ECOLOGICAL, GENOMIC, AND SOCIAL FACTORS IMPACTING WILDLIFE CONSERVATION

by

SARA ELIZABETH HEISEL

(Under the Direction of John P. Wares)

ABSTRACT

To better understand social and ecological factors surrounding wildlife conservation, I used a combination of comparative (meta-analysis), field, molecular, and interview techniques to, 1) examine associations between genomic variation and disease in wild mammals, 2) assess environmental context effects on stress and infection in an endangered equid, and 3) examine how socio-cultural perceptions of wildlife conservation align across cultures. For ***goal 1***, I performed a meta-analysis using empirical studies on the association between genomic variability and disease measures in mammalian wildlife species. Candidate (i.e., coding) genomic regions, but not putatively neutral (i.e., non-coding) regions of the genome, showed greater associations with disease measures, indicating that candidate regions may be more useful in predicting disease response and forces shaping disease response, than frequently used microsatellite-based studies of anonymous genome-wide heterozygosity. For ***goal 2***, I investigated how environmental and host factors contribute to differences in stress hormone levels and parasite infection rates in the endangered Grevy's zebra. Stress and parasitism were affected by water, but not food, availability. Anthropogenic activity from tourism and pastoralism were correlated with increased stress hormones. Grevy's zebra are arid-adapted, thus lack of water may indicate an overlooked factor important for their conservation. Pastoralism and sympatric livestock are often cited as causes of conservation concern; these findings shed light on the need to consider tourism as a source of environmental stress. For ***goal 3***, I conducted interviews across three community conservancies in Samburu District, Kenya. International wildlife conservation program strategies typically reflect the ecological understandings and conservation motivations held by Western conservationists who design them. Socio-cultural factors, such as knowledge perceptions, locus of control, and motivations may not be shared by people who live alongside wildlife, but these factors are known to impact pro-environmental behavior. Incongruent with Western conservation ideas, knowledge perceptions regarding extinction and species' rarity did not resonate with Samburu residents, however most residents did feel they had an influence on wildlife populations, which aligns to a core presumption of Western conservation. Regarding motivating factors, economic factors were listed as the primary reason to conserve among Samburu residents, however this could reflect influence of Western conservation actors.

INDEX WORDS: genomic variation, infectious disease, Grevy's zebra (*Equus grevyi*), wildlife conservation, environmental effects, stress physiology, social factors

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DEDICATION

To all the wildlife – in particular, Grevy's zebra – in Kenya that I had the good fortune to see in their natural habitat.

I also dedicate this work to my nephew, Sam Heisel, who brought so much laughter and love to my life.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

One of the primary factors driving current extinction rates is habitat loss and degradation from anthropogenic and climatic changes (Barnosky et al. 2012; Pimm et al. 2014). Due in part to such environmental changes, it is estimated that 52 IUCN Red List wildlife species move a threat status closer to extinction each year (Hoffmann et al. 2010). With these rapid changes to population status', there is a dire need to gain a better understanding of the factors pushing species towards extinction. Beyond the direct and immediate impacts from loss of habitat, environmental change can lead to cascading effects, such as loss of genomic diversity, increased stress and disease, and can negatively impact human-wildlife interactions (Daszak et al. 2001; Acevedo-Whitehouse & Duffus 2009; Hammond et al. 2018). Conservation research is often focused on only a single component that affects species' survival in the wild. However, integration of the multiple ecological and social factors influencing

Figure 1.1: Grevy's zebra in Samburu National Reserve, Kenya (photo credit: Sara Heisel).

survival are necessary for long-term recovery of wildlife populations (Balmford & Cowling 2006).

I addressed genomic, ecological, and social factors influencing wildlife conservation in my thesis, thereby contributing to a more holistic understanding of factors shaping wildlife conservation status. In my first chapter, I used meta-analytical techniques to compare how different aspects of genomic diversity affect disease across wild mammal systems. In the second chapter, I used field-collected samples to assess the impact of different natural and anthropogenic factors on stress and infection in a wild endangered equid, the Grevy's zebra (*Equus grevyi*). Finally, because there are potentially misalignments of perceptions and beliefs between international conservation actors and local communities being asked to participate in wildlife conservation, I conducted interviews to discern how people living in a rural region of Kenya perceive wildlife and wildlife conservation in the area. While each chapter represents a knowledge gap in wildlife and Grevy's zebra conservation, together they represent a holistic analysis that will allow me to draw broader conclusions about wildlife conservation than from any one of these studies alone.

Study Systems and Area

The majority of my dissertation field work was conducted in central and northern Kenya, which has the highest concentration of threatened and endangered large mammal species in East Africa (Sundaresan et al. 2012), including Grevy's zebra (*Equus grevyi*), wild dogs (*Lycaon pictus*), lions (*Panthera leo*), and elephants (*Loxodonta africana*) – making it a critical area for wildlife conservation.

For my work on environmental and demographic factors that impact stress and infection in wildlife (Chapter 3), I studied the endangered Grevy's zebra (*Equus grevyi*) (Figure 1.1), an arid-adapted wild equid whose core populations are in central and northern Kenya (Williams 2002). Grevy's zebra are the largest extant wild equid (average body size 350-450 kg) and live in arid and semi-arid grass or shrub land where they can access water (Rubenstein 1986; Williams 2002; Sundaresan et al. 2008). They are predominantly grazers, however during droughts or in areas that are overgrazed, browse can comprise up to 30% of the Grevy's zebra diet (Estes 1997). Their social organization is a fission-fusion structure, meaning that animals are often found in groups, but there are no long-term bonds (Ginsberg 1988). The lack of permanent social bonds, translates into large variability in the amount different individuals move, with selection of core areas of use based on varying resource needs between different reproductive classes (Rubenstein 1986; Ginsberg 1989; Sundaresan et al. 2007). Reproductive females form unstable groups and move among male territories (i.e., choose mates) based on the quality of resources (e.g., forage and water) within that territory (Rubenstein 1986; Ginsberg 1989). Lactating females require daily water intake and

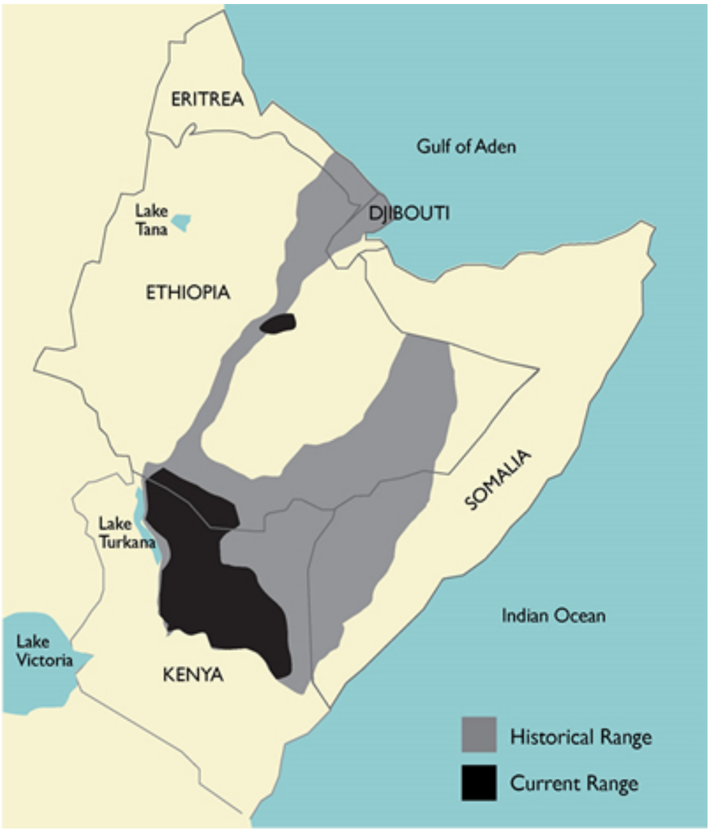


Figure 1.2: Historical and current range of Grevy's zebra (grevyszebratrust.org)

cannot move long distances with foals, thus most often remain in areas near water with greener and shorter grass (Sundaresan et al. 2008). Bachelor males tend to use the same areas as lactating females, perhaps to gain access to females coming into estrus (Ginsberg 1988; Ginsberg & Rubenstein 1990). Territorial male Grevy's zebra are the only individuals that do not roam freely, but defend territories between 2-12 km^2 (Ginsberg 1989).

Grevy's zebra are listed as endangered on the IUCN Red List owing to a drastic decrease in population numbers from 14,000 in the 1970s to an estimated 2,500 today (Williams 2002). Many factors contributed to their rapid decline, including hunting for meat and skins (KWS 2008). More recently, anthrax outbreaks have killed large numbers of Grevy's zebra (e.g., 53 animals (~6% of global population) died in 2005-2006) (Muoria et al. 2007). Currently, competition from humans and livestock are thought to be the primary threats to their existence. In addition to the severe drop in population size, their range has also undergone a dramatic contraction (Williams 2002). Grevy's zebra were once found across the entire Horn of Africa, however now 93% of the world's population is found in central and northern Kenya (Figure 1.2). In addition, over the past 40 years, their range within Kenya has shifted southward into the less arid Laikipia plateau (Williams 2002) (average annual rainfall 500 mm compared to 375 mm annually in the more northern Samburu district (Low et al. 2009)).

Although Kenyan populations of Grevy's zebra have stabilized, the species still faces severe threats from environmental changes, related to anthropogenic and climatic changes across their core range (KWS 2008). Grevy's zebra habitat choice in relation to environmental factors has been studied (Sundaresan et al. 2012), however the physiological impacts that could directly impact survival and reproduction have not. I used differences in land-use types across the Grevy's zebra core region to test the impact of varying types and levels of ecological and anthropogenic factors on stress and disease in Grevy's zebra. The majority of land-use is centered around livestock production, wildlife tourism, or a mix of these activities. However, among these land-use types, the density of livestock, the number and type of human settlements, and management regimes (i.e., whether the land is managed exclusively for livestock, exclusively for wildlife, or for both livestock and wildlife) differ substantially (Georgiadis et al. 2007; Kinnaird & O'Brien 2012).

For interviews on perceptions of wildlife and wildlife conservation (Chapter 4), I worked with Samburu people in three community conservancies in the Samburu District of northern Kenya. People living in northern Kenya, including Samburu, are primarily semi-nomadic pastoralists (i.e., many move seasonally in search of grazing pasture for their cattle) and live across an extensive rangeland, characterized by extreme aridity and increasingly more frequent and extended droughts (Boruru et al. 2011). Samburu use ecological knowledge, such as managing livestock through extended periods of drought to persist in this extremely variable and drought-prone environment (Kameri-Mbote 2005; Ocholla et al. 2016). However, despite Samburu having extensive understanding of the northern Kenya rangelands, including many species of wildlife found there, limited studies have examined their perceptions of wildlife and how this might be relevant for wildlife conservation (Oguge et al. 2006). Integrating knowledge and voices of individuals residing in the region is critical, because this is a tightly linked social-ecological system in which human livelihoods, the health of the landscape, and the survival of many wildlife species are integrally linked (Ocholla et al. 2016). Additionally, local communities are the most impacted by conservation actions and more immediately feel the consequences of sharing a landscape with sometimes dangerous or destructive species of wildlife (Sundaresan et al. 2012).

Study Overview

Because multiple factors influence survival of wildlife species, conserving wildlife is a complex task. This is especially true for small and endangered populations as they are more likely to have lost genomic variability, inhabit degraded environments, and be directly impacted by anthropogenic factors (Hilton-Taylor 2000; Spielman et al. 2004a). Conservation of threatened and endangered species thus requires a multi-faceted and interdisciplinary approach.

Individual genomics is an integral determinant of fitness – survival and reproduction – and helps to determine how animals will respond to disease (Frankham 1995; von Hardenberg et al. 2007; King and Lively 2012). Resistance and tolerance to disease in populations with limited genomic variability may be compromised leaving such populations at increased risk of extinction when faced with disease (Altizer et al. 2003; Smith et al. 2006). Recent work has pointed to an increasing list of examples where infectious diseases have caused declines in previously thriving populations, and been implicated in endangerment and extinction, in particular for already declining populations (Altizer et al. 2003; Smith et al. 2009) – and in some cases this has been linked to low levels of genomic variation (Coltman 1999; Spielman et al. 2004b). For example, devil facial tumor disease (DFTD), due to limited levels of genetic diversity at a specific immune locus in the Tasmanian devil (*Sarcophilus harrisii*), has caused population declines, changes in distribution, and localized extinctions (McCallum 2008; Siddle et al. 2007).

I augmented my field work with a meta-analysis exploring the relationship between genomic variability and disease measures in natural systems. Because there is no clear picture of how different measures of genomic variation can be used to predict an animal's response to infectious disease, one goal of the work was to compare empirical studies in wild mammals to determine if putatively neutral genomic regions were as useful in predicting disease measures as variability at candidate loci. Illuminating how and which genomic factors influence the host disease response is critical for developing strategies to mitigate the effect of disease on wildlife populations and for evaluating evolutionary consequences (e.g., adaptive potential and evolutionary trajectory) (Hoelzel et al. 2019). As such, determining the genomic basis for the disease response helps inform, in the immediate timeframe, conservation management decisions, and over longer timescales, how a population or species might evolve in response to disease pressures (i.e., evolutionary potential). Despite multiple empirical studies assessing the relationship between genomic variability and disease in wildlife species (Spielman et al. 2004), there is not yet a clear picture of which approaches to the study of genomic variation most efficiently contribute to understanding differences in disease outcome across study systems.

Alongside genomic factors, environmental conditions, both natural and anthropogenic, can have strong negative impacts on fitness and measures of fitness in wildlife (Wikelski & Cooke 2006). Environmental change may exacerbate the negative fitness consequences of two common measures of fitness in wildlife populations – stress and infection (Young et al. 2017; Hammond et al. 2018). Consistent exposure to stressful environments can elevate stress hormone levels, which has been associated with depressed immune function, decreased body condition, and reduced reproduction and survival (Sapolsky 2000; Dhabhar 2009). Likewise, parasites cause significant morbidity, mortality, and reduced fecundity in wildlife (Dobson & Hudson 1992; Voegeli et al. 2012; Coulson et al. 2018). Although increasing environmental disturbances are compromising the fitness of a wide range of wildlife species (Acevedo-Whitehouse & Duffus 2009; Cooke et al. 2014), there is still a poor understanding of how specific aspects of environmental change impact wildlife fitness and measures of fitness (Breuner et al. 2013; Madliger et al. 2015).

Although the main threats to wildlife populations and species diversity throughout the world are driven by human factors, humans are also the most integral determinant of successful conservation (Hicks et al. 2015). Wildlife conservation programs have historically rarely accounted for the culture and values of local communities, even when human populations share space with species of endangered wildlife (Waylen et al. 2010). Recent work highlights that challenges faced by community-based conservation programs may be in part due to the failure to incorporate human psycho-social factors (DeCaro & Stokes 2008; Waylen et al. 2010). Typical endangered species conservation programs emphasize biological assessments and solutions over "human social, psychological, and cultural factors" (Kellert 1985; Kittinger et al. 2012). Appreciating local community members' ecological knowledge, perceptions, values, and motivations can enhance conservation outcomes in a number of ways, including: (a) helping conservationists and communities develop a broader, shared understanding of the issues, which is known to strengthen cooperation; (b) understand how communities view their role and agency to engage in wildlife conservation, which can reveal barriers and leverage points for conservation strategies, and (c) reveal what incentives for conservation are more likely to be credible, salient and legitimate – and therefore more motivational – for people living alongside and interacting with wildlife (Cash et al. 2003).

Summary

My dissertation work examines multiple facets of endangered species conservation and potential threats facing endangered species. The main goal of this work is to better understand the complex factors involved in wildlife conservation, in particular of endangered species living in environments that are changing ecologically and culturally. First, I reviewed the literature on how genomic variation impacts disease processes. Because there would be too few studies involving only endangered species, I included all studies on mammalian hosts to gain a better understanding of the genomic basis for parasite resistance and tolerance across study systems (Chapter 2). Next, I focused on Grevy's zebra (*Equus grevyi*), an endangered equid found only in a small area of the Horn of Africa, to determine how environmental factors (including natural features, such as water and forage availability, as well as anthropogenic factors), impact levels of stress hormones and parasite burden (Chapter 3). The final chapter of my thesis focused on the social context of endangered species conservation in remote regions of Kenya (Chapter 4). Taken together, these chapters inform multiple aspects of endangered species conservation. The meta-analysis indicates which genomic information can help best discern aspects of genomic variability that might benefit species facing disease risks. The field study on Grevy's zebra informs what factors of the environment might be most negatively impacting Grevy's zebra stress and infection. Lastly, the interviews conducted with local Samburu people elucidate how local individuals living near endangered species may view those animals and the benefit to preserving them and contrasts this with international views on conservation. The results of all work conducted on Grevy's zebra and in Samburu communities will be communicated back to local Kenyan conservation organizations and communities where this work was conducted through a series of community meetings to be held in Kenya in 2020.

CHAPTER 2

IS IT TIME TO MOVE WILDLIFE STUDIES INTO THE GENOMIC ERA?: A META-ANALYSIS ON GENOMIC VARIATION-DISEASE ASSOCIATION

Abstract:

Individuals with limited genomic variability often show lowered resistance and tolerance to disease, which can translate to population decline. Given this, it is crucial to understand how variability across the genome influences diseases in individuals and populations. There are three main genomic components that influence disease response: 1) coding loci (i.e., candidate genes); 2) genome-wide levels of variation at putatively neutral (i.e., non-coding) locations; and 3) complex interactions at both types of loci throughout the genome. Surveilling these genomic components has been used to help inform, in the immediate timeframe, conservation management decisions as they relate to disease, and over longer timescales, how a population or species might evolve in response to disease pressures (i.e., evolutionary potential). It is unclear, however, whether surveilling certain genomic components can provide significantly improved insight on the association with disease over other genomic components. Also unclear is whether and how study system-specific factors (e.g., study species, parasite taxa) might influence the association between disease and specific genomic components. We performed a meta-analysis on the association between genomic variation and measures of disease in wild mammals – taking into account whether studies used candidate gene loci or genomic variability at putatively neutral genomic locations. Across studies, specific alleles of candidate loci were strongly associated with disease measures. Specifically, alleles present at a low frequency in populations (i.e., rare alleles) were commonly associated with increased resistance and tolerance to disease. Heterozygosity (i.e., possession of two different alleles per locus) at candidate gene loci, but not at putatively neutral loci across the genome (i.e., genome-wide heterozygosity), was linked to higher levels of resistance and tolerance to infectious disease. Associations of rare alleles with disease measures suggests a role for frequency-dependent or balancing selection acting to maintain specific alleles within populations. The association of candidate loci heterozygosity with disease measures suggests that heterozygote advantage may be acting at candidate, but not neutral loci, to maintain variability at functional genomic loci. These results increase our understanding of the genomic components associated with disease in wild populations, thus can help inform the design of future empirical studies.

1. Introduction

Infectious diseases represent a threat to wild populations that can rapidly reshape communities and ecosystems (Altizer et al. 2003; Frick et al. 2015; Langwig et al. 2015). Recent work has pointed to an increasing list of examples where infectious diseases have caused declines in previously thriving populations, and these diseases have been implicated in endangerment and extinction of these species (Altizer et al. 2003; Smith et al. 2009). Wildlife epidemics such as devil facial tumor disease (DFTD) in the Tasmanian devil (*Sarcophilus harrisii*) (McCallum 2008), bacterial hemorrhagic septicemia in saiga antelopes (*Saiga tatarica tatarica*) (Kock et al. 2018), chytridiomycosis in amphibians (Skerratt et al. 2007), and white-nose syndrome in multiple species of bats (Blehert et al. 2009) provide examples in which infectious diseases have caused population declines, changes in distribution, and species' extinctions (McCallum &

Dobson 1995; Daszak et al. 1999; Daszak & Cunningham 1999; Lafferty & Holt 2003; Pounds et al. 2006).

While wild animals have behavioral mechanisms to avoid and tolerate parasitic infections, individual genomics is an inherent and integral determinant of resistance and tolerance to disease at both the individual and population levels (Spielman et al. 2004a). Variation throughout the genome drives differences in host immune responses which – along with environmental factors – generates various disease outcomes for individual animals (Tavalire et al. 2019). The genomic component of the disease response can be determined by loci that are specifically linked to disease (i.e., candidate genes), genome-wide levels of variation at putatively neutral (i.e., non-coding) locations, and by complex interactions at loci throughout the genome. Illuminating how and which of these components determine the host disease response in any given wildlife system is critical for developing strategies to mitigate the effect of disease on populations and for evaluating evolutionary consequences (e.g., adaptive potential and evolutionary trajectory) (Hoelzel et al. 2019).

