colorado State University Institutional Review Board (IRB) under protocol number 20-9752H. All respondents gave free and informed consent to be surveyed (Appendix I). To ensure anonymity, respondents were assigned a random number ID at the start of an interview and names were not collected. The exact locations of respondent's homes and village names are not included in our Results to protect the privacy of respondents.

Study Area

The study region covers 1,500km^2 of the Greater Mara Ecosystem (GME) between the Maasai Mara National Reserve (MMNR) to the west and the Naimina Enkiyio forest in the east in Narok county, Kenya (Figure 3.1). The population is dominated by two Maasai sub-tribes, Purko in the west and Loita (*Iloitai*) Maasai in the east, and population density is relatively low (median =11.8 people or 1.3 households /km^2, WorldPop, 2020). Maasai both herd livestock and farm, but as a result of national land privatization policies many have also diversified their livelihoods through leasing of land parcels for either commercial agriculture or wildlife conservation and tourism through community conservancies (Homewood 2002). The study region includes Olderkesi conservancy (28.3 km^2) bordering the MMNR within the former Olderkesi group ranch, but in the remainder of the study region there are no conservancies (Figure 3.1). Most of the study area has not yet been privatized with Naikarra group ranch as the exception. Narok county supports an estimated 30% of Kenya's wildlife and many species rely on habitat outside of the MMNR, including the study region which is known as a wildlife dispersal area and elephant movement corridor (Ogutu *et al.* 2016; Waweru *et al.* 2021). The Naimina Enkiyio forest is one of the few ungazetted forests in Kenya and is managed by Maasai community leaders. It is also a vital dry season grazing resource for livestock and wildlife and contains rare endemic plant and wildlife species including elephants.

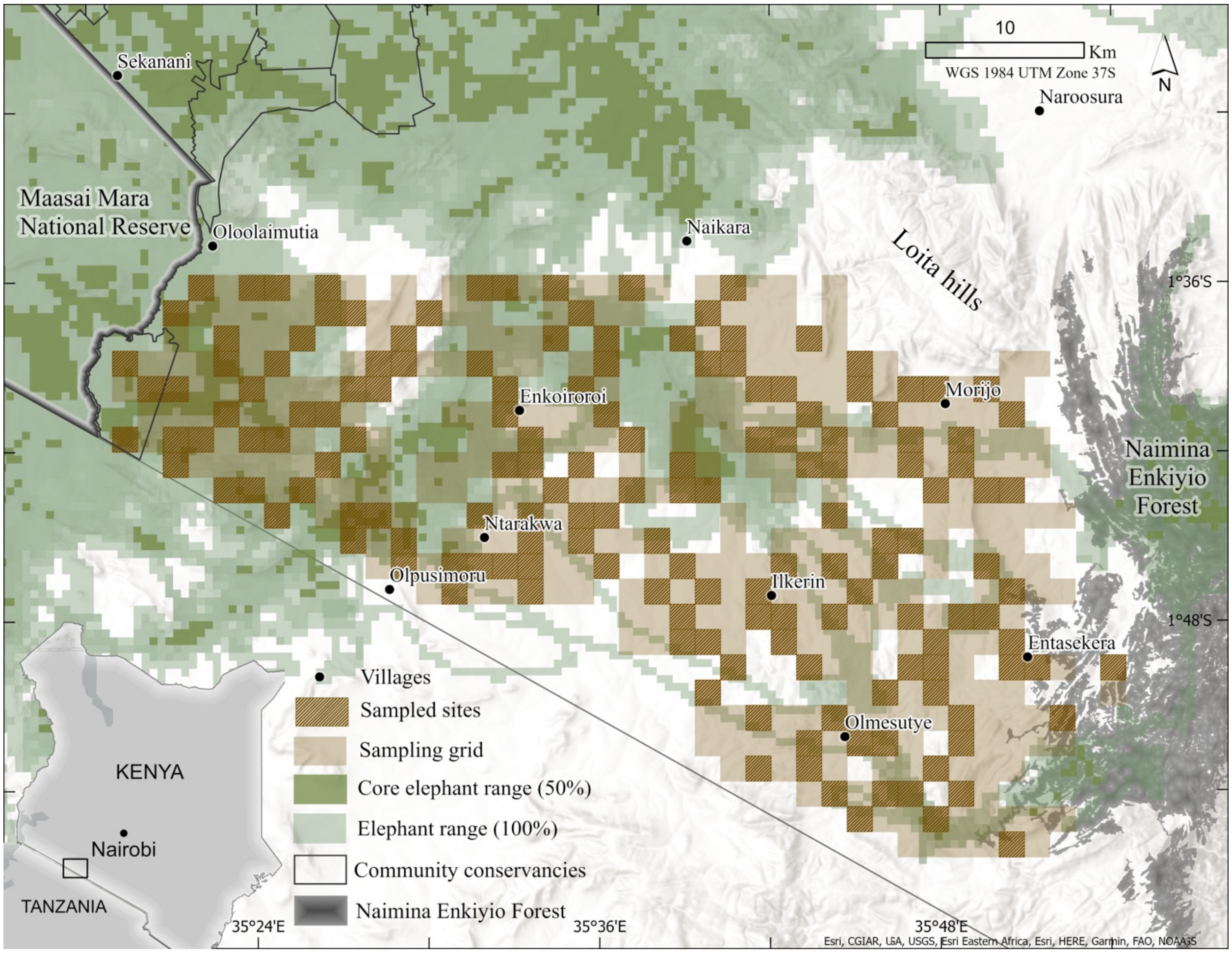

Figure 4.1. Study area map with spatial sampling grid and 160 sample cells (1.6km^2) where questionnaires were conducted overlaid with known African elephant core range (50%) and overall range (100%) estimated from over 1.4 million GPS relocations collected from 51 elephants from 2011-2020.

Survey Instrument

We developed a semi-structured questionnaire to address our research objectives. Because we sought to both quantify attitudes towards elephants and gain a deeper understanding of what drives attitudes, we included structured, Likert scale questions as well as open-ended questions (Appendix III). Likert questions were posed in the form of a statement to which respondents rated their level of agreement on a five-point scale to provide a consistent method of observing attitudes (Frank *et al.* 2015; Vasudev & Goswami 2020). Open-ended questions addressed beliefs, values, and experiences with elephants, for example, to understand sociocultural values and beliefs associated with elephants we asked, “Are elephants important in your culture?” and “If so, how, and why? What is the role of elephants in your culture?”. We developed the questionnaire in English, translated it into Maa, and then edited questions using back-translation to ensure accuracy.

Sampling design and data collection

Prior information on the location of occupied bomas (traditional Maasai homes) in the study area was not available, so we used QGIS *v.3.8* to create a uniform grid of 1.6 km^2 cells across the region bounded by the Loita hills to the north, the Naimina Enkyio forest to the east, and the Tanzania border to the south (Figure 3.1). The region is remote with limited infrastructure and low population density, so we constrained sampling to reasonably accessible areas for the safety of our field team. We overlaid roads, paths, and tracks from OpenStreetMap (OpenStreetMap contributors, 2020) with gridded estimated population density (WorldPop, 2020) in QGIS and selected grid cells that either: (a) intersected a path with connectivity to road, or (b) had an estimated population density that exceeded the median and was ≤ 2km from a connected road. We acknowledge that bomas in unselected cells are a potential source of non-response bias, however this is likely minor given low population density in these areas. We used a Generalized Random Stratified Tessellation sampling algorithm executed in R (R Core Team 2022) with the package *spsurvey* (Kincaid & Olsen 2011) to randomly select 160 sample cells in a spatially balanced manner to avoid spatial bias and sample evenly across the study region (Stevens Jr & Olsen 2004).

We developed the questionnaire in January 2020 and pre-tested it in Oloolamutia village near the sampling grid. We adjusted the questionnaire following the pre-test, and after delays due to the

COVID-19 pandemic, interviews were conducted by two trained local team members from June - August 2020. We used the KoboCollect app (Pham *et al.* 2014) to create digital questionnaire forms accessible on interviewer mobile phones for remote data collection and we used CyberTracker to create a navigation app for interviewers with a list of assigned sample sites. We stratified survey effort according to population density and interviewed at least one household per sample cell, or two-three if the density estimate exceeded the median for the study region. We redeployed the form four times during the collection period with a new random ordering of Likert questions to minimize potential bias in responses due to the order in which Likert questions were asked by interviewers.

Data Analysis

Hierarchical modeling of attitudes towards elephants

We implemented a hierarchical Bayesian model developed by Vasudev & Goswami (2020) to estimate the probability that a person holds a positive attitude towards elephants (Vasudev & Goswami 2020). We use this approach to (1) directly account for response bias in self-reported attitudes while investigating what drives attitudes, and (2) to distinguish locally positive attitudes (i.e., willingness to share space) from attitudes that are positive in a general or abstract sense (what we refer to as *notional* attitudes; Vasudev and Goswami 2020). For example, a person may be generally in favor of elephant conservation inside parks while also being against elephants using land near their home, and so measuring only their attitude towards elephants in general (*notional* attitude) would not accurately reflect their attitude about living with elephants at a local level. Thus, we consider notional attitudes to be loosely related to value orientations (Manfredo 2008) towards elephants that may or may not give rise to a willingness to share space with elephants at a local scale, which we consider here to be a locally positive attitude.

We seek to understand a person's true attitude toward elephants which we consider to be a latent random variable that can take on a positive or non-positive value. To separate local attitudes from notional attitudes, we modeled each as a latent variable with a hierarchical structure where the probability of a person to hold a local positive attitude towards elephants depends on their notional attitude; people who are notionally negative cannot be locally positive. We estimate the probability that the true attitude is positive with observations of attitudes from answers to Likert questions, which can result in two possible forms of response bias: (a) a false positive error where a person who is not positive towards elephants reports a positive attitude, or (b) a false negative error arising from a person who is truly positive towards elephants but reports a non-positive attitude. For example, a person may report a falsely positive attitude because of social desirability bias related to depicting a positive image for the wildlife tourism industry. To account for such errors, we use the 'multiple detection method' from ecological occupancy models (Miller *et al.* 2011, 2013). Using multiple methods of observation where at least one method (here, a *certain* Likert question) has a discrete error form allows for the estimation of false positive and false negative error rates and thus reduces bias in estimates of the true state of interest (Miller *et al.* 2013).

We used both positive and negative Likert statements about elephants in the questionnaire, so we converted all responses to a positive scale (e.g., a positive response to a negative statement about elephants became a negative response). We then converted responses to the binary scale of non-positive (0) or positive (1) treating neutral on this scale as non-positive. For n =177 respondents, the observation model of responses (x_i) to notional statements are described by a Binomial distribution:

$$x_i \mid (\alpha_i = 1) \sim \begin{cases} Binom\ (J_c, p_c^{11}) \\ Binom\ (J_{uc}, p_{uc}^{11}) \end{cases} \text{, given the true notional attitude state is positive}$$

$$x_i \mid (\alpha_i = 0) \sim \begin{cases} Binom\ (J_c, p_c^{01}) \\ Binom\ (J_{uc}, p_{uc}^{01}) \end{cases} \text{, given the true notional attitude state is non-positive}$$

where p_c^{11} is the probability of true positive reporting for the *certain* notional statement i.e., the probability that a person's response is positive when they truly have a positive notional attitude. For uncertain statements (e.g., all other Likert statements), p_{uc}^{11} is the probability of true positive reporting, and if the true notional attitude state is non-positive, p_{uc}^{01} is the probability of false positive reporting (the probability that a person gives a positive response when they truly do *not* have a positive notional attitude towards elephants). Responses to local attitude statements (z_i) also follow a Binomial probability distribution with reporting probabilities (q) similar that of notional attitudes, except that by design of the certain local statement, the probability of *false positive* reporting for *certain local* statements is zero ($q_c^{01} = 0$, appendix III).

To understand what drives notional attitudes, we controlled for sociodemographic factors that we expected to influence notional attitudes based on evidence from the literature, specifically, a person's age group (a_i), access to formal education (e_i), gender (g_i), and religious beliefs (r_i) may influence the likelihood of that person to be notionally positive towards elephants (Kideghesho *et al.* 2007; Hazzah *et al.* 2009; Browne-Nunez *et al.* 2013; Western *et al.* 2019). In addition, we posited that sociocultural values and beliefs associated with elephants could influence positive attitude probabilities (Kioko *et al.* 2015). We used coded responses to an open-ended question about sociocultural roles of elephants to identify respondents who believe that elephants have sociocultural value (c_i). We modelled positive notional attitude probability as a Probit function of individual covariates such that:

$$\mathrm{P}(\psi_i = 1) = \Phi(\beta_0 + \beta_1 a_i + \beta_2 e_i + \beta_3 g_i + \beta_4 r_i + \beta_5 c_i) \qquad \text{Eq. 4.1}$$

We expected that local attitudes towards elephants may be most strongly driven by individual or within household experiences. For example, we expected households that cultivate (x_i) to be less positive because of the potential for crop loss due to wildlife (Browne-Nunez *et al.* 2013). We expected people who had experienced problems caused by elephants (i.e., conflict) to be less positive (z_i) and those that identified benefits derived from elephants may be more positive (y_i). We anticipated that people living near core elephant ranges may have more interactions with elephants (positive or negative), so we identified which of our respondents were from bomas within 5km of known core elephant ranges (p_i). We expected that people who had experienced conflict with any species may be less positive towards all wildlife including elephants (w_i). Finally, we tested if formal education (e_i) influenced local attitudes because formal education access may be considered as an indirect benefit of the wildlife tourism industry and has been associated with positive attitudes in other studies in Maasailand (Western *et al.* 2019). The probability of a respondent to have a locally positive attitude was thus given by the Probit model:

$$\mathrm{P}(\phi_i = 1) = \Phi(\beta_0 + \beta_1 e_i + \beta_2 x_i + \beta_3 y_i + \beta_4 z_i + \beta_5 p_i + \beta_6 w_i) \qquad \text{Eq. 4.2}$$

Misreporting probabilities (e.g., q_{uc}^{01}) can also be estimated as a function of covariates, so we controlled for an effect of interviewer identity on local attitude misreporting probabilities. Some covariates of interest were spatially correlated so we proceeded with a set of covariates that best indexed our hypotheses and did not include correlated variables in the same level of the model.

We developed a second, landscape model for local attitudes to understand variation in positive attitudes across the study area. We used the same notional attitude model structure as above and included an effect of interviewer on misreporting probabilities, but instead modelled local positive attitude probabilities for six sub-regions that we expected could have different attitudes towards elephants based on land cover and land-use, cultural differences, and land sub-division (appendix II). This allowed us to both evaluate what drives attitudes and to make spatially explicit predictions of positive attitude probabilities at a scale that can be useful to community leaders, land managers, and conservation organizations.

We used Bayesian Markov Chain Monte Carlo (MCMC) simulations with a Metropolis-Hastings algorithm to estimate model parameters. We set normal, vague priors on all model coefficients with mean 0. For each model, we ran three MCMC chains for 20,000 iterations with a thinning interval of 4 and a burn-in of 4,000 retaining 12,000 samples per chain for analysis. We examined trace plots of MCMC chains to ensure mixing and assessed convergence by calculating the Gelman-Rubin statistic for every parameter and assessed model specification with graphical posterior predictive checks for all detection parameters (61; appendix III). We used results from the drivers model to evaluate variation in attitudes among respondents and we used results from the landscape model to map local attitudes.

Because all covariates were nominal, we evaluated differences in mean positive attitude probabilities between groups by calculating the pairwise difference between group mean parameters at each MCMC iteration as a derived quantity. We used the posterior mean of that quantity for hypothesis testing and measured the strength of the effect by calculating the posterior probability for the difference between groups as the proportion of parameter estimates for a given group that were larger than the reference group across all MCMC iterations (Hobbs & Hooten 2015). We used R v.4.0.5 (R Core Team 2022) for modeling and MCMC analysis.

Qualitative Analysis

We conducted thematic analysis (Braun & Clarke 2006; Clarke & Braun 2013) on qualitative responses to open-ended questions using MaxQDA software v.20.4.0. We created analytical categories guided by our research questions (e.g., living with elephants, conflict experiences, benefits, sociocultural values, and beliefs) and conducted an initial round of structural coding and then used *in vivo* coding to develop detailed sub-codes from the data (Clarke & Braun 2013). We identified final axial and sub-codes and tallied the frequency of codes across respondents. Sample sizes for qualitative results in our Results section reflect the number of people who answered a given question because we designed our form using a skip-logic framework that led some respondents to different sets of questions based on their answers and respondents could decline to answer some questions.

Co-interpretation

We returned to the study area in the fall of 2021 and attended public meetings to discuss and share our preliminary findings to local leaders and community members (David-Chavez & Gavin 2018). We distributed handouts with infographics and gave presentations explaining the content of the infographics in English and Maa. We then held two informal focus-group interviews with a subset of participants to qualitatively assess how our interpretation of the results aligned with and/or deviated from local interpretations (i.e., member checking). The interpretations that we present in the Results and Discussion sections are thus informed by these discussions.

4.3. RESULTS

Respondent Demographics

We analyzed data from a sample of 177 adult residents, 75 (42.3 %) of which were women and 102 (57.6%) men. Most respondents were household heads or wives of household heads. The mean age of respondents was 37 (SD = 11.63; range = 19–70), and the mean residence time in the study area was 13.7 years (SD=12.2; range = 2 – 49). When asked to identify livelihood activities and sources of income, 99% of respondents identified livestock husbandry, 71% identified crop cultivation, 21% identified small businesses (e.g., shops, livestock sales), 7% mentioned employment, and 6% reported other sources of income such as timber sales. For 150 (84.7%) respondents, livestock husbandry was the most important source of income, whereas 24 (13.5%) reported crop cultivation as most important and five (1 %) reported small business activities. About 31% of respondents (n=55) reported that they or someone in their household were members of a conservancy with most of these at Olderkesi (n=44) as well as Siana and Olare Orok. Most respondents had received no formal education 112 (63.2 %); 42 (23.7 %) had completed only primary school, 12 (6.7 %) completed secondary school, and 11 (6.2 %) had attended a college or university. Most respondents, 140 (79.1 %), reported their religious beliefs as Christian and 37 (20.9 %) reported holding traditional Maasai beliefs.

Notional Attitudes Towards Elephants

Overall, respondents were moderately positive towards elephants at a notional level (i.e., expressed support for elephant conservation in general). The average probability of a respondent to hold a positive notional attitude (ψ) ranged from 0.34 [95% CI=0.25–0.65] to 0.84 [95% CI=0.56–0.96] across sociodemographic groups (Figure 4.2a). Respondents who believe that elephants have sociocultural value (Table 4.1) had the highest mean positive attitude probabilities, on average 0.28 higher than those who did not believe that elephants have sociocultural value with posterior probability 0.90 (Figure 4.2b), indicating strong support for this effect. The most frequently reported sociocultural values of elephants were ecological (38.9 %) and economic (37%), though over 18% of respondents also reported cultural importance of elephants related to environmental conservation and Maasai oral literature and traditions (Table 3.1). For example, several respondents explained that elephants typically occupy forested areas, and their presence is a deterrent to potential illegal logging and burning in forests by outsiders. Posterior probabilities suggest other differences between sociodemographic groups were mostly weak (Figure 3.2b). Individuals who had received formal education were slightly more likely to be positive than those who had not with a mean increase in positive attitude probability of 0.12, with posterior probability 0.78 (Figure 4.2b). Individuals from older age-sets (age 48 – 70 and 34 – 47, respectively) were more likely to have positive attitudes that those aged 18 – 33, and women were on average slightly less likely to be positive than men (Figure 3.2). We did not detect an effect of religious beliefs on positive notional attitude probabilities.