Reduced variation (i.e., heterozygosity) throughout an individual's genome can arise thru inbreeding – a demographic process that often results from small population size or fragmented populations – and is often measured using microsatellite or other codominant markers located in non-coding regions of the genome (Slate & Pemberton 2002; Balloux et al. 2004). Microsatellite markers have been widely used in wildlife studies to estimate inbreeding, but this diversity at selectively neutral, anonymous loci is also often used as a proxy for diversity at harder to identify, candidate genes (Piertney & Webster 2010). Thus, heterozygosity determined from microsatellite markers is often assumed to reflect genome-wide heterozygosity (Grueber et al. 2008). A wide body of literature has examined the association between heterozygosity and fitness or proxies of fitness in wildlife populations (heterozygosity-fitness correlations, HFC hereafter) (Hansson et al. 2002; Grueber et al. 2008; Chapman et al. 2009; Szulkin et al. 2010) – with disease frequently used as a proxy of fitness (e.g., Brambilla et al. 2018). In such studies, lower levels of heterozygosity have been associated with increased incidence of disease and greater disease-related mortality (Spielman et al. 2004a). For example, inbred Soay sheep (*Ovis aries*) had higher parasite burdens and lower survival than more outbred individuals (Coltman et al. 1999), and in wild banded mongoose (*Mungos mungo*) more heterozygous individuals had reduced parasitic infections (Mitchell et al. 2017).

Although microsatellite-derived heterozygosity has been useful in some cases to detect associations with disease, directly measuring diversity of candidate genes may be better indicators of how an individual animal will respond to disease (Hedrick 2003; Manlik et al. 2019). This is because candidate genomic loci may be directly involved in disease resistance and tolerance (Tavalire et al. 2019; Roffler et al. 2016) and genomic variation at these loci are shaped by selective pressures, thus may differ in levels of variation from putatively neutral loci (Spurgin & Richardson 2010). Heterozygosity at candidate gene regions is often used to infer disease outcome (Trowsdale 2011) and in some cases can point to associations between genomic variability and disease that may be missed by the use of putatively neutral heterozygosity alone. For example, in bighorn sheep (*Ovis canadensis*), overall heterozygosity calculated across multiple microsatellite loci was not associated with lungworm infection; however, heterozygosity at single, a specific locus was correlated with infection burden (Luikart et al. 2008). In other instances, specific alleles (i.e., alternative forms of a gene that control the same character) of candidate genes, rather than heterozygosity, have been linked to differing disease outcomes and can provide information on associations with disease measures that are not revealed from assessment of heterozygosity at either putatively neutral or candidate gene loci (Harf & Sommer 2005). For instance, in the spotted suslik (*Spermophilus suslicus*), heterozygosity at Major Histocompatibility Complex loci (hereafter, MHC), a gene complex directly involved in the adaptive immune response of vertebrates (Apanius et al. 1997; Sommer 2005), was not related to infection status with the blood parasite *Haembartonella* sp, however specific MHC alleles were related to prevalence and infection intensity (Biedrzycka & Kloch 2016).

Despite the existence of multiple empirical studies that assess the relationship between genomic variation and disease in wildlife species, there is no clear picture of which components of genomic variation contribute most closely to differences in disease outcome across wildlife study systems (Hohenlohe et al. 2019). Additionally, empirical studies have shown equivocal results (Hansson & Westerberg 2002; Chapman et al. 2009). Some studies have revealed the expected negative association, that disease measures are lower in animals with higher levels of heterozygosity (e.g., Coltman et al. 1999). However, other show no association or show a positive association in which animals with higher levels of heterozygosity have a greater incidence of disease (e.g., Acevedo-Whitehouse et al. 2018). Due to such equivocal results, our our ability to design genomic variation-disease association studies in wildlife systems that will aid in understanding aspects of genomic variation involved in resistance and tolerance to disease is currently limited. Here, we performed a phylogenetically controlled meta-analysis of empirical studies in free-ranging, naturally-infected wildlife to test whether genomic variation measured at non-coding loci or genomic variation measured at candidate loci showed stronger associations with disease measures. Additionally, we tested if different taxonomic classes of parasites or the disease measure (infection status, parasite burden, parasite richness, and disease-related illness and mortality) recorded per study impacted the association between genomic variation and disease. Understanding if there are patterns with regards to the direction and magnitude of effect across empirical studies and what factors moderate those patterns will aid in the design of future genomic variation-disease studies. Our results elucidate how different measures of genomic variability associate with parasite resistance and tolerance across studies, and can shed light on the ways in which disease susceptibility is influenced by host and pathogen attributes.

Table 2.1: Categories of genomic variation and disease measures.

Genomic variation categories	
Form of diversity	**Definition**
Heterozygosity: candidate gene	Heterozygosity measured across a disease-related gene (e.g. MHC)
Heterozygosity: genome-wide	Heterozygosity at putatively neutral markers; in this meta-analysis all empirical studies used microsatellite markers
Allelic diversity	Nucleotide or amino acid differences between two alleles at a specific locus
Specific alleles: common	Assessment of specific alleles present in the individual (common ≥ 15% frequency in population)
Specific alleles: rare	Assessment of specific alleles present in the individual (rare ≤ 15% frequency in population)
Disease Measure categories	
Infection status	Whether animal was infected or not (yes/no)
Parasite burden	Number of parasites of a specific spp. or multiple spp. (from fecal egg counts or necropsy)

Parasite richness	Number of different spp. of parasite in host
Disease-related illness or mortality	Recording of illness known to be associated with the infection (e.g. lungworm-related anemia in sea lions); or mortality known to be due to infection and infection-related complications.

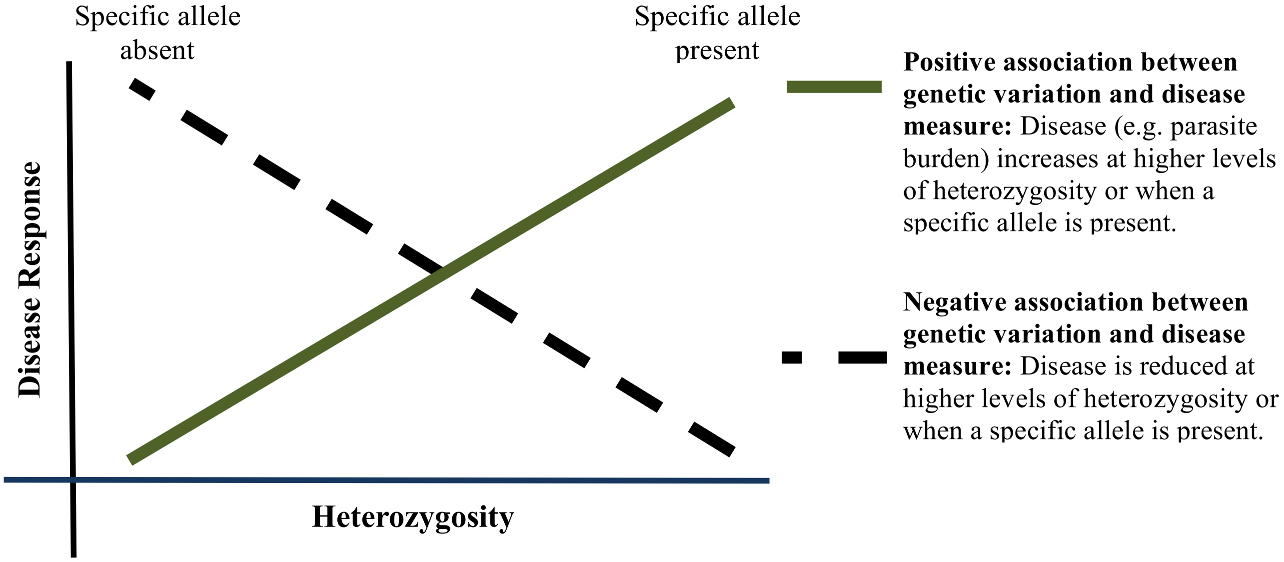


Figure 2.1: Hypothetical relationships for positive and negative associations between genomic variation and measures of disease. Positive genomic variation-disease associations indicate a negative outcome for the host (i.e. increasing levels of heterozygosity or the presence of a specific allele lead to increased disease measures.) Negative associations between genomic variation and measures of disease indicate a positive outcome for the host (i.e. increasing levels of heterozygosity or the presence of a specific allele lead to increased disease measures.)

2. Materials and Methods:

Literature survey and statistical approach

We performed a systematic review of available literature on the association of genomic diversity and disease measures in free-ranging, wild mammals. We focused on mammals, because few metazoans have received as much attention for management, disease risk, and evaluation of genomic variation across a breadth of study organisms. Additionally, the vertebrate MHC in particular has been explicitly evaluated in a number of such studies, along with typical anonymous loci - often in the same study system – allowing some control for study design (e.g., Winternitz et al. 2014). Scholarly articles were identified through Web of Science and EBSCO (includes: MEDLINE, CAB Abstracts, Environment Complete, Wildlife & Ecology Studies Worldwide, Agricola) searches using strings of terms relevant to genomic diversity and disease (Supplemental Figure 2.1: PRISMA diagram, Supplemental Document 2.1). Our systematic search identified 65 studies meeting initial criteria for inclusion, of which relevant information was only available from 28 studies. Initial criteria for inclusion were that the study had to have quantified genomic variability and had to include a measure of naturally-occurring infectious disease in wild mammals. The 28 studies used in our analyses included statistical relationships between individual genomic variability (measure of heterozygosity at a single locus or multiple loci, or the presence of absence of a specific allele at a focal genomic region) and disease measures (infection status, abundance, parasite richness, or a measure of disease outcome, such as disease-related mortality). From each study, we recorded the test statistics and direction of effect for the relationship between genomic variability and the disease measure along with information on the focal genomic region used to assess genomic variability, parasite taxa (ectoparasite, bacteria, helminth, protozoa, virus) and functional characteristics (macro or microparasite; extra or intracellular), disease response measure, mammalian host species, and study characteristics (i.e., study site, duration of study, and sample size). Because many studies reported data for multiple measures of genomic variability, multiple pathogens, or multiple measures of disease response, our data set included 386 records, where each record consisted of a particular genomic variability-disease measure combination. Further details on search procedures, criteria for study inclusion, and categorical assignments are reported in the Supplemental Data (Supplemental Document 2.1).

With regards to information on genomic variability, we categorized data into two broad groups: studies that used heterozygosity as a summary statistic, and those that used specific alleles as indicators. The former group being studies that examined diversity at a single or multiple loci using heterozygosity (i.e., possessing different alleles at a locus or at multiple loci across the genome) as the metric of genomic variation. We further categorized heterozygosity into three types: (1) 'genome-wide heterozygosity' for putatively neutral markers such as microsatellites used as a proxy for heterozygosity throughout the genome, (2) 'candidate gene heterozygosity' for heterozygosity at a single candidate gene-linked locus or at a candidate gene locus such as MHC, or (3) 'allelic diversity' for diversity between two alleles at a given locus (e.g., amino acid distance or nucleotide diversity). Because heterozygosity from multiple loci (i.e., genome-wide heterozygosity) can be calculated using different formulas (Slate & Pemberton 2002), and studies frequently report more than one measure, we checked each manuscript to ensure that reported measures were consistent with each other. In our meta-analysis, there were no studies reporting multiple measures of heterozygosity in which measures differed with statistical significance, we thus recorded only one measure for each record.

The second broad group used to categorize genomic variability was the presence of specific alleles at a locus. These studies examined the association between disease measure and the presence or absence of a specific allele at focal genomic regions. In our meta-analysis, with the exception of 3 records for Tlr4 (Toll like receptor 4; Toll like receptors are genomic regions involved in activating the innate immune system (Kopp & Medzhitov et al. 1999)), the only focal genomic region used for specific allelic analysis was the MHC region. We recorded only those studies that tested the effect of a single allele (as opposed to genotype). We did not collect data for specific allele association tests that compared the effect of two alleles (i.e., pairwise comparisons). Additionally, for specific alleles, we categorized the frequency of the allele in the population or study and categorized these as "common" or "rare" in frequency. We used the cut-offs <15% to denote a rare allele and $\geq$15% for "common". These delimitations were assessed with other values to retain some statistical balance but determine if the results are sensitive to the value chosen. If the study reported a category for allele frequency (e.g., reported as rare), we used this reported category. Allele frequencies could not be determined for the three Tlr4 records as this data was not available (Gavan et al. 2015), thus only MHC records were used in distinguishing differences between common and rare alleles with regards to associations with disease measure.

Lastly, we only included associations that showed a linear response between genomic variability and disease (i.e., strictly positive, negative, or true null effects), thus some associations were excluded. For instance, when an intermediate number of alleles per individual was found to provide the best protection against disease, this provided test statistics for a quadratic effect and could not be converted to an effect size and direction for inclusion in our study. Ten observations were eliminated due to non-linearity.

Disease measures included: infection status (yes/no), infection intensity (e.g., fecal egg counts, count of infected blood cells), parasite richness (i.e., the number of different parasites counted within a given individual), disease-related illness or mortality. All measures were taken at the individual level to use in the meta-analysis. Population-level measures of genomic variability-disease associations (e.g., infection prevalence) were excluded from this study. For disease measures, we also recorded the parasite type according to three different classification schemes. These were: (1) bacteria, helminth, protozoa, ectoparasite ('virus' was excluded, because there was only one record representing a viral infection), (2) extra-cellular or intra-cellular parasite, and (3) microparasite and macroparasites. When multiple parasites were used in one association, this was coded as "multiple".

We used the reported test statistics (e.g., r^2, odds ratios, t, χ^2) and sample sizes for each genomic variability-disease measure to obtain standardized effect sizes through the correlation-based r (Rosenthal & DiMatteo 2001; Bonett 2007). We assigned positive values to correlations when the disease measure (e.g., parasite abundance) was greater at higher levels of genomic variability. In contrast, when the disease measure was greater at lower levels of diversity, we noted this as a negative correlation. Likewise, for specific alleles, if the presence of the allele was associated with an increased disease measure, we noted this as a positive association and vice versa (Figure 2.1). Directional r effect sizes were transformed into Fisher's Z_r to stabilize variance (Fisher 1921) and to estimate the sampling variances for the statistical models.

We used phylogenetically-controlled hierarchical models to explain variation in disease measures across the 29 unique host species (Supplemental Table 2.2). We used the *rotl* (Michonneau et al. 2016) and *ape* (Paradis & Schliep 2018) packages in R to obtain a branch-length based phylogeny for our 29 hosts from the Open Tree of Life (Lajeunesse 2009; Sanchez et al. 2018). Host species was included as a random effect, with the covariance structure specified by the correlation matrix of our phylogeny. Observation and study were included as a nested set of random effects to account for unit-level heterogeneity and the multiple effect sizes per study (Konstantopoulos 2011; Nakagawa & Santos 2012). All models were fit with restricted maximum likelihood to obtain unbiased estimates of variance component and included weighting by sampling variance. We used the R package *metafor* for r-to-Z_r effect size conversions, and hierarchical statistical models (R Core Team 2013; Viechtbauer 2010).

To infer the average effect of genomic variability (all measures) on disease measures across the entire data set (n=295), we first used a univariate random-effects model (REM; Model A). We calculated I^2 (i.e., a measure of the heterogeneity in effect sizes) to quantify the relative contribution of true heterogeneity to the total variance in effect size. Next, to assess how different measures of genomic variability moderate effect size, we ran three separate mixed-effects models (MEM) using genomic variability measures as moderator variables. The first MEM tested whether effect size varied between the two broad classes of genomic variability: specific allelic responses or heterozygosity across all genomic regions (Model B; n=295). We ran this same model using only records containing MHC genomic regions ($n=188$). This tested for effect size differences between specific alleles and heterozygosity at the immune region used in the majority of studies. The second MEM tested for an association between the frequency of specific alleles (i.e., common or rare) and effect size (Model C; n=189). All but one of these studies was an allele of the MHC region. This model was not run with MHC-only data due to the unlikelihood of one record impacting the model output. The third MEM (Model D) tested whether the focal genomic region used to determine heterozygosity (i.e., genome-wide heterozygosity, candidate gene heterozygosity, allelic diversity) was associated with the relationship between genomic variability and disease measure (Model D; $n=106$).

We also fit a suite of MEMs to test if the metrics used to classify ‘disease’ (i.e., parasite taxonomy and disease measure) were important moderators of effect size. We first fit MEMs with each ‘parasite taxa’ classification schema. This was to understand whether there was a difference in the genomic diversity-disease measure association between parasite taxonomic classes. We first tested if there were differences in effect size among bacteria, helminth, protozoa, and ectoparasite infections (Model E1, *n=229*) ('virus' was excluded, because there was only one line of data representing a viral infection). Models E2 and E3 tested for differences in effect size between extra- and intracellular parasites (*n=229*) and micro- and macroparasites (*n=229*), respectively. Last, we included the category of 'disease response' as a moderator variable to understand whether disease measure (abundance, infection status, parasite richness, disease related-illness or mortality) had an effect on the relationship between genomic variability and disease measure (Model F; *n=231*).

Because sample sizes varied per model based on missing values for some moderators, we fit separate univariate models rather than multivariable models. Missing values for some moderators also precluded a model comparison approach. We instead quantified the variation in effect size explained per each univariate moderator by calculating the proportional reduction in the summed variance components from each MEM compared to the summed variance components of a comparable REM (i.e., the model without moderators fit to the same dataset), equivalent to a pseudo-R^2 value (Lopez-Lopez et al. 2014). Lastly, we obtained the predicted means and their 95% confidence intervals for each level of our moderator variables (Table 2.2).

3. Results:

3.1 Associations between genomic variability and disease measures

When the REM was fit to the entire dataset (Model A), there was no significant overall relationship between genomic variability and disease (overall correlation, z=-1.1054, p=0.27). However, there was significant heterogeneity among associations between genomic variability and disease measures (I^2=88.43%, Q=1653.56, df=260, p<0.0001), which we investigated further by testing whether effect sizes varied with (1a) types of genomic variability, (1b) focal genomic region used to calculate heterozygosity, (1c) allele frequency, (2) parasite taxa, (3) disease response measures, and (4) host phylogeny.

3.2 Effect of types of genomic variability

3.2.1 *Heterozygosity vs. specific alleles*

The first MEM (Model B) found that the two broad classes of genomic variability – heterozygosity or specific allelic responses at any genomic region – were significantly different from each other in effect size (Q=16.48, df=1, p <0.0001; Figure 2.2a). Heterozygosity had an overall negative relationship with disease (i.e., less disease), while specific alleles had both positive and negative mean relationships (i.e., the 95% confidence interval crossed zero) with disease outcome. This relationship was still significant and maintained the same directionality when the model was run with studies that looked only at heterozygosity or specific alleles of the MHC region (Q=9.36, df=1, p=0.002).

3.2.2 *Allele Frequency (rare vs. common alleles)*

Allele frequency significantly explained variation in effect size (Q=23.06, df=1, p<0.0001; Figure 2.2b), highlighting a difference in disease measures between common and rare alleles. Common alleles ($\geq$15% representation in the population) had a positive association (i.e., more disease) with disease measure, whereas rare alleles (<15% representation in the population) had a negative association (i.e., less disease) with disease measures. For common alleles this indicates they are more frequently associated with higher parasite burden or richness, or with a positive infection status. For rare alleles, the mean effect size was negative, however the 95% confidence interval crossed the zero line, indicating that there are also positive associations (i.e., more disease) with disease and rare alleles. This indicates diverse disease outcomes in response to rare alleles.

3.2.3 *Focal genomic region used to calculate heterozygosity*

There were no significant differences between effect sizes dependent on the focal genomic region used to calculate heterozygosity (i.e., candidate-gene heterozygosity, genome-wide heterozygosity, allelic diversity; Q=3.02, df=2, p=0.2214; Figure 2.2c) However, heterozygosity at candidate genes, such as MHC, showed a negative association (i.e., less disease) (z =-0.1331, SE=0.078, p=0.08) with disease measure. Neither allelic diversity or genome-wide heterozygosity were significantly associated with disease measure across studies. Allelic diversity had mean effect sizes that showed positive and negative associations with disease measure. Genome-wide heterozygosity (i.e., based on putatively neutral loci) had negative mean effect sizes, but was not significantly different than zero.

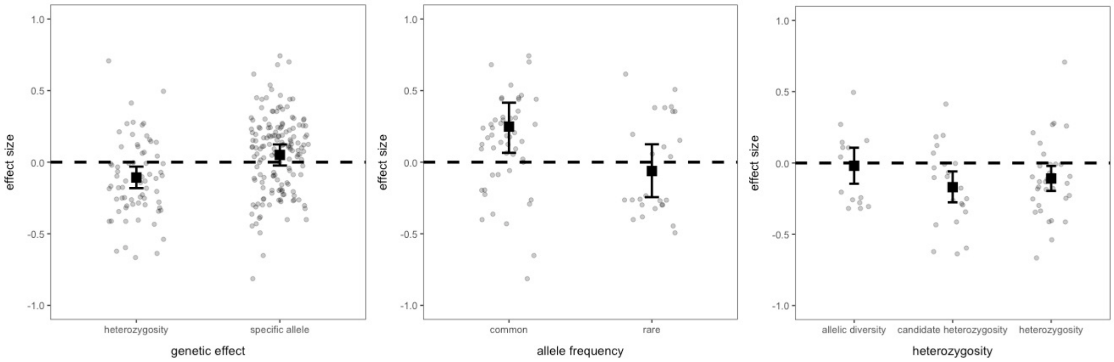


Figure 2.2: Distribution of effect sizes according to (a) genomic effect type (Model B), (b) allele frequency (Model C), and (c) focal genomic region used to determine heterozygosity (Model D). Plots show the mean predicted effect size and bars indicate 95% confidence intervals. The dashed horizontal line represents no association between genomic variability and disease measure (*r*=0). A positive effect size represents increased disease measure (e.g., parasite burden) with increasing genomic variability or the presence of an allele. A negative effect size represents decreasing disease measure with increasing genomic variability or the presence of a specific allele.

3.3 Parasite taxa and genomic variability-disease associations

No significant differences in effect sizes in genomic variability-disease measure associations were found using any method of categorizing parasites as a moderator variable (Model E1 – helminths, protozoa, bacteria, ectoparasite: Q=2.18, df=3, p=0.536; Model E2 – extra/intracellular parasites: Q=2.06, df=2, p=0.358; Model E3 – macro/microparasites: Q=0.484, df=1, p=0.487). Because no differences were found in the genomic variability-disease measure associations between parasite taxa, we did not conduct further analyses to test whether there were pairwise differences between different types of genomic variability.

3.4 Disease measures and genomic variability-disease associations

When categories of 'disease measure' (parasite burden, parasite richness, infection status, disease-related illness and mortality) were included as a moderator variable, we found no significant association with effect size (Q=1.93, df=3, p=0.588). We therefore did not further test whether there was a difference between specific alleles or heterozygosity, or whether allele frequency or the focal region used to calculate heterozygosity impacted the genomic variability-disease measure relationship.

3.5 Effect of host phylogeny

Sigma^2 estimates for host species across all mixed effects models was zero, suggesting there was no influence of host phylogeny on the relationship between disease measure and genomic variability. This further suggests that the effect of genomic variability on disease measures is a general phenomenon and is unlikely to be restricted to certain clades within our phylogeny.

Table 2.2: Pseudo-R^2 values, predicted mean effect sizes, and 95% confidence intervals for Models B, C, and D using the predict package in R.

Model (n)	*Pseudo-R^2*	*Moderator variable*		*Predicted Mean effect size*	*95% confidence intervals*
Model B (n=295)	0.12	Genomic effect type	- Heterozygosity	-0.113	-0.18 – -0.43
			- Specific alleles	0.036	-0.313 – 0.10
Model C (n=188)	0.02	Specific alleles	- Common	0.230	0.07 – 0.38
			- Rare	-0.03	-0.19 – 0.13
Model D (n=106)	0.02	Heterozygosity	- Candidate heterozygosity	-0.17	-0.27 – -0.06
			- Genome-wide heterozygosity	-0.019	-0.15 – 0.107
			- Allelic diversity	-0.109	-0.20 – -0.02

4. Discussion:

Predicting how wild host populations will respond to parasites is challenging, because it requires understanding the genomic basis for host resistance and tolerance and the drivers of these traits (Altizer et al. 2003). We performed a meta-analysis across studies of wild mammalian populations to determine if genome-wide heterozygosity (based on putatively neutral loci), candidate heterozygosity or the presence of specific alleles were linked to measures of resistance and tolerance to infectious diseases. We found that while higher levels of both genome-wide and of candidate gene heterozygosity are negatively associated with disease measures (i.e., less disease), when candidate gene heterozygosity was analyzed alone, there was a stronger association (i.e., larger (more negative) effect size) with disease measures. When looking at the relationship between disease and specific alleles, both positive and negative effects sizes were noted, with a mean effect size near zero. However, parsing of alleles into categories based on the frequency of that allele in the population in which it was sampled revealed that there was a difference between common and rare alleles in their association with disease. While common alleles were more commonly positively associated with disease (i.e., greater disease), rare alleles had a negative association with disease (i.e., less disease). Our findings suggest that targeting specific candidate genes either through the determination of heterozygosity at those loci or through the identification of specific alleles will provide better resolution than putatively neutral heterozygosity when attempting to predict disease responses in wild mammalian populations. Additionally, identifying the genomic components involved in disease responses allows inference into the modes by which genomic variability linked to disease is either being maintained or is diminishing. These findings suggest that incorporation of genomic techniques into wildlife disease studies will provide two large benefits: 1) it will increase our ability to understand the genomic basis of disease and 2) will therefore lend insight into the demographic and evolutionary forces shaping the genomic architecture involved in the disease response (i.e. resistance and tolerance to disease).

4.1 Using genomics to increase our understanding of the genomic basis of disease responses

Since the inception of genetic studies in wildlife, such research has relied primarily on the use of markers located in putatively neutral regions of the genome (i.e., microsatellites or other markers types (e.g., allozymes)) (Goldstein & Schloetterer 1999). While the use of genomic methods (i.e., next-generation sequencing of full genomes or of candidate genes of interest) has become commonplace in human and model organism studies (Flint & Eskin 2012), the integration of such genomic methods is not yet widely accessible to researchers whose study systems include non-model organisms (Ellegren 2014), which includes most species of wildlife. The studies used in our meta-analysis is evidence of this, as many rely on microsatellite markers to assess genome-wide heterozygosity. Additionally, all but one study used MHC loci as the candidate gene of interest in reference to disease, reflecting the fact that outside of this genomic region, little is know about other loci that might have as strong as an effect on resistance and tolerance to disease in non-model wildlife systems (Acevedo-Whitehouse et al. 2006). There is an expectation that the incorporation of genomic era techniques, with their associated higher number (hundreds to thousands) of markers and/or ability to sequence whole genomes or genomic regions, would reveal distinct results and the improve the ability to uncover quantitative trait linkages (e.g., Vilas et al. 2014).

4.1.1 *Specific alleles & candidate gene heterozygosity associations with disease responses*

While multiple genes are involved in the disease response to parasites (Wrightsman et al. 1982), all but one study in our meta-analysis investigated the role of candidate genes using The Major Histocompatibility Complex genes (MHC) as the focal genomic region. Here we will focus on discussions of MHC, while recognizing the need to broaden our understanding of genes beyond MHC that are involved in resistance and tolerance to disease. The MHC has been widely used in wildlife studies as it has been broadly studied in model and non-model systems, and determining the genomic basis of other traits of interest, even in model systems, has proven difficult (Gebremedhin et al. 2009; Spurgin & Richardson 2010). Links between MHC heterozygosity and disease measures have been found across a wide range of taxa (MacDougall-Shackleton et al. 2005; Oliver et al. 2009), and it is widely accepted that variation at MHC plays an integral role in the response to multiple diseases (Spurgin & Richardson 2010b; Bujanic´ & Konjevic´

2015). Our results support stronger associations between genomic variation (both the presence of specific alleles and heterozygosity) at candidate loci and the disease measure than at putatively neutral loci. Because the candidate locus studies involved in our meta-analysis used MHC almost exclusively, our findings underscore the importance of MHC in disease resistance and tolerance. By extension this may point to a stronger association between disease and all candidate genomic regions, however this finding also illuminates the need to link greater numbers of candidate genomic regions to functional traits in wildlife, including disease, to gain a broader understanding of how genomics underpins resistance and tolerance.

4.1.2 *Putatively neutral genomic variation (microsatellite-based heterozygosity) and association with disease measures*

Microsatellite markers have historically been used as a proxy for genome-wide levels of heterozygosity (Dewoody & Dewoody 2005; Miller et al. 2014), and as an inference into inbreeding (Robinson et al. 2013). An increasing number of empirical studies indicate that individuals with limited heterozygosity at one or multiple loci, relative to the overall genomic diversity of the population or species, experience disproportionately negative impacts on fitness and from disease (Coltman 1999; Chapman et al. 2009). For example, in male Alpine ibex (*Capra ibex*), burden of intestinal nematodes was linked to heterozygosity across the genome, which was assessed with 37 microsatellite loci (Brambilla et al. 2015). These results fit with expectations, because more diverse individuals are expected to express fewer recessive deleterious alleles and/or to carry more adaptive alleles to resist parasites (Coltman 1999; Cassinello et al. 2001; Brambilla et al. 2015). Despite many published reports of associations between putatively neutral heterozygosity and genomic variation, we did not detect an overall significant association between genome-wide heterozygosity assessed by microsatellite markers and disease measure. This provides further evidence that candidate genomic loci are more informative to understand how individuals may respond to disease. However, it is also possible that the low number of microsatellite markers (range: 1-37) used in many studies included in our meta-analysis led to a lack of power to detect associations with disease. Slate and Pemberton (2002) found that when less than ten microsatellites were used, there was low power to detect any type of heterozygosity-fitness correlations. In our study only 26 of 106 records for putatively neutral heterozygosity included the use of more than ten microsatellite markers.

It is also possible we did not find evidence for genome-wide heterozygosity-disease associations across our data set, because associations between genome-wide heterozygosity based on microsatellite markers and disease measures may be driven by different mechanisms, including not just the effect of genome-wide heterozygosity on disease (i.e., general effects), but also from the effects of single markers that are in or linked to candidate genes (i.e., single locus effects) (Chapman et al. 2009). For example, Acevedo-Whitehouse et al. (2005) found that heterozygosity across the genome in wild boars (*Sus scrofa*) was linked to resistance to bovine tuberculosis (bTB) and played a role in limiting disease progression once individuals were infected (Acevedo-Whitehouse et al. 2005). Similarly, in the alpine ibex (*Capra ibex*), parasite resistance to nematodes (measured by fecal egg counts) was greater in more heterozygous animals (Brambilla et al. 2015). However, in both examples, effects of heterozygosity on disease response were interpreted to be due to general effects as well as to single locus effects. Given this, it is not always clear if heterozygosity-disease measure associations are due to genome-wide heterozygosity or to heterozygosity at a specific microsatellite locus that may be linked to a locus involved in disease.

4.2 Demographic and evolutionary forces shaping the genomic architecture behind disease responses

Genomic architecture and variation is shaped by demographic and evolutionary forces. Because different processes play a role in shaping the genomic components associated with disease, genomic variability-disease associations can be used as inferences into whether demographic or evolutionary forces are working within a given population to shape the genomic architecture underpinning resistance and tolerance to disease. Demographic factors, such as small population size or population fragmentation, can lead to inbreeding or genetic drift resulting in lower genome-wide heterozygosity (Slate & Pemberton 2002; Balloux et al. 2004). In contrast to the demographic processes that drive genome-wide heterozygosity, evolutionary processes – in particular different forms of pathogen-mediated selection – can maintain genomic variation at functional loci involved in aspects of the disease response (Apanius et al. 2017). Pathogen-mediated selection at the MHC and other candidate loci involved in resistance and tolerance to disease can be driven in three distinct, but potentially overlapping ways: 1) heterozygote advantage (i.e., being heterozygous is generally advantageous because heterozygotes can recognize and bind a wider range of antigens than homozygotes) (Doherty & Zinkernagel 1975)), 2) rare-allele advantage (negative-frequency dependent selection and new alleles confer an advantage since parasites rapidly evolve to overcome more common resistance alleles) (Slade & McCallum 1992)) and 3) fluctuating selection (spatial and temporal variability in pathogen exposure leads to differences in alleles that are advantageous in a given system) (Portanier et al. 2019). The stronger negative association with candidate gene heterozygosity over putatively neutral heterozygosity suggests there is evidence across the mammalian study systems in our meta-analysis for pathogen-mediated selection in the form of heterozygote advantage. The negative association between disease measures and rare alleles, suggests there is pathogen-mediated selection for specific alleles, with rare alleles conferring an advantage against disease and common alleles conferring a disadvantage (i.e., higher parasite burdens/richness and positive infection status) across systems. While we found evidence across studies for pathogen-mediated selection in the form of heterozygote advantage and rare allele advantage (Bujanic´ & Konjevic´ 2015), because these studies represent a snapshot in time, it is difficult to determine if this is indicative of fluctuating or balancing selection (Spurgin & Richardson 2010).

4.3 Genomic basis of resistance across parasite taxa and disease measure

Parasites have very diverse life cycles, can infect the host in a multitude of ways, engage different immune pathways, and cause differing pathologies (Spielman et al. 2004a; Cizauskas et al. 2014; Portanier et al. 2019). Because of these differences, parasites can elicit immune responses that rely on different underlying genomic components (e.g., different classes of MHC) (Portanier et al. 2019). We thus tested whether the genomic basis of resistance differed across parasite taxa. We classified parasites in three ways, however found no differences in the association with disease response when we tested between (1) ectoparasites, helminths, bacteria, and protozoa, (2) extracellular and intracellular parasites, or (3) microparasites and macroparasites. Although it is unclear whether limited sample size across parasite taxa or across different measures of genomic variation contributed to the lack of significant association with parasite taxa in our study, differing associations with parasite taxa have been found in other systems. For example, in the Mediterranean mouflon (*Ovis gmelini* x *Ovis* sp.), genome-wide heterozygosity (from 16 microsatellite markers), heterozygosity and rare alleles at MHC were associated with resistance to gastrointestinal nematodes (macroparasitic nematodes), but not to coccidian (intracellular protozoa) (Portanier et al. 2019). In this case, the authors attributed the genomic variation-nematode resistance association to the fact that the particular MHC locus employed in their study is linked to extracellular parasite-driven peptide presentation (Piertney & Oliver 2006).

Additionally, genomic variation can impact different aspects of the disease response (i.e. whether an animal becomes infected (infection status), parasite abundance, parasite richness, or disease-related illnesses and mortality) (Acevedo-Whitehouse et al. 2005). However, we found no differences between the type of disease response measured and the genomic basis of resistance.

4.4 Conclusions – implications for conservation and future directions

It is unclear how many species or populations are directly threatened with disease (Smith et al. 2006), but it is known that populations with limited genomic variability experience unusually large impacts from infectious disease (Altizer et al. 2003). Historically, putatively neutral loci have been implemented across HFC studies and many have found strong associations between heterozygosity and fitness (Chapman et al. 2009), however neutral loci cannot provide direct information on selective processes or adaptive potential (van Tienderen et al. 2002). In contrast, candidate gene variability reflects evolutionary and adaptive processes, and therefore will be more useful in studies of the association between genomic variation and disease (Cote et al. 2005). Although MHC is frequently used as a model for studying the maintenance and effect of immune-related genomic variation in wild populations (Spurgin & Richardson 2010), association studies between disease measures and other candidate loci involved in resistance and tolerance will help elucidate the role of genomic variation in disease. Going forward, incorporating disease-related regions of the genome, beyond MHC, in genomic variation-disease studies (Acevedo-Whitehouse & Cunningham 2006) can help elucidate the connection between other genomic regions and disease. For instance, specific genotypes and increased heterozygosity of toll-like receptor (TLR) were more predictive of fitness in a species of bird (*Petroica australis rakiura*) than MHC profiles (Grueber et al. 2015). Schiebelhut et al (2018) found single-nucleotide polymorphisms that changed following high mortality from sea star wasting disease. Such studies highlight the role of non-MHC immune genes in overall fitness, a contributing factor to the disease response, and highlight the advantage of surveilling more and different regions of the genome beyond what has been done in the recent past. With increasing availability of next-generation sequencing, genome-wide association studies (GWAS) will be facilitated, that can identify new genomic regions of interest in wildlife disease.

CHAPTER 3

ENVIRONMENTAL AND DEMOGRAPHIC CORRELATES OF STRESS AND INFECTION IN THE ENDANGERED GREVY'S ZEBRA

Abstract:

Understanding the role of the environment in shaping individual fitness is critical for conservation given that more than 85% of IUCN-listed species are threatened by habitat destruction and degradation. Environmental changes, including anthropogenic disturbance and climate changes, can have sweeping effects on wildlife, altering many facets of individual physiology. Using the Grevy's zebra (*Equus grevyi,* an endangered equid) which lives in a matrix of diverse land-use types as a model, we investigated how parasite infection (strongyle nematodes and lungworms) and physiological stress (fecal glucocorticoid metabolites [fGCMs]) are influenced by environmental context. We also asked whether individual responses to environmental context depend on demographic status (e.g., reproductive status). Our data suggest that anthropogenic factors and water limitations may be key factors influencing stress hormones and parasite infection in Grevy's zebra – with forage availability playing a less important role. Water availability and anthropogenic activity were the primary drivers of fGCM levels, whereas water and forage availability (predicted by Normalized Difference Vegetation Index [NDVI]) were predictors of lungworm infection status. Our results on physiological response to lack of water are important to consider in light of climate change scenarios under which water scarcity will be a greater concern for wildlife species, especially those such as Grevy's zebra living in arid regions. Additionally, our findings that fGCMs increase in the presence of both pastoralist and tourist activity is important to consider as tourism continues to

increase regionally, while pastoralist activities are being curbed as a premise to conserve wildlife. Water availability and tourism are factors previously not considered in Grevy's zebra conservation strategies; our results suggest they should be.

1. Introduction

Environmental conditions, both natural and anthropogenic, can affect animal physiology with implications for fitness (Wikelski & Cooke 2006). Habitat alterations due to human activity and changing climates are among the leading causes of biodiversity declines worldwide (Allan et al. 2019; Oliver & Morecroft 2014; Mantyka-Pringle et al. 2015). As such, increasing environmental disturbances pose a problem for a wide range of species (Acevedo-Whitehouse & Duffus 2009; Cooke et al. 2014). For example, in Cape mountain zebra (*Equus zebra zebra*) poor habitat quality was linked to increased stress hormone levels and decreased population growth rate (Lea et al. 2018). Despite the negative impact environmental factors can exert on fitness there is still a poor understanding of how specific aspects of environmental change affect wildlife physiology and fitness (Breuner et al. 2013; Madliger et al. 2015). Physiological metrics that are correlated with individual survival and reproduction are often used as proxies of fitness in wildlife, and may help illuminate the fitness implications of environmental change (Homyack 2010; Madliger et al. 2018).

Two physiological metrics that are often used as proxies of fitness in wildlife are parasite infections and levels of stress hormones (i.e., glucocorticoids, GCs hereafter). Both metrics directly affect survival and reproduction, thus can provide information about the fitness of individual animals (Breuner et al. 2008; Chapman et al. 2015). Importantly, both chronically elevated GCs and increased rates of parasite infection have been linked to environmental degradation – meaning that as environments are rapidly being altered by anthropogenic and climatic disturbances, this could lead to further negative fitness consequences in wildlife (Hammond et al. 2018; Young et al. 2017). Exposure to consistently stressful or rapidly changing environments can lead to chronically elevated GCs, which has been associated with depressed immune function, decreased body condition, and reduced reproduction and survival (Sapolsky 2000; Dhabhar 2009). Likewise, environmental changes associated with habitat disturbance and climate change can enhance disease transmission, increase levels of parasite infection in wildlife, and facilitate the emergence of infectious diseases, which can lead to morbidity, mortality, and fecundity declines (Dobson & Hudson 1992; Voegeli et al. 2012; Coulson et al. 2018).

The environment is a critical determinant of GC levels. In wildlife GCs are often measured as fecal glucocorticoids and metabolites (fGCMs hereafter) as this represents a composite measure of stress experienced over time, and is therefore representative of chronic stress, whereas GCs in blood are indicative of short-term stressors (Wasser et al. 2000). Chronically elevated fGCM levels have been linked to multiple natural and anthropogenic factors, including human disturbance (e.g., logging, snowmobile use, tourism), resource (i.e., food and water) scarcity, high population density, and high levels of predation (Creel et al. 2013). For example, in white-bearded wildebeest (*Connochaetes taurinus*), the combination of low levels of forage (estimated from plant biomass measures) and high levels of anthropogenic disturbance contributed to elevated fGCMs. In the same study, new plant growth, indicating available forage, was associated with lowered levels of fGCMs (Stabach et al. 2015). Alongside environmental factors, demographic factors, such as sex, age, and reproductive status also influence fGCM levels, thereby modulating an animal's stress response to the environment (Lea et al. 2018). During energetically demanding life stages (e.g., lactation and late stage gestation), baseline fGCMs may rise, thereby triggering further elevation of fGCMs under stressful environmental contexts (McEwen & Wingfield 2003; Busch & Hayward 2009; Creel et al. 2013). For example, in brown lemurs (*Eulemur collaris*), the highest measured fGCM levels were in gestating females found in degraded forests indicating that a combination of ecological and reproductive stressors may act synergistically to raise fGCMs (Balestri et al. 2014).