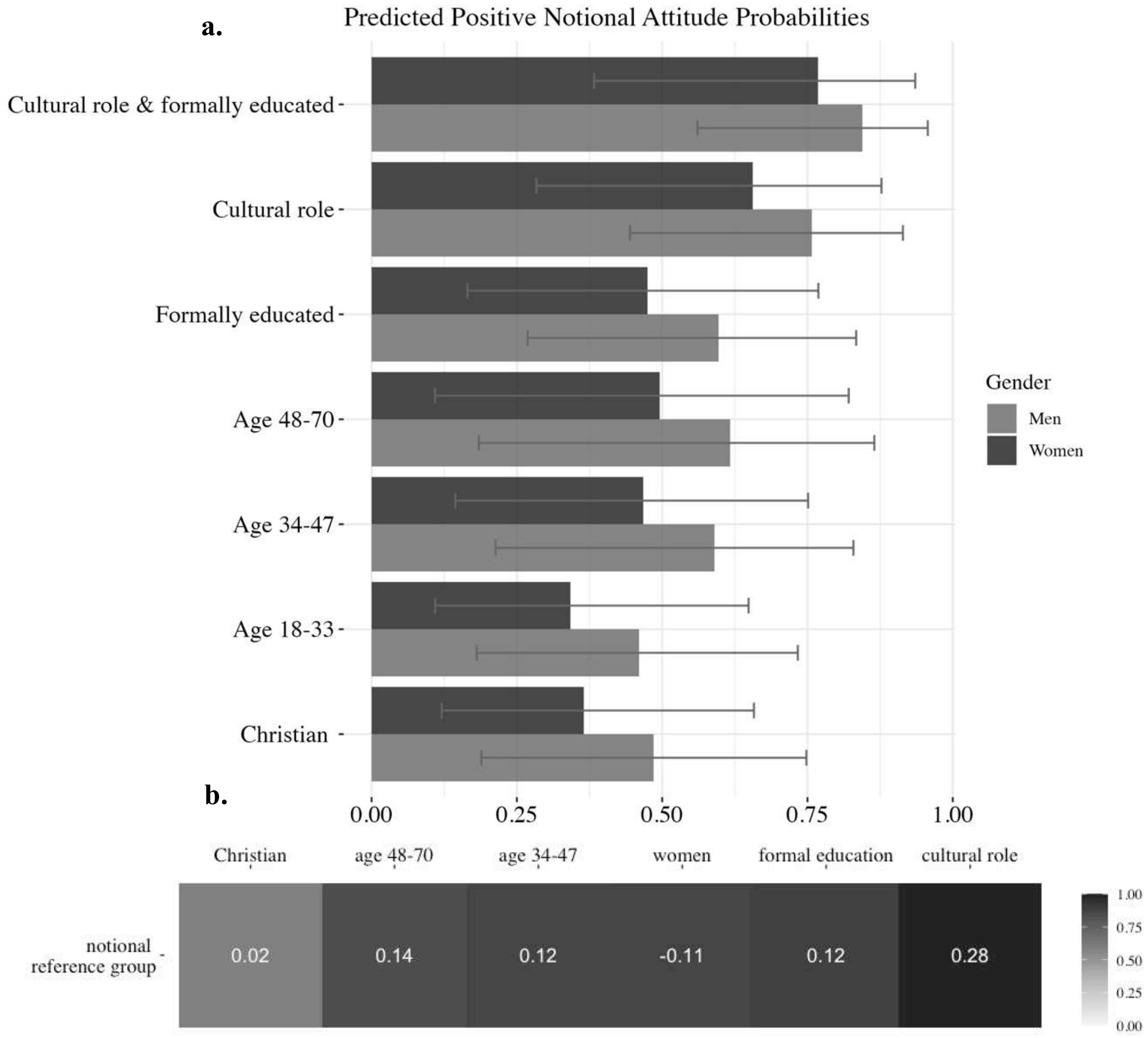

Figure 4.2. **(a)** Predicted posterior mean positive notional elephant attitude probabilities and 95% credible intervals (CI) across common sociodemographic groups. (**b**) Posterior mean difference in positive notional attitude probability for each group compared to the reference group (men aged 18-33 without a formal education who did not identify sociocultural roles of elephants). The posterior probability for the mean difference between groups is displayed as a heat map with darker hues indicating stronger evidence for the difference associated with a covariate.

Table 4.1 Sociocultural values and beliefs about elephants identified by respondents who believe elephants have sociocultural value (n= 108, 61.1%) with example quotations.

Coded sociocultural value and the percentage of respondents who identified each value.	**Example quotations**
Ecological (38.9 %) *	[1] *"Elephants clear the thick bushes and pave the way for new plant growth."* [2] *"[Elephants] increase soil fertility through their dung deposition."*
Economic (37.0 %)	[1] *"Elephants attracts the tourists which bring income to Kenya's economy and also to [the] community."* [2] *"[Elephants] bring income in terms of employment to many [Maasai] and earnings from land leases [through conservancies]."*
Resource conservation (18.5%)	[1] *"Elephants are important because they protect the forest that is highly destroyed by people by burning charcoal and also [making] fencing posts."* [2] *"Elephants are important in providing security and also in protecting forests which are water catchment area[s]."*
Oral literature & traditions (18.5 %)	[1.] *"[The elephant's] size, strength, and wisdom have inspired many tales, sayings, and riddles with these virtues, such as Meek olenkaina ilala lenyanak, which means [in Maa] the elephant never tires of his tusks."* [2.] *"Elephants represent and name Maasai clans."*
Use of elephant products (10.2 %)	[1] *"Elephant dung is/was [used] as traditional medicine."* [2] *"If the afterbirth of an elephant is found it is seen as a good omen and may be used for ceremonial purposes."*

*Note that percentages do not sum to 100 because respondents could identify multiple roles.

Local Attitudes Towards Elephants

Local positive attitude probabilities were lower than notional estimates, indicating that people with positive notional attitudes were not always willing to share space with elephants at a local level. Mean local positive attitude probabilities (ϕ) ranged from 0.16 [95% CI= 0.04 – 0.60] to 0.56 [95% CI= 0.25 – 0.88] (Figure 3.3a). Human-wildlife conflict experience with any species had the strongest effect on local attitudes; individuals (n=156) who had experienced conflict with any species of wildlife were less positive towards elephants by .20 on average with posterior probability 0.96 indicating strong evidence for this difference (Figure 3b). Hyenas (*Crocuta crocuta*) were the most frequently reported conflict species (78%), followed by baboons (*Papio Anubis*) (46%), buffalo (*Syncerus caffe*) (40%), and leopards (*Panthera pardus*) (35%). Additionally, individuals with some formal education were more locally positive by 0.16 on average with posterior probability 0.90. Posterior probabilities indicated that other covariate effects at the local level were weak (Figure 4.3 a and b). Model results showed no evidence that individuals who felt that they receive benefits derived from elephants were more likely to be locally positive, nor evidence that experiencing HEC made people less positive towards elephants (Figure 4.3). Cultivation did not influence local attitude probabilities.

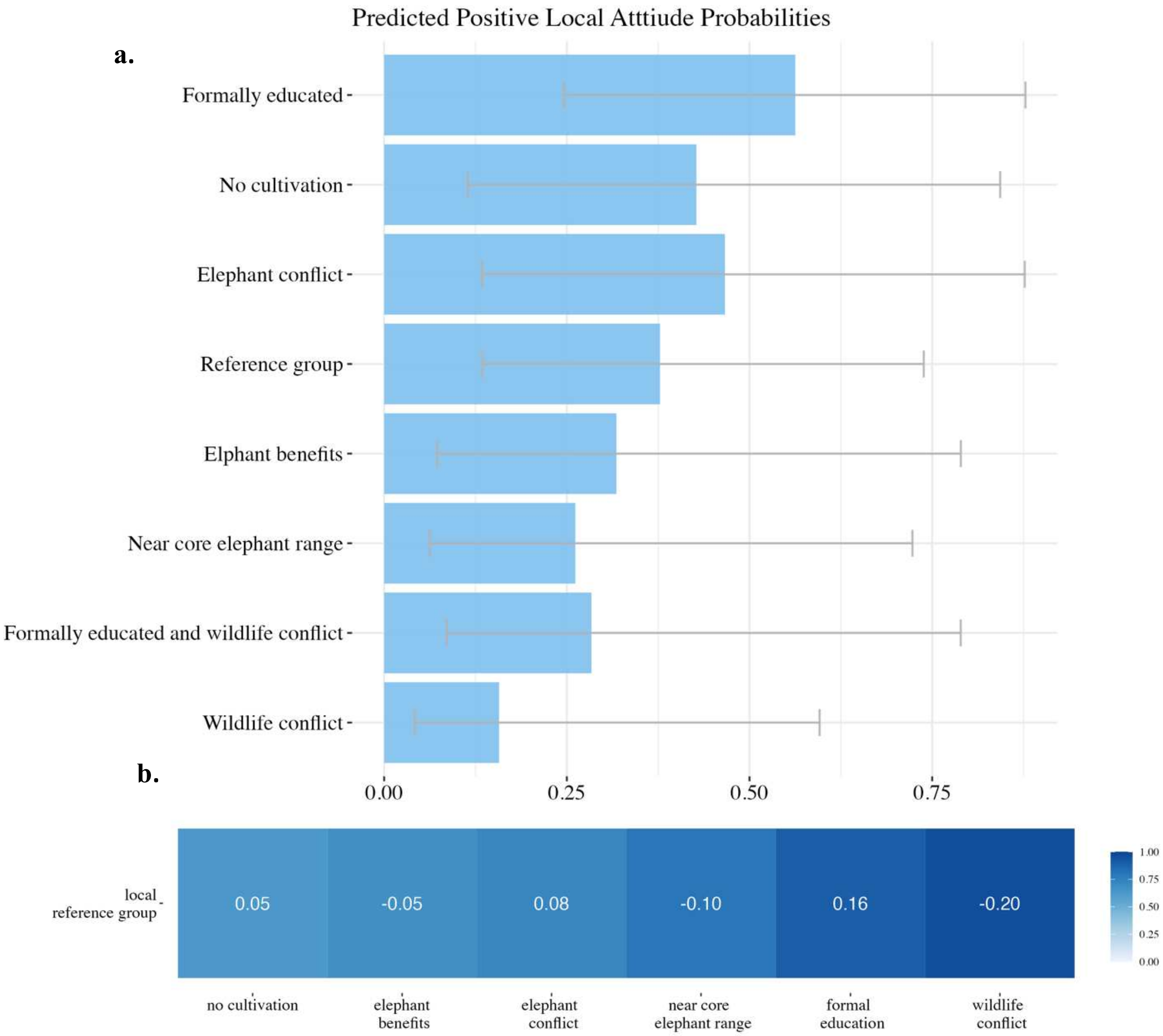

Figure 4.3. **(a)** Predicted posterior mean positive local elephant attitude probabilities and 95% credible intervals (CI) across common sociodemographic groups. **(b)** Posterior mean difference in positive local attitude probability for each group compared to the reference group (no formal education, no conflict, no benefits, etc.). The posterior probability for the mean difference between groups is displayed as a heat map with darker blues indicating stronger evidence for the mean difference associated with a covariate.

Mapping Local Attitudes

We used the landscape model to predict true local positive attitude probabilities across the study area for the sub-regions of Olderkesi, Naikarra, Enkoiroroi, Ilkerin, Loita north, and Olmesutye.

Mean positive attitude probabilities ranged from 0.32 to 0.41 across sub-regions but differences were weak (Figure 4.4). Respondents from Loita north and Olmesutye were the most likely to report positive attitudes (mean positive attitude probabilities of 0.41 and 0.40, respectively) and respondents from Naikarra and Ilkerin were the least likely to report positive attitudes (0.22 and 0.23, Figure 4.4). We found no evidence of a difference in the probability to be positive among respondents from Enkoiroroi, Ilkerin, and Naikarra (Figure 4.4). We found weak evidence that respondents from Loita North and Olmesutye were more likely to be positive than those from Enkoiroroi by 0.08 and 0.09 on average with posterior probabilities of 0.70 and 0.71.

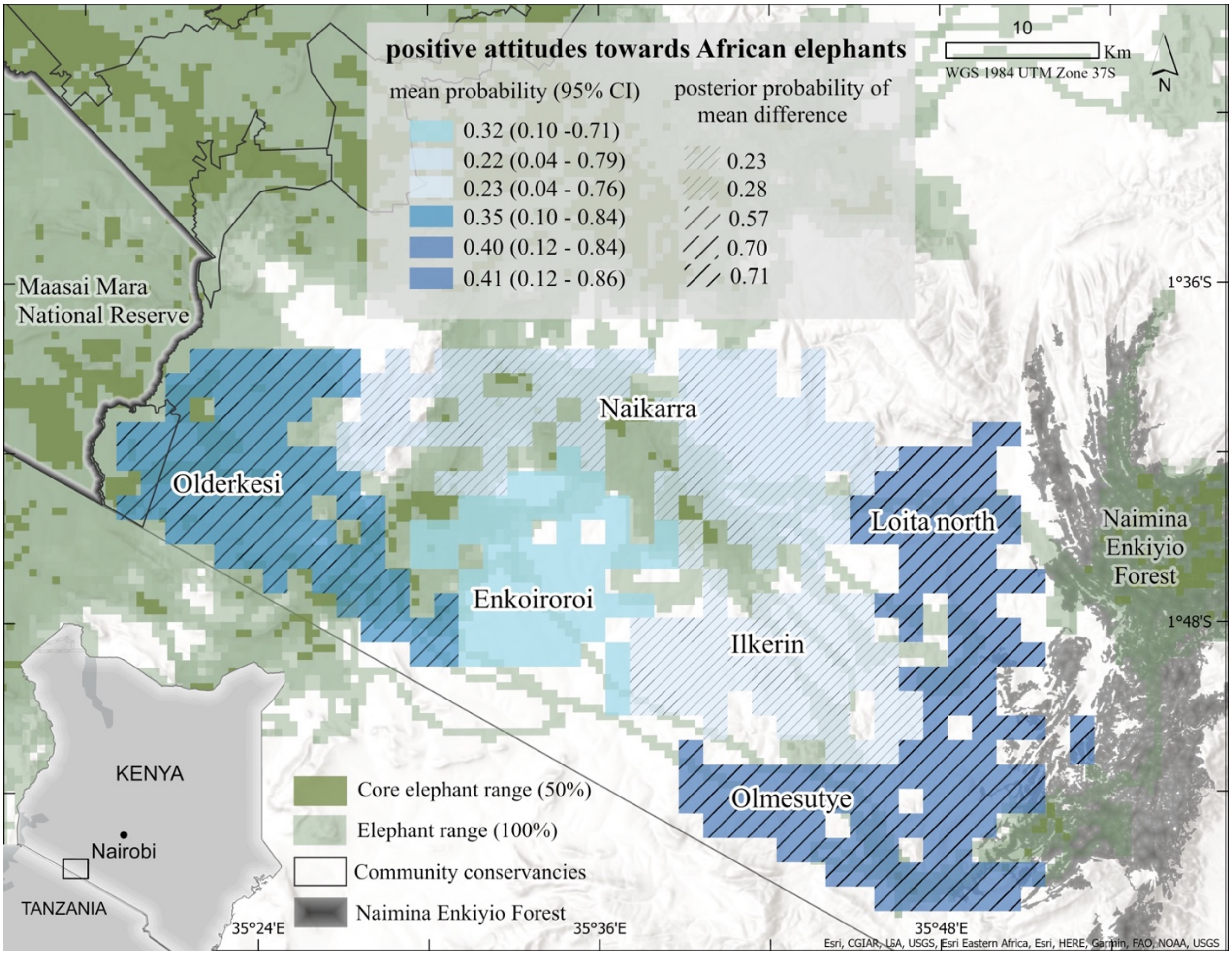

Figure 4.4. Predicted marginal posterior mean positive local attitude probabilities for six sub-regions from the landscape model. Darker blues indicate higher mean positive attitude probabilities and bolder hashing indicates stronger evidence for a difference in mean positive attitude probability for that region compared to Enkoiroroi.

Attitude Misreporting

The model estimated mean false positive reporting probability for notional attitudes towards elephants was 0.55 [95% CI= 0.47–0.62] whereas the mean false negative reporting probability was 0.32. At the local level, misreporting varied substantially between interviewers and false-negative probabilities were generally higher. The mean false-negative reporting rate of local attitudes was lower for interviewer A (q_{ucA}^{10} = 0.41) than interviewer B (q_{ucB}^{10} = 0.64), whereas the false positive rate was higher for interviewer A (q_{ucA}^{01} = 0.53, 95% CI= 0.50–0.56) than interviewer B (q_{ucB}^{01} = 0.30, 95% CI= 0.26–0.34). Inferring attitudes from raw Likert scores would have resulted in overestimation of positive notional attitudes for most sociodemographic groups at the notional level and underestimation positive local attitudes for most groups at the local level. For example, the mean raw notional attitude Likert score for men aged 18-33 was 84% positive but the model estimated mean positive attitude probability after accounting for misreporting was 46% (95% CI 0.18-0.73; Appendix III).

Living with elephants

All but eight respondents (95%) had seen elephants at least once. Respondents repeatedly described elephants as “destructive” and “dangerous”, and 57% said they would prefer fewer elephants in their area, whereas 43% preferred no change and only 14% favored an increase in elephant numbers. Those with preferences for fewer elephants explained that elephants are a threat to their safety, livestock safety, and crops. Those who preferred no change in numbers rarely saw elephants and worried that an increase would cause conflicts, whereas those who preferred more elephants were concerned about the loss of elephant populations due to poaching and habitat loss or hoped that more elephants would increase revenue from wildlife tourism. Over 73% of respondents (n=130) believed that elephants impact daily life in their communities when they are nearby, and the most frequently reported emotion associated with elephant presence was fear. The most frequently described impact of elephants was people changing their activities due to fear of encountering elephants (92%), which caused herders to avoid preferred grazing routes and areas where access was effectively ‘blocked’ by the presence of elephants, parents to keep children home from traveling to school because of fear that children would encounter elephants, and everyone avoiding travel to markets and water sources. Other impacts included crop and property destruction (e.g., fences) (38%), loss of livestock life (< 1%) and loss of human life (<0.5%).

Only 22% of respondents (n=39) had directly experienced conflict with elephants. Crop destruction was most frequently cited as the biggest problem (69%), followed by restricting movements of people and livestock (26%), threatening human safety (15%), killing livestock (1%), and causing injury to or loss of human lives (< 1%). Amongst respondents that cultivate and had experienced crop loss during the 2019 and 2020 growing seasons (n=89), all reported that some loss was caused by wildlife. However, only 31% selected wildlife as the biggest cause compared to weather, pathogens, and insects. When asked which animal caused the most damage, zebra were the most frequently reported species (31.6%), followed by baboons (20%), warthogs (16.5%), and elephants (12.7 %).

Benefits derived from elephants were reported by 41% of respondents (n=73) but most people described the benefits as indirect. The most frequently reported (indirect) benefit was that elephants attract tourists to Narok County and therefore support the economy (51%), which some respondents believed can increase the value of livestock at markets due to an influx of cash from employment in tourism. About a quarter (27%) of respondents reported jobs in tourism or conservation as benefits (held mostly by relatives but seen as more direct) and 12% mentioned community development projects funded through tourism or conservation NGOs. A minority of respondents described non-economic benefits from elephants, for example that when elephants push down trees to feed on roots, they make easily accessible firewood.

Perceptions of Human, Elephant, and Livestock Coexistence

Perceptions about coexistence among respondents (n=177) were mixed, but only 22% favored coexistence in their communities. Most respondents in favor of coexistence said it was a result of tradition and precedent that should be continued to benefit future generations (47%). One respondent described it this way: "*elephants have been staying many years with people and livestock and that is* [evidence] *that they can still live together for many years to come*". Others mentioned economic benefits of elephants through community conservancies, and a few respondents cited rights of wildlife, for example, one respondent explained: "*wildlife have a right to move freely*". But most who favored coexistence also identified challenges and threats to coexistence, as one respondent described: "*wildlife are the backbone of the Kenya economy, especially the Narok economy, but local people are suffering a lot from losses causes by wildlife*". Another respondent commented on how relationships with elephants have changed over time because of increased competition for space and resources: "*there was a time when harmony was maintained between elephants and Maasai, problems between them were minimal in comparison to now. But that was when the human population was lower, and competition for land and resources was less, but now, because of human population increases, there is increased demand* *for food and* [this] *causes* [habitat] *of elephants to be encroached for reason of food resulting in conflict*".

Most respondents who were not optimistic about coexistence (83%) voiced that conflict is a certain outcome of people, elephants, and livestock sharing space because of threats to human safety, livestock safety, and crops, for example: "*elephants can kill both livestock and people and also destroy crops*". Another respondent stated: "*it is people who should coexist with livestock, not elephants*". Other challenges to coexistence included concern over competition for water and pasture between livestock and elephants (9%), and a lack of tangible benefits from wildlife generally (10%). Finally, an emergent theme across responses was a sense of exclusion from power and decision-making. For example, one person described their frustrations and concerns this way: "*the government needs to involve local people in decision making regarding wildlife conservation, as they have coexisted together with wildlife for long time, and we feel we are not included or important*."

4.4 DISCUSSION

Accurate estimates of local attitudes in communities living with and near wildlife is directly relevant for conservation. Our study demonstrates that the accuracy of self-reported attitudes is improved by accounting for response bias, and that when interpreted with the deeper context provided by qualitative data, this can provide robust information about attitudes and what explains attitudes. Although many people expressed notional support for elephant conservation, most were not also positive about sharing space with elephants at a local scale, and our approach allows for quantification of this difference. People who identified sociocultural values associated with elephants were more notionally positive, but at the local level, conflict experience with any wildlife species lowered the probability of people to be positive towards elephants. Qualitative data highlighted that concerns about safety, well-being, and autonomy likely contribute to lower positive local attitudes. Overall, our results suggest that conservation approaches focused on sustaining existing sociocultural values and relationships with wildlife while also investing in human well-being and safety measures and could improve conservation outcomes in shared landscapes. We include recommendations for conservation practitioners to directly support conservation planning in the region given that land privatization and zoning is currently underway.

Our results provide evidence that a greater focus among conservation practitioners on sustaining sociocultural values and traditions while adapting approaches as values change could lead to better conservation outcomes (Dickman *et al.* 2014; Fernandez-Llamazares *et al.* 2020; Melubo 2020; Dheer *et al.* 2021). People who believed elephants have sociocultural value were the most likely to be notionally positive about elephant conservation, which aligns with research showing that values can be strong predictors of wildlife-related attitudes (Manfredo 2008; Teel & Manfredo 2009). The most important values people ascribed to elephants were economic or ecological and tied to traditional ecological knowledge of elephant roles. Many respondents who expressed optimism about coexistence cited tradition and the precedent of coexistence with wildlife as a practice that should be continued and linked this to the concept of *eramatare*, a Maasai ethos of relationship and reciprocity between people, rain, land, vegetation, cattle, and wildlife (Melubo 2020). In other societies (mostly North America) economic valuation of wildlife has been associated with a 'domination' wildlife value orientation meaning that the person tends to have a utilitarian view of wildlife and prioritize human needs and well-being (Teel & Manfredo 2009;

Manfredo *et al.* 2021). But it is not clear in Maasai communities how economic valuations might contrast with or complement other sociocultural values of elephants and traditional ecological knowledge, suggesting that more research into wildlife values in Maasailand is needed (Western *et al.* 2019; Dheer *et al.* 2021).