Similar to the impact that environmental context and demographic factors have on stress hormone levels, these factors can also alter infection dynamics in wildlife (Lewis et al. 2017; Young et al. 2017). From an environmental perspective, factors such as limited availability of resources, exposure to stress, and social factors, such as high population density, can limit an animal's investment in resistance or tolerance to parasitic infection, or increase transmission (Koski et al. 1999; Coop et al. 2001; Beldomenico et al. 2008). Limited resources can impair the host's nutritional status, resulting in decreased immunity and increased susceptibility to disease (Parker et al. 2009; Becker et al. 2015). High levels of stress due to predation or other natural or anthropogenic factors, can lower host immunity, thereby increasing disease susceptibility and severity (Hing et al. 2016). Additionally, high population density may increase contact rates (Ramsey et al. 2002) and parasite prevalence and diversity (Altizer et al. 2003). Because immunity varies with age, sex, and reproductive status, environmental context interacts with demographic factors in determining whether an animal will become infected and the extent of infection. Across mammals, sex and age are correlated with parasites and disease, with males and older animals having greater prevalence of disease (Zuk & McKean 1996; Wilson 2002).

In our study, we examined how natural and anthropogenic environmental variation affects fitness-associated physiological traits in the endangered Grevy's zebra (*Equus grevyi*).

The Grevy's zebra is an important species in which to understand the impact of environmental context on fitness. This species is of conservation concern due to a limited population size (~2,500 individuals range wide) and contraction of their previous range to a small region of central and northern Kenya (primarily Laikipia and Samburu Districts) (Williams 2002). (Grevy's zebra are also found in limited numbers in Ethiopia, however our study focuses on the Kenyan population.) The Laikipia and Samburu Districts and neighboring regions are rapidly increasing in human and livestock populations and tourism, creating potentially high levels of ecological and anthropogenic stress for all wildlife in the region (Williams 2002; Low et al. 2009). Additionally, climatic factors such as variable rainfall patterns lead to high levels of temporal and spatial variation in the amount of forage available for livestock and wildlife (Vetter 2005) and cause many sources of water to be ephemeral (Augustine et al. 2010). Across the Grevy's zebra range, resources (i.e., food and water) and levels of disturbance (i.e., tourism and pastoralist activity) vary, creating variable anthropogenic and climatic contexts (Kinnaird & O'Brien 2012). This matrix of environmental contexts provides an opportunity to measure how specific environmental factors independently and synergistically affect fGCMs and parasite infections. For Grevy's zebra, anthropogenic factors, vegetation, and availability of water are key environmental features affecting their distribution (Sundaresan et al. 2008; Kinnaird & O'Brien 2012; Levikov 2014), but it is unknown how these same factors impact fitness or fitness-associated measures. We investigated how anthropogenic disturbance (tourism and pastoralism-associated factors), ecological differences, and demographic factors (reproductive status) affect fGCM levels and the infection burden and status of two endoparasites (strongyle nematodes and lungworms, respectively). We used a non-invasive fecal sampling approach to monitor stress and infection across twelve different sites that varied in levels of anthropogenic disturbance (tourism and pastoralism) and resource availability (forage and water). Using these data, we: (1) assessed how environmental context impacted fGCMs and parasite infection; and (2) determined whether demographic status (e.g., reproductive status) modulated how an individual responded to their environmental context.

2. Methods

2.1 *Study area*

We sampled Grevy's zebra from June-September 2014 and June-December 2015 at 12 sites in Laikipia, Samburu, Marsabit, and Isiolo Counties, Kenya (Table 3.1; Figure 3.1). The entire region is considered semi-arid, however, seasonally and spatially variable rainfall patterns create high levels of temporal and spatial variation in the amount of forage available for livestock and wildlife (Vetter 2005). Grevy's zebra alter their use of the land to maximize their distance from human and livestock activity, yet remain in proximity to water sources. Previous research shows that they select habitats away from active livestock *bomas* (i.e., corrals where cattle and small stock are kept overnight) (Kinnaird & O'Brien 2012; Levikov 2014; Sundaresan et al. 2008) and shift the times they visit water points to the night to avoid livestock even though this is when risk of predation is highest. Additionally, water dependency varies between reproductive groups. Aside from lactating females who need to drink daily, other reproductive status groups only need to drink every five days (Williams 1988).

Seven of the twelve sites were sampled on two or more separate occasions; and five sites were sampled once (Table 3.1). Because seasonality varies from year to year, and from central to northern Kenya, we used 30-day sampling periods to define independent sampling units rather than classifying sampling periods by season. The 12 sampling sites represent different land-use types with differing intensities of anthropogenic activity (e.g., livestock density, road and settlement density; Table 3.1) and environmental conditions (e.g., vegetation quality, availability of water).

Table 3.1: Sampling location characteristics for the 12 sites (representing five different land-use classifications) that were sampled within the Grevy's zebra core range in Kenya.

Land-use classification	**Sampling site** (sample size; #of times sampled)	**Livestock Density** (head/km^2)	**Manyatta Density** (%area covered)	**Private compound density** (%area covered)	**Road Density** (m/km^2)	**PC1***
private ranch	Mpala (85; 4)	133-298	0-.03	0-.04	1.99-9.51	-1.9-2.13
	Ol Jogi (75; 4)	107-296	0-.001	0-.07	2.40-7.55	-3.19- -.14
community conservancy	West Gate (50; 5)	968-4287	0-.03	0	.32-5.64	.81-4.32
	Meibae (22; 1)	1074-2371	.002-.02	0	1.50-2.17	1.41-3.41
National Reserve	Samburu (54; 1)	0	0	0-.01	4.07-23.95	-2.83- -.43
	Buffalo Springs (24; 2)	289-913	0-.007	.002-.005	2.88-3.97	-.34-.72
private reserve	Pyramid (12; 2)	184-310	0	0-.003	6.83-7.85	-.72- -.59
	Lewa (50; 3)	276-881	0	0-.01	4.63-7.54	-.92-.21
	Mugie (7; 1)	601-881	0-.0009	0	3.93-5.19	.09-.18
open rangeland	El Barta (42; 1)	892-1721	0-.006	0	0-3.61	.47-1.47
	Laisamis (29; 2)	128-198	.0002-.006	0-.009	.85-4.60	-.23-.46
	South Horr (4; 1)	16	.008	0	.34	.74

Sample size represents the total number of samples collected from a given location. # of times sampled represents the number of different 30-day periods during which a site was sampled. If a site was sampled during the same 30-day period (i.e., month) over two consecutive years, it was counted as having been sampled twice. Environmental parameters represent the range of values across all sampling locations within a site.

*PC1 represents a principal component consisting of manyatta density, livestock density, road density, and density of private compounds (Table 3.2).

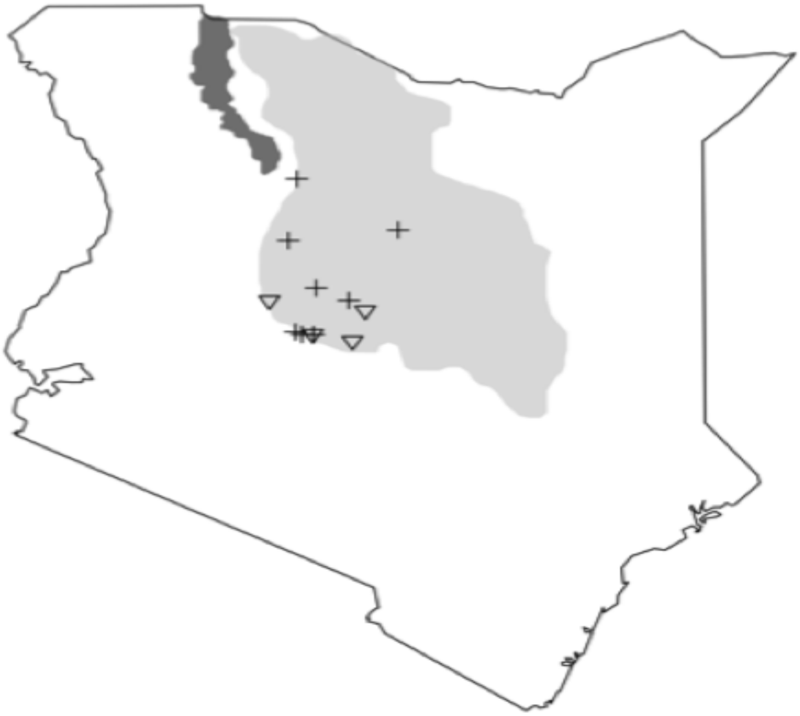


Figure 3.1: Map of Kenya depicting the Grevy's zebra core range in light grey. Sampling sites are indicated with + (areas where wildlife is not official protected) and upside down triangles (areas where wildlife is officially protected, including two national reserves – Buffalo Springs and Samburu National Reserves, and three private reserves – Lewa Wildlife Conservancy, Pyramid, and Mugie Conservancy). Lake Turkana is in dark grey for reference.

2.2 *Sampling methods*

Fresh fecal samples were collected from individually monitored animals at each study site. Repeat sampling of the same individuals was minimized by avoiding sampling of groups of the same size and composition on consecutive days. Samples were retrieved within 30 minutes of a defecation event to prevent desiccation, stored on cool packs in the field, and then processed within 8 hours. For sample retrieval, we inverted a clean plastic bag and collected as much of the fecal material as possible while avoiding soil or other potentially contaminating material. The location of sampling (GPS coordinates) was recorded for each individual and when possible, information on individual sex, age class (i.e., adult or sub-adult), and reproductive status were also recorded. Age classification was based on body size and group membership with animals less than two years old classified as sub-adult and those older than two as adults. Age classification was based on unpublished data from the Princeton Equid Team. Male reproductive status was classified for adults as territorial or bachelor. Bachelor males were identified based on membership in a herd of males, while solitary males or a single male with a herd of females was considered territorial. For adult females, reproductive status was classified as pregnant, lactating, or non-lactating. Lactating females were those with a suckling foal. Pregnant females were those visibly pregnant. Adult females not visibly pregnant and without a foal, were classified as non-lactating.

2.3 *Parasite analysis*

A portion of each fecal sample (3g for strongyles; 10g for lungworms) was used to quantify two common equid helminth parasites: strongyle nematodes, which reside in the intestinal tract, and lungworms, which infect the respiratory tract (Round 1976). Both are transmitted through a fecal-oral route whereby a host sheds eggs or larvae in the feces, which develop in the external environment and are ingested by a new host during foraging (Foreyt 2001). Strongyle egg output was quantified using a modification of the McMaster fecal egg counting technique (Ezenwa 2003). Lungworms were quantified using a beaker-modified Baermann technique (Forrester & Lankester 1997).

2.4 *Fecal glucocorticoid metabolite analysis*

The use of fGCMs to indicate exposure to stress has previously been validated in Grevy's zebra (Franceschini et al. 2008). Upon collection, approximately half of the fecal material collected for each individual was homogenized and immediately frozen on dry ice (in the field) for fGCM analysis. Between collection and lyophilization samples were stored at -20 C (Chinnadurai et al. 2009). Samples were kept at -20 C for up to 18 months before lyophilization. Samples were lyophilized for $\geq$ 48 hrs, after which they were sifted to remove non-fecal material (i.e., large pieces of grass, sticks, etc.). fGCMs were extracted using 0.2 g of dried fecal material by agitating in 5 mL of 70% ethanol for 30 minutes, then re-extracting the pellet in 3 mL of 70% ethanol for 15 minutes. Supernatants were combined, dried down, and resuspended in 1 mL 100% methanol using a combination of vortexing and sonication. Extracts in methanol were frozen at -80 C until assayed. fGCMs were quantified using the MP Biomedicals radioimmunoassay kit (Corticosterone double antibody radioimmunoassay (^{125}I) kit (MP Biomedicals 07-221102)). Each sample was run in duplicate and data were retained if the intra-sample coefficient of variation (CV) was $\leq$ 10% (range: 0.02-10%; average = 4.27%). Samples were run in twelve different batches and inter-assay variability was 7.24 and 10.53%, for the high- and low-dose standards, respectively. Assays were validated by performing a parallelism assay of serially diluted hormone extracts (Supplemental Figure 3.1).

2.6 *Environmental data*

Data on environmental conditions associated with each fecal sample were obtained from a 1.175 km radius buffer area surrounding each sampling location. The 1.175 km radius buffer area is based on the average 24 hour movement distance of four collared Grevy's zebra from one of the

12 sampling sites (Rubenstein, unpublished data). We used three metrics to assess landscape variability: Normalized Difference Vegetation Index (NDVI, to represent available forage), the presence of water, and the type of water (Table 3.2). Because water is a limiting resource in many of our sampling locations and one which animals must travel to access, we used a different buffer distance (5.25 km, the maximum 24 hr movement distance) to assess water availability. All data were extracted from publicly available data sources or were mapped using ArcGIS (version 10.5.1) (Table 3.2). To assess anthropogenic activity, we quantified livestock (cows, goats, and sheep) density, road density, the density of manyattas (i.e., traditional pastoralist homesteads), and the density of private compounds (i.e., research and tourist buildings). We included airstrips and airplane hangars in the latter.

NDVI is often used as a measure of forage availability (Ryan et al. 2012) and we ground-truthed this assumption by quantifying thyroid hormone. Thyroid hormone provides a complement to fGCMs by illuminating the contribution of nutritional deficiencies to overall stress (Keech et al. 2010; Wasser et al. 2010; Gobush et al. 2014; Brinkmann et al. 2016). We used a subset (n=47) of the hormone samples extracted to measure fGCMs to quantify thyroid hormone (free T3) with the MP Biomedicals radioimmunoassay kit (T3 (Triiodothyronine)) solid phase radioimmunoassay kit (MP Biomedicals 06B2587-CF). The kit was validated by performing a parallelism assay of serially diluted samples with a set of control standards. The assay was biologically validated for use in Grevy's zebra by comparing samples from sites with large differences in nutrient quality, as assessed by NDVI (Supplemental Figure 3.2). As with the fGCM, samples were run in duplicate and data was retained if the intra-sample CV was $\leq$ 10%. Samples were run in two batches and inter-assay variability was 3.45 and 6.23%, for the high- and low-dose standards, respectively.

Table 3.2: Environmental and host variables derived from remotely-sourced data and field observations taken during sample collection to relate to physiological measurements of health in Grevy's zebra (*Equus grevyi*). All anthropogenic and landscape variables were extracted from a buffer of 1.175 km radius from the sampled individual, except for 'access to water'. For this variable, we used a maximum distance of 5.25 km to define whether an animal had access to water or not. This is because most Grevy's zebra, except for lactating females, only need to drink every 5 days and thus will travel further to find water than they do daily.

Variable	**Definition**
Landscape variables	
NDVI	Normalized Difference Vegetation Index (NDVI) is a satellite-based measure of primary productivity (Pettorelli et al. 2011) that measures the density of green leaves on surface vegetation and can be used as an indicator of vegetation health (Justice et al. 1985). NDVI data was obtained for the 16-day window closest to the sampling date. Data source: MODIS.
Access to water	Presence of water within 5.25 km (av. max distance traveled based on collar data) of the sampling location. Data source: Digitization in ArcMap (base map download, 15 March 2018).
Water source-type	Water sources were classified in 5 types: dry river (seasonal), dam (man-made), river, stream, or none. Data source: Digitization in ArcMap (base map download, 15 March 2018)
Anthropogenic activity	
Livestock density	Biomass of cows, goats, and sheep at a 1km resolution, extracted using the *raster* package in R (R core team 2013) and then summed (units = head/km^2). Data source: 2014 Gridded Livestock of the World (Robinson et al. 2014).
Road density	Roads were digitized in ArcMap, classified as large or small. Large roads were assigned a weight of 2, small roads a weight of 1 and then summed and represented as meters of road per km^2. Total weighted road density is used in models. Data source: Digitization in ArcMap (base map download, 15 March 2018).
Manyattas (i.e. traditional pastoralist homesteads)	Settlements were distinguished by type, because a typical pastoralist settlement (i.e. manyatta) is comprised of many individuals and heads of livestock, yet takes up a small land area compared to a private compound, which are occupied typically by only a few individuals. Density of each buffer area covered by manyattas was included in models. Data source: Digitization in ArcMap (base map download, 15 March 2018).
Private compounds (i.e. research buildings, private ranch houses, hotels, air strips)	Methods for calculating percent area covered by private compounds was the same as above. Density of private compounds is included in models. Data source: Digitization in ArcMap (base map download, 15 March 2018).
Principal Component 1 (PC1)	Principal component consisting of manyatta density and livestock density, which are positively correlated, and road density and density of private compounds, which are negatively correlated for the first two components. PCA performed in JMP v 13.2.0
Host factors *(individual host information collected by visual observation in the field)*	

Age	Animals were classified as adult or subadult (i.e. juveniles and foals)
Sex	Male/Female
Reproductive Status	Females were classified in four categories: pregnant, lactating, non-lactating, sub-adult. Males were classified in three categories: territorial, bachelor, sub-adult.

2.7 *Statistical Analysis*

The four measures of anthropogenic activity (livestock density, road density, manyatta density, private-compound density) were correlated with one another (n=454, Pearson's r range = -0.29 – 0.41, $p \leq 0.04$), so we used a principal component analysis to condense these measurements into a single integrated measure of anthropogenic activity. The first principal component (PC1) explained 42% of the variance in all four anthropogenic measures, with positive loadings for *manyatta* (0.72) and livestock density (0.82) and negative loadings for road density (-0.55) and density of private compounds (-0.40).

To examine the effect of environmental variables on fGCMs and parasites, we used linear (LMMs) and generalized (GLMMs) linear mixed models. Linear mixed models were used to model fGCM levels, whereas generalized linear mixed models (GLMMs) were used to model parasite responses since these variables did not meet the assumptions of normality. Strongyle models were run using a negative binomial error distribution. Given a moderate prevalence of infection (57.8%), lungworm data were coded as a binary variable (infected or uninfected) and run using a binomial error distribution. Five environmental terms (access to water, NDVI, $NDVI^2$, PC1, $PC1^2$) were included as fixed effects in these models. Since preliminary data exploration revealed a non-linear relationship between the response variables and NDVI and PC1, we included linear and squared terms for both variables in all models. NDVI was centered and then squared to account for collinearity of the linear and squared terms. PC1 was squared to account for the non-linear relationship of these variables with each of our response variables. Location and month were included as random effects in all models because we were interested in determining the effect of specific environmental and host factors on physiological responses rather than the effect of location or time period. The fit of all models was evaluated by graphing the residuals using normality plots (Zuur 2009).

In addition to testing the effect of access to water on fGCM and parasites in the environmental models described above, we also tested for an effect of the type of water source (dam, stream, Ewaso river, dry river, or no water). To do this, we first ran LMMs or GLMMs (depending on the response variable, see above) with 'water type' as a fixed effect, and month and location included as random effects.

After running models with only environmental variables (as described above), we added demographic predictors to the main environment-only models to examine whether sex or reproductive status modulated the physiological response to environmental context. First, we tested whether there was a difference in how males and females responded to environmental context for each response variable. As fixed effects in these models, we included environmental variables that emerged as significant in the relevant environment-only models, sex, and an interaction term for each environmental variable and sex. Location and month were again included as random effects. These environment-sex models were run for fGCM and lungworm response variables. No strongyle model was run because no environmental terms emerged as significant in the initial environment-only model.

To ask whether reproductive status within each sex (for females: pregnant, lactating, non-lactating, or sub-adult; and for males: territorial, bachelor, or sub-adult) further modulated the physiological response to environmental context, we ran an additional set of models for males and females. For these environment-reproductive status models, we included environmental variables that emerged as significant in the relevant sex-environment model as well as interactions between reproductive status and each environmental variable. In total, four models were run – two models (fGCM and lungworms) for each sex. As was the case for the sex-environment model, we did not run a strongyle model.