Experiencing conflict with any wildlife (most respondents; n=156) significantly reduced the probability of respondents to have positive local attitudes towards elephant conservation. Though our results showed that formal education can increase the likelihood of being locally positive, formally educated respondents who had experienced conflict were less positive than those who had not experienced conflict irrespective of formal education. Contrary to our expectations, experiencing conflict with elephants alone did not influence positive attitude probability. However, open-ended responses revealed high levels of perceived threats to human life, livestock, and crop destruction associated with elephants and these threats lowered optimism for human-elephant coexistence. For example, 73% of respondents believed that elephants negatively impact daily life in their communities when elephants are known to be nearby although only 22% reported experiencing HEC, and among those who lost crops to wildlife, elephants were not the most frequently reported species causing the most crop loss. These results indicate that though HEC is relatively infrequent in the region, the risk of conflict and the perception that elephants and other wildlife often negatively impact the lives, well-being, and livelihoods of others were likely drivers of lower local positive attitude probabilities.

When HEC does occur, those who are impacted can suffer severe financial losses and/or physical and emotional trauma (Kaelo 2007; Cassidy & Salerno 2020; Nyumba *et al.* 2020) and many respondents suggested that they feel their safety is not a priority of wildlife officials. For example, on respondent said: "[The] *government loves the wildlife more than life of people and they give much attention to wildlife more than the people who are losing their live[s] and properties from wildlife*". This sentiment was echoed during co-interpretation discussions, when a participant asked and others then agreed: "*why does the government respond quickly when a person kills an elephant, but not when an elephant kills a person*?" Similarly, Western et al. (2019) found that elephants were perceived to pose the greatest threat to human life compared to any other species across Maasai communities in other parts of Kenya, and studies from North America and Europe have found that perceived risks/threats reduce acceptance and tolerance for other large mammals (Frank *et al.* 2015; Adams Knopff *et al.* 2016; Western *et al.* 2019). Elephant conservation initiatives that directly address safety concerns and perceived risks/threats in addition to conflict mitigation could lead to better conservation outcomes. For example, government agencies and NGOs could employ local community rangers that specifically provide security for communities living near elephant core areas. This was a potential strategy to support coexistence suggested by three respondents and strongly supported in co-interpretation discussions.

Model estimates showed no evidence that respondents who do not cultivate were more positive about elephants than those who do. But qualitative responses exposed that crop destruction by elephants was perceived to be a ubiquitous problem and a barrier to coexistence even though only 24% of respondents reported crop cultivation as their primary income source. This aligns with findings that the adoption of cultivation has shifted Maasai attitudes towards wildlife over time and generally resulted in less positive attitudes (Okello 2005; Browne-Nunez *et al.* 2013; Fernandez-Llamazares *et al.* 2020). Our results also highlight that the perceived threat that elephants pose to crops was greater than reported rates of elephant crop damage. It is also noteworthy that elephants were widely perceived as a threat to the lives of livestock. Elephants killing livestock has been reported (Thouless 1994) but little information on this behavior exists and more research is needed to understand it.

Experiencing benefits attributed to elephants did not increase local positive attitude probabilities towards elephants, and a key theme that emerged from open-ended responses and co-interpretation was that the costs of living with elephants outweigh the benefits in the region. Open-ended responses from conservancy members revealed that though benefits exist, most thought they were too little or indirect to be impactful, whereas others expressed dissatisfaction with conservancy leadership and stated that benefits are not equally distributed. These findings suggest that elite capture (Sheely 2015) and conservancy governance issues (Galvin *et al.* 2020) may temper perceived benefits. However, we note that employment in conservation and tourism (the most frequently reported direct benefit), was especially low when interviews occurred due to the COVID-19 pandemic. The lack of benefits from elephants and other wildlife was also identified by some non-conservancy members as a challenge to coexistence, whereas others suggested that benefits would improve coexistence. Overall, we found that benefits were less salient than concerns about human safety, well-being, and conflict in explaining attitudes towards elephants and this was confirmed in co-interpretation discussions. These findings are consistent with growing evidence that compensation or payment programs alone may not sustain coexistence between people and conflict-prone wildlife species, particularly when well-being and safety concerns remain unaddressed (Nyhus *et al.* 2005; Hoare 2012; Galvin *et al.* 2018; Karanth *et al.* 2018; Fernandez-Llamazares *et al.* 2020).

We found limited evidence that attitudes varied spatially between sub-regions and variance within sub-regions was high. Positive attitudes towards elephants were lowest in Naikarra and Ilkerin. Open-ended responses revealed little to no perceived benefits from tourism or conservation and many respondents reported that elephants frequently used ideal livestock grazing areas in these regions. Respondents from Olderkesi were slightly more positive than Enkororoi. While there are more benefits from conservation and tourism in Olderkesi, there was also greater potential to experience loss from wildlife or have poor experiences with the conservancy. In contrast, open-ended responses suggested that attitudes were slightly more positive in the east (Loita north and Olmesutye) due to few negative experiences with elephants and a positive perception of community conservancies. Respondents in these communities described elephants use of their lands as seasonal and infrequent, and many had heard about the success of community conservancies in western Narok County and expressed optimism about the potential for wildlife conservation-based income, for example through tourism of the Naimina Enkiyio forest.

A benefit of our approach is that positive attitude probabilities are standardized measures that can be directly compared across contexts and landscapes. For example, we found that local attitudes towards African elephants in our study were about 14% lower on average than attitudes towards Asian elephants across tea estates in northeast India, but our estimates of misreporting rates were similar (0.30 – 0.63 this study, 0.22–0.68 in Vasudev & Goswami 2020). We found strong evidence that false reporting of local attitudes varied between interviewers, suggesting different social perceptions of interviewers influenced response bias that could be related to social desirability. For example, an interviewer who is well-known in the study area as a person who works in wildlife conservation and tourism may be more likely to illicit falsely positive responses. Our estimate of a 30% minimum rate of false reporting in addition to variation across interviewers underscores the importance of accounting for misreporting bias when making inference about attitudes towards wildlife.

We acknowledge that reducing attitudes to positive or non-positive is a simplification of the complexity of attitudes towards wildlife which can be diverse and shaped by traditional and indigenous knowledge systems or historical and political dimensions that we may not have fully captured in our study (Hill *et al.* 2012; Fernandez-Llamazares *et al.* 2020; Kioko *et al.* 2022). It is also possible that other factors not captured in our interviews could influence attitudes. For example, measuring and including the HEC experiences of kin and neighbors in addition to the sample household in the model may result in a better representation of perceived HEC experiences given that Maasai tend to have strong social networks (Homewood *et al.* 2009; Baird *et al.* 2021). Additionally, positive attitude probability estimates from the hierarchical models did not have high precision, particularly at the local level. This is likely due in part to high rates of false-negative reporting of local attitudes in our study area (Cruickshank *et al.* 2019; Vasudev & Goswami 2020) and high individual variation in attitudes, but future work could focus on strategies to improve the precision of estimates with survey techniques that result in lower false-negative reporting rates.

Despite this, our approach provides a repeatable and spatially explicit, rigorous assessment of local attitudes that can directly inform spatial conservation plans that better support the well-being of both people and elephants. For example, our map of positive attitude probabilities could be used with ecological data and elephant movement data to prioritize suitable corridors in the region based on both ecological and social factors (Ghoddousi *et al.* 2021). It could also be used for targeted implementation of community engagement and conflict mitigation where attitudes are majority non-positive. Decades of research focused on HEC mitigation suggest that the most impactful strategies must include direct cooperation with impacted communities designed such that those communities have real agency in the process (Dickman 2010; Hoare 2015; Cassidy & Salerno 2020). Ideally, this community-oriented approach to HEC mitigation should be paired with sophisticated land-use planning that addresses the resource use and needs of both people and elephants that can be integrated into policy at relevant scales of governance. The future of at-risk wildlife will depend on whether local communities decide that there is a place for wildlife in their future and on the success of social institutions to ensure that this decision is not a choice between human well-being and coexistence.

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CHAPTER 5

CONCLUSIONS AND RECOMMENDATIONS

This dissertation investigates interactions between African elephants, people, and their livestock in multi-use savanna landscapes in east Africa with a specific focus on the Greater Mara Ecosystem (GME) in southwest Kenya. The GME is a globally important ecosystem given its biodiversity, large wildlife populations, and rich cultural history. However, the GME is also facing declining wildlife populations, land privatization and land development, the expansion of mechanized agriculture, growing livestock populations, increasing fencing and deforestation, and increasing human-elephant conflict (Serneels & Lambin 2001; Reid *et al.* 2004; Ogutu *et al.* 2016; Løvschal *et al.* 2017; Veldhuis *et al.* 2019; Tiller *et al.* 2021; Tyrrell *et al.* 2022). Thus, the research in this dissertation addresses several knowledge gaps that have direct implications for African elephant conservation in the GME in the context of global change, and others across the continent where elephants, pastoralists, and livestock share space through the application of a holistic, social-ecological systems approach. Specifically, the research in chapters 2– 4 contribute new understanding about: (1) the influence of livestock in shaping spatiotemporal patterns of elephant occurrence, (2) the roles water availability, ecosystem productivity, and people in shaping elephant movement behaviors, and how elephants adjust their movement with variation in these factors across ecoregions, (3) the identification of specific habitat types that are important for elephant movement, (4) how local people living with elephants relate to elephants and elephant conservation, and (5) how elephants impact the lived experience of local people and how these experiences influence their willingness to coexist with elephants. This research also provides several map products that can be distributed to conservation practitioners, wildlife officials, and land managers to inform conservation decision making. Chapters 2– 4 thus advance research across multiple sub-disciplines of conservation science and spatial ecology that are relevant for African elephant conservation. In the sections below, I reflect on key takeaways for conservation practitioners and researchers from chapters 2– 4, I also reflect on the process of conducting this research, and finally, I discuss remaining questions and future research directions.

5.1.SUMMARY OF RESEARCH FINDINGS AND BROADER IMPLICATIONS FOR AFRICAN ELEPHANT CONSERVATION

In Chapter Two, we used data from a remote camera trap survey collected across two years (2018 and 2019) to evaluate the effects of land management and the presence of livestock on the spatiotemporal patterns of African elephant space use in the Greater Mara Ecosystem. Two separate analyses confirmed that elephants were more likely to use the Mara Triangle protected area than community conservancies where livestock are present. This pattern was reflected in the total number of detections of elephants during the study period in addition to daily estimates of elephant occupancy across land management types. For 2018, we also found evidence that elephants likely avoid areas that are most heavily used by sheep and goats, as well as cattle, though we note our estimates of these effects had low precision. Yet, our finding that elephants also avoided open grassland in community conservancies during the day and favored riparian areas which tend to have more canopy cover and denser woody vegetation also supports the hypothesis that elephants may avoid livestock because cattle are typically grazed in large herds in open grassland in Mara Conservancies. Interestingly, our results from Chapter 3, in which we analyzed high-resolution tracking data, also suggest that riparian/riverine woodlands are critical habitat for elephants in the GME. Thus, we recommend that maintaining elephant access to riparian areas and riverine woodlands in community conservancies should be a management priority, particularly given the high number of fences that have been erected near Olare Orok conservancy (Løvschal *et* *al.* 2022) .Though we consider our finding that elephants avoid livestock in the GME to be preliminary, this suggests that uncontrolled grazing in conservancies in terms of the total number of livestock and the intensity of grazing could result in stronger spatial avoidance of conservancies by elephants which may have cascading ecological impacts due to concentration of elephant use in other areas of the landscape such as the Mara Triangle (Sitters *et al.* 2009; Veldhuis *et al.* 2019). In addition, data from camera traps showed consistent cattle grazing across most camera sites for the duration of the study period in both years. This finding, in addition to the relatively high number of sheep and goat detections, suggests that although grazing plans exist for each conservancy, they are likely not strictly enforced, and this could risk the sustainability of elephant coexistence with livestock in these areas.

In Chapter 3, we use GPS-tracking data to identify core areas for elephants (e.g., the areas that elephants used with high intensity based on the tracking data) and movement corridors that are important for ecosystem wide connectivity in the GME. Overall, our results showed that elephants consistently and strongly avoid human settlements in the GME, and that human presence also impacted the types of movement behaviors likely to be observed. Elephants in the GME avoided areas with high densities of human settlements and we found that fast, directional movements by elephants were more likely to be observed in areas near villages and towns. Additionally, results from this analysis indicate that forests and bush thickets on hillsides in addition to riparian woodlands are important habitats for elephants. Because our novel method for analyzing movements allowed us to identify multiple types of movement according to speed, directionality, and structural components (e.g., connectivity) we found interesting insights for other researchers interested in movement connectivity. Contrary to common ideas in the connectivity conservation literature about what movement corridors should or do look like (e.g., long, narrow connectors between core areas that are used occasionally), we found that elephant-defined corridors in the GME were common on the landscape and elephants used them primarily to transit within home ranges or to augment core habitats. This is important because though elephants also make long-distance movements, some of the most important locations for ecosystem-wide connectivity were small patches (1km^2) in the middle of the ecosystem that elephants crossed coming from and going to many directions, likely reflecting preferred transit routes. Another common idea in the movement connectivity literature is that animal-defined corridors should be identified by fast, linear movements. While we did identify corridors with fast, linear movement, our inclusion of structural metrics revealed that not all fast linear movements are also important for connectivity. We also observed fast, linear movements in locations with low-use intensity and low connectivity value. Thus, ignoring structural and use intensity metrics when identifying potential wildlife corridors could result in incorrectly prioritizing areas for conservation that are unlikely to be used as corridors by wildlife or may have low connectivity value. Our maps of core elephant areas, and elephant corridors can support land management plans that account for elephant movement and can help managers to prioritize the most important locations for elephant movement connectivity.

Also in Chapter 3, we compare the factors that most strongly influenced elephant movement behaviors in the mesic Greater Mara Ecosystem with the factors that most strongly influenced elephant movements in the xeric Samburu-Laikipia ecosystem. We found that water availability and vegetation productivity and predictability strongly influenced core areas for both male and female elephants in Samburu and were more influential than anthropogenic factors. Although vegetation productivity also influenced elephant core area use in the Mara, predictability did not, and human presence and canopy cover strongly influenced core area use in the Mara more strongly than water availability. Overall, these findings indicate that elephants in the Mara are likely less constrained by water and forage availability than elephants in Samburu and have more flexibility to access these key resources while minimizing the risks posed by people. However, some elephants in the Mara also used cropland, which is not present in Samburu. These results indicate potentially important trade-offs in terms of where and with whom (agriculturalists vs pastoralists) elephants may be most likely to come into conflict. Elephants in Samburu appear to have more direct resource overlap with pastoralists and thus conflict at water points and for forage during droughts may be more likely, whereas in the Mara, elephants appear to be able to avoid people and still access key resources except for when cropland encroaches on or replaces elephant habitat.

Finally, some of the most important contributions for the practice of elephant conservation from this research come from the findings of Chapter 4 and particularly, the process of co-interpretation of the research with local community members. In Chapter 4, we use mixed methods and interviews with pastoralists to understand local attitudes towards elephants in communities east of the Maasai Mara National Reserve. Respondents raised several problems that elephants can pose for pastoralists in this landscape that have been rarely reported in the past. Specifically, we found that for many people inhabiting this densely vegetated landscape, the fear of encountering elephants was a large concern, and that this fear impacted how people used the landscape when elephants were known to be nearby. We also found that many people believed that elephants pose a direct threat to the lives of livestock because aggressive elephants sometimes kill sheep and goats. We found that people who believed that elephants had sociocultural value were the most likely to be positive towards elephant conservation in general, but experiencing conflict with any wildlife lowered the probability that respondents have a positive attitude towards sharing space with elephants at a local scale. We also note that though we sought to explore the relationship between people and elephants, our model results revealed that conflict experience with any wildlife species, including elephants, was the strongest predictor of lowered willingness to sharing space with elephants at a local scale, and was more influential than experience with elephant conflict alone. This result may be due to relatively infrequent conflict with elephants in the study region. However, this result also suggests that people in agropastoral communities in Kenya may draw on interactions and experiences with any wildlife species and all past experiences with conservation efforts when forming attitudes towards the conservation of a particular species. Based on these findings, we recommend that conservation practitioners may need to take a more holistic approach to addressing conflict with wildlife and the impacts of conflict and wildlife conservation on lived experiences with a species-agnostic approach. Qualitative data revealed that safety and well-being concerns related to the perceived threats that elephants pose to human life, livestock, and crops, coupled with few social and economic incentives to support elephant conservation in community and private lands also contribute to low local positive attitudes. Overall, our results suggest that conservation approaches focused on sustaining existing sociocultural values and relationships with wildlife while also investing in human well-being and safety measures and could improve conservation outcomes in shared landscapes. As one of the most novel contributions of this research, we include a map product detailing estimated social acceptance of elephant conservation across the landscape with associated uncertainty measures to support the integration of social variables into land use and conservation planning.

5.2 REFLECTION ON THE RESEARCH PROCESS

In this section, I describe my efforts to engage in collaborative research with stakeholders of wildlife conservation in the Greater Mara Ecosystem in southwest Kenya. I discuss the ways in which I was successful in pursuing this approach as well as the aspects of this approach that could be improved upon in future collaborative research efforts. For myself, a goal of this section is to reflect on how I might improve my future collaboration with stakeholders to co-produce research, including agropastoral communities, conservation practitioners, and other scientists. My hope is that this section may also be useful to other researchers interested in pursuing a similar approach. I feel it is important to first acknowledge a fundamental tension at the center of this research, which is that each participant and stakeholder has different values, perspectives, goals, biases, and intentions for the research process which are likely shaped by their positionality or the social, political, and spatiotemporal context of their lived experience. In the case of conservation research focused on species that can negatively impact people such as elephants, often times the goals and intentions of conservationists and sometimes researchers are diametrically opposed to the goals and intentions of other stakeholders including some agropastoralist communities. As a conservation researcher, I fundamentally believe that wildlife conservation is necessary and important, and this belief, certainly even if unintentionally, influenced my research topics and decisions. Additionally, as a student researcher with limited time and funding to manage such that I could meet the requirements of the PhD degree and develop skills to help me reach future career goals, there were some aspects of the research on which I did not compromise.

My goals and intentions were to find collaboration opportunities that matched my research interests related to interactions between people and wildlife, African elephant spatial ecology, and community-based conservation. I was also determined to conduct research that could be meaningfully applied to support conservation efforts, and I strived to design my research such that I would have the opportunity to develop specific types of skills that would be beneficial to my career development. Thus, I want to acknowledge that engaging in collaborative conservation research, particularly as a graduate student, does not necessarily change or alleviate this fundamental tension. I felt this tension throughout the research process. However, I strongly believe that working to understand the perspectives, lived experiences, and values and goals of others, and striving to finding openings where compromise might be possible and mutual understanding between stakeholders is increased, is a worthwhile endeavor and is necessary to improve the practices of conservation and conducting conservation research.

Collaboration

I partially guided my approach to collaborative research based on the work outlined by David-Chavez and Gavin (2018), in which the authors offer key indicators for researchers for responsible community engagement and present a scale of Indigenous community participation in the research process ranging from "contractual" (least amount of community participation), through "consultative" and "collaborative" to Indigenous (highest level of Indigenous community participation; David-Chavez & Gavin 2018). David-Chavez and Gavin define collaborative participation in this context as a research process in which community members and researchers work together on the research, but researchers have primary authority over the process (David-Chavez & Gavin 2018). My goal was to at minimum achieve a fully collaborative level of participation with communities, and to design my process while to ensure that I: (1) do no harm, (2) follow ethics standards, (3) do work that was relevant to the concerns and interests of communities, (4) give due credit, and (5) to share and discuss research findings with community members and stakeholders.

I made an effort to initiate collaboration with local stakeholders in Kenya to identify a location to conduct research that met my research interests and could be beneficial for to stakeholders. I first traveled to Kenya in July of 2018 and visited three different parts of the country where mixed-use savannas, elephants, and community-based conservation occur. Through the connections of and with the help of my advisor, I met with government officials and scientists at Kenya Wildlife Service, the Department of Resource Surveys and Remote Sensing, researchers and scientists and the University of Nairobi, multiple conservation organizations and wildlife researchers, and several leaders of community-based conservation efforts in Kenya including conservancy managers. These meetings were crucial to understand what research was already underway so as to not duplicate efforts, to identify potential collaborators, to acknowledge and learn from Kenyan expertise on the topic of wildlife conservation in Kenya, and to identify potential research needs that could serve Kenyan institutions and communities. However, I want to acknowledge that without my advisor's reputation and connections, these initial connections would have likely been much more difficult to make. In the Greater Mara Ecosystem, this trip included a brainstorming session with people working in community-based conservation to identify key research needs in the ecosystem. I took detailed notes at most meetings and found this trip and my notes to be crucial to identifying which region had the most overlap of opportunity and research needs that met my interests and goals. Based on this trip, I decided to work in the Greater Mara Ecosystem and center my research on collaboration with Mara Elephant Project (MEP), an elephant conservation organization. I was also pursing collaboration with other academic institutions for data sharing, and my research plan was very flexible and somewhat unclear. This was initially unnerving but ended up being somewhat of an asset because everything changed when I returned to Kenya and of course, after the breakout of the COVID-19 pandemic.

I returned to Kenya in mid-January of 2020, ready to start planning and implementing my field research. I was in the Mara for about 6-weeks before I had to make an emergency trip home due to the outbreak of COVID-19. During this time, I made a major pivot in my research plan to focus much of my research on a remote region in the eastern Greater Mara Ecosystem to adapt to the research needs outlined by Mara Elephant Project's CEO and Director of Research and Conservation. I also made this pivot because I discovered that another researcher was just wrapping up near identical research on community attitudes towards and issues with elephants in the central Mara conservancies. Though 6 weeks was much less time than I expected to have in the field, I managed to forge critical connections with MEP, other scientists, and a few community members working in conservation and community development that I ended up hiring as field researchers, including one person who was from the Olderkesi area in the new region where I would conduct research. However, it was a major challenge to shift my study area to a remote location where we all, myself, MEP, and some of my research team, were less familiar and less integrated with the communities. All of us except one were complete outsiders, and the logistics of working in this remote place was difficult.