All models were run in R version 3.4.4 (R Core Team 2016) using the R packages *lme4* (Bates et al. 2015) and *glmmTMB* (Brooks et al. 2017) for fGCM and lungworm analyses, respectively.

3. Results

3.1 *Impact of environmental variables on physiological responses*

3.1.1 *Fecal glucocorticoid metabolite (fGCM) levels*

We found that environmental context influenced fGCMs in Grevy's zebra. The squared principal component term ($PC1^2$) and access to water (i.e., areas with versus without permanent water) were significantly associated with fGCM levels, whereas NDVI was not (Table 3). First, $PC1^2$ was positively associated with fGCM levels (Figure 3.2). Specifically, fGCM levels were highest in areas where there was pastoralist (positive PC1 values) or tourist activity (negative PC1 values). Second, access to water was negatively associated with fGCM levels (Figure 3.3a). fGCM levels were lowest in areas where water was present within a 5.25 km radius. Interestingly, water source-type also affected fGCM levels (Table 3.4). Animals sampled within a 1.175 km radius of a dry river, no water, or near the only major river in the region (Ewaso river) all had significantly higher fGCM levels than those sampled near dams or streams (Figure 3.3b).

When we tested whether fGCM responses to environmental factors were sex-dependent, we found that males had significantly lower fGCM levels when water was accessible, whereas females were not affected by water availability (Table 3.5). Specifically, males had lower fGCM levels when water was accessible. When we ran separate models for males and females to test whether the stress response to environmental factors was reproductive-status dependent, we found no effect of male reproductive status on the relationship between access to water and fGCMs: all males (i.e., territorial, bachelor, and non-reproductive males) had lower fGCM levels when water was accessible (Supplemental Table 3.1). This contrasts with females, who responded differently to access to water based on reproductive status (Supplemental Table 3.2), as shown by a significant interaction between female reproductive status and access to water in which non-lactating females had higher fGCM levels when water was accessible, while all other females responded to water access similarly to males (i.e., with lower fGCM levels where water was present).

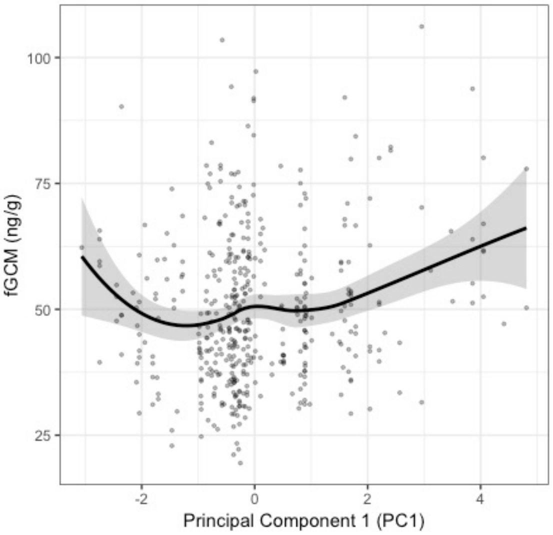


Figure 3.2: Effects of PC1 on fGCM levels. Data points are shown with a loess smoother (solid line) and standard error in grey.

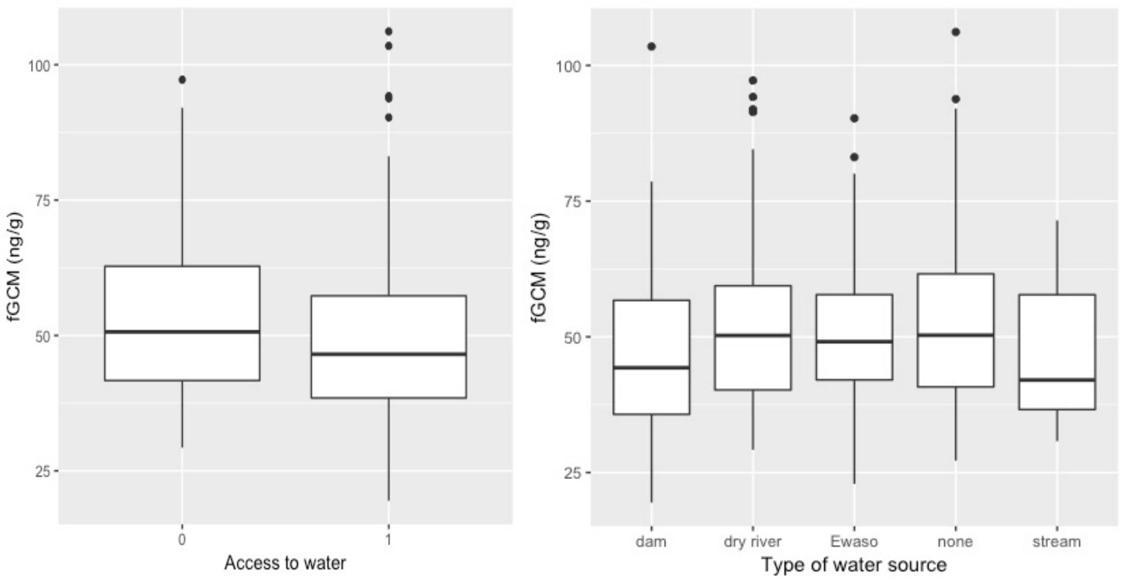


Figure 3.3: Effects of (a) access to water', and (b) type of water source on fecal glucocorticoid metabolites (fGCMs) across all individuals. Bars represent the mean for each category and lines represent 95% confidence intervals.

Table 3.3: Results for the environment-only model representing the effect of environmental variables on the three response variables. Data for each response variable was analyzed separately using generalized linear mixed effects models with location and month included as random effects. All environmental terms were included in models for each response variable. Significant effects are in bold.

	fGCM (N=447)			Strongyle burden (N=454)			Lungworm infection status (N=446)		
	β estimate ± SE	t value	P	β estimate ± SE	Z value	P	β estimate ± SE	Z value	P
NDVI	-8.28 ± 28.96	-0.29	0.78	-0.95 ± 1.21	-0.79	0.43	3.38 ± 4.05	0.83	0.405
NDVI^2	66.42 ± 66.36	1.00	0.32	2.50 ± 2.92	0.86	0.39	-15.96 ± 9.09	-1.76	0.079
PC1	-0.03 ± 0.90	-0.031	0.98	-0.02 ± 0.04	-0.56	0.57	-0.22 ± 0.13	-1.63	0.103
PC1^2	0.72 ± 0.29	2.50	**0.01**	0.002 ± 0.01	0.18	0.86	-0.04 ± 0.04	-0.96	0.338
access to water	-6.77 ± 2.20	-3.07	**0.003**	-0.05 ± 0.09	-0.60	0.55	-0.67 ± 0.33	-2.04	**0.041**

Table 3.4: Results for the water-type model representing effect of the ‘type of water’ within the 1.175 km radius of each animal on the three response variables. Data for each response variable was analyzed separately using generalized linear mixed effects models with location and month included as random effects. The reference level for water-type is “Dam”. Significant effects are in bold.

	fGCM (N=447)			Strongyle burden (N=454)			Lungworm infection status (N=446)		
	β estimate ± SE	t value	P	β estimate ± SE	Z value	P	β estimate ± SE	Z value	P
Dry river	4.91 ± 2.57	1.91	0.057	-0.01 ± 0.01	-0.13	0.894	0.93 ± 0.40	2.34	**0.019**
Ewaso river	7.27 ± 2.47	2.94	**0.003**	-0.04 ± 0.10	-0.45	0.650	0.65 ± 0.39	1.66	0.096
none (no water)	3.84 ± 1.93	1.99	**0.047**	0.02 ± 0.02	0.30	0.763	0.60 ± 0.29	2.03	**0.042**
stream	-5.24± 4.62	-1.13	0.258	0.13 ± 0.17	0.73	0.465	0.04 ± 0.68	0.06	0.955

3.1.3 *Strongyle parasite burdens*

None of the environmental variables had a significant effect on strongyle nematode burdens (Table 3.3). The type of water within a 1.175 km radius of each animal, also had no effect on levels of this parasite (Table 3.4). Because the environment-only models showed no significant effects, we did not run subsequent models testing for sex or reproductive status-based variation.

3.1.4 *Lungworm infection status*

We found that environmental context influenced lungworm infection status in Grevy’s zebra. Access to water was associated with infection status, whereas anthropogenic activity (PC1 and $PC1^2$) was not. There was a positive relationship between access to water and lungworm infection status, with animals more likely to be infected when there was no access to permanent water with a 5.25km radius (Table 3.3). Additionally, “water source type” was significantly associated with lungworm infection status. Animals in areas where there was no water or where there was a dry river were more likely to be infected than animals in regions where there were streams or dams (Table 3.4). Finally, there was a tendency for animals in areas with lower NDVI (less available forage) to be lungworm positive (Table 3.3).

Lungworm infection status in male, but not female Grevy's zebra, was impacted by access to permanent water and NDVI. Males in areas with no water had a higher likelihood of being infected with lungworms, however females showed no difference in infection status between areas with and without water (Table 3.5). Likewise, males showed a significant decrease in the likelihood of infection in areas with higher NDVI. Although the likelihood of infection for females also decreased with increasing NDVI levels, this effect was not significant (Table 3.5). When we ran separate models for males and females to determine whether reproductive status modulated lungworm infection status in response to NDVI or access to water, we found no significant interactions (Supplemental Tables 3.1 and 3.2).

Table 3.5: Results for the sex and environment model representing whether the sexes are impacted differently by environmental variables for the two response variables. Data for each response variable was analyzed separately using linear mixed effects models (fGCM) and generalized linear mixed effects models (lungworm infection status) with location and month included as random effects in all models.

Predictor	**Level**	fGCM (N=370)			Lungworm infection status (N=369)		
		β estimate ± SE	t value	P	β estimate ± SE	Z value	P
NDVI	na	-	-	-	-6.05 ± 6.34	-0.95	0.340
NDVI^2	na	-	-	-	2.88 ± 14.24	0.20	0.840
PC1	na	-1.73 ± 1.06	-1.63	0.10	-	-	-
PC1^2	na	0.39 ± 0.35	1.11	0.27	-	-	-
access to water	na	-2.40 ± 2.57	-0.93	0.35	0.06 ± 0.47	0.13	0.895
Sex	male female (ref)	0.15 ± 3.17	0.05	0.96	-3.89 ± 2.40	-1.62	0.106

NDVI*sex	NDVI*male NDVI*female (ref)	-	-	-	17.05 ± 8.81	1.94	**0.053**
NDVI^2*sex	NDVI^2*male NDVI^2*female (ref)	-	-	-	-33.17 ± 19.56	-1.70	0.090
PC1*sex	PC1*male PC1*female (ref)	0.70 ± 1.40	0.50	0.62	-	-	-
PC1^2*sex	PC1^2*male PC1^2*female (ref)	0.43 ± 0.49	0.89	0.37	-	-	-
access to water*sex	access to water*male access to water*female (ref)	-8.10 ± 3.90	-2.08	**0.04**	-1.34 ± 0.65	-2.06	**0.039**

Only terms that were significant in the environment-only model for each response variable were carried forward to the sex and environment model. Environmental terms not used in this model for a given response variable are indicated with a -. We did not run a sex and environment model for strongyle nematodes because there were no significant effects of the environment on strongyle burden. For categorical variables, the reference level is noted in the Level column with (ref). Continuous variables with no interaction have no associated level, and are thus noted with ‘na’. Significant and marginally significant effects are in bold.

4. Discussion

We investigated how environmental and host factors contribute to differences in fGCM levels and parasite infection rates. Surprisingly, we found that stress and parasitism in Grevy’s zebra were affected predominantly by water availability and to a lesser extent by the availability of food. Additionally, both tourist and pastoralist activity were correlated with increased fGCMs. Stress and parasitism in response to environmental variables were modulated by reproductive status of the individual animal. Given the physiology of Grevy’s zebra as an arid-adapted animal, elevated fGCMs in response to lack of water may indicate an overlooked environmental factor important for their conservation. Further, under the current conservation paradigm, pastoralism and associated higher densities of livestock are often cited as causes of conservation concern for

Grevy's zebra and other species of wildlife (Homewood & Rogers 1984; Riginos et al. 2012). This study sheds light on the need to consider tourism as an additional source of potential environmental stress as well as to begin to integrate considerations of this anthropogenic activity into conservation management plans.

4.1.1 *Effects of water availability and type on fGCMs*

fGCM levels were higher in areas where there was no access to water within the maximum 24 hour movement distance of Grevy's zebra (i.e., 5.25 km radius.) Interestingly, this effect was driven not just by lack of water, but also by the type of water source present (measured within a 1.175 km radius). fGCM levels were highest for animals where there was no water present and in areas with the largest river in the region (Ewaso river). In contrast, animals sampled near dams or streams (permanent to semi-permanent sources of water) had lower fGCM levels. It is possible that the effect of water availability and water type on the stress response may be driven by at least two separate phenomena: 1) resource limitations (i.e., water or forage) in areas where no water is present or, (2) social stress from high levels of resource competition and predation in areas where water and forage are abundant (i.e., near the Ewaso river.)

Increased fGCM levels in response to resource limitations have been found in other ungulate systems, either as a direct effect of inadequate nutrition or from increased energetic expenditures from having to travel long distances to locate resources (Busch & Hayward 2009). While studies in domestic and laboratory animals (i.e., mice) studies have shown increased levels of stress hormones in response to short-term water deprivation (Houpt et al. 2000), to our knowledge, there are no studies in wildlife on the stress response to water limitation or deprivation. In contrast to the short-term water deprivation studied in laboratory animals Grevy's zebra in the wild could experience longer bouts of water deprivation. This in combination with increased travel to access drinking water may lead to chronically elevated fGCMs. Although Grevy's zebra are arid-adapted and adult animals (with the exception of lactating females) can go without water for up to five days (Becker & Ginsberg 1990), our results indicate that due to potentially synergistic factors, Grevy's zebra may show greater negative physiological impacts from water deprivation than expected.

Because of variation in energetic demands faced by animals in different reproductive states (Madliger & Love 2016), we expected to find differences in fGCM levels among reproductive groups in response to the same environmental contexts. In addition to lactation being an energetically-demanding stage, lactating Grevy's zebra females need to drink daily and cannot move long distances with foals (Sundaresan et al. 2008). Together these factors might indicate that lack of water would be detrimental for lactating females. We did not find evidence for this in our study, however, as only non-lactating females had increased fGCM levels when water was present compared to areas without water. All other females (i.e., pregnant, lactating, and non-reproductive females) had decreased average fGCM levels when water was present. Although, it is unclear why non-lactating females would have increased fGCMs when water was present, it is expected that lactating females, which are most dependent on water (Sundaresan et al. 2008), had the greatest decrease in average fGCM levels (as observed) between areas with water and areas with no water. In males, all reproductive groups had lower fGCM levels when they had access to water.

In contrast to areas with no water, we also detected higher fGCM levels in animals sampled near the Ewaso river where water is typically available. It is possible that elevated fGCMs in these areas may be due to social context, including higher levels of intra- and interspecific competition and increased predation, rather than resource limitation. Within parts of our study region, the Ewaso is often the only source of water and therefore would draw other species of wildlife (including ungulates and carnivores) to the area. When resources are limited or patchy, inter- and intraspecific competition can be increased due to increased competition for food or mates. Correspondingly, fGCMs are usually higher when population densities and predation risks are high (Forristal et al. 2012; Creel et al. 2013; Caslini et al. 2016; Seeber et al. 2018; Boonstra et al. 1998; Scheuerlein et al. 2001; Clinchy et al. 2004; Mateo 2007.)

4.1.2 *Effects of water availability and type on lungworm infection*

When there was no access to water within the 5.25 km buffer zone, animals were more likely to be infected with lungworms, and this effect was specific to males. Additionally, all males, irrespective of reproductive status, showed the same increase in infection probability when they did not have access to water, suggesting that how lungworm infection status responds to access to water in males is not a product of behavioral or hormonal differences, but rather is driven largely by environmental context. Consistent with the finding of male infection likelihood being higher in areas with no water, our analysis of water source type showed that Grevy's zebra (pooled analysis of males and females) had a greater likelihood of being infected with lungworms when they were in areas with no water or a dry river. Increased energy expenditure from traveling greater distances to water, could depress condition and immunity, thereby decreasing resistance and tolerance to infection. This corresponds to findings that parasite loads are higher in the dry season due largely to declines in condition and immune function (Ezenwa 2004).

4.1.3 *Effects of anthropogenic activity on fGCMs*

Anthropogenic disturbance has been linked to elevated glucocorticoid levels in a number of wild ungulates (e.g., woodland caribou and moose in oil-drilling areas (Wasser et al. 2011), elk in response to snowmobile activity (Creel et al. 2002). In agreement with those findings, Grevy's zebra had the lowest fGCM levels in areas where there was limited anthropogenic activity. The region where we conducted our study is a mix of pastoralist and tourist activities, however for the most part, these activities are spatially segregated (Kinnaird & O'Brien 2012). To address how different human factors might be impacting stress in wildlife, we measured pastoralist activity and tourist activity as two separate variables and combined the associated environmental factors into one principal component (PC1). In areas of higher pastoralist or tourism activity, fGCMs were highest. While many studies on fGCMs in wildlife combine types of anthropogenic stress (Creel et al. 2013), we were able to distinguish between two distinct activities by sampling animals in discrete land-use types and measuring specific environmental factors associated with each land-use type. While we found an increase in fGCMs in response to pastoralist and tourist/research activity, other studies have found that pastoralism has a greater impact on fGCMs. For example, in wild spotted hyenas (*Crocuta crocuta*), fGCM levels were highest in areas of pastoralist activity, while no elevation was seen in tourist areas (Van Meter et al. 2009).

4.1.4 *Effects of forage variability (NDVI) on lungworm infection*

Grevy's zebra in areas with the lowest NDVI values (i.e., least available forage), had a significantly greater likelihood of being infected with lungworms, but this pattern was only true for males. Low food availability has been linked to increased parasite infection across multiple species (sheep, snowshoe hare, and primates) (Gulland 1992; Murray et al. 1998; Chapman et al.

2006; Santiacchi et al. 2015), and this effect may be particularly pronounced for species which feed on low-quality forage, such as Grevy's zebra (Sundaresan et al. 2012). Indeed, Ezenwa (2004) found that under drought conditions, species, such as hartebeest (*Alcelaphus buselaphus*) and waterbuck (*Kobus defassa*), which, like Grevy's zebra, feed on low-quality forage have higher gastrointestinal parasite burdens, while those feeding on higher quality forage showed no difference. Such effects might also be more pronounced in males due to well-known sex biases in immunity in mammals, where males tend to have lower levels of various immune responses (Zuk & McKean 1996).

4.1.5 *Conclusions*

Together, our data suggest that anthropogenic factors and water limitations may be key factors influencing stress hormones and parasite infection in Grevy's zebra – with forage availability playing a less important role. The effects of lack of water on stress and infection have implications for climate change scenarios under which water may become more scarce. Understanding which species are most water-dependent can shed light on how spatial distribution and extinction potential of certain species may be influenced in the future. For instance, Veldhuis et al. (2019) predicted that under extreme drought conditions, larger, water-dependent grazers, may be replaced by smaller, less water-dependent species. Given the results from our current study, it is possible Grevy's zebra should be considered water-dependent and therefore may have heightened risks to their persistence in areas where water is currently very limited. However, this requires further study to understand which specific factors (i.e., increased competition, no access to a limiting resource) are contributing to increased stress and infection responses. Future work could illuminate the pathways by which lack of water is impacting these two important physiological measures and could have important implications for Grevy’s zebra conservation. Our finding that stress is impacted by both pastoralist and tourist activity is critical for Grevy’s zebra conservation efforts. Pastoralist activity has been widely cited as detrimental to wildlife conservation, through disturbance effects (Homewood & Rogers 1984; Riginos et al. 2012), while tourism is often promoted as financially benefiting conservation (Whitelaw et al. 2014).