Thus, what was most missing from the initial trip to Kenya and the 6-weeks I spent trying to get my bearings in the field was the opportunity to talk more directly with conservancy members and agropastoralists from the communities that we visited and those where we planned to conduct research. The individuals from Maasai communities that we did speak with tended to be those who were already working in or connected to conservation, and those with higher formal education and wealth than the average person. In hindsight, I can see how this lack of community representation likely contributed some bias in identifying research needs in initial meetings (e.g., talking almost exclusively to other people who also believe that wildlife conservation is necessary and important) and may also have contributed to a positively biased view of community-based conservation programs in the Mara and how they were working for Maasai communities.

Overall, I think that I was successful in collaborating with local conservationists and pursuing research topics that were highly relevant to conservation practitioners and leaders of community-based conservation in Kenya. However, my research was not necessarily driven by what was most relevant for local Maasai communities. I feel strongly that more time, and thoughtful conversations with a greater diversity of people from the communities in which I plan to work would be an important step to improve any future collaborative research with communities. However, I think that achieving this would require more time to truly get to know people, and funding for this type of activity is not typically available. Evaluating my research process based on the scale of engagement with communities (discussed above) rather than organizations and institutions, I think my research process was closer to 'consultative' than 'collaborative', because my research team and I made all decisions about the content and topic of the research in the design process and data collection process. While my research team included two local Maasai, who helped to shape the research, additional community involvement in designing the research did not happen, and this was the biggest shortcoming of my collaborative research effort. In the future, I would improve my process by integrating more community participation at the design and planning stages. However, I would note that this type of activity and research conduct is not typically logistically or financially supported for most graduate students.

Remote Research

Shifting unexpected to fully remote research was difficult, and I do not recommend a fully remote approach if it can be avoided. However, I think there can be value in partially remote research. In my case, I felt particularly well set-up to succeed because I had worked over the previous year to solidify my collaborations and connections in Kenya, and I did get some time in the field. For my collaborations with MEP and other academics, I tried to attend all virtual group, lab, and research meetings to keep conservations going. Most importantly, I had been able to hire experienced co-researchers in Kenya right before my departure. Both had experience with social surveys and working in their communities in the conservation and community development space. However, conducting the research remotely did heighten cultural and language barriers that sometimes impacted the efficiency and quality of the research. To overcome these barriers and ensure that quality data was collected, I created various media that I shared digitally with my team primarily via WhatsApp and video-call software. I created training and orientation documents for interviewers, and guide to all the important aspects of the research for my field manager to teach interviewers during training. This included videos showing how to use remote data collection software on mobile phones, complete with tutorials for how to complete specific tasks using mobile app data collection software, how to interact with potential respondents, how to ease into questions and how to obtain free prior informed consent from potential respondents. I also requested photographic and video evidence of completed tasks and training, and checked-in often, sending messages nearly every day during data collection to ask about what was working and not working in the process.

The biggest hurdle was trying to hire a new researcher remotely who I had not meet in-person. It became clear after about three weeks of trying to communicate with this person via mobile phone, and reviewing the data they had submitted, that this person was not interested in the position and was not preforming research tasks up to standard. I ended up losing some research funds and having to throw out poor quality data. Also, upon my return to Kenya in 2021, I learned that this person had offended some community members while trying to preform research tasks and left some people with a bad experience with our research project. So, I did not fully succeed in causing no harm in my research efforts and I regret this deeply. In the future, I will ensure that any co-researchers and research assistants are also equipped to do no harm. In the end, what made the remote research possible was working with high-quality research team members, flexibility, embracing technology, constant communication, and on-demand problem solving during data collection.

Co-interpretation and sharing findings with communities

In August of 2021, I was finally able to return to Kenya. During this trip I managed to somewhat succeed in sharing the findings of the research with members of those communities that had participated in the interviewers. Another goal of sharing was to engage in co-interpretation to discover if my conclusions and interpretations of the content of interviews resounded as relatively true and accurate with local people, to identify where people might disagree with our findings, and to ensure that there was no obvious misrepresentations or potentially harmful information that I was planning to share with a wider audience. A major challenge was trying to find creative ways of sharing social survey data in accessible formats so that it was understandable and interesting to others, including those with low literacy. My strategy was to create a 2-page summary of the findings, with limited text and a focus on infographics. We then organized two meetings in different regions where we conducted interviews, invited members of the community, and gave attendees a color copy of the summary. I then gave a presentation that closely followed the content of the summary, and had a colleague live -translate the presentation in Maa language, highlighting where on the handout we were in the content. At one meeting, we had a projector and used a PowerPoint, but at the other meeting held outside, we relied on the handouts. This approach seemed to work OK, but in the future, I may try another format oriented more like a discussion than a presentation. Because I relied on my colleagues and co-researchers to use their social networks to help organize and invite people to the meetings, it is likely that there was some bias in who attended. There were between 10-30 attendees across meetings and meetings including the discussion lasted 1-2 hours. After sharing the findings, we held informal focus-group interviews with a smaller group of attendees (7-10) to co-interpret the information. I had a dry-erase board where I took notes and wrote down different prepared statements summarizing my key takeaways from the interview responses. Attendees then discussed as a group the extent to which they felt the statement was true or not, and why, or how they would change it to make it more accurate.

It was encouraging to find that overall, attendees agreed with our interpretations of the interview data, and in some cases, were willing to ask questions and voice their opinions, even when they disagreed with another attendee or something we discussed. However, I got the sense that cultural norms, including deference to older, influential, and male participants may have curtailed individuals from speaking up and voicing contradictory viewpoints. My presence as an outsider, also likely contributed to this and I had not previously met most of the attendees. Some insights from this process were very valuable to improving the relevance of our work to local people. However, I also received a clear message that for some people, issues with elephants were not a primary concern, and that issues with government personnel, or other wildlife-conflict such as carnivore predation of livestock were more pressing topics. My concern that my research was not driven primarily by local concerns of regular people in these regions was thus apparent. Also, because of logistics and limited funding, we only reached a small proportion of people for sharing and co-interpterion. In the future, it would be ideal to plan for more sharing with a greater number of people. In Loita, the most remote community that participated in the research, attendees expressed that this was the first time a researcher had ever returned to their community in an attempt to return and share research findings back with them.

Interdisciplinary research

From the start of my PhD program, I was insistent that I wanted interdisciplinary training because human-wildlife interactions research is a multidisciplinary field and I felt understanding both wildlife and human components at a deep level is necessary to advancing this field. But despite the now wide recognition for better integration of human and social processes in conservation science, there are several barriers to achieving this integration, and there remains relatively little discussion of these barriers in the literature though see Niemiec et al. (2021). One barrier is the lack of interdisciplinary training at the graduate level to facilitate the development of interdisciplinary scientists. The reality I experienced as a student interested in multiple disciplines was that the only option was to work and try to train in multiple disciplines, e.g., to double my learning efforts. Mostly, I did this extra learning on my own with limited support. Based on my experience as a student and now applying for jobs, my opinion is that there is still little room for interdisciplinary, social-ecological wildlife scientists, particularly outside of the tenure track career path. I also feel that the academic community continues to encourage and reward evermore narrow and deep expertise, and that interdisciplinary work done by an individual, rather than a team of researchers where each contributes something from their discipline, continues to be critiqued as insufficiently deep. Thus, I strove to dive deep into multiple disciplines. The downside of this approach was that it took considerably more time, and was considerably more difficult, than pursing research that fell neatly in one discipline and focused on working with a single data type or analysis method. The positives of having taken this approach are that I have finished my degree with a broad skillset for research in multiple disciplines important in conservation, as well as experience and competence at working with varied datasets and analysis tools to answer research questions. I also gained invaluable insight and understanding into the human side of human-elephant interactions, and pursuing that experience and understanding is something I would choose to do again. I hope that in the future I will have the opportunity to continue to develop my interdisciplinary research.

5.3 REMAINING QUESTIONS AND FUTURE RESEARCH DIRECTIONS

One of my goals in this dissertation was to more directly integrate the wildlife and human components of social-ecological savanna ecosystems to support spatial planning (e.g., integrated spatial ecology, Chapter 1). However, partially due to the difficulties and limitations discussed in the above section, I did not have the time or resources to complete the task of fully integrating these different components into a new research product. I also assert that integrating social, wildlife, and landscape components to produce new meaningful information is a challenging, cutting-edge research project on its own. Thus, I view working on the integration of the spatial data products that I have developed in this dissertation to support conservation planning as the biggest future direction for my research. The biggest remaining question is exactly how might we do this? The elephant movement connectivity and corridor maps produced in this dissertation provide an important empirical estimate of where elephants are most likely to move through the landscape. However, these estimates do not incorporate other key factors essential to wildlife corridor design and conservation landscape planning such as administrative boundaries, social acceptability, legal and political requirements, and effective corridor width. To begin, I plan to integrate my social acceptability maps with the elephant corridor maps and experiment with different approaches to prioritize specific areas of land that are most suitable for protection based on social acceptability and elephant ecology. For example, one approach could be to integrate the data layers using a weight-based ranking system, that can allow for spatial-prioritization of potential corridors based on weighting rules (Cushman *et al.* 2018; Sinclair *et al.* 2018). The goal of such as approach would be to identify areas that are both ecologically and socially suitable for conservation intervention.

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APPENDIX I

SUPPLEMENTAL INFORMATION FOR CHAPTER 2

1.1 Overall Performance of Machine Learning Model Used to Classify Camera Trap Images

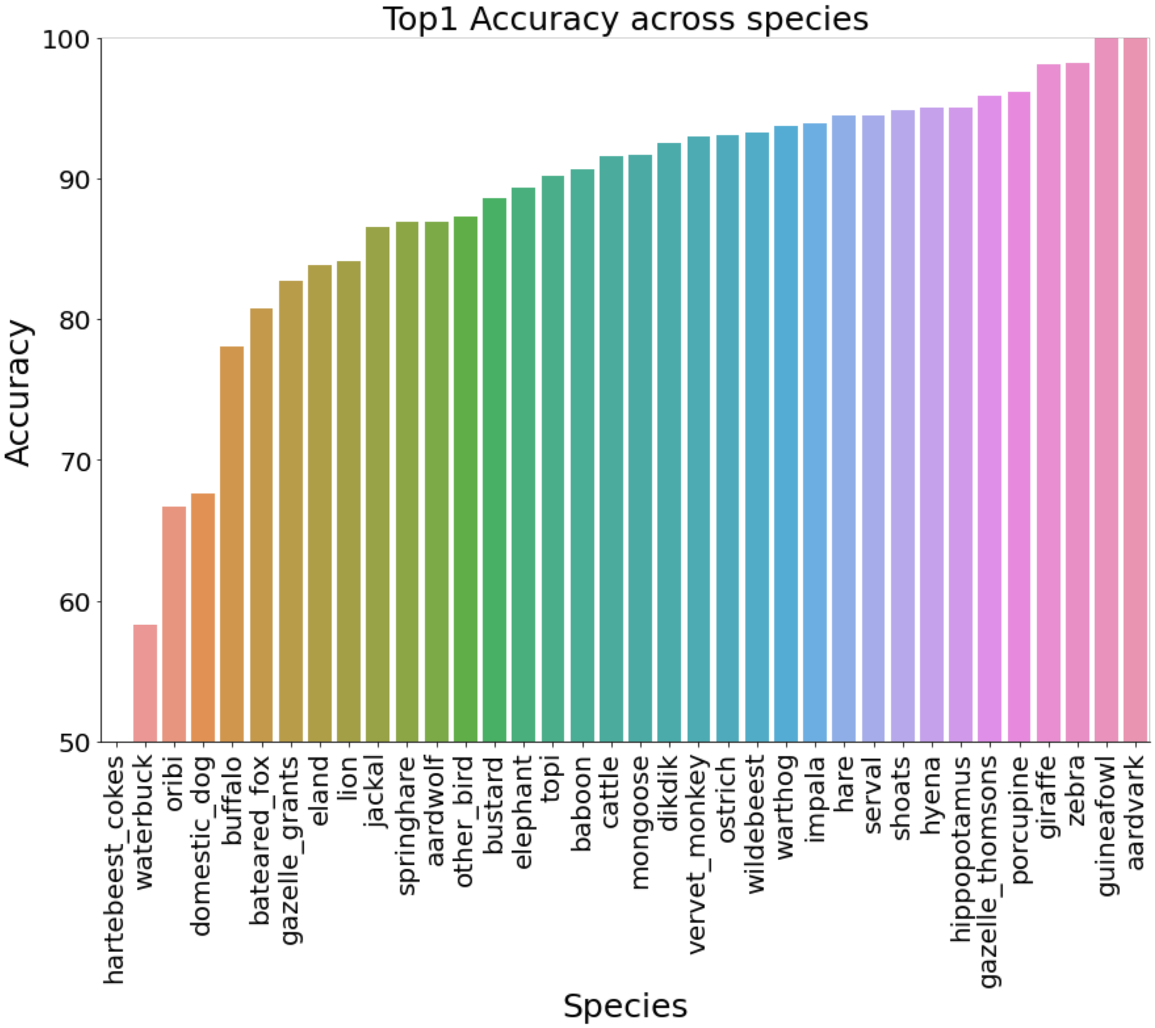


Figure S1.1. Top one accuracy for all species and species groups in the test dataset (n = 25,000 animal image crops) labeled by machine learning using a 90% confidence threshold for machine learning labels with increasing accuracy scores from left to right across species groups.

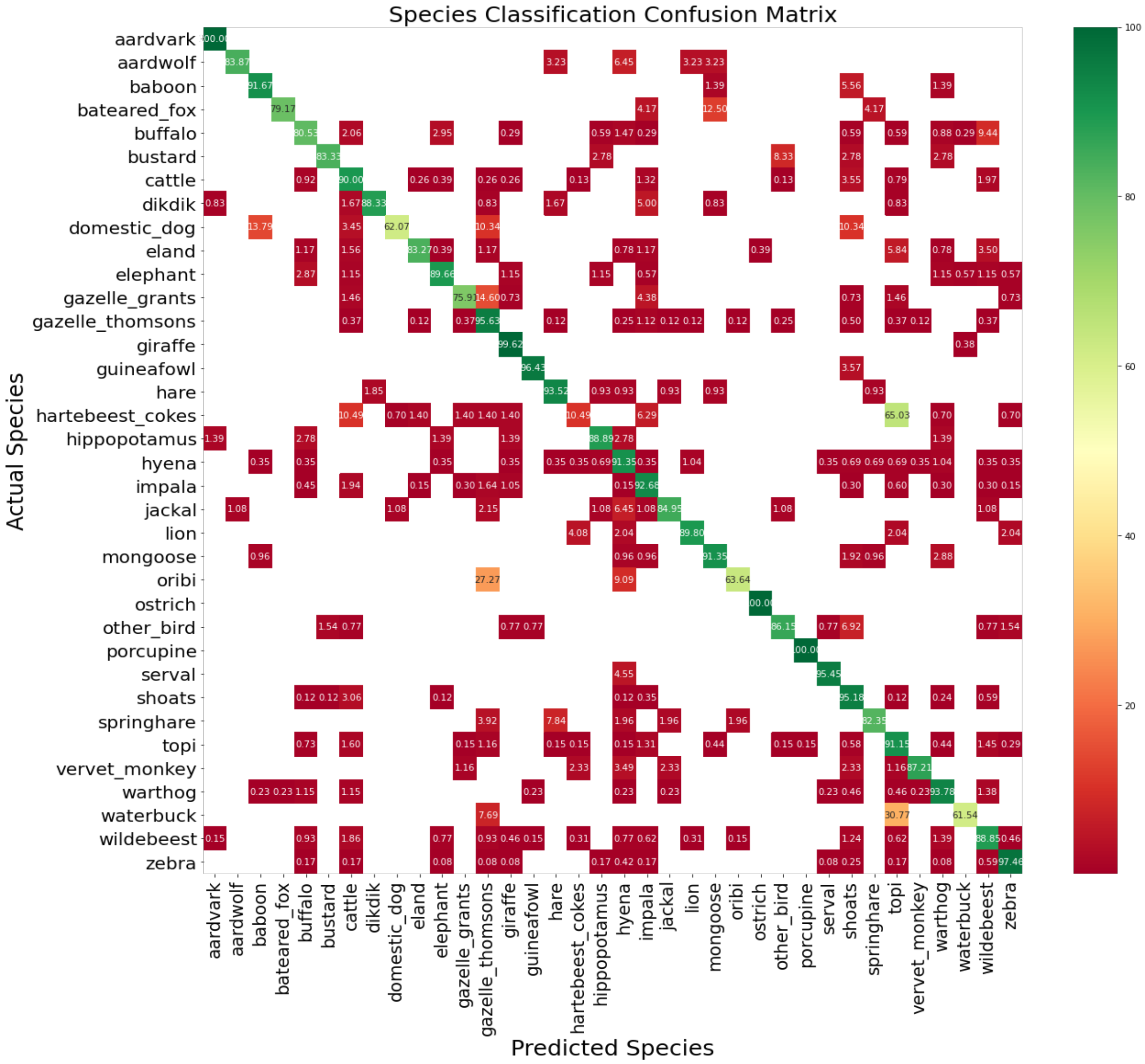


Figure S1.2. Confusion matrix for all species (or species group) showing the proportion of correctly classified labels and the proportion of misclassified labels by species for the test dataset labels generated by the machine learning model.

1.2 Validation of Machine Learning Labels in Ecological Models

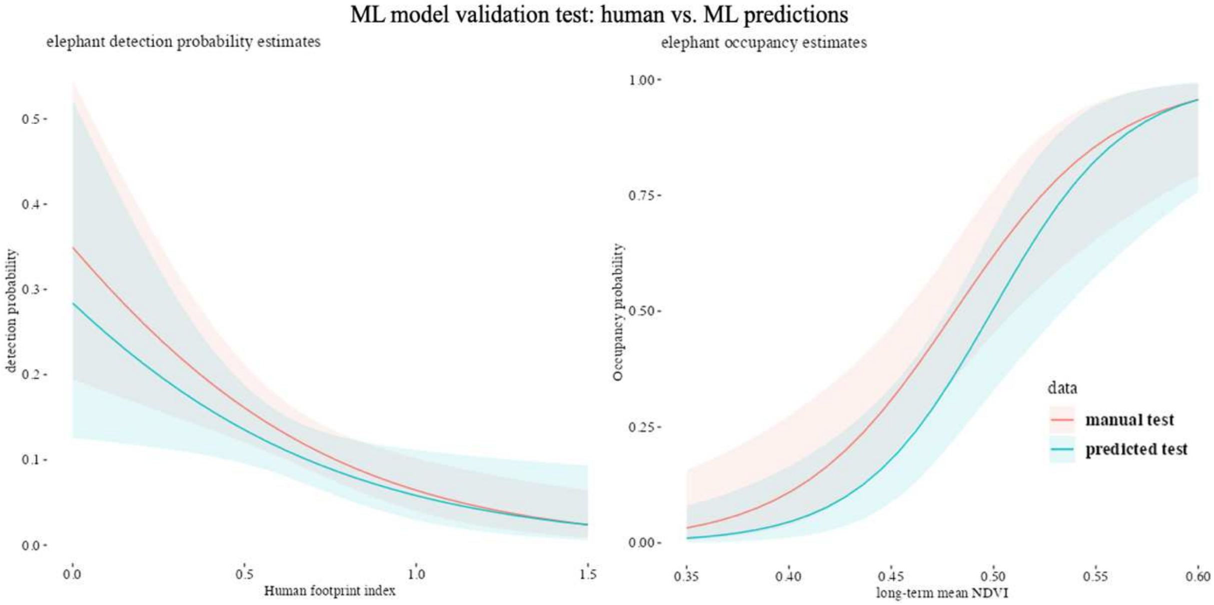


Figure S1.3 Plots comparing estimated detection probability for African elephants (left) and occupancy probability (right) with associated 95% confidence intervals for the human labeled test data (manual test) and the machine learning generated labels (predicted test) for the test data in an occupancy model with covariates on both parameters at a 90% confidence threshold for the machine learning labels.

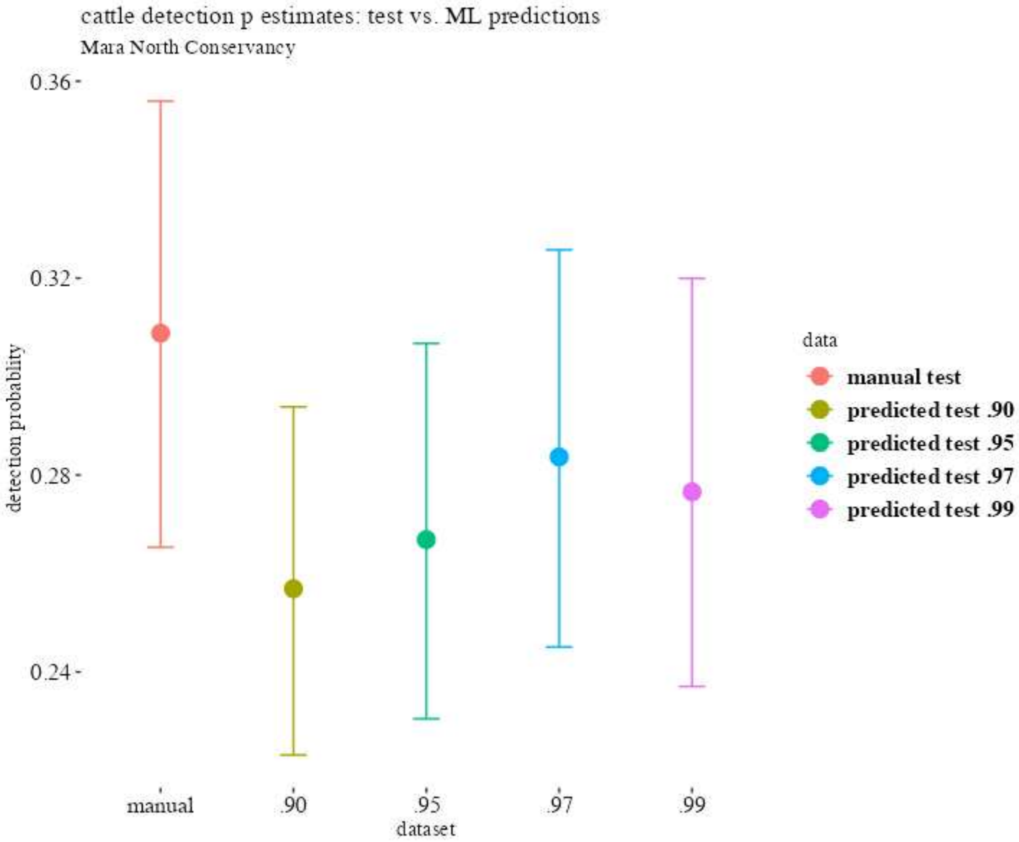


Figure S1.4 Plot comparing the estimated detection probability for cattle in Mara North Conservancy between the human labeled test data (manual test) and the machine learning generated labels (predicted test) at confidence thresholds of .90, .95, .97, and .99 for the machine learning labels.

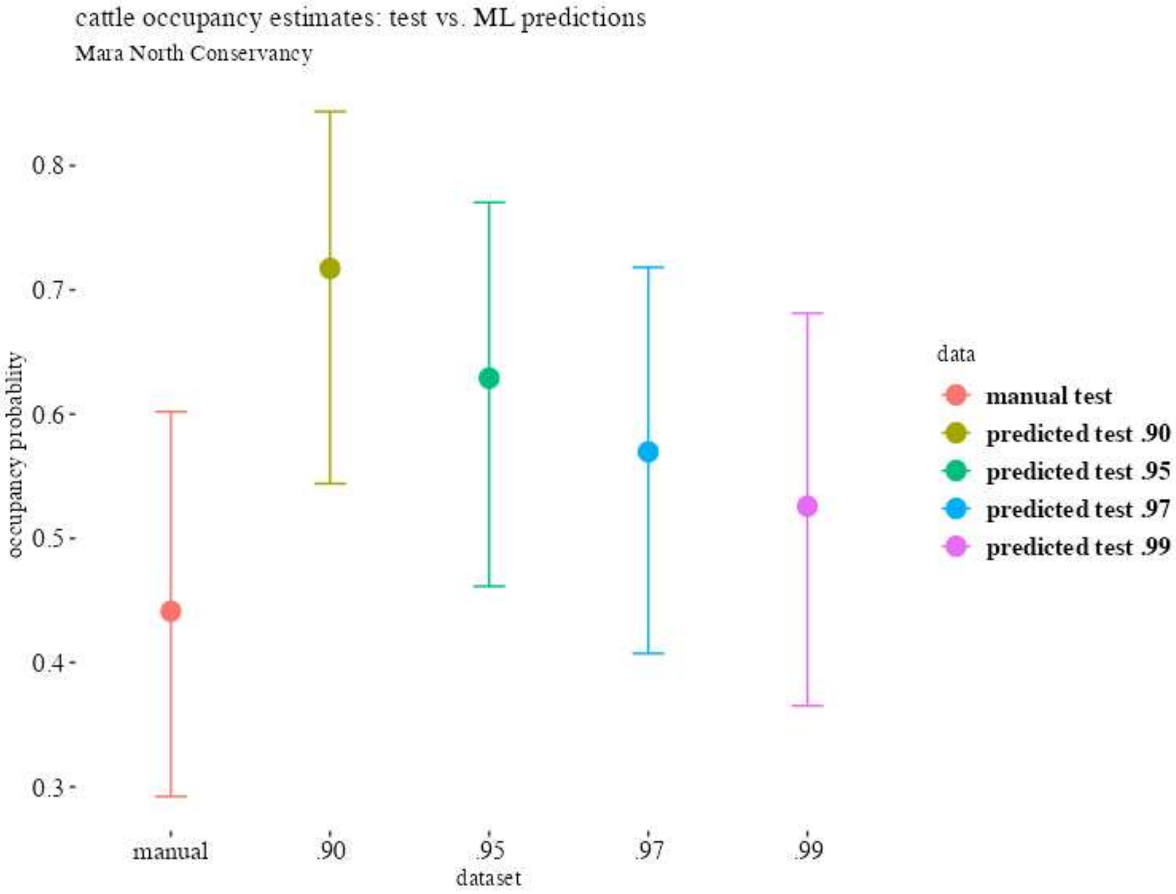


Figure S1.5 Plot comparing the estimated occupancy probability for cattle in Mara North Conservancy between the human labeled test data (manual test) and the machine learning generated labels (predicted test) at confidence thresholds of .90, .95, .97, and .99 for the machine learning labels.

1.3 Components and Weighting Scheme for Local Human Footprint Analysis

The spatial data layers used to create a local human footprint layer were downloaded and extracted from the public Landscape Dynamics database as described in Tyrrell *et al.* (2022). The tables below include additional detail for the classification of each feature or land-use type used in analysis.

Table S1.1. Geospatial layers and weight for each layer used in a weighted sum to estimate the local human footprint in the Greater Mara Ecosystem.

Layer	Weight
Boma density in a 500m radius	0.30
Distance to town center, lodge, or hotel	0.25
Fence density (classification in Table 1.2)	0.10
Roads (classification in Table 1.3)	0.25

Table S1.2 Weights used for combining fence density layers into a weighted sum based on fence type with density of fence lines calculated for each 30m^2 pixel.

Fence Type	Weight
Wire Fence	0.3
Electric Fence	0.5
Other Fence	0.2

Table S1.3 Classification values used for proximity to primary, secondary, and tertiary roads before combining all roads layers using a weighted sum.

Distance	Primary roads	Secondary roads	Tertiary roads
> 5.0 km	5	3	2
.75 – 1km	4	2	1
0.50 - .75 km	3	1	1
0.25 - 0.50 km	2	1	0
0.1 - 0.25 km	1	1	0
0 - 0.1 km	5	0	0

1.4 Full Model Selection Results

The following tables contain the full model selection results for the candidate false-positive occupancy models used for 2018 and 2019 occupancy estimation. All tables include the model formulae, the negative log-likelihood value (LogL**),** the number of estimated parameters (K), the

AIC value, the delta AIC value (Δ AIC), the model weight, and the cumulative weight (CumWt) of candidate models.

Table S1.4. Univariate model selection table for occupancy (*ψ)* false-positive occupancy models for African elephants at all camera sites in 2018 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., *b* (~1), and p_{10} (~1) in all models).

Model	**LogL**	**K**	**AIC**	**Δ AIC**	**Weight**	**CumWt**
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~dist2drain)	1686.35	7.00	3386.69	0.00	0.39	0.39
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean250)	1687.03	7.00	3388.05	1.36	0.20	0.59
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean500)	1687.50	7.00	3389.00	2.30	0.12	0.72
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~open500)	1688.52	7.00	3391.04	4.34	0.04	0.76
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~open250)	1688.63	7.00	3391.26	4.56	0.04	0.80
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~wildebeest)	1688.74	7.00	3391.48	4.79	0.04	0.84
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~1)	1689.75	6.00	3391.50	4.80	0.04	0.87
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~Zone)	1689.10	7.00	3392.21	5.51	0.02	0.90
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~HFI500)	1689.51	7.00	3393.02	6.33	0.02	0.92
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~HFI250)	1689.59	7.00	3393.19	6.49	0.02	0.93
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~cover_2070_500)	1689.59	7.00	3393.19	6.49	0.02	0.95
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~cover_2070_250)	1689.64	7.00	3393.27	6.58	0.01	0.96
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~conservancy)	1687.73	9.00	3393.45	6.76	0.01	0.97
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~closed250)	1689.74	7.00	3393.48	6.79	0.01	0.99
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~closed500)	1689.75	7.00	3393.50	6.80	0.01	1.00

Table S1.5 Final candidate model selection for false-positive occupancy models for African elephants at all camera sites in 2018 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., b=1, and p_{10} = 1 in all models). The most supported model used for inference is highlighted.

Model	**LogL**	**K**	**AIC**	**Δ AIC**	**Weight**	**CumWt**
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ Zone)	1678.96	11	3379.91	0	0.28	0.28
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ open500)	1679.7	11	3381.4	1.49	0.13	0.42
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~Zone + wildebeest + NDVI_mean250)	1678.92	12	3381.85	1.94	0.11	0.53
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ wildebeest)	1679.94	11	3381.88	1.97	0.11	0.63
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ dist2drain)	1679.97	11	3381.93	2.02	0.1	0.74
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ open500 + dist2drain + Zone)	1678.5	13	3383	3.09	0.06	0.8
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ wildebeest + open500)	1679.53	12	3383.06	3.15	0.06	0.86
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ open500 + dist2drain)	1679.69	12	3383.38	3.47	0.05	0.91
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ wildebeest + dist2drain)	1679.94	12	3383.88	3.97	0.04	0.94
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean+ open500 + dist2drain + Zone + wildebeest)	1678.28	14	3384.55	4.64	0.03	0.97
p(~conservancy + NDVI250m + wildebeest) psi(~dist2drain)	1686.35	7	3386.69	6.78	0.01	0.98
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~NDVI_mean250)	1687.03	7	3388.05	8.14	0	0.99
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~Zone + wildebeest + open500)	1682.21	12	3388.41	8.5	0	0.99

p_{11}(~conservancy + NDVI250m + wildebeest) psi(~wildebeest + Zone)	1683.64	11	3389.27	9.36	0	0.99
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~open500 + Zone)	1683.9	11	3389.81	9.89	0	1
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~dist2drain + Zone)	1684.35	11	3390.7	10.79	0	1
p_{11}(~conservancy + NDVI250m + wildebeest) psi(~open500)	1688.52	7	3391.04	11.13	0	1
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~Zone + wildebeest + dist2drain)	1683.55	12	3391.1	11.19	0	1
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~wildebeest)	1688.74	7	3391.48	11.57	0	1
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~wildebeest + open500)	1691.4	11	3404.79	24.88	0	1
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~wildebeest + dist2drain)	1693.42	11	3408.85	28.94	0	1
p_{11} (~conservancy + NDVI250m + wildebeest) psi(~open500 + dist2drain)	1694.68	11	3411.35	31.44	0	1

Table S1.6 Univariate model selection table for occupancy (ψ) false-positive occupancy models for African elephants at all camera sites in 2019 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., b (~1), and p_{10} (~1) in all models).

Model	**LogL**	**K**	**AIC**	**Δ AIC**	**Weight**	**CumWt**
p_{11} (~Zone + NDVI250m) psi(~NDVI_mean250)	1740.11	6	3492.22	0.00	0.28	0.28
p_{11} (~Zone + NDVI250m) psi(~NDVI_mean250)	1740.27	6	3492.55	0.33	0.24	0.52
p_{11} (~Zone + NDVI250m) psi(~conservancy)	1738.48	8	3492.96	0.74	0.19	0.71
p_{11} (~Zone + NDVI250m) psi(~dist2drain)	1741.69	6	3495.38	3.17	0.06	0.77
p_{11} (~Zone + NDVI250m) psi(~wildebeest)	1742.07	6	3496.13	3.92	0.04	0.81
p_{11} (~Zone + NDVI250m) psi(~1)	1743.23	5	3496.45	4.24	0.03	0.85
p_{11} (~Zone + NDVI250m) psi(~Zone)	1742.45	6	3496.91	4.69	0.03	0.87

p_{11} (~Zone + NDVI250m) psi(~open250)	1742.59	6	3497.17	4.96	0.02	0.90
p_{11} (~Zone + NDVI250m) psi(~closed500)	1742.89	6	3497.77	5.56	0.02	0.91
p_{11} (~Zone + NDVI250m) psi(~open500)	1742.91	6	3497.82	5.60	0.02	0.93
p_{11} (~Zone + NDVI250m) psi(~cover_2070_500)	1743.04	6	3498.08	5.86	0.02	0.95
p_{11} (~Zone + NDVI250m) psi(~cover_2070_250)	1743.04	6	3498.08	5.87	0.02	0.96
p_{11} (~Zone + NDVI250m) psi(~closed250)	1743.17	6	3498.35	6.13	0.01	0.97
p_{11} (~Zone + NDVI250m) psi(~HFI250)	1743.21	6	3498.43	6.21	0.01	0.99
p_{11} (~Zone + NDVI250m) psi(~HFI500)	1743.22	6	3498.44	6.22	0.01	1.00

Table S1.7 Final candidate model selection table for false-positive occupancy models for African elephants at all camera sites in 2019 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., b=1, and $p_{10} = 1$ in all models). The most supported model used for inference is highlighted.

Model	LogL	K	AIC	Δ AIC	Weight	CumWt
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +wildebeest + Zone)	1712.30	8	3440.60	0.00	0.21	0.21
p_{11} (~Zone + NDVI250m psi(~wildebeest + Zone)	1713.45	7	3440.91	0.30	0.18	0.40
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +wildebeest)	1713.46	7	3440.92	0.32	0.18	0.58
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 + dist2drain + Zone + wildebeest)	1711.90	9	3441.81	1.20	0.12	0.70
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +wildebeest + dist2drain)	1713.36	8	3442.73	2.12	0.07	0.77
p_{11} (~Zone + NDVI250m psi(~conservancy + wildebeest)	1712.48	9	3442.96	2.35	0.07	0.84
p_{11} (~Zone + NDVI250m psi(~conservancy + wildebeest + NDVI_mean250)	1711.52	10	3443.04	2.43	0.06	0.90
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +wildebeest + conservancy)	1711.52	10	3443.04	2.43	0.06	0.97

p_{11} (~Zone + NDVI250m psi(~conservancy + wildebeest + dist2drain)	1712.34	10	3444.68	4.08	0.03	1.00
p_{11} (~Zone + NDVI250m) psi(~NDVI_mean250 +Zone)	1718.83	7	3451.66	11.06	0.00	1.00
p_{11} (~Zone + NDVI250m) psi(~NDVI_mean250 +Zone)	1718.83	7	3451.66	11.06	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~ Zone)	1720.25	6	3452.50	11.89	0.00	1.00
p_{11} (~Zone + NDVI250m) psi(~NDVI_mean250 +dist2drain)	1719.37	7	3452.73	12.13	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +dist2drain + Zone)	1718.78	8	3453.56	12.95	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 +Zone + dist2drain)	1718.78	8	3453.56	12.95	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~wildebeest + dist2drain)	1723.33	7	3460.67	20.06	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~dist2drain + Zone)	1723.46	7	3460.92	20.32	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250 + dist2drain)	1723.46	7	3460.92	20.32	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~NDVI_mean250)	1740.27	6	3492.55	51.94	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~dist2drain)	1741.69	6	3495.38	54.78	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~wildebeest)	1742.07	6	3496.13	55.53	0.00	1.00
p_{11} (~Zone + NDVI250m psi(~open500)	1742.91	6	3497.82	57.21	0.00	1.00

Table S1.8. Univariate model selection table for occupancy (*ψ)* false-positive occupancy models for African elephants during daylight hours in community conservancies in 2018 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., *b* (~1), and p_{10} (~1) in all models).

Model	**LogL**	**K**	**AIC**	**Δ AIC**	**Weight**	**CumWt**
p_{11}(~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~livestock)	751.22	10	1522.44	0.00	0.63	0.63
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~shoats)	752.87	10	1525.74	3.31	0.12	0.75
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~NDVI_mean250)	753.12	10	1526.24	3.80	0.09	0.85

p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~NDVI_mean500)	753.30	10	1526.60	4.16	0.08	0.92
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~wildebeest)	754.20	10	1528.40	5.96	0.03	0.96
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~cattle)	755.53	10	1531.07	8.63	0.01	0.96
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~open250)	755.83	10	1531.66	9.22	0.01	0.97
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~1)	756.94	9	1531.89	9.45	0.01	0.98
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~open500)	756.20	10	1532.40	9.96	0.00	0.98
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~cover_2070_250)	756.31	10	1532.61	10.17	0.00	0.98
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~closed500)	756.64	10	1533.27	10.84	0.00	0.99
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~cover_2070_500)	756.67	10	1533.34	10.90	0.00	0.99
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~closed250)	756.81	10	1533.63	11.19	0.00	0.99
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~dist2drain)	756.93	10	1533.86	11.42	0.00	0.99
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~HFI500)	756.94	10	1533.88	11.44	0.00	1.00
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~HFI250)	756.94	10	1533.88	11.44	0.00	1.00
p_{11} (~ NDVI250m + open250+ shoats + wildebeest + cattle) psi(~conservancy)	756.18	11	1534.36	11.93	0.00	1.00

Table S1.9 Final candidate model selection table for false-positive occupancy models for African elephants during daylight hours in community conservancies in 2018 with the most supported covariates for p_{11}. Model formulas omit constant detection parameters present in every model (e.g., b=1, and p_{10} = 1 in all models). The most supported model used for inference is highlighted.

Model	**LogL**	**K**	**AIC**	**Δ AIC**	**Weight**	**CumWt**
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + wildebeest + cattle+ NDVI_mean250 + dist2drain)	746.93	14	1517.85	0.00	0.29	0.29
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + wildebeest + NDVI_mean250 + dist2drain)	746.87	13	1519.74	1.89	0.11	0.41
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + wildebeest + NDVI_mean250)	748.34	12	1520.68	2.83	0.07	0.48

p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + NDVI_mean250 + dist2drain)	748.41	12	1520.82	2.97	0.07	0.54
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + wildebeest + NDVI_mean250)	748.62	12	1521.24	3.39	0.05	0.60
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + NDVI_mean250)	749.71	11	1521.42	3.57	0.05	0.65
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + wildebeest)	749.74	11	1521.48	3.62	0.05	0.70
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + shoats + wildebeest + NDVI_mean250 + dist2drain)	746.79	14	1521.58	3.73	0.05	0.74
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + open250)	749.96	11	1521.92	4.06	0.04	0.78
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + wildebeest + NDVI_mean250 + open250)	748.12	13	1522.24	4.39	0.03	0.81
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock)	751.22	10	1522.44	4.59	0.03	0.84
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + NDVI_mean250)	750.67	11	1523.34	5.49	0.02	0.86
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~wildebeest + shoats)	750.77	11	1523.54	5.69	0.02	0.88
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~livestock + wildebeest + NDVI_mean250 + open250)	748.88	13	1523.76	5.91	0.02	0.89
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + open250)	750.97	11	1523.94	6.09	0.01	0.91
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + shoats + wildebeest + NDVI_mean250)	749.00	13	1524.01	6.15	0.01	0.92
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats + cattle)	751.06	11	1524.12	6.27	0.01	0.93
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(wildebeest + NDVI_mean250)	751.19	11	1524.38	6.53	0.01	0.94
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + shoats + NDVI_mean250 + open250)	749.29	13	1524.58	6.73	0.01	0.95

p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + shoats + wildebeest + NDVI_mean250 + dist2drain)	748.57	14	1525.13	7.28	0.01	0.96
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + shoats + wildebeest + NDVI_mean250 + open250)	748.59	14	1525.18	7.33	0.01	0.97
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + wildebeest + NDVI_mean250)	750.87	12	1525.74	7.89	0.01	0.98
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~shoats)	752.87	10	1525.74	7.89	0.01	0.98
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~wildebeest + NDVI_mean250 + open250)	751.09	12	1526.18	8.33	0.00	0.99
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~NDVI_mean250)	753.12	10	1526.24	8.39	0.00	0.99
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + wildebeest + NDVI_mean250 + open250)	750.80	13	1527.60	9.75	0.00	0.99
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + NDVI_mean250 + open250)	752.10	12	1528.20	10.35	0.00	0.99
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~wildebeest + cattle)	753.20	11	1528.40	10.54	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~wildebeest)	754.20	10	1528.40	10.55	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + NDVI_mean250)	753.66	11	1529.32	11.46	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~wildebeest + open250)	753.97	11	1529.94	12.09	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle)	755.53	10	1531.07	13.22	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~NDVI_mean250 + open250)	754.54	11	1531.07	13.22	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~cattle + open250)	754.71	11	1531.42	13.57	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~open250)	755.83	10	1531.66	13.81	0.00	1.00
p_{11} (~ NDVI250m + cover_20_250 + shoats + wildebeest + cattle) psi(~dist2drain)	756.93	10	1533.86	16.01	0.00	1.00

APPENDIX II

SUPPLEMENTAL INFORMATION FOR CHAPTER 3

Table S2.1. Model selection tables for final mixed-effects logistic regression candidate models comparing full models containing the most parsimonious sets of both environmental and social covariates, environmental only, social only, and a null model containing only a random intercept for individual elephants and the spatial autocovariate.