CHAPTER 4

KNOWLEDGE PERCEPTIONS, LOCUS OF CONTROL, AND MOTIVATIONS REGARDING WILDLIFE AND WILDLIFE CONSERVATION IN SAMBURU, KENYA

Abstract:

International wildlife conservation program strategies typically reflect the ecological understandings and conservation motivations held by Western conservationists who design them. Their knowledge, perceptions, and motivations, however, may not be shared by people who live alongside wildlife. Since conservation program success typically relies on the cooperation and behavioral modification of local residents and stakeholders, failure to recognize and account for misalignments between the views of local communities and the assumptions behind western-derived conservation strategies can undermine the effectiveness of conservation efforts. We conducted interviews in Samburu, Kenya, an area with multiple active international conservation programs, to assess whether three categories of local perceptions did in fact align with the perspectives that underpin Western conservation programs strategies. The factors were (a) residents' ecological knowledge and perceptions, (b) perceptions of locus of control, or personal responsibility and agency in affecting wildlife, and (c) motivations for wildlife conservation. These were targeted because each is known to have an impact on pro-environmental behavior. We found that the Western notion of rarity and extinction, a fundamental ecological and normative premise for wildlife conservation, did not resonate with residents. Most residents felt they do have an influence on wildlife populations, which aligns with another core presumption of Western conservation. There was partial alignment between the economic incentives that conservation strategies use to encourage pro-conservation behavior, and the values that residents reported as motivations for conservation. It remains unclear, however, whether conservation programs in the area may have already influenced residents' motivational structures, and we conclude with cautionary notes regarding the ethics and potential unintended consequences of 'motivation crowding' by powerful exogenous agents.

1. Introduction

Wildlife conservation is rarely, if ever, solely an ecological problem; it also entails negotiating the interface between people and wildlife. International conservation efforts, particularly in rural areas, may affect livelihoods in communities that share landscapes with wildlife, and the success of conservation programs may depend on local stakeholders' cooperation and behavioral changes (Barrett et al. 2011). Wildlife conservation programs, even those involving community engagement, have typically focused on ecological assessments and strategies that reflect the scientific knowledge and values of Western conservationists (Kellert 1985; Kittinger et al 2012). When conservation programs are based on Western knowledge and values, but implemented with non-Western stakeholders, this can lead to a misalignment of conservation messages and strategies with local people's ecological knowledge, perceptions, values, and motivations, a problem that may contribute to poor or unexpected outcomes in many community-engaged conservation programs (DeCaro & Stokes 2008; Waylen et al. 2010). There is, however, growing recognition that taking steps to appreciate locally-held (a) knowledge, (b) perceptions of environmental influence, and (c) motivations regarding endangered wildlife species can enhance conservation outcomes.

First, sharing knowledge can help conservationists and communities develop a broader, shared understanding of the issues, which is known to strengthen cooperation (Biggs et al. 2011).

One dominant knowledge source for wildlife conservation organizations is information regarding species' rarity or vulnerability to extinction. Emphasis is often placed on protecting species classified as rare or extinction-prone according to the IUCN Red List for endangered and threatened species (Butchart et al. 2006). The Red List classifications for threat status (e.g., vulnerable, threatened, endangered, critically endangered) are based largely on biological assessments of rarity (indicated by population sizes and distributions), threats, and temporal trends in populations (Primack 2012), which are used to project the likelihood that a species will go extinct if conditions remain the same (Mace et al. 2008). However, classifications of species as “rare” based on their global range or total population size may not resonate with knowledge held by local residents, who may understand wildlife dynamics in their region on finer spatial or different temporal scales than traditional scientific research (Kellert 1985; Ziembicki et al. 2013; Magurran 2007; Hartley & Kunin 2003).The scientific community may consider, for example, an endemic species to be at risk of extinction because of its restricted global distribution, declines in abundance, and existing threats across its range, but local residents' spatial and temporal frames of reference may not indicate those patterns, or they may not make the same causal inference about extinction risk (Gagnon & Berteaux 2009; Bennett 2016). Local community members’ ecological perceptions regarding the rarity or endangerment of wildlife species are among many factors that may influence conservation outcomes (Hicks et al. 2015). If recognized, divergences between locally held and Western scientific perceptions are not necessarily an impediment to conservation; they can be an asset (Fazey et al. 2006; Ziembicki et al. 2013). For example, indigenous Maori people in New Zealand knew the past locations of extirpated populations of endemic tuatara reptiles (*Sphenodon spp.*) that were otherwise unknown to scientists. Their knowledge helped establish a broader understanding of population status and declines within the taxa (Ramstad et al. 2007). Despite the potential complementarity of scientific and local ecological knowledge to inform conservation (Berkes et al. 2000; Berkes 2004; Fraser et al. 2006; Gagnon & Berteaux 2009; Gilchrist et al. 2005), scientifically-based assessments of species' status are often prioritized over local knowledge (Reid et al. 2009).

Second, understanding how people in local communities view their role in influencing their environment can reveal barriers and leverage points for conservation strategies. Wildlife conservation programs are commonly based on the implicit assumption that humans can influence the outcome of wildlife populations through their actions (St John et al. 2010). However, for conservation programs to initiate pro-environment behavior, local partners must also believe their actions will have an impact on the desired outcome. Indeed, studies in environmental psychology have found that an individual's beliefs regarding whether they can bring about change through their actions, has an impact on pro-environmental behavior (Kollmuss & Agyeman 2002). Locus of control is a term used to describe "an individual's perception of his or her ability to bring about change through his or her behavior." (Hines et al. 1987). Those with an internal locus of control believe their actions are impactful, whereas people with an external locus of control tend to believe that they cannot effect change, but that change is externally driven, for example by more powerful people, natural forces, or deities (Carver 1997). For example, Trivedi et al (2015) found that people with an internal locus of control pertaining to the environment were more willing to pay for more environmentally-friendly products, suggesting that locus of control may be linked to pro-environmental behavior (Trivedi et al. 2015). Perceived locus of control can vary among cultures, and among segments of society. The Western conservation paradigm is dominated and motivated by the belief that humans are a significant cause of wildlife endangerment, and that humans can (and should) play a role in conserving wildlife. These two assumptions about locus of control are so fundamental, however, that conservationists may not recognize that either or both beliefs may not be shared by local partners (Barnes et al. 2011). The perceived legitimacy of a conservation program and partners' likelihood to adopt its recommended behaviors can be undermined if local partners do not share these beliefs.

Third, when programs seek to incentivize cooperation and behavioral changes, understanding local stakeholders' values and motivations are a key issue, as they influence what incentives are likely to be more acceptable and effective (Cetas & Yasue 2017). A literature review by DeCaro & Stokes (2008) showed that offering economic incentives is the predominant paradigm adopted by conservation organizations for promoting community-based conservation in developing countries. However, programs using economic incentives as the primary motivating factor may be less successful than other forms of incentives inspired by the perspectives and contributions of local partners (Rode et al. 2015). For example, a project in Amboseli, Kenya adopted two programs for improving local communities’ tolerance of lions, and found greater short- and long-term success when community and cultural values were incorporated. One program used financial incentives – compensating residents for killed livestock – which led to 87-91% reduction in lion killings. But the other program integrated employment of men as wildlife guardians, tapping their knowledge to track animals and their social stature to influence others' behavior, which resulted in a 99% reduction (Hazzah et al. 2014). Because motivating factors strongly influence acceptance and longevity of pro-environmental behavior, but can differ among cultures (reviewed in Rode et al. 2015), it is important to identify appropriate incentives when designing and implementing conservation strategies.

Samburu (a Nilotic people of north-central Kenya) pastoralists in the drylands of northern Kenya depend heavily on livestock and local environmental resources for their livelihoods (Ocholla et al. 2016). Northern Kenya, including Samburu County, is also an important region for wildlife conservation because there are more threatened and endangered large mammal species in Samburu County than anywhere else in East Africa, including Grevy's zebra (*Equus grevyi*), wild dogs (*Lycaon pictus*), lions (*Panthera leo*), and elephants (*Loxodonta africana*) (Sundaresan et al. 2012). Samburu people directly experience livelihood consequences of sharing a landscape with wildlife, as well as the consequences of conservation actions (Sundaresan et al. 2012). For decades, various conservation programs have engaged with Samburu pastoralists in efforts ranging from school outreach, to employment of wildlife scouts, to facilitating tourism enterprises. However, few studies have examined the relevance or use of Samburu indigenous knowledge in wildlife management (Oguge et al. 2006), and it is difficult to ascertain from existing literature the degree to which their perceptions, motivations, and values have been ascertained or incorporated in the process of designing and implementing conservation programs.

In a wildlife-rich area in Samburu County, Kenya, we conducted semi-structured interviews with residents to assess the degree of alignment between their knowledge, perceptions, and values, and the views and assumptions commonly held by conservation organizations. We focused on: their knowledge and perceptions of wildlife rarity, endangerment, and risk of extinction; their views regarding whether humans are responsible for past and current wildlife abundance trends, indicating perceived locus of control; and factors that would motivate them to conserve wildlife. We targeted these concepts because they are often misaligned between international conservation actors and local communities, yet all have been shown to have an impact on pro-environmental behavior and compliance with conservation strategies (Bennett 2016).

2. Materials and Methods

2.1 *Ethics Statement*

This research protocol was approved by the Institutional Review Board (IRB) at the University of Georgia. We obtained informed oral consent from all informants before beginning all interviews. In-country research permission was provided through the first author's affiliation with the Kenya Wildlife Service and a research permit granted by National Commission for Science, Technology and Innovation (NACOSTI) in Kenya. Additionally, the West Gate, Kalama, and Meibae Community Conservancy Committees granted permission to conduct research within conservancy borders by signing a Prior Informed Consent (PIC) form.

2.2 *Study Area & Communities*

The Samburu ecosystem is semi-arid and covers 17,100 km^2 in northern Kenya (Figure 4.1). Our study area within this region encompassed three contiguous community conservancies – Meibae, West Gate, and Kalama Community Conservancies – which together cover a total of 2,023 km^2 (Bruyere et al. 2018). In recent decades, the Northern Rangelands Trust (NRT), a non-governmental organization (NGO) with substantial international backing, has promoted the formation of community conservancies in northern Kenya as a means to improve wildlife conservation, land management, and livelihood of people living there (https://www.nrt-kenya.org). As practiced in Samburu County on lands owned by residents under collective title, community conservancy formation entails the delineation of fenceless borders; adoption of specific land use, conservation, and governance plans, drawn up with guidance from NRT; and registration with the government.

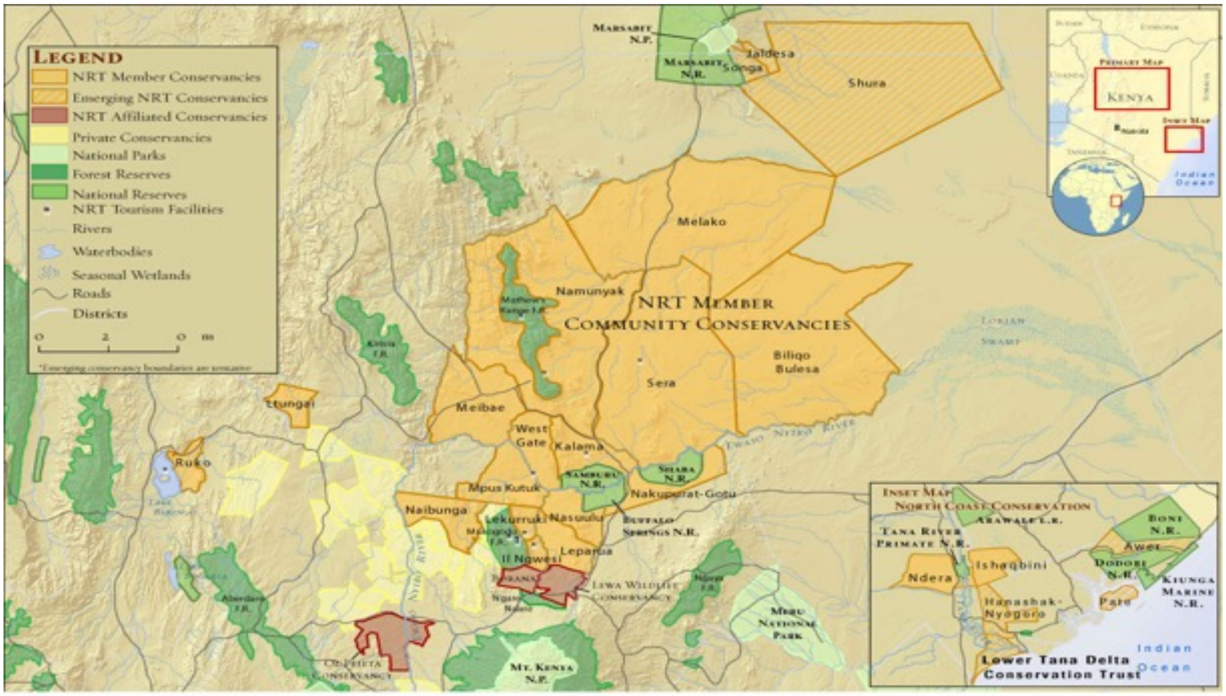


Figure 4.1: Map shows locations of Meibae, West Gate, and Kalama conservancies. Notably, Meibae is the most remote of the three conservancies included in our interviews and does not border a national reserve, which is a major draw for wildlife tourism. (Map downloaded from Northern Rangelands Trust www.nrt-kenya.org/map.)

The three community conservancies in this study have different levels of eco-tourism and investment from conservation organizations. Two of the conservancies, West Gate and Kalama, neighbor the unfenced Samburu National Reserve, which is a IUCN-listed Wildlife Reserve that attracts international wildlife tourism (Figure 4.1). During rainy seasons, wildlife disperses from the park into these two neighboring community conservancies. Thus, tourists often visit Kalama and West Gate conservancies to view wildlife. With external financial investment, both West Gate and Kalama have established tourism markets with at least one tourist lodge on each community conservancy. Meibae, although the largest of the three conservancies, is more remote, does not border a wildlife reserve, and does not currently have an established base of tourism or tourist facilities of any kind. The conservancies vary in distance to a populous, urban area, thus have varying access to commercial goods and services, with Kalama having the greatest and Meibae having the least access (https://www.nrt-kenya.org; Table 1). All three community conservancies are characterized by pastoralism as the main livelihood, which makes up approximately 80% of income in Samburu (Bruyere et al. 2018).

Table 4.1: Descriptions of three conservancies used as study locations; Data from https://www.nrt-kenya.org.

Conservancy	Area (approx.)	Population (approx.)	Tourism assets	Urban Access
Kalama	50,000 ha	11,300	Lodge, adjacent national reserve	High
West Gate	36,000 ha	3,000	Lodge, adjacent national reserve	Medium
Meibae	101,000 ha	10,000	None	Low

2.3 *Interviews*

Field research was conducted between June and December 2015. We first conducted focus group discussions in West Gate and Kalama in order to develop thematically appropriate questions for semi-structured interviews with individuals. Four discussions were held with groups of elder men, and five with groups of women. Each focus group was comprised of 4-6 individuals and lasted between 1 and 2 hours. The focus groups discussed knowledge about wildlife and residents' interactions with wildlife and with conservation organizations; contents of focus group discussions were not analyzed further in the study.

Within each conservancy, we selected 4 villages (residential areas with loose clusters of homesteads, delineated as part of conservancy formation) to conduct semi-structured interviews. Using maps held at conservancy headquarters, we selected four villages within each conservancy that occurred at varying distances from the conservancy headquarters and from the core conservation areas (i.e., areas reserved from livestock grazing to promote wildlife abundance), without considering other criteria. We took this stratified approach because proximity to either core conservation regions or to headquarters could influence individual perceptions of the benefits or costs to conserving wildlife, and we wanted interviews to sample the range of perspectives held in the community. We found no trends associated with village proximity to conservancy headquarters or to conservation areas, so village proximity is not considered further in analyses presented.

We conducted a total of 74 semi-structured interviews. Interviewees were identified opportunistically by approaching homesteads as they occurred along travel routes, and inquiring if any residents wished to participate. We interviewed one to three residents per homestead, but never more than two of the same gender to maintain gender parity. Interviews were conducted in the Samburu language, and consisted of 3 demographic questions, 4 categorizing activities, and 12 categorical or open-ended questions relating to conservation. Interviews were conducted by one English-speaking researcher and a translator fluent in English and Samburu, and lasted between 45 minutes and 2 hours each. Interviews were conducted by the first author and by Camilla Ryan. Concordance in technique was established by conducting multiple interviewers together. During the interview, the participant’s response to a given question was immediately back-translated from Samburu to English and transcribed in English. This protocol allowed the English-speaking interviewer to ask for clarification or to ask follow-up questions immediately. Voice recordings of interviews were attempted initially, but the available equipment was unable to produce audible recordings under the wind and external noise conditions experienced.

Demographic data ascertained for each interviewee were gender, age set, formal education level, and direct or family employment in conservation. Gender and age also served as criteria for participation. Overall, we interviewed 37 men and 37 women, but were unable to get exact gender parity within each conservancy. We limited participation to individuals known or inferred to be over 18 years of age. Samburu customarily regard age in terms of age sets; these are named cohorts that men enter when they are initiated into the warrior age class (Ocholla et al. 2008); each named cohort of warriors lasts about 14 years. The dates associated with each age set are the years during which that age set functioned as the warrior age class in the society, not the birth years of members. Thus, while the age set durations do correspond to known calendar years and are thus very helpful for defining historical time frames (Ocholla et al. 2016), men can enter those age sets 8 to 18 years after their birth year, depending on their age at initiation (circumcision), so the categories are less specific for inferring individuals' ages in year. We selected men who were elders (no longer in the warrior age class and appeared to be above the age of 18), and women who were above the age of 18 (inferred from related mens' or husbands' age sets or reported directly if known). Table 2 describes number of interviewees by gender and their associated age set. We inquired about each individual's level of formal education. We also inquired whether participants were themselves employed in a conservation-related field or if they had any relatives employed in conservation, since either could influence their financial benefits from conservation, their perceptions of wildlife, or their familiarity with exogenous concepts regarding wildlife conservation.

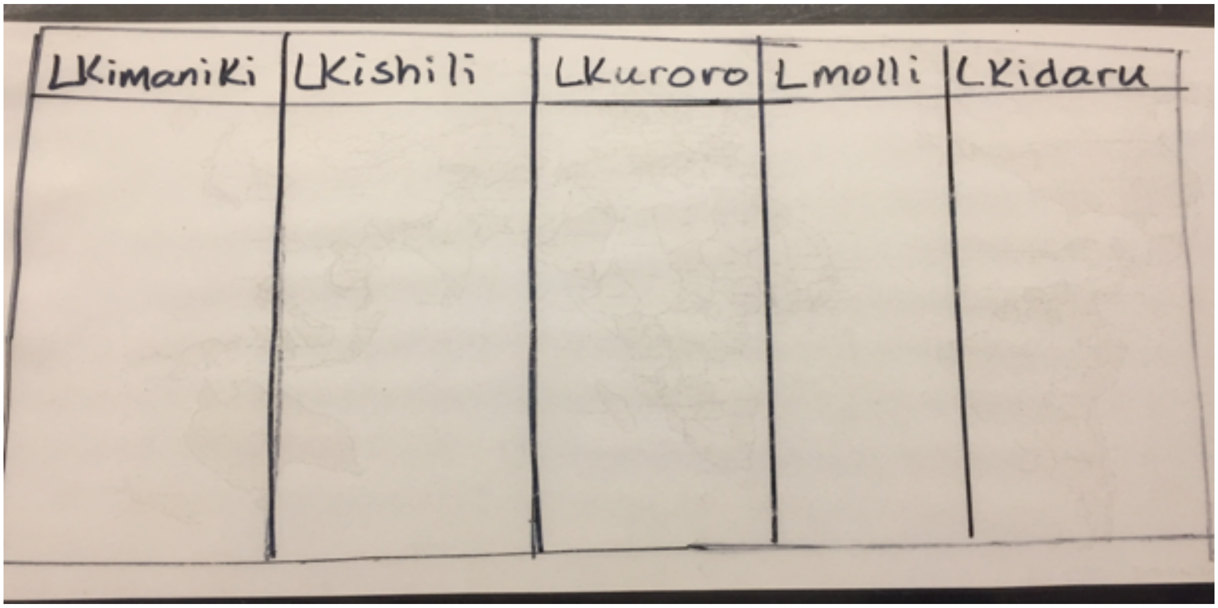
Table 4.2: Number of interviewees associated with each age set (and gender) within the three conservancies. Year spans were the years during which the age sets were warriors in the Samburu age class system (Ocholla et al. 2016). See Methods for full description of age sets and their use in historical accounting.