High vs. medium and low use

females		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Full (Environmental and Social)	-8026.304	16227.459	0.000	1.000
	2	Environmental	-8204.764	16543.238	315.779	0.000
	3	Social	-8270.893	16613.784	386.325	0.000
	4	Null	-8468.391	16988.208	760.749	0.000
males		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Full (Environmental and Social)	-8026.304	16227.459	0.000	1.000
	2	Environmental	-8204.764	16543.238	315.779	0.000
	3	Social	-8270.893	16613.784	386.325	0.000
	4	Null	-8468.391	16988.208	760.749	0.000

Directed corridor vs. high, medium, and low use

females		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Environmental	-6,315.254	12,754.814	0.000	0.935
	2	Full (Environmental and Social)	-6,312.736	12,760.138	5.324	0.065
	3	Social	-6,402.201	12,845.838	91.023	0.000
	4	Null	-6,405.518	12,862.830	108.016	0.000
males		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Environmental	-6,315.254	12,754.814	0.000	0.935
	2	Full (Environmental and Social)	-6,312.736	12,760.138	5.324	0.065
	3	Null	-6,402.201	12,845.838	91.023	0.000
	4	Social	-6,405.518	12,862.830	108.016	0.000

Fast corridor vs. high, medium, and low use

females		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Full (Environmental and Social)	-7893.639	15891.042	0.000	0.998
	2	Environmental	-7905.118	15903.624	12.582	0.002
	3	Social	-8029.124	16120.507	229.465	0.000
	4	Null	-8040.997	16133.877	242.835	0.000
males		***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
	1	Environmental	-8099.642	16283.654	0.000	0.533

2	Full (Environmental and Social)	-8094.503	16283.923	0.268	0.467
3	Social	-8124.402	16312.083	28.428	0.000
4	Null	-8130.139	16313.010	29.355	0.000

Medium vs. low use

females	***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
1	Full (Environmental and Social)	-12540.905	25244.301	0.000	1.000
2	Environmental	-12640.838	25403.543	159.243	0.000
3	Social	-13009.521	26110.442	866.142	0.000
4	Null	-13139.139	26329.056	1084.756	0.000
males	**Model**	**logLik**	**BIC**	**delta BIC**	**weight**
1	Full (Environmental and Social)	-13,683.532	27,563.874	0.000	1.000
2	Social	-14,025.860	28,144.945	581.071	0.000
3	Environmental	-14,034.698	28,224.772	660.898	0.000
4	Null	-14,514.932	29,081.655	1,517.782	0.000

Fast vs. directed corridors

females	**Model**	**logLik**	**BIC**	**delta BIC**	**weight**
1	Environmental	-1900.239	3868.662	0.000	0.939
2	Full (Environmental and Social)	-1898.709	3874.124	5.462	0.061
3	Null	-1964.180	3970.975	102.313	0.000
4	Social	-1962.286	3975.709	107.047	0.000
males	**Model**	**logLik**	**BIC**	**delta BIC**	**weight**
1	Full (Environmental and Social)	-1883.254	3877.743	0.000	0.996
2	Environmental	-1893.137	3888.953	11.210	0.004
3	Social	-1946.984	3945.308	67.565	0.000
4	Null	-1957.962	3958.707	80.965	0.000

Low use (fast) vs. low use (slow)

females	**Model**	**logLik**	**BIC**	**delta BIC**	**weight**
1	Full (Environmental and Social)	-7749.428	15615.729	0.000	0.635
2	Environmental	-7754.853	15616.841	1.111	0.365
3	Social	-7932.526	15923.488	307.759	0.000
4	Null	-7938.705	15926.106	310.377	0.000
males	***Model***	***logLik***	***BIC***	***delta BIC***	***weight***
1	Full (Environmental and Social)	-8903.230	17947.734	0.000	1.000
2	Environmental	-8932.636	17976.271	28.537	0.000
3	Social	-9016.991	18114.709	166.975	0.000
4	Null	-9061.349	18173.152	225.418	0.000

Table S2.2 Coefficient estimates and 95% confidence intervals (log-odds scale) for male and female African elephants from the most supported mixed-effects logistic regression models evaluating the effects of landscape variation and conspecific use on the probability of observing different functional movement types. Land management is abbreviated as UP (unprotected), PA (Protected Area), and CC (Community Conservancy), NDVI refers to the mean NDVI.

	Females			**Males**		
corridor	*fast corridor vs. directed*	*medium use vs. low use*	*low use (fast) vs. low use (slow)*	*fast corridor vs. directed corridor*	*medium use vs. low use*	*low use (fast) vs. low use (slow)*
(Intercept) (UP)	2.44 (-0.13 to 5.01)	-0.38 (-1.28 to 0.51)	-2.75 (-4.18 to -1.33)	1.46 (-0.97 to 3.90)	-2.04 (-2.63 to -1.46)	-4.03 (-6.06 to-1.99)
CC	0.31 (-0.04 to 0.67)	0.29 (0.18 to 0.41)	0.01 (-0.14 to 0.15)	0.60 (0.37 to 0.84)	0.14 (0.04 to 0.24)	0.03 (-0.08 to 0.15)
PA	-0.37 (-0.71 to -0.04)	-0.16 (-0.29 to -0.04)	0.06 (-0.11 to 0.22)	1.00 (0.72 to 1.27)	-0.16 (-0.32 to 0.01)	0.25 (0.11 to 0.39)
mean NDVI	-0.31 (-0.38 to -0.23)					
NDVI * UP		0.11 (0.06 to 0.15)	-0.48 (-0.56 to -0.41)	-0.64 (-0.84 to -0.45)	0.46 (0.33 to 0.58)	-0.22 (-0.32 to -0.12)
NDVI * CC		0.48 (0.32 to 0.64)	0.16 (-0.05 to 0.37)	0.97 (0.61 to 1.32)	0.43 (0.28 to 0.57)	-0.38 (-0.58 to -0.19)
NDVI * PA		0.63 (0.41 to 0.86)	-0.65 (-0.96 to -0.35)	0.90 (0.42 to 1.38)	-0.12 (-0.36 to 0.11)	-0.11 (-0.34 to 0.12)
boma density		-0.18 (-0.24 to -0.12)			-0.14 (-0.17 to -0.10)	
distance to village center				0.39 (0.22 to 0.56)	0.07 (0.02 to 0.13)	
distance to drainage	0.27 (0.18 to 0.36)				-0.17 (-0.21 to -0.14)	0.07 (0.03 to 0.11)
closed (>70% cover)		0.08 (0.04 to 0.13)	0.08 (0.03 to 0.13)		-0.08 (-0.13 to -0.02)	0.18 (0.11 to 0.26)

open (<20 % cover)		-0.39 (-0.43 to -0.34)	0.26 (0.21 to 0.32)		-0.19 (-0.24 to-0.15)	0.28 (0.23 to 0.32)
crop			-0.08 (-0.13 to -0.03)	-0.24 (-0.32 to -0.17)	-0.20 (-0.25 to -0.15)	
slope		0.15 (0.11 to 0.18)		0.14 (0.06 to 0.23)	-0.11 (-0.15 to -0.06)	
distance to roads	0.37 (0.27 to 0.46)			0.24 (0.14 to 0.33)		
high use		0.95 (0.45 to 1.45)		1.90 (0.96 to 2.83)	1.99 (1.71 to 2.26)	-0.90 (-1.41 to -0.39)
high use females only		0.97 (0.74 to 1.19)			0.65 (0.49 to 0.81)	-0.40 (-0.64 to -0.16)
high use males only		0.93 (0.75 to 1.11)	-0.50 (-0.82 to -0.19)		1.42 (1.29 to 1.54)	-0.70 (-0.93 to -0.47)
corridor males only		0.41 (0.23 to 0.58)			0.19 (0.05 to 0.34)	
spatial autocovariate	-0.88 (-1.03 to -0.72)	1.22 (1.17 to 1.27)	-0.82 (-0.89 to -0.75)	-0.50 (-0.59 to-0.41)	0.86 (0.82 to 0.90)	-0.66 (-0.70 to -0.61)
individual variance	30.41	3.90	8.96	26.02	1.55	18.04
AUC	**0.907**	**0.814**	**0.777**	**0.918**	**0.801**	**0.834**
n=1	2,793	8,761	4,207	2,543	7,398	4,794
n=0	2,236	16,974	12,767	2,658	24,123	19,329

APPENDIX III

SUPPLEMENTAL INFORMATION FOR CHAPTER 4

1.1 Survey Methods, Questionnaire, and Informed Consent Process

Notional attitude statements		Attitude measurement	Attitude direction
1. J_c	*Elephants are intelligent animals.*	*Empathy/ respect for elephants*	positive
2.J_{uc}	Elephants only cause problems for society.	Societal norm of elephants as a problem animal	negative
3.J_{uc}	Elephants should be protected.	General conservation concern	positive
4.J_{uc}	It is beneficial to my spiritual wellbeing to know elephants live here.	Religious or spiritual beliefs	positive
5.J_{uc}	Conservation is important because it protects the environment that we depend on.	General importance of conservation for human societies	positive
6.J_{uc}	Conservation of land and wildlife is compatible with keeping livestock.	General compatibility of conservation with tradition of pastoralism	positive

Local attitude statements

1. K_c	*Elephants cause damage to our property and people's livelihoods.*	*local negative elephant impacts to livelihoods*	*negative*
2.K_{uc}	It is good for the health of the environment to have elephants around here.	local perception of elephant ecological impacts	positive
3.K_{uc}	People and livestock should live alongside elephants.	local coexistence with wildlife including elephants	positive
4.K_{uc}	Elephants are important because they attract tourism to this area.	local positive elephant impacts to livelihoods	positive
5.K_{uc}	People around here think that elephants should not live here.	local social norms around acceptability of elephants	negative
6.K_{uc}	When elephants are around here, I feel unsafe and unhappy.	local safety and well-being concerns	negative

7.K_{uc}	There are no benefits from wildlife conservation to people around here.	local assessment of economic benefits to community	negative
8.K_{uc}	Wildlife tourism could be a good alternative income source around here.	local perception of potential economic benefits from wildlife tourism	positive

Selected Open-ended Questions:

1. Are elephants important in your culture? If so, how and why? What is the role of elephants in your culture? [Iletipat iltomia tolkuak linyi?]
2. Have you ever seen a wild elephant? [Itodua aikata oltome le ntim?]
3. Can you tell me about that experience? When was this? What happened? How did it make you feel? [Ikin'dim atoliki kainyoo nataase teina rishata?]
4. Do elephants have any effect on your day-to-day life? If so, how do elephants impact your daily activities? [Keetae enkipirta nayau iltomia te nkishui ino e poki olong'? ore tenaa keetai, kaa kipirta kiyaki iltomia too mb'aa niasita?]
5. Would you prefer the number of elephants around here to increase, stay the same, or decrease? [Iyie naa keponari, keton ake enaa enatiu ashu kedoiyio esiana o ltomia tena murua?]
6. Can you explain why that is your preference? [Kaaidim ajo kaa naji inkashie?]
7. Are there any good things or benefits that you get from elephants? [Keetai ake ntoking sidan nitumito to ltomia?]
8. What (or would) you do if an elephant comes near your livestock while grazing? [Kainyoo naaji ias teneloto oltome enkalo enedaare swam inonok?]
9. What (or would) you do if an elephant came near your home? [Kainyoo naaji ias teneloto oltome enkalo enkang ino?]
10. Are there any elephants causing problems in your area? [Keetae iltomia oogira aayau enyamali te emurua ino?]

Consent

We are conducting a research study on local perspectives on conservation, elephants, and land use and would like to ask you some questions. Can I tell you more about the study? {Await confirmation}. If you say yes, what will happen is that we will have a conversation about elephants, conservation, and land. The information you provide will be used to write a scientific report representing your opinions that will teach us about what ideas, experiences, and issues you have with elephants in your area. The information you provide is confidential. This means that we will not publish your name or any personal information about you. After the interview, I will remove your personal information so that no one will know what your answers are. Your participation is voluntary, and you can end the interview at any time, or you may withdraw your consent to participate at any time without any negative consequences. The interview will last for 20-40 minutes. There are no monetary benefits to you for participating, but we will use this information to develop ways to reduce any conflicts you have with elephants and to better conserve elephants.

Documentation of oral consent: Before we proceed with the interview, do I have your permission to conduct this interview?

Enkigeroto o lomon le nyorraroto: Ore eton eitu kipou dukuya tena kilikuanare, kaata orusa lino peyie aas ena kilikuanare? Yes [Eeh] No [Meetai]

1.2 Developing certain statements

To develop the *certain* questions, we worked as a team to discuss potential causes of response bias to Likert questions based on our collective knowledge of the culture, history, and context regarding attitudes towards elephants and conservation. We developed a reasonably comprehensive list of potential reasons for (sub-) conscious response bias:

Reasons for false positives could be:

- Social norm of *Eramatare*: a Maasai cultural ethos of the cosmic links between people, land, cattle, and wildlife, wildlife such as elephants are intrinsic part of these dynamics and belong in relationship with people and cattle.

- Social norm of a "new conservation culture" in which conservation should be viewed as good because NGOs, tourism companies, and conservancies can support education, jobs and infrastructure development. In this context, protecting wildlife is a socially desired opinion or perceived to be a socially desirable opinion. This is 'new', because the 'old' tradition of nonviolence against wild animals and earth/soil has changed with colonial conservation actions, and some Maasai responded with violence against wildlife to protest new rules.

- Positivity bias: people may respond positively because they may perceive that a positive response is the 'correct' answer.

- Agreement bias: if the statement about elephants is positive people may agree because agreement is the 'easiest' response to give.

- Positive image for tourism: tourism boosts the income of some communities from land lease payments or employment and tourists come to see wildlife, thus is important to project an image of oneself as a protector of nature and wildlife, because tourists expect this from Maasai based on media representations and tourism company advertising.

Reasons for false negatives could be:

- Expectation of compensation for loss or damage of property including livestock or crops, thus exaggerating negative experiences to increase the likelihood of compensation or amount of compensation (traditionally it is offensive for Maasai to penetrate the earth, but some areas people plant crops).

- Telling foreign researchers about problems they believe researchers want to hear about given a history of research focused exclusively on conflicts.

- Perceiving a social norm of negativity towards elephants, and conforming answers to a perceived social norm of negativity towards elephants given that interviewers are also Maasai from the region.

- Agreement bias: for negative statements, people may agree because agreement is the ‘easiest’ response to give.

- Knowledge that the report/paper will be shared with conservation NGOS, Kenya Wildlife Service, and eventually published, thus some people may want to convey a need for help and/or compensation to increase potential for financial support in their communities.

After identifying these potential causes of response bias (i.e., misreporting), we formulated attitude statements about which we were confident that responses would have one type of error, either a false positive or a false negative response, but not both.

J_c: Elephants are intelligent animals.

If respondents notionally agree that elephants are intelligent animals, then there is no cultural, political, or contextual reason for them to report that they disagree with the statement. If however, they do *not* agree that elephants are intelligent, they may answer either way. They might truthfully report a negative response (disagree), or they many report a false-positive attitude to 'be nice', or because they perceive that agreement is the 'correct' answer. Therefore, there is only one type of misreporting error: false-positive.

Kc: Elephants cause damage to our property and people's livelihoods.

If respondents agree that there is damage to property and livelihoods in their communities, there is no cultural, political, or contextual reason for them to disagree with the statement. If they don't think there is any damage, they might respond either way (agree or disagree) because of a perception of elephants as problem species, telling researchers about conflict, or to increase chances of compensation for any damages. Therefore, there is only one type of misreporting error: false-negative.

1.3 Derivation of Conditionals

Defining variables

Latent states

α_i = {0,1} = Notional attitude → Latent state

λ_i = {0,1} = Local attitude → Latent state

Attitude probabilities

ψ = Pr $(\alpha_i = 1)$ = Probability that notional attitude is positive (Psi)

ϕ = Pr $(\lambda_i = 1)$ = Probability that local attitude is positive (Phi)

Misreporting probabilities: Notional

Generally, p = Probability of reporting positive notional attitude

p_c^{11} = Pr(positive reporting for certain questions | positive notional attitude state) = True positive reporting of notional attitudes for certain questions

$p_c^{10} = 1 - p_c^{11}$ = Pr(non-positive reporting for certain questions | positive notional attitude state) = False negative reporting of notional attitudes for certain questions

p_c^{01} = Pr(positive reporting for certain questions | non-positive notional attitude state) = False positive reporting of notional attitudes for certain questions

p_{uc}^{11} = Pr(positive reporting for uncertain questions | positive notional attitude state) = True positive reporting of notional attitudes for uncertain questions

$p_{uc}^{10} = 1 - p_{uc}^{11}$ = Pr(non-positive reporting for uncertain questions | positive notional attitude state) = False negative reporting of notional attitudes for uncertain questions

p_{uc}^{01} = Pr(positive reporting for uncertain questions | non-positive notional attitude state) = False positive reporting of notional attitudes for uncertain questions

Misreporting probabilities: Local

Generally, q = Probability of reporting positive local attitude

q_c^{11} = Pr(positive reporting for certain questions | positive local attitude state) = True positive reporting of local attitudes for certain questions

$q_c^{10} = 1 - q_c^{11}$ = Pr(non-positive reporting for certain questions | positive local attitude state) = False negative reporting of local attitudes for certain questions

q_c^{01} = Pr(positive reporting for certain questions | non-positive local attitude state) = False positive reporting of local attitudes for certain questions

q_{uc}^{11} = Pr(positive reporting for uncertain questions | positive local attitude state) = True positive reporting of local attitudes for uncertain questions

$q_{uc}^{10} = 1 - q_{uc}^{11}$ = Pr(non-positive reporting for uncertain questions | positive local attitude state) = False negative reporting of local attitudes for uncertain questions

q_{uc}^{01} = Pr(positive reporting for uncertain questions | non-positive local attitude state) = False positive reporting of local attitudes for uncertain questions

Questions

J_c = number of certain questions for notional attitudes

J_{uc} = number of uncertain questions for notional attitudes

K_c = number of certain questions for local attitudes

K_{uc} = number of uncertain questions for local attitudes

The process

Latent attitude states

α_i = Bernoulli (ψ_i) → The notional (latent) attitude state of respondent i is a Bernoulli process determined by a respondent-specific probability ψ_i

$\psi_i = \Phi(\beta \times w_i)$ → Respondent-specific probability ψ_i can be determined by a Probit function of covariates w_i and coefficients / impacts of the covariates β

$\lambda_i \mid (\alpha_i = 1)$ = Bernoulli (ϕ_i) → The notional (latent) attitude state of respondent i is a Bernoulli process determined by a respondent-specific probability ϕ_i and is conditional on notional state α_i

If α_i = 0, then λ_i = 0

$\phi_i = \Phi(\beta \times w_i)$ → Respondent-specific probability ϕ_i can be determined by a Probit function of covariates w_i and coefficients / impacts of the covariates β

Reporting

$x_i \mid (\alpha_i = 1) = \begin{cases} Binomial\ (J_c, p_c^{11}) \\ Binomial\ (J_{uc}, p_{uc}^{11}) \end{cases}$ → Determines responses when true notional attitude state is positive

$x_i \mid (\alpha_i = 0) = \begin{cases} Binomial\ (J_c, p_c^{01}) \\ Binomial\ (J_{uc}, p_{uc}^{01}) \end{cases}$ → Determines responses when true notional attitude state is non-positive

Either p_c^{11} = 1 → No false negative reporting for certain questions on notional attitudes, or p_c^{01} = 0 → no false positive reporting for certain questions on notional attitudes.

$z_i \mid (\lambda_i = 1) = \begin{cases} Binomial\ (K_c, q_c^{11}) \\ Binomial\ (K_{uc}, q_{uc}^{11}) \end{cases}$ → Determines responses when true local attitude state is positive

$z_i \mid (\lambda_i = 0) = \begin{cases} Binomial\ (K_c, q_c^{01}) \\ Binomial\ (K_{uc}, q_{uc}^{01}) \end{cases}$ → Determines responses when true local attitude state is non-positive

Either q_c^{11} = 1 → No false negative reporting for certain questions on local attitudes, or q_c^{01} = 0 → no false positive reporting for certain questions on local attitudes.

Y = (X, Z) = Complete reporting data, a matrix with number of rows → number of respondents; number of columns → J + K

Scenarios of misreporting for certain questions

Scenario 3: NFP-LFN

Notional false positive, ie., no false negative, ie., $p_c^{11} = 1$

Local false negative, ie., no false positive, ie., $q_c^{01} = 0$

Confusion Matrix

$\alpha_i = \rightarrow$ $x_{ij} = \downarrow$	0	1
0	$(1-\psi)\,(1-p_c^{01})$	$\psi\,(1-p_c^{11})$
1	$(1-\psi)\,p_c^{01}$	$\psi\,p_c^{11}$

$\alpha_i, \lambda_i = \rightarrow$ $z_{ij} = \downarrow$	$\alpha_i, \lambda_i = 0$	$\alpha_i = 1, \lambda_i = 0$	$\alpha_i, \lambda_i = 1$
0	$(1-\psi)\,(1-q_c^{01})$	$\psi\,(1-\phi)\,(1-q_c^{01})$	$\psi\,\phi\,(1-q_c^{11})$
1	$(1-\psi)\,q_c^{01}$	$\psi\,(1-\phi)\,q_c^{01}$	$\psi\,\phi\,q_c^{11}$

Deriving the conditionals

$$[\beta_\theta, \alpha, \lambda \mid Y] = [\beta_\psi] \times [\beta_\phi] \times [\beta_{p_c^{01}}] \times [\beta_{p_c^{11}}] \times [\beta_{p_{uc}^{01}}] \times [\beta_{p_{uc}^{11}}] \times [\beta_{q_c^{01}}] \times [\beta_{q_c^{11}}]$$
$$\times [\beta_{q_{uc}^{01}}] \times [\beta_{q_{uc}^{11}}] \times [\propto \mid \beta_\psi] \times [\lambda \mid \beta_\phi, \alpha] \times [X_c \mid \beta_{p_c^{01}}, \beta_{p_c^{11}}, \alpha]$$
$$\times [X_{uc} \mid \beta_{p_{uc}^{01}}, \beta_{p_{uc}^{11}}, \alpha] \times [Z_c \mid \beta_{q_c^{01}}, \beta_{q_c^{11}}, \lambda] \times [Z_{uc} \mid \beta_{q_{uc}^{01}}, \beta_{q_{uc}^{11}}, \lambda]$$

$$[\beta_\theta, \alpha, \lambda \mid Y] = \frac{1}{2\pi}\, e^{-\beta_\psi{}^2} \times \frac{1}{2\pi}\, e^{-\beta_\phi{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{p_c^{11}}{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{p_c^{01}}{}^2}$$
$$\times \frac{1}{2\pi}\, e^{-\beta_{p_{uc}^{11}}{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{p_{uc}^{01}}{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{q_c^{11}}{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{q_c^{01}}{}^2}$$
$$\times \frac{1}{2\pi}\, e^{-\beta_{q_{uc}^{11}}{}^2} \times \frac{1}{2\pi}\, e^{-\beta_{q_{uc}^{01}}{}^2} \times$$

Normal, un-informative, 0-mean priors for all parameters

$$\prod_{i=1}^{m} \psi_i{}^{\alpha_1} \times (1 - \psi_i)^{(1-\alpha_i)} \times$$

$[\alpha \mid \beta_\psi]$

$$(\phi_i \alpha_i)^{\lambda_i} \times (1 - \phi_i \alpha_i)^{(1-\lambda_i)} \times$$

$[\lambda \mid \beta_\phi, \alpha]$

$$\left(\left(\alpha_i p_{c,i}^{11}\right) + \left((1 - \alpha_i) p_{c,i}^{01}\right)\right)^{X_{c,i}}$$
$$\times \left(1 - \left(\alpha_i p_{c,i}^{11}\right) - \left((1 - \alpha_i) p_{c,i}^{01}\right)\right)^{J_c - X_{c,i}} \times$$

$[X_c \mid \beta_{p_c}, \alpha]$

Either $p_c^{11} = 1$ (FP), or $p_c^{01} = 0$ (FN)

$$\left(\left(\alpha_i p_{uc,i}^{11}\right) + \left((1 - \alpha_i) p_{uc,i}^{01}\right)\right)^{X_{uc,i}}$$
$$\times \left(1 - \left(\alpha_i p_{uc,i}^{11}\right) - \left((1 - \alpha_i) p_{uc,i}^{01}\right)\right)^{J_{uc} - X_{uc,i}} \times$$

$[X_{uc} \mid \beta_{p_{uc}}, \alpha]$

$$\begin{aligned}&\left(\left(\lambda_i q_{c,i}^{11}\right) + \left((1-\lambda_i) q_{c,i}^{01}\right)\right)^{Z_{c,i}} \\ &\qquad \times \Bigl(1 - \left(\lambda_i q_{c,i}^{11}\right) \\ &\qquad - \left((1-\lambda_i) q_{c,i}^{01}\right)\Bigr)^{K_c - Z_{c,i}} \times\end{aligned}$$

$[Z_c \mid \beta_{q_c}, \lambda]$

Either $q_c^{11} = 1$ (FP), or $q_c^{01} = 0$ (FN)

$$\begin{aligned}&\left(\left(\lambda_i q_{uc,i}^{11}\right) + \left((1-\lambda_i) q_{uc,i}^{01}\right)\right)^{Z_{uc,i}} \\ &\qquad \times \Bigl(1 - \left(\lambda_i q_{uc,i}^{11}\right) \\ &\qquad - \left((1-\lambda_i) q_{uc,i}^{01}\right)\Bigr)^{K_{uc} - Z_{uc,i}}\end{aligned}$$

$[Z_{uc} \mid \beta_{q_{uc}}, \lambda]$

Conditionals for Metropolis-Hastings F

1. β_ψ

$$\log[\beta_\psi \mid .] = -\frac{{\beta_\psi}^2}{2} + \sum_{i=1}^{n} \alpha_i \log \psi_i + (1-\alpha_i)\log(1-\psi_i)$$

2. β_ϕ

$$\log[\beta_\phi \mid .] = -\frac{{\beta_\phi}^2}{2} + \sum_{i=1}^{n} \lambda_i \alpha_i \log \phi_i + (1-\lambda_i)\alpha_i \log(1-\phi_i)$$

3. $\beta_{p_c^{11}}$

$$\begin{aligned}\log[\beta_{p_c^{11}} \mid .] = &-\frac{{\beta_{p_c^{11}}}^2}{2} \\ &+ \sum_{i=1}^{n}\sum_{j=1}^{J_c} x_{ij}\log(\alpha_i p_c^{11} + (1-\alpha_i)p_c^{01}) \\ &+ \left(1 - x_{ij}\right)\log(1 - \alpha_i p_c^{11} - (1-\alpha_i)p_c^{01})\end{aligned}$$

4. $\beta_{p_c^{01}}$

$$\log[\beta_{p_c^{01}} \mid .] = -\frac{{\beta_{p_c^{01}}}^2}{2} + \sum_{i=1}^{n}\sum_{j=1}^{J_c} x_{ij}\log(\alpha_i p_c^{11} + (1-\alpha_i)p_c^{01}) + \left(1-x_{ij}\right)\log(1-\alpha_i p_c^{11} - (1-\alpha_i)p_c^{01})$$

5. $\beta_{p_{uc}^{11}}$

$$\log[\beta_{p_{uc}^{11}} \mid .] = -\frac{{\beta_{p_{uc}^{11}}}^2}{2} + \sum_{i=1}^{n}\sum_{j=J_c+1}^{J} x_{ij}\log(\alpha_i p_{uc}^{11} + (1-\alpha_i)p_{uc}^{01}) + \left(1-x_{ij}\right)\log(1-\alpha_i p_{uc}^{11} - (1-\alpha_i)p_{uc}^{01})$$

6. $\beta_{p_{uc}^{01}}$

$$\log[\beta_{p_{uc}^{01}} \mid .] = -\frac{{\beta_{p_{uc}^{01}}}^2}{2} + \sum_{i=1}^{n}\sum_{j=J_c+1}^{J} x_{ij}\log(\alpha_i p_{uc}^{11} + (1-\alpha_i)p_{uc}^{01}) + \left(1-x_{ij}\right)\log(1-\alpha_i p_{uc}^{11} - (1-\alpha_i)p_{uc}^{01})$$

7. $\beta_{q_c^{11}}$

$$\log[\beta_{q_c^{11}} \mid .] = -\frac{{\beta_{q_c^{11}}}^2}{2} + \sum_{i=1}^{n}\sum_{k=1}^{K_c} z_{ik}\log(\lambda_i q_c^{11} + (1-\lambda_i)q_c^{01}) + (1-z_{ik})\log(1-\lambda_i q_c^{11} - (1-\lambda_i)q_c^{01})$$

8. $\beta_{q_c^{01}}$

$$\log[\beta_{q_c^{01}} \mid .] = -\frac{{\beta_{q_c^{01}}}^2}{2} + \sum_{i=1}^{n}\sum_{k=1}^{K_c} z_{ik}\log(\lambda_i q_c^{11} + (1-\lambda_i)q_c^{01}) + (1-z_{ik})\log(1-\lambda_i q_c^{11} - (1-\lambda_i)q_c^{01})$$

9. $\beta_{q_{uc}^{11}}$

$$\begin{aligned}\log\left[\beta_{q_{uc}^{11}} \mid .\right] = & -\frac{{\beta_{q_{uc}^{11}}}^2}{2} \\ & + \sum_{i=1}^{n} \sum_{k=K_c+1}^{K} z_{ik} \log(\lambda_i q_{uc}^{11} + (1 - \lambda_i) q_{uc}^{01}) \\ & + (1 - z_{ik}) \log(1 - \lambda_i q_{uc}^{11} - (1 - \lambda_i) q_{uc}^{01})\end{aligned}$$

10. $\beta_{q_{uc}^{01}}$

$$\begin{aligned}\log\left[\beta_{q_{uc}^{01}} \mid .\right] = & -\frac{{\beta_{q_{uc}^{01}}}^2}{2} \\ & + \sum_{i=1}^{n} \sum_{k=K_c+1}^{K} z_{ik} \log(\lambda_i q_{uc}^{11} + (1 - \lambda_i) q_{uc}^{01}) \\ & + (1 - z_{ik}) \log(1 - \lambda_i q_{uc}^{11} - (1 - \lambda_i) q_{uc}^{01})\end{aligned}$$

Gibbs functions for α_i and λ_i

Detection Scenario: NFP-LFN

Notional false positive, ie., no false negative, ie., $p_c^{11} = 1$

Local false negative, ie., no false positive, ie., $q_c^{01} = 0$

CF-Notional

$\alpha_i = \rightarrow$ $x_{ij} = \downarrow$	0	1
0	$(1 - \psi)\,(1 - p_c^{01})$	0
1	$(1 - \psi)\, p_c^{01}$	ψ

CF-Local

$\alpha_i, \lambda_i = \rightarrow$ $z_{ij} = \downarrow$	$\alpha_i, \lambda_i = 0$	$\alpha_i = 1, \lambda_i = 0$	$\alpha_i, \lambda_i = 1$

0	$(1-\psi)$	$\psi\,(1-\phi)$	$\psi\,\phi\,(1-q_c^{11})$
1	0	0	$\psi\,\phi\,q_c^{11}$

α_i

If:	α_i = ; or probability of being 1	Because:
$x_i = 0$	0	There is 0 probability of α_i being 1
$x_i > 0$ and $z_i > 0$	1	There is 0 probability of α_i being 0 if $z_i > 0$
$x_i > 0$ and $z_i = 0$	$\frac{\psi\,\phi\,(1-q_c^{11})^{K_c}}{Num\;+\;\psi\,(1-\phi)+(1-\psi)(p_c^{01})^{X_{c,i}}}$	+ve and all-0 local reports / num + non-positive X 1-reports + non positive local

λ_i

If:	α_i = ; or probability of being 1	Because:
$z_i > 0$	1	There is 0 probability of λ_i being 0
$z_i = 0$	$\frac{\phi\,(1-q_c^{11})^{K_c}}{Num\;+\;(1-\phi)} \times \alpha_i$	+ve and all-0 reports / num + true negative reports * α_i (as λ_i = 0 when α_i = 0

Table S3.1. Covariates Used in Hierarchical Models of Positive Attitudes Towards Elephants and Hypotheses.

Covariate	Hypotheses	Explanation	Evidence
		NOTIONAL ATTITUDES	
Gender	Less positive if woman	Women collect firewood and so could be more fearful of encountering elephants. Women are also less likely to have direct income from conservation, which traditionally goes only to male heads of households.	Gore & Kahler 2012; Khumalo & Yung 2015
Formal education	More positive	Formal education might increase positivity about conservation and about wildlife, because of a stronger connection to national economy and local wildlife tourism-based economy.	Browne-Nunez et al. 2013; Western et al. 2019
Age	More positive with age	Traditionally, Maasai society is structed in age-sets. Older groups maybe be more positive about living with elephants because of traditional cultural links and more experience living with wildlife.	Kioko et al. 2015, 2022
Religion	Less positive if Christian	Colonialism including the shift to Christianity, has been linked to a shift in values from indigenous belief systems to a domination-based valuation of nature and wildlife, resulting in more negative views of wildlife.	Gillingham & Lee 1999; Hazzah et al. 2009
Sociocultural values of Elephants	More positive	Sociocultural values of wildlife can be strong predictors of attitudes; those who believe there are important roles for elephants (positive roles) may be more positive about elephants generally.	Teel & Manfredo 2009; Kioko et al. 2015; Manfredo et al. 2021
		LOCAL ATTITUDES	
Elephant Problems	Less positive	Those who have experienced problems caused by elephants (i.e., conflict) will be less positive.	Hoare 2015; Nyumba et al. 2020
Elephant Benefits	More positive	Those who have experienced benefits, economic or otherwise, will be more positive.	Kaelo 2007; Reid et al. 2016

Wildlife problems	Less positive	Those who have experienced problems caused by any wildlife species will be less positive.	Redpath et al. 2015; Nyumba et al. 2020
Formal Education	More positive	Formal education is an experience with the potential to strongly shape ones' worldview. In the study area, most primary schools have been built with funds from wildlife-conservation related donations so education could strongly influence local positive attitude probability.	Browne-Nuñez et al. 2013; Western et al. 2019
Cultivation	Less positive if cultivating	Cultivation creates the possibility for additional or new conflict with wildlife associated with crop damage and livelihood insecurity.	Okello 2005; Browne-Nuñez et al. 2013
Proximity to core elephant range (5km)	Either way	Strong variation exists in the proximity of respondent residences to known core elephant ranges. Those who live closest could be more likely to encounter elephants herding, etc., and could have more experiences that were negative or positive. We used a buffer of 5km based on mean daily distance traveled by tracked elephants.	

Table S3.2 Number of respondents across covariate groups for attitude drivers model (N = 177).

Notional	**Age 18-33**	**Age 34-47**	**Age 48-70**	**Christian**	**Formal education**	**Sociocultural value**
MEN	44 (24.8 %)	41 (23.2%)	17 (9.6 %)	78 (44.1%)	47 (26.6 %)	68 (38.4 %)
WOMEN	30 (16.9 %)	32 (18.1%)	13 (7.4 %)	62 (35.0%)	18 (10.2 %)	42 (23.7 %)
Local	**Elephant conflict**	**Elephant benefits**	**Wildlife conflict**	**Near core elephant range**	**Formal Education**	**Household cultivation**
YES	39 (22%)	73 (41.2 %)	156 (88.1 %)	106 (59.8%)	36 (20.3 %)	120 (67.8%)
NO	138 (78 %)	104 (58.8 %)	21 (11.8 %)	71 (40.1 %)	141 (79.6)	47 (26.6 %)

1.4 Defining sub-regions to predict positive attitude probabilities for the landscape model

The study region covers roughly 1,500km^2 and has a diversity of communities across the landscape. Thus, we defined six appropriate sub-regions based on our collective knowledge of the recent cultural, administrative, and political context and on what might be the most practical for landscape planning. The study area in eastern Narok county is split by two Maasai sub-tribes or sections, Purko Maasai in the west and north and Loita Maasai, a smaller section, in the east and southeast of the study area. Loita Maasai (*Iloitai* in Maa) are a ‘section’ of Maasai, referring to both the people and the area where they live, which administratively is Loita Ward of Narok county.

Loita ward is currently undergoing land adjudication, the process of privatizing community land into individually owned parcels. To define the Loita North, Olmestuye, and Ilkerin sub-regions, we extracted all cells from the sampling grid that fell within Loita ward adjudication section polygons. Loita North partially covers the Entasekara and the Morijo sections, and Olmesutye and Ilkerin are separate sections. In the north, west, and central part of the study area, we used group ranch boundaries to define sub-sections. Specifically, the study area overlaps with Naikarra GR in the north, Siana in the northwest, and Olderkesi GR in the southwest. Olderkesi and Siana group ranches have both created community conservancies whereas Naikarra has not. Given that subdivision of group ranches is either very recent (2020) or ongoing due to challenges in the courts, we divided sub-regions based on group ranch boundaries. However, we included the few cells that overlap Siana GR as a part of Olderkesi, since there were not enough individuals to model Siana as a separate group.

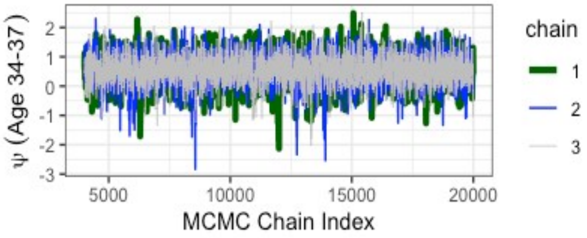
Table S.3.3 Number of respondents from each sub-region for the landscape model (N = 177).

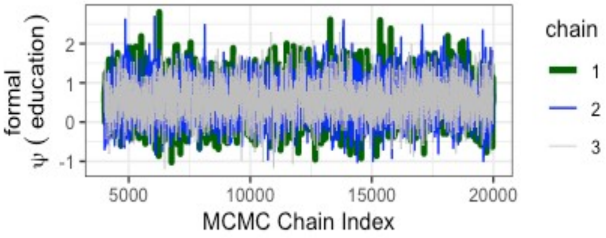
Enkoiroroi	25 (14.2%)
Olderkesi	41 (23.2 %)
Olmesutye	23 (12.9 %)
Ilkerin	26 (14.7 %)
Loita North	23 (12.9 %)
Naikarra	39 (22 %)

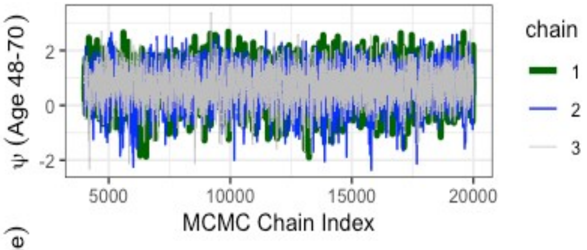
1.5 Bayesian Model Results and Model Checking

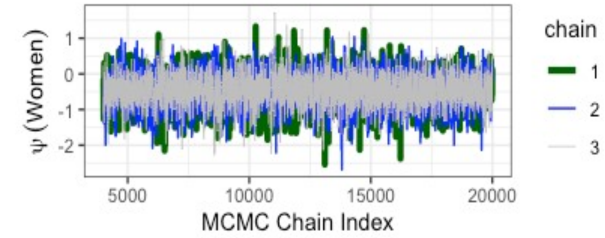
Table S3.4. Gelman-Rubin statistic and effective sample size (ESS) for all parameters for the drivers of attitudes towards elephants model.

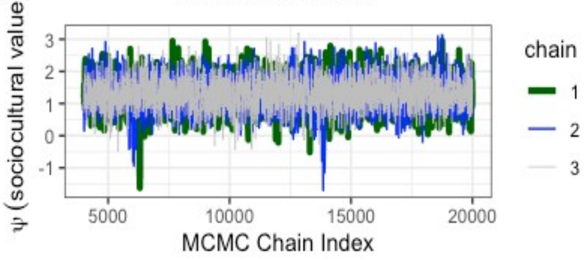
	$\hat{R}$ point est.	$\hat{R}$ Upper C.I.	Effective Sample Size
Intercept (ψ)	1.01	1.03	770.59
Women (ψ)	1.00	1.01	1528.36
Age 34-47 (ψ)	1.00	1.01	1226.68
Age 48-70 (ψ)	1.00	1.01	1231.75
Sociocultural value (ψ)	1.01	1.02	1617.45
Christian (ψ)	1.00	1.01	2129.02
Formal education (ψ)	1.00	1.00	1874.75
Local Intercept (ϕ)	1.00	1.00	930.58
Formal education (ϕ)	1.00	1.02	1450.90
No cultivation (ϕ)	1.00	1.00	1560.29
Elephant benefits (ϕ)	1.00	1.01	1486.42
Elephant problems (ϕ)	1.00	1.01	1478.96
Wildlife problems (ϕ)	1.00	1.00	1149.62
Near core elephant range (ϕ)	1.00	1.01	1256.00
Bp01c	1.03	1.09	300.33
Bp11uc	1.01	1.03	568.96
Bp01uc	1.00	1.01	724.60
Bq11c Interviewer A	1.00	1.00	471.18
Bq11c Interviewer B	1.00	1.01	4354.72
Bq11uc Interviewer A	1.00	1.00	2311.09
Bq11uc Interviewer B	1.00	1.00	2447.07
Bq01uc Interviewer A	1.03	1.03	1474.66
Bq01uc Interviewer B	1.01	1.01	5628.92
Adot	1.01	1.05	206.51
Ldot	1.05	1.08	124.80
CondLdot	1.03	1.05	126.68
Multivariate psrf	1.03		

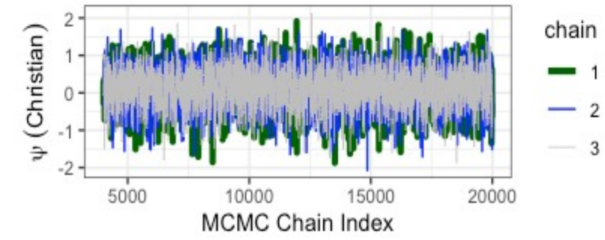

ψ (Age 34-37)
2
1
0
-1
-2
-3
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

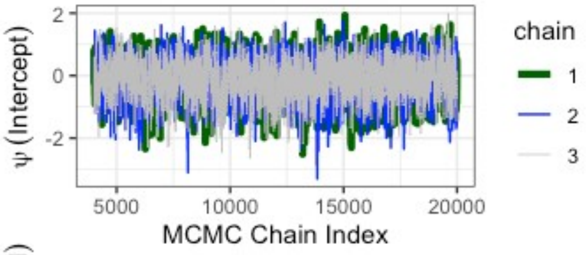

ψ (formal education)
2
1
0
-1
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

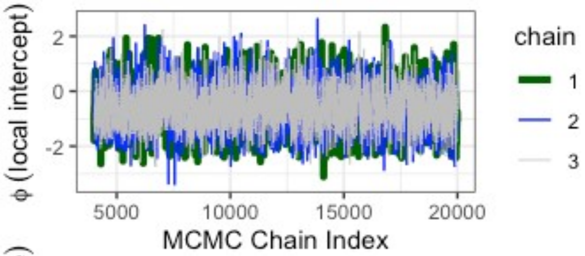

ψ (Age 48-70)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

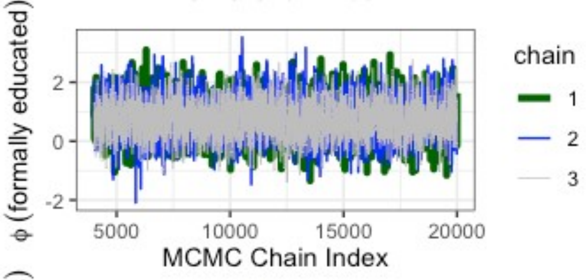

ψ (Women)
1
0
-1
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

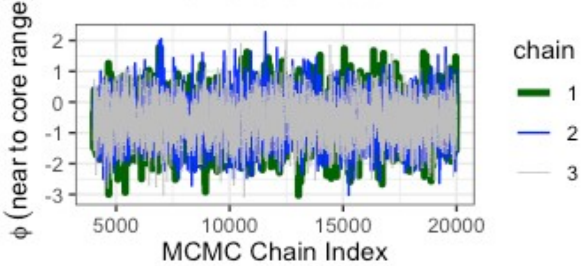

ψ (sociocultural value)
3
2
1
0
-1
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