Conservancy	Lkimaniki 1947-1958	Lkishili 1959-1974	Lkuroro 1975-1898	Lmolli 1990-2005	Lkidaru 2006-	***Total***
Kalama	4 (2f, 2m)	4 (4f, 0m)	8 (2f, 6m)	8 (4f, 4m)	0	***24 (12f, 12m)***
West Gate	2 (1f, 1m)	10 (5f, 5m)	6 (3f, 3m)	5 (2f, 3m)	0	***23 (11f, 12m)***
Meibae	3 (2f, 1m)	9 (6f, 3m)	6 (3f, 3m)	9 (3f, 6m)	0	***27 (14f, 13m)***
Total	***9 (5f, 4m)***	***23 (15f, 8m)***	***20 (8f, 12m)***	***22 (9f, 13m)***	***0***	*74 (37f, 37m)*

2.4 *Interview Topics*

Interviews were designed to gain information on three key themes: (1) ecological perceptions regarding trends in local wildlife abundance and diversity, spatial ranges of species, and concepts of rarity and extinction; (2) locus of control, *vis a vis* interviewees' beliefs that they personally, or humans generally have influence over the outcome of wildlife conservation; (3) reasons for conserving wildlife, including asking specifically if “rarity” was a motivating factor. The aim of the study was to evaluate the degree to which interviewees' knowledge, perceptions, and values aligned with those commonly encountered and espoused in Western conservation paradigms. The interview protocol therefore included objects, ideas, and categories from Western conservation thinking, such as maps and notions of abundance, diversity, and extinction, rather than taking an elicitation approach that would avoid such external frames of reference. The interview protocol and questions are listed in Appendix A.

To evaluate ecological knowledge and perceptions of wildlife population trends, we first used a graphical sorting activity to elicit perceptions of temporal trends in wildlife *abundance* (the overall amount of wildlife in the region) over their *lifetime*, and *currently* (from approximately 2006, during last age set listed on the table), and changes in wildlife *diversity* (i.e., number of different species) over their *lifetime*. We began by introducing a table with age sets labeling each column (Figure 4.2), then gave the interviewee ten pebbles and asked them to place the pebbles on the table to represent how they perceived wildlife *abundance* changes over their *lifetime*. We recorded the represented trend as either “increased,” “decreased,” or "stable" over their lifetime. We then asked participants to focus on wildlife *abundance* trends in the *current* time period (Lkidaru, which began in 2006), and describe whether they believed it is currently increasing, decreasing, or stable. Finally, we repeated the pebble exercise using the age set table, asking them to represent their perceptions of trends in wildlife *diversity* over their *lifetime*, and recording their illustrated trend as “increased,” “decreased,” or "stable” over their lifetime.



LKimaniKi	LKishili	LKuroro	Lmolli	LKidaru

Figure 4.2: Grid used for assessing wildlife abundance and diversity trends over interview participant's lifetime. The right-most column, Lkidaru, corresponds to the current age set, and participants were asked to describe their perceptions of wildlife abundance trends within its time span (approximately the last 10 years).

To assess knowledge and perceptions regarding geographic distributions of wildlife at national and international scales, we introduced an exercise that used three graphical components: a panel of photographs of 9 wildlife species, a world map, and a map of Kenya (Figure 4.3). The extent of the assessment varied from individual to individual; we only pursued questions relating to the components that the participants felt comfortable using. We first presented the wildlife photos (8 species occurring in the Samburu region and one species, rhinoceros, that occurred historically, Figure 4.3). We discussed the names of each animal to establish that participants understood which animals were represented in the photos. We then showed participants a global map (Figure 4.3), and we named and pointed out the different continents. We asked if the participants wanted to share their perceptions of which wildlife species occurred in which continents. If the answer was no, we recorded that and any spontaneously offered explanations, and moved to the next step. For those who answered yes, we went through the species one by one, and recorded the continents they indicated in association with any species whose distribution they chose to describe. The next step followed the same protocol as the previous, but focused on the national scale using a map of Kenya divided into five general regions (Figure 4.3). Participants were asked if they wanted to describe the occurrence of wildlife species in different regions; we recorded their reply, and for those who elected to do so, their species-by-region responses were recorded. In our results, we report the percentage of interviewees who opted to participate in these exercises as an indirect indicator of community members' comfort or interest in the topic; specific responses about distributions were not analyzed.

Figure 4.3: Cards of the nine species used to ask interview participants about their perceptions of global (continental) and national (five regions within Kenya) distribution.

To assess participant's views on the ecological concept of extinction, we asked participants, "If a species existed only in this region (Samburu), do you think it would be possible for a species to go extinct?" and explained that extinction meant there would be no more of this animal left in the world.

We assessed locus of control by analyzing responses from three different open-ended interview questions. The first two questions were "What do you believe are the primary reasons for changes in the *abundance* of wildlife over their *lifetime*?" and "What do you believe are the primary reasons for the *current* trends in wildlife *abundance*?" These two questions were asked following the temporal trend exercise in which they reported the temporal trends they perceived. We recorded all reasons mentioned, then categorized each reason as “human-induced” (e.g., bushmeat, poaching) or “not human-induced” (e.g., drought, God). Based on all the reasons the participant provided, we scored their overall causal attribution as human-induced, not human-induced, or both. The third question regarding locus of control was, "What personal actions can have a positive or negative impact on the ability of a species to survive here?" We recorded any relationships described. For example, an individual could state that a particular action, such a grazing livestock could have both a positive and a negative impact depending on how it was managed, or they could state that they do not interact at all with wildlife and thus have “no impact” on the ability of wildlife species to survive in the region. For each interviewee, we summarized the impacts they identified as all positive, all negative, both, or neither.

We evaluated motivations underlying wildlife conservation using open-ended questions. We first asked, "If you learned that a particular species were rare, meaning it is found only in this region and nowhere else in the world, how do you feel about that? Should that species receive more care than other species, or more care than it is currently receiving?" and we recorded any responses. Then we asked "What factors or reasons would motivate you to conserve a species of wildlife?" and recorded the free-listed responses. We classified these reasons as “economic only,” “non-economic only,” or “both economic and non-economic reasons.” Economic reasons included reasons such as school bursaries, tourism-related employment or income, whereas non-economic reasons were aesthetic or related to cultural practices or values.

2.5 *Data Analysis*

Answers for each participant were recorded in an Excel spreadsheet for data summarization and analysis. We used the English-language transcript of each interview to further categorize answers as described above. We also recorded any spontaneous explanations or reasons given for any answer. To analyze categorical responses, we tallied the number of respondents providing different answers, then performed separate chi-squared contingency tests for each question to determine if responses varied by gender, age set, or conservancy. To increase statistical power for age set tests, Lkimaniki and Lkishili were grouped as “older age sets”, while Lkuroro and Lmolli were grouped as “younger age sets.”

3. Results

3.1 *Education and Employment trends*

Of the participants interviewed, 62 provided information about their education, of which 53 (85%) reported having no formal education. When we inquired about education through seminar courses, 37 of 50 participants (74%) responded that they had not participated in a seminar of any kind. Only 8 of 74 participants (11%) were themselves employed in conservation, whereas 35 of

74 (47%) had a relative employed in conservation. Neither education levels nor employment in conservation varied among conservancies.

3.2 *Ecological Perceptions*

Overall, 88% (65/74) and 82% (61/74) of all interview participants perceived that wildlife abundance (Figure 4.4) and diversity, respectively, had decreased over their lifetime. Perceptions of lifetime trends in wildlife abundance varied by gender ($X^2 = 6.75$, df = 2, $p = 0.034$, N=74), but not conservancy or age set. 78% of women (29/37) and 97% (36/37) of men stated that wildlife abundances had decreased over their lifetime, while 14% (5/37) of women and no men (0/37) believed that lifetime wildlife abundances had increased over their lifetime. Perceptions of lifetime trends in wildlife diversity differed by conservancy ($X^2 = 12.70$, df = 4, $p = 0.032$, N=74), but not by age set or gender. More residents of Meibae (93%; 25/27) believed that lifetime wildlife diversity had decreased than did residents of Kalama (67%; 16/24) or West Gate (87%; 20/23). Further, many interviewees remarked that local declines were due to animals moving or being moved elsewhere, rather than believing animals were declining in number overall.

In contrast to perceptions of lifetime trends in wildlife abundance, the majority of participants perceived that currently, wildlife abundance is increasing. 75% (53/71) of participants reported that wildlife abundance is increasing in the current age set-period (i.e., since 2006). Perceptions of current wildlife abundance trends differed by conservancy ($X^2 = 17.36$, df = 4, p-value = 0.002, N=71; Figure 4), but not by age set or gender. 95% (21/22) and 83% (20/24) of interviewees in West Gate and Kalama Conservancies, respectively, believed wildlife abundance was increasing, whereas only 48% (12/25) of interviewees in Meibae Conservancy stated that abundances were increasing.

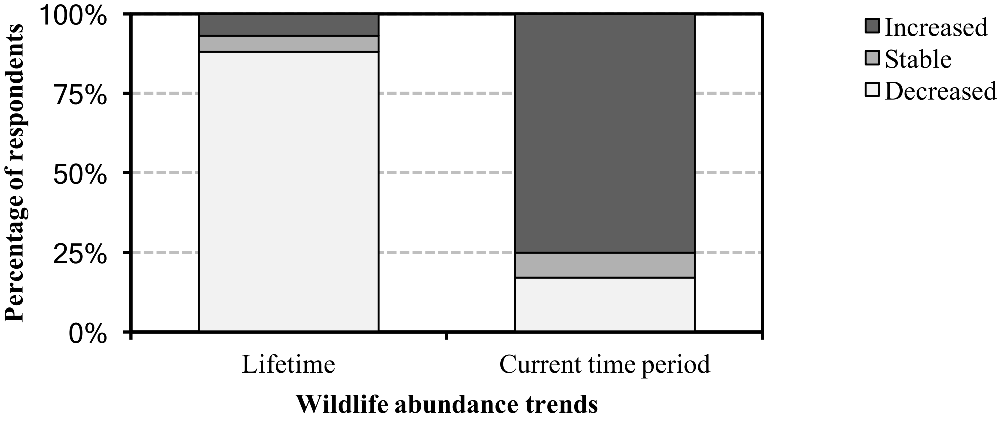


Figure 4.4: Across all participants, the majority of interviewees perceived that wildlife abundance had decreased over their lifetime, but is currently increasing.

All interviewees opted to participate in the activity describing the distribution of wildlife species within Kenya, with 34% (24/71) completing the activity fully and 66% (47/71) restricting their responses to regions they were familiar with. In contrast, only 45% (32/71) of interviewees chose to participate in the activity addressing global distribution of wildlife species, while most who declined stated that they did not have knowledge of other continents. Of the 32 who participated, 13 completed the activity.

Most interview participants (65%; 46/71) expressed that extinction of a wildlife species was not possible (Figure 4.5). Perceptions of extinction possibility differed marginally by conservancy ($X^2 = 5.11$, df = 2, $p = 0.077$, N=71) and gender ($X^2 = 3.34$, df = 1, $p = 0.067$, N=71), but not by age set. Relative to participants from Meibae and Kalama Conservancies, the participants from West Gate more frequently stated that extinction was possible. 52% (12/23) of all participants from West Gate believed extinction was possible, while from Meibae and Kalama, it was 31% (5/24) and 33% (8/24), respectively. Between men and women interview participants, men (46%; 16/35) were more likely to state that extinction is possible than women (25%; 9/36).

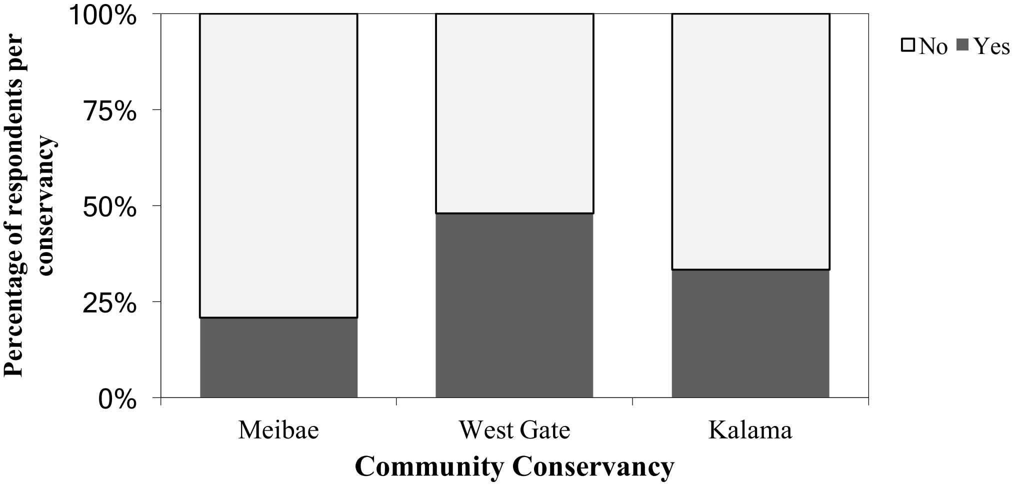


Figure 4.5: Interview participant's perceptions of whether wildlife species occurring in their region could go extinct. The majority did not believe that extinction was possible, but this varied by site.

3.3 *Locus of Control*

Participants free-listed what they perceived as the primary reasons for changes in wildlife abundance over their lifetime and currently, and their stated set of reasons were categorized as human-related, non-human related, or both. These perceptions of human impacts on wildlife populations trends were interpreted as general indicators of internal vs. external locus of control over wildlife populations. The majority of interviewees stated that human-related factors played a role in both trends. For lifetime wildlife abundance trends, 51% (37/73) said they were solely due to human-related factors; 40% (29/73) said they were due to both human- and non-human-related factors, whereas only 10% (7/73) said they were due solely to non-human-related factors (Figure 4.6). When asked about causes of current wildlife abundance trends, 83% (54/65) of participants stated that wildlife abundance trends are due to human-related causes; 6% (4/65) attributed abundance changes to both human- and non-human factors, and 11% (7/65) said they were not related to human factors (Figure 4.6). Responses for lifetime trends were similar across conservancies, but responses for current trends differed significantly among conservancies (X^2 = 10.14, df =4, *p* =0.038, N=65), 100% of respondents from West Gate (19/19) attributed the current trends solely to human-related causes, whereas for Kalama and Meibae, 88% (21/24) and 64% (14/22) attributed current wildlife abundance trends to human-related causes, respectively. Age and gender were not associated with differences in human vs. nonhuman attribution rates for lifetime or current trends.

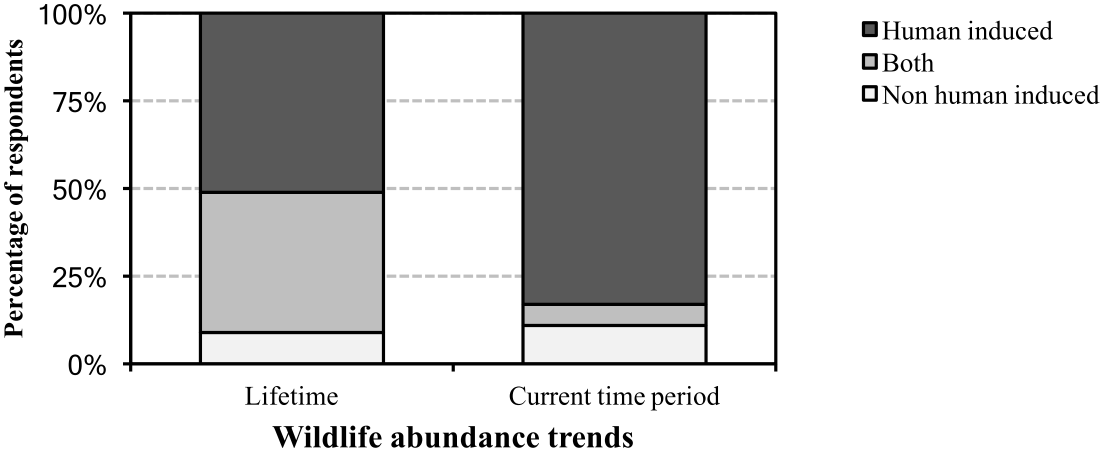


Figure 4.6: Percentage of respondents across all conservancies who indicated that lifetime wildlife abundance trends and current wildlife abundance trends (over last 10 years) were due to human-related causes, non-human-related causes, or a combination of both.

When asked directly whether their own activities can have an impact on wildlife, the majority of people stated that they can have an impact on wildlife populations (68%; 49/72). For those that stated that they did have an impact on wildlife (n=49), 45% (22/49) stated that the only impact they have on wildlife is negative, while 35% (17/49) stated that the impact was positive, and 21% (10/49) stated that their impact was both positive and negative, depending on the action. Beliefs about whether interviewees can have an impact on wildlife did not differ by age set or gender, but varied among conservancies ($X^2 = 7.87$, df = 2, $p = 0.020$, N=72), with 88% (23/26) of Meibae residents, 58% (14/24) of Kalama residents, and 55% (12/22) of West Gate residents, respectively, expressing that their actions do impact wildlife. Whether the impact was considered positive, negative, or both, did not differ by age set, gender, or conservancy.

3.4 *Motivations*

When people were asked directly if they would care more for a species if it were "rare", 59% (42/71) responded affirmatively and indicated that a rare species should receive more care, while 34% (24/71) said that a rare species should receive the same amount of care as it currently receives, acknowledging that rare species currently do receive more care than other wildlife. Only 7% (5/71) said it should receive no more care than other species of wildlife that are more common (Figure 4.7). The response rates did not differ by age set, conservancy, or gender.

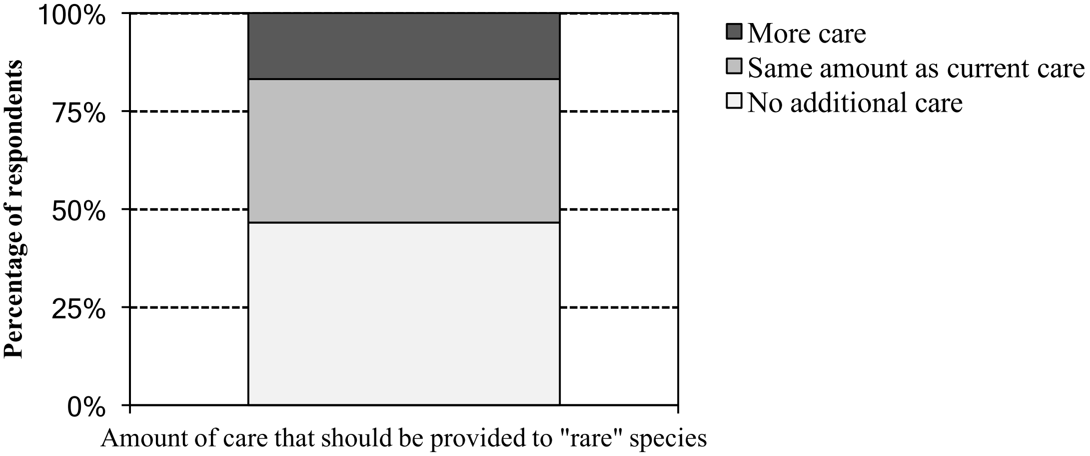


Figure 4.7: Interviewees were asked how much care should be given to a species if it were "rare" respondents said they would give a 'rare' animal more care than those that were common.

When interview participants were asked to free-list why they would be motivated to conserve wildlife, the majority (64%) listed both economic reasons and non-economic reasons, and 33% gave only economic reasons (e.g. tourism-based income, wildlife-related jobs, school bursaries) (Table 4.3). Very few respondents (3%) presented only non-economic reasons (e.g. aesthetics, security, "they've always been there"). Notably, among all the reasons given for wildlife conservation, none represented ideas about rarity, endangerment, or the prevention of extinction. Among interview participants stating either economic-only or both economic and non-economic reasons, motivations for wildlife conservation differed by age set ($X^2 = 8.48$, df =3, p =0.037, N=67) and by conservancy ($X^2 = 5.95$, df = 2, p =0.051, N=67), but not by gender. (The two respondents listing non-economic-only reasons were removed due to the small sample size n=2.) The two respondents who listed only non-economic reasons belonged to older-generation age sets and resided in Meibae. The majority of participants in the older age sets listed both economic and non-economic reasons to conserve wildlife (71%), and fewer members of older age sets listed economic-only reasons (21%). In contrast, younger age sets more commonly listed economic-only reasons (41%) and none listed only non-economic reasons (Table 4.3a). Among the conservancies, residents of West Gate more commonly listed only economic-only reasons to conserve wildlife (55%) compared to Kalama (25%) and Meibae (22%). (Table 4.3b).

Table 4.3: Number of interview participants listing non-economic only, economic-only, or both reasons for conserving wildlife, broken down (a) by age set and (b) by conservancy.