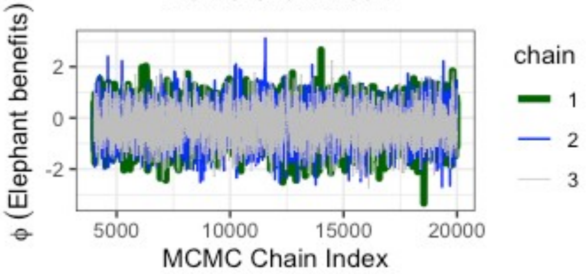

ψ (Christian)
2
1
0
-1
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

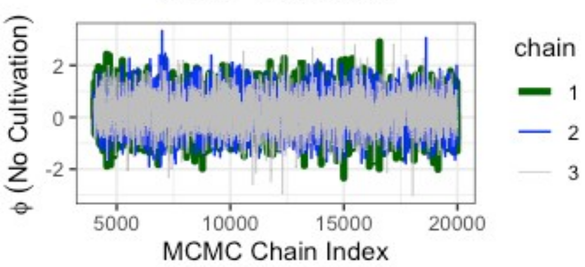

ψ (Intercept)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


φ (local intercept)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


φ (formally educated)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


φ (near to core range)
2
1
0
-1
-2
-3
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


φ (Elephant benefits)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


φ (No Cultivation)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

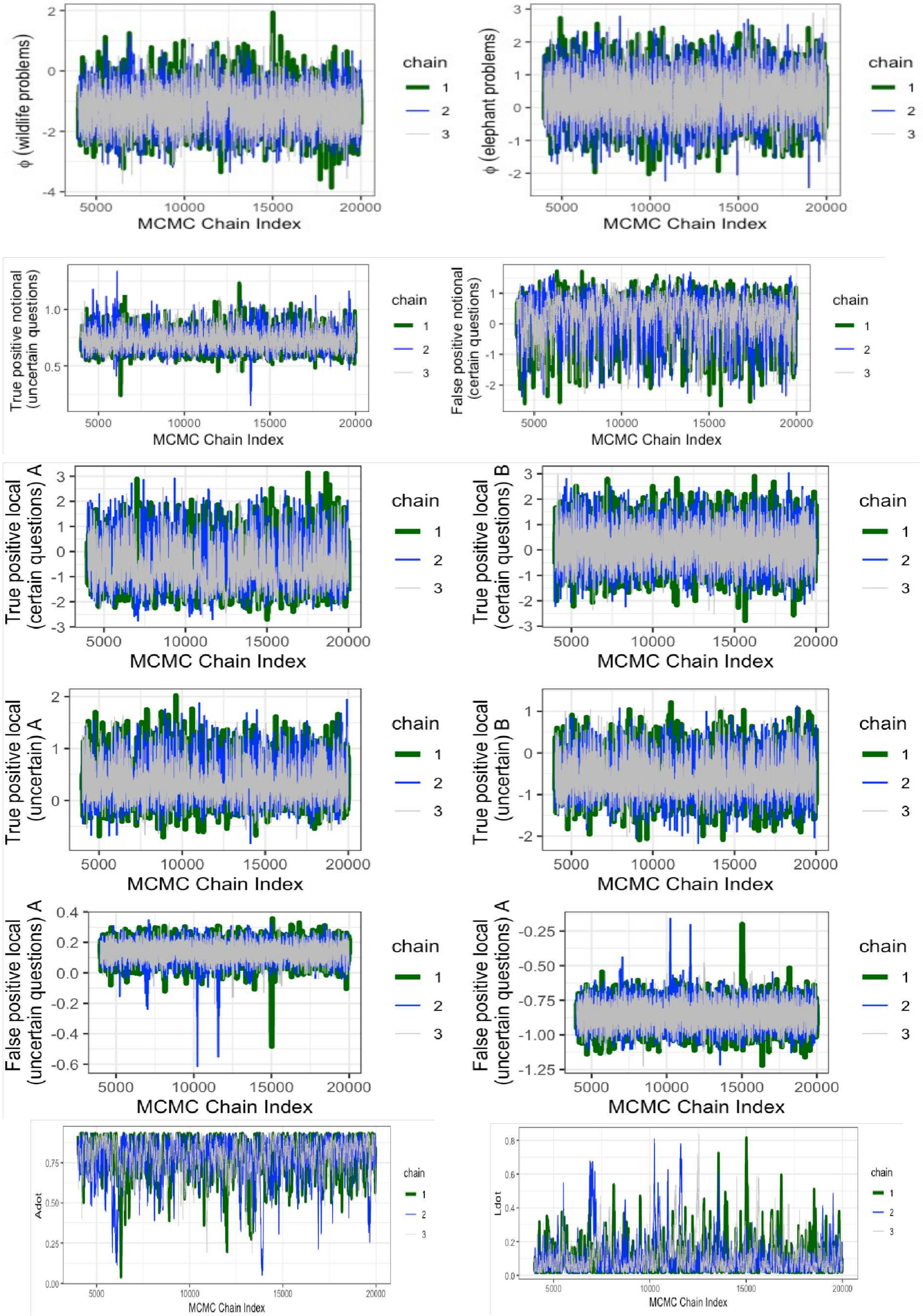
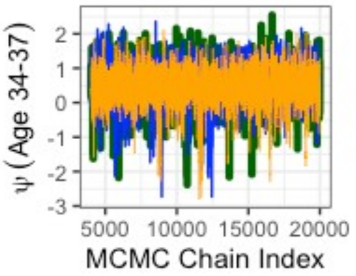
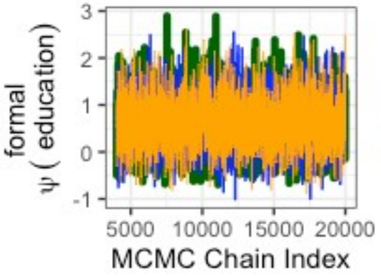
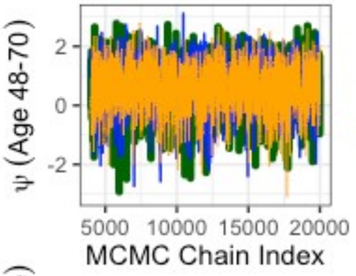
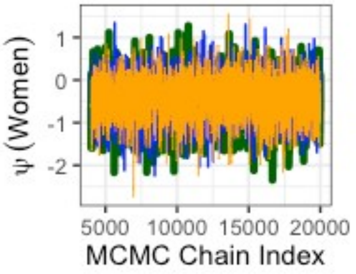


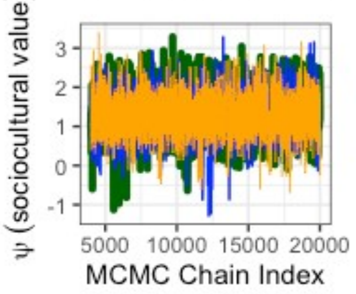
Figure S3.1. MCMC Chain Trace Plots for drivers of elephant attitudes model.

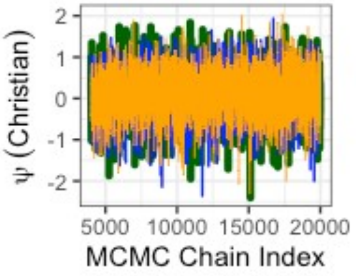

ψ (Age 34-37)
2
1
0
-1
-2
-3
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

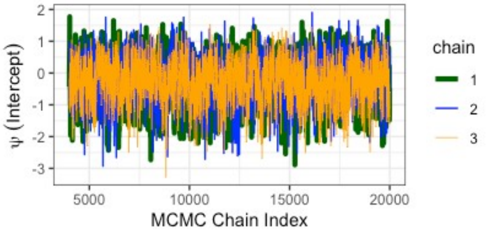

ψ (formal education)
3
2
1
0
-1
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

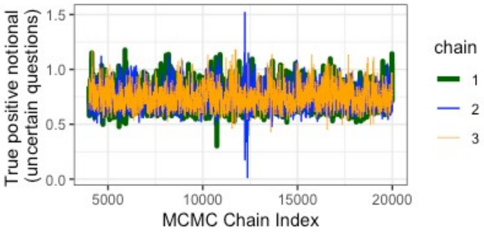

ψ (Age 48-70)
2
0
-2
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

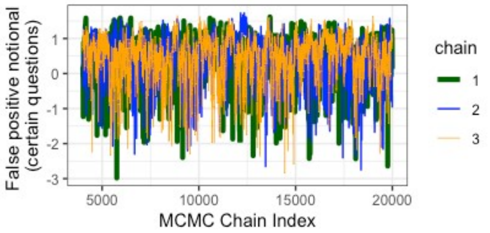

ψ (Women)
1
0
-1
-2
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

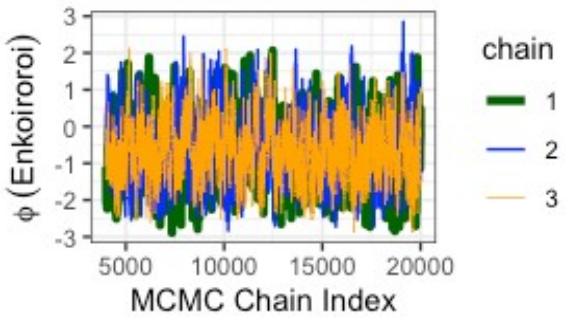

ψ (sociocultural value)
3
2
1
0
-1
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

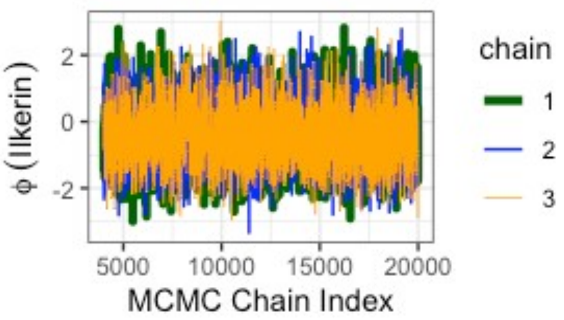

ψ (Christian)
2
1
0
-1
-2
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

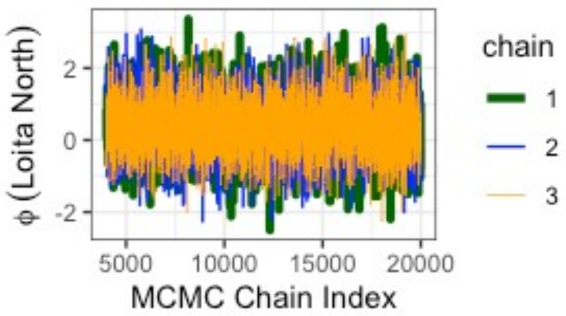

ψ (Intercept)
2
1
0
-1
-2
-3
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

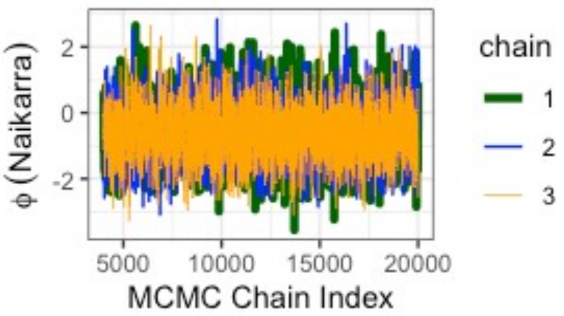

True positive notional (uncertain questions)
1.5
1.0
0.5
0.0
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

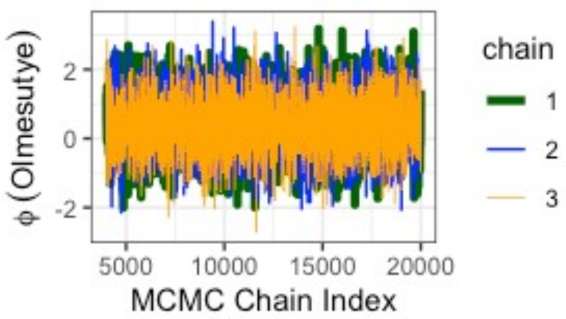

False positive notional (certain questions)
1
0
-1
-2
-3
5000 10000 15000 20000
MCMC Chain Index
chain
1
2
3

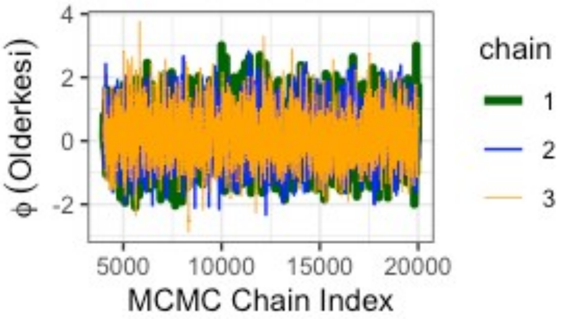

ϕ (Enkoiroroi)
3
2
1
0
-1
-2
-3
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

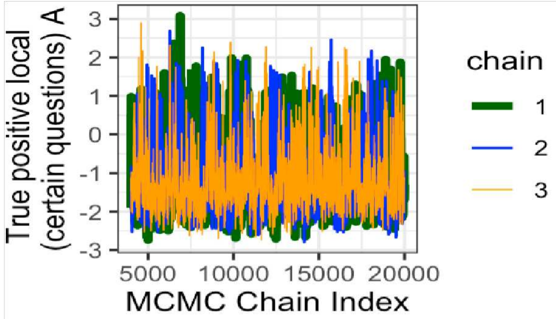

ϕ (Ilkerin)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

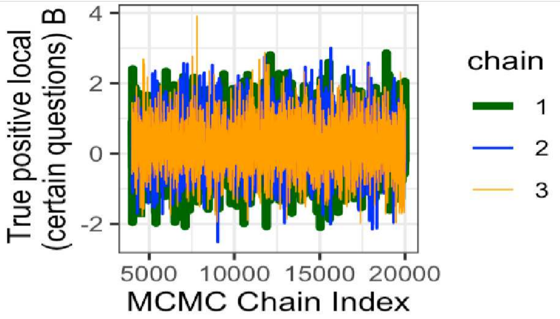

ϕ (Loita North)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

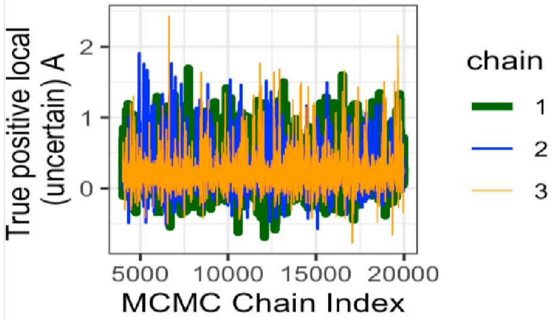

ϕ (Naikarra)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

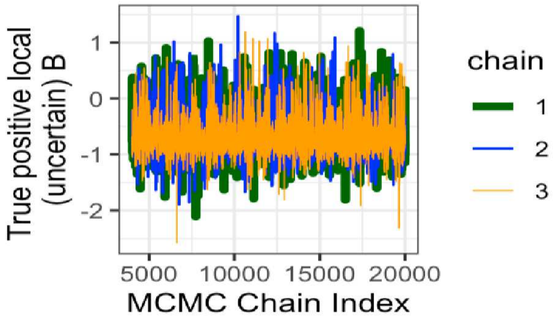

ϕ (Olmesutye)
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


ϕ (Olderkesi)
4
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


True positive local (certain questions) A
3
2
1
0
-1
-2
-3
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


True positive local (certain questions) B
4
2
0
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


True positive local (uncertain) A
2
1
0
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3


True positive local (uncertain) B
1
0
-1
-2
5000
10000
15000
20000
MCMC Chain Index
chain
1
2
3

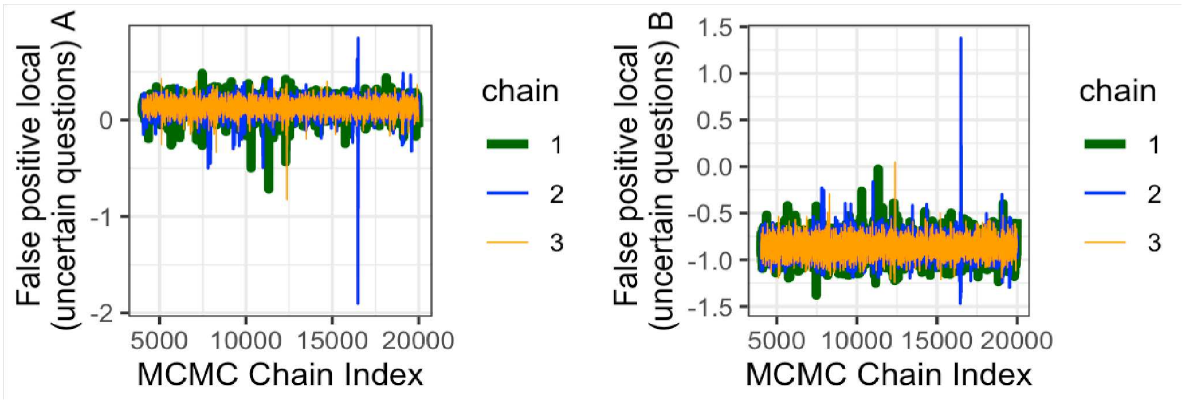


Figure S3.2. MCMC Chain Trace Plots for Regional Elephant Attitudes Model.

Understanding Community Perspectives On & Attitudes Towards Elephants & Conservation

Introduction and Methods

In Narok county, Kenya, wildlife including elephants frequently use habitat outside of protected areas. As human populations increase in the region, people and elephants are increasingly sharing space which often results in human-elephant conflict.

Understanding community perspectives on and attitudes towards elephants and conservation is needed to effectively address and mitigate conflict and identify community supported methods.

We used a questionnaire to interview 177 adults in 2020 by visiting randomly selected bomas (homesteads) across Maasai community lands in southeast Narok county.

Fig. 1. Map of Kenya highlighting Narok county and the study area.

RESULTS: The Complexity of Living With Elephants

- Most people (95%) believe elephants should be protected and have important roles in Maasai culture (61%). Figure 2 shows the most important roles of elephants.
- However, most people (73%) were not positive about living with elephants, and 57% of people would prefer if elephant numbers decreased in the area where they live.
- Figure 3 shows the most reported problems that elephants cause. The size of each box is proportional to number of people that discussed the problem.

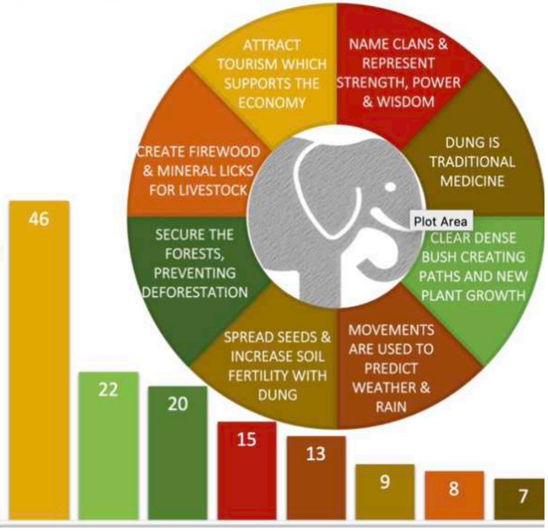
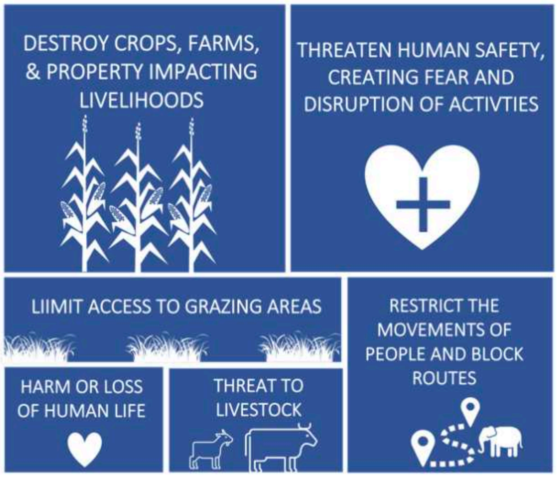


Fig. 2. Importance and roles of elephants.



DESTROY CROPS, FARMS, & PROPERTY IMPACTING LIVELIHOODS

THREATEN HUMAN SAFETY, CREATING FEAR AND DISRUPTION OF ACTIVTIES

LIIMIT ACCESS TO GRAZING AREAS

RESTRICT THE MOVEMENTS OF PEOPLE AND BLOCK ROUTES

HARM OR LOSS OF HUMAN LIFE

THREAT TO LIVESTOCK

Figure 3. Biggest problems caused by elephants.

- The perception that elephants are dangerous & destructive was widespread though just 22% of people reported experiencing or witnessing human-elephant conflict themselves.
- A major theme across responses was that the costs of living with elephants can be severe and are not balanced by benefits. When losses do occur, there is no recourse or help for they majority of people who are impacted.

research by Sarah Carroll, for more information, email at slcarrol@colostate.edu

Figure S3.3 Handout and Infographic Created for Sharing Results of Chapter 4 With Communities.