		Economic-only	**Both economic and non-economic**	**Non-economic only**
All participants (N=69)		23	44	2
a) By Age Set				
	Older (Lkimaniki & Lkishili) (n=28)	6	20	2
	Younger (Lkuroro & Lmolli) (n=41)	17	24	0
b) By Conservancy				
	West Gate (n=22)	12	20	0
	Kalama (n=24)	6	18	0
	Meibae (n=23)	5	16	0

4. Discussion

Our interview questions and activities sought to explore three categories of factors that may influence efficacy of stakeholder-engaged wildlife conservation programs: ecological knowledge, perceived locus of control, and motivating factors. We were primarily interested in whether residents' responses aligned with, or diverged from, commonly-held Western understandings and mindsets that underpin international wildlife conservation. Their responses were sometimes aligned, but often distinctly divergent from Western conservation understandings and perspectives.

4.1 *Ecological perceptions – local and global ecological knowledge*

By asking questions about particular forms of ecological knowledge regarding wildlife distributions and trends, this study sought to assess whether conservancy residents' perceptions reflected Western notions of population declines over time, rarity, and extinction risk, which are the most common ecological motivations for conservation prioritization. Most respondents perceived that wildlife abundance trends had declined over a participant's lifetime. This reflects views typically held by conservation biologists – that species are declining in number and diversity in the region. In contrast to lifetime trends, the majority of interview participants perceived wildlife to be increasing over the last 10 years. It is difficult to accurately assess whether interview participants' views on lifetime and current wildlife abundance trends agree with traditional scientific assessments, as those numbers are not available for the distinct regions in which our interviews were conducted. Residents often remarked that increases and decreases in abundance were likely due to animals migrating in and out of the area, rather than changes in total population size, which is partly consistent with scientific ecological understandings. African ungulates, of which all of nine species in our study were, migrate in response to drought and seasonally shifting forage availability (Ogutu et al. 2003). The global and national wildlife distribution exercise revealed variable, but generally unresolved perceptions of wildlife abundances in areas and at scales beyond the Samburu region. Thus, we saw little alignment with Western understandings of rarity, which is a key motivator for conservation measures. The most notable divergence from the Western scientific viewpoint was residents' ecological perception that wildlife species could not become extinct, even if the local region was a species' entire range. While at odds with conservation biology theory, their viewpoint on extinction is logically consistent with their perceptions that observed population decreases are due to animals migrating away, not necessarily becoming less numerous. The idea that when species decline locally, they may still not be globally rare or at risk of extinction is also concordant with a previous survey by Sundaresan et al (unpublished data), in the same conservancies as our study, which found that less than 17% of people were aware that the Grevy's zebra (*Equus grevyi*) is globally rare and considered endangered, despite being locally common. This low level of awareness is despite a conservation organization – The Grevy's Zebra Trust – operating in that area for over a decade, explicitly for conservation of that species. Overall, local ecological knowledge did not align with the assumed Western conservation reasoning that rarity and population declines of wildlife species in Samburu are placing those species at risk of extinction. In other natural resource management contexts, such misalignments have been associated with ineffective conservation outcomes (Barnes et al. 2011; Bennett 2016)

4.2 *Locus of Control*

In western models of conservation, the idea that humans can both positively and negatively impact wildlife individuals and populations is prevalent (Newhouse 1990). Although, during our interviews, some participants invoked "God" or "fate" as a reason for lifetime wildlife abundance declines, a majority of these people also mentioned a human-related cause for the decline. In fact, most interview participants attributed decreases in lifetime wildlife abundance as well as increases in current wildlife abundance to human-related factors. While lifetime trends were primarily attributed to poaching and killing of wildlife in the past, current trends were primarily attributed to the establishment of local wildlife conservancies, of which seventeen have been established in northern Kenya since 2013 (https://www.nrt-kenya.org/wildlife).

Interviewees expressed that not only are the conservancies actively conserving wildlife, but they are integral in the decline of illegal hunting and poaching. When asked directly if humans impact wildlife, the majority expressed the belief that humans do impact wildlife, but whether this impact is positive or negative (or both) differed based on the activity. While many Samburu believe in God as a source of punishment and protection and use of “Shamans” in cases of illness and misfortune, our interviews also indicate that they believe their own actions can have an impact on wildlife and wildlife conservation and that survival or extinction is not dependent on matters outside of their control. This internal locus of control is consistent with the basic premise of Western conservation – that humans are part of both the cause and the solution to species endangerment.

4.3 *Motivations*

Although most people were not aware of species’ global distribution or rarity, when the concept of rarity was explained, the majority of respondents said they would value rare animals more than those that are common. Concepts of rarity, aesthetic appreciation, and highlighting ecological roles of species as reasons to conserve are based on Western ideals (Hartley & Kunin 2003). As local communities may not identify with categories such as rare, endangered, or threatened, it is unclear whether being informed of a species’ global rarity would create an impetus for conservation. For instance, Sundaresan et al (2012) found that conventional species’ status classifications (i.e., endangerment status) based on IUCN recommendations did not play a role in local people’s attitudes towards the endangered Grevy’s zebra. Rather, attitudes were correlated with demographic factors, with men and individuals with fewer livestock expressing more favorable attitudes towards Grevy’s zebra (Sundaresan et al. 2012). During our interviews, when participants were asked to free-list reasons they would be motivated to conserve wildlife, rarity and endangerment were not mentioned. Instead, the primary motivations for conservation were economic incentives such as wildlife-related employment, tourism income, and school bursaries, but the majority also mentioned non-economic factors as well. Non-economic reasons were more common among older age sets, suggesting generational shifts in motivations, or perhaps more familiarity with, or access to, economic benefits from conservation activities. It is increasingly recognized that the introduction of economic incentives for conservation can feed back to influence and restructure people's intrinsic motivations. So-called "motivation crowding" can facilitate conservation efforts when stakeholders do not hold strong intrinsic, non-economic motivations. However, there are tenuous ethical questions that should be weighed carefully when a Western conservation organization, with many forms of subtle and overt power, decides to impose an exogenous value system that may undermine existing motivation structures, which may also carry values related to cultural identity, sense of place, sense of autonomy, or social leverage (Rode et al. 2015).

4.4 *Impact of Community Conservancy, Age Set, and Gender on ecological perceptions, locus of control, and motivations for conservation*

Interestingly, we found the most significant differences between ecological perceptions, locus of control, and motivations for conservation between conservancies rather than gender or age. This lends support to the fact that the involvement from conservation NGOs and the community conservancy staff themselves may have an impact on the perceptions and outlooks that people form regarding conservation. In West Gate, the community conservancy with the most tourism, largest presence of conservation NGOs, and involvement from conservancy staff (field notes from S. Heisel), 100% of participants stated that increasing current wildlife abundance trends are due to human-related causes. Congruently, more people in West Gate stated that extinction was possible than in the other conservancies. These two responses suggest a stronger internal locus of control regarding wildlife in West Gate residents compared to residents of the other conservancies. Additionally, in West Gate participants were the most likely to list only economic motivations for wildlife conservation. These trends together suggest that while in West Gate the presence of conservation actors may be shifting ecological perceptions and locus of control in a way that advantages conservation, the motivations for conservation actions are primarily seen as economic, which may in the long-term have negative implications for conservation in the area (Gebara & Agrawal 2017). Based on the work of DeCaro & Stokes (2008), economic-only incentives are less likely to achieve long-term success, because focusing solely on economics ignores the psychological bases of individual behavior that is necessary for long-term positive outcomes. In contrast to West Gate, Meibae residents were the only participants who listed non-economic-only incentives for conservation and also had the least number of people who believe wildlife abundance trends are currently increasing. Comparing these two community conservancies, that are distinct in the amount of external conservation activity, can shed light on how these actors are influencing ecological knowledge, locus of control, and what people perceive as motivations to conserve wildlife.

4.5 *Conclusions: Linking Scals of Knowledge & Concepts – Implications for Conservation*

While local Samburu residents recognize the role humans play in wildlife declines, our interviews suggest they do not connect population declines to endangerment or the possibility of extinction. One potential reason for this is the spatial and temporal scale on which local knowledge is being formed. The majority of our interview participants had not traveled outside of the region where they live. The exception to this were a few men who had traveled to work in other regions (mostly the Maasai Mara or the Kenyan coast) as wildlife tourism guides or in other aspects of the tourism industry. Furthermore, ecological perceptions of why species decline in abundance (e.g., moved away, migrated) are congruent with the semi-nomadic pastoralist lifestyle and could underscore why rarity is not deemed as an important variable in the context of conservation and that extinction is perceived as something largely not possible.

Although we did not note a connection between perceptions about observed wildlife population declines and endangerment or extinction across our interview data, the locus of control for improving wildlife conservation in the region was noted in our interviews in that recent increases in wildlife abundance were almost strictly attributed to humans (Dove et al. 2008). Overall, we found extensive knowledge of wildlife across our interviews, but that perceptions of abundance trends, rarity, and extinction may vary based the spatial and temporal extents at which perceptions are formed. In many cases traditional ecological knowledge (TEK) from these differing scales has been successfully integrated with scientific data for species conservation and it has been suggested that this information be incorporated into IUCN Red List assessments (Wong 2016; Ziembicki et al. 2013).

CHAPTER 5

CONCLUSIONS

By incorporating field, meta-analytical, and interview approaches, this research represents an integrative approach to gaining a better understanding of the multiple factors impacting wildlife fitness and conservation efforts. Although the meta-analysis of associations between genomic variability and disease in wild mammals did not reveal results that were surprising – that candidate gene loci provide more information on how individuals will respond to disease than putatively neutral genomic loci – it represents the first compilation of empirical results studying these associations. Given that disease in wild populations is increasing, thus increasing extinction risks, this is an important area of study and these results will increase our understanding of the genomic components associated with disease in wild populations, thus helping to inform the design of future empirical studies. Additionally, results described here lend support to the prediction that environmental factors known to influence behavior in Grevy's zebra, can also profoundly affect stress and infection in Grevy's zebra. Importantly, results from this work indicate that factors, such as water limitations impact stress and infection more than forage limitations. This is surprising given that Grevy's zebra are an arid-adapted species. Our research also suggests that pastoralist and tourism activity have impacts on stress. Because we were able to separate the impacts of these two activity-types, our study supports conservation actions that also focus on limiting tourism activities, whereas historically, livestock densities due to high levels of pastoralism were targeted for reduction under wildlife conservation programs. These findings offer insights on how conservation actions could be targeted to specific components of the Grevy's zebra habitat. My interview findings point to incongruencies between perceptions of wildlife and wildlife conservation between conservation actors and Samburu communities. By understanding where these incongruencies are present it becomes possible to integrate perceptions of communities being asked to participate in conservation of wildlife into conservation programs – thereby giving hope for a more holistic approach to conservation that integrates detailed traditional knowledge with scientific understandings.

There is currently a lack of research on endangered species conservation that integrates multiple factors. By addressing genomic, ecological, and social factors influencing wildlife conservation in my thesis, I hoped this might lead to a more holistic understanding of factors shaping wildlife conservation status. Throughout the course of my PhD research, I worked in close collaboration with The Grevy's Zebra Trust (GZT), a conservation organization in Samburu, Kenya dedicated to co-existence of wildlife in the region – in particular the Grevy's zebra – with traditional pastoralist lifestyles. I sought collaboration with this organization, because they are closely aligned with Samburu culture and also with understand in detail the threats facing Grevy's zebra. By working with them, I was able to focus my research on relevant areas of concern for both people and wildlife. Throughout my time in Kenya, I participated in meetings with local community members and with the Kenya Wildlife Service (KWS) directed at better monitoring disease in Grevy's zebra populations. In 2020, I will return to Kenya to share results with communities where this work was conducted, local conservation organizations (including GZT), and KWS. It is my hope that findings from this research will highlight environmental factors to which Grevy's zebra (and perhaps other arid-adapted species) may be vulnerable and thus be useful in guiding future research as well as in the development of conservation management plans. Likewise, by sharing the results of the interviews, I hope to shed light on the discrepant perceptions that seem to exist between conservation actors communities residing in these areas.

SUPPLEMENTARY TABLES

CHAPTER 2: SUPPLEMENTAL TABLES

IS IT TIME TO MOVE WILDLIFE STUDIES INTO THE GENOMIC ERA?: A META-ANALYSIS ON GENOMIC VARIATION-DISEASE ASSOCIATION

Supplemental Table 2.1: Unique host species included in the meta-analysis and the number of records included for each species.

Host species (genus species)	**N (records included in study)**
Ailuropoda melanoleuca	27
Apodemus flavicollis	12
Arvicola amphibius	3
Arvicola terrestris	2
Bison bonasus	8
Canis lupus	6
Capra ibex	6
Cervus elaphus	1
Cheirogaleus medius	18
Equus quagga	16
Gerbillurus paeba	1
Gracilinanus microtarsus	3
Leopoldamys sabanus	4

Marmosops incanus	1
Meles meles	1
Microcebus murinus	23
Microtus montanus	2
Myodes glareolus	2
Noctilio albiventris	13
Ovis aries	7
Ovis canadensis	18
Phoca vitulina	2
Phocarctos hookeri	6
Procyon lotor	1
Rangifer tarandus	4
Rhabdomys pumilio	36
Spermophilus suslicus	78
Sus scrofa	2
Zalophus californianus	26

CHAPTER 3: SUPPLEMENTAL TABLES

ENVIRONMENTAL AND DEMOGRAPHIC CORRELATES OF STRESS AND INFECTION IN THE ENDANGERED GREVY'S ZEBRA

Supplemental Table 3.1: Results for the male and environment model representing whether the reproductive status groups for males are impacted differently by environmental variables for the two response variables. Data for each response variable was analyzed separately using generalized linear mixed effects models with location and month included as random effects.

Predictor	Level	fGCM (N=165)			Lungworm prevalence (N=165)		
		β estimate ± SE	t value	P	β estimate ± SE	Z value	P
NDVI	-	-	-	-	15.74 ± 13.61	1.16	0.247
NDVI^2	-	-	-	-	-39.63 ± 38.45	-1.03	0.303
PC1	-	-	-	-	-	-	-
PC1^2	-	-	-	-	-	-	-
access to water	-	-8.79 ± 3.28	- 2.68	**0.008**	-3.11 ± 1.47	-2.11	**0.035**
Male	subadult	1.33 ± 6.38	0.21	0.834	1.85 ± 2.37	-0.39	0.698
	territorial bachelor (ref)	-0.68 ± 4.72	-0.14	0.886	2.35 ± 5.95	0.40	0.693
NDVI*male	NDVI*subadult	-	-	-	10.07 ± 39.08	0.26	0.797
	NDVI*territorial NDVI*bachelor (ref)	-	-	-	-7.49 ± 22.59	-0.33	0.740
NDVI^2*male	NDVI^2*subadult	-	-	-	-25.24 ± 93.42	-0.27	0.787
	NDVI^2*territorial NDVI^2*bachelor (ref)	-	-	-	28.03 ± 52.71	0.53	0.595
PC1*male	PC1*subadult	-	-	-	-	-	-
	PC1*territorial PC1*bachelor (ref)	-	-	-	-	-	-
PC1^2*male	PC1^2*subadult	-	-	-	-	-	-
	PC1^2*territorial PC1^2*male (ref)	-	-	-	-	-	-
access to water*male	access to water*subadult	-4.42 ± 7.15	-0.62	0.537	-25.24 ± 93.42	0.78	0.434
	access to water*territorial access to water*bachelor (ref)	7.14 ± 5.43	1.32	0.190	28.03 ± 52.71	0.13	0.901

Only terms that were significant in the sex and environment model were carried forward. Terms not used in this model for a given response variable are indicated with a -. We did not run a male and environment model for strongyle nematodes because there were no significant effects of the environment on strongyle burden. For categorical variables, the reference level is noted in the Level column with (ref). Continuous variables with no interaction have no associated level, and are thus noted with 'na'. Significant effects are in bold.

Supplemental Table 3.2: Results for the female and environment model representing whether the reproductive status groups for females are impacted differently by environmental variables for the two response variables. Data for each response variable was analyzed separately using generalized linear mixed effects models with location and month included as random effects.

Predictor	**Level**	**fGCM (N=154)**			**Lungworm prevalence (N=152)**		
		β estimate ± SE	t value	P	β estimate ± SE	Z value	P
NDVI	na	-	-	-	12.45 ± 23.73	0.53	0.600
$NDVI^2$	na	-	-	-	-42.85 ± 48.33	-0.89	0.375
PC1	na	-	-	-	-	-	-
$PC1^2$	na	-	-	-	-	-	-
access to water	na	-10.52 ± 5.17	-2.04	**0.044**	0.85 ± 1.62	0.53	0.598
Female	non-lactating	-16.38 ± 6.41	-2.55	**0.012**	1.30 ± 6.73	0.19	0.847
	subadult	0.59 ± 6.30	0.09	0.926	1.54 ± 7.06	0.22	0.827
	pregnant lactating (ref)	2.76 ± 6.20	0.45	0.656	-0.60 ± 7.02	-0.09	0.932
NDVI*female	NDVI*non-lactating	-	-	-	-5.30 ± 27.15	-0.20	0.845
	NDVI*subadult	-	-	-	-8.33 ± 28.48	-0.29	0.770
	NDVI*pregnant NDVI*lactating (ref)	-	-	-	-3.08 ± 27.09	-0.11	0.910
$NDVI^2$*female	$NDVI^2$*non-lactating	-	-	-	25.94 ± 55.74	0.47	0.642
	$NDVI^2$*subadult	-	-	-	17.60 ± 60.09	0.29	0.770
	$NDVI^2$*pregnant $NDVI^2$*lactating (ref)	-	-	-	14.39 ± 55.88	0.26	0.797
PC1*female	PC1*non-lactating	-	-	-	-	-	-
	PC1*subadult	-	-	-	-	-	-
	PC1*pregnant PC1*lactating (ref)	-	-	-	-	-	-
$PC1^2$*female	$PC1^2$*non-lactating	-	-	-	-	-	-
	$PC1^2$*subadult	-	-	-	-	-	-
	$PC1^2$*pregnant $PC1^2$*lactating (ref)	-	-	-	-	-	-
access to water*female	access to water *non-lactating	21.11 ± 7.71	2.74	**0.007**	-1.32 ± 2.04	-0.65	0.514
	access to water *subadult	3.41 ± 7.59	0.45	0.654	-1.36 ± 2.09	-0.65	0.513
	access to water *pregnant access to water*lactating (ref)	5.41 ± 7.41	0.73	0.466	0.18 ± 1.85	0.10	0.923

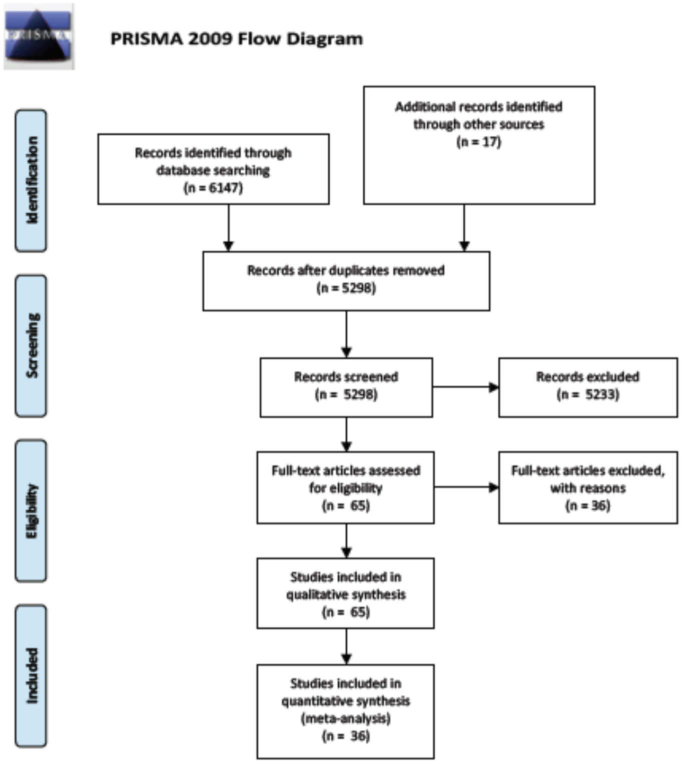
Only terms that were significant in the sex and environment model were carried forward. Terms not used in this model for a given response variable are indicated with a -. We did not run a female and environment model for strongyle nematodes because there were no significant effects of the environment on strongyle burden. For categorical variables, the reference level is noted in the Level column with (ref). Continuous variables with no interaction have no associated level, and are thus noted with ‘na’. Significant effects are in bold.

SUPPLEMENTARY FIGURES

CHAPTER 2: SUPPLEMENTAL FIGURES

IS IT TIME TO MOVE WILDLIFE STUDIES INTO THE GENOMIC ERA?: A META-ANALYSIS ON GENOMIC VARIATION-DISEASE ASSOCIATION

Supplemental Figure 2.1: PRISMA diagram detailing search results for genetic variation-disease association meta-analysis.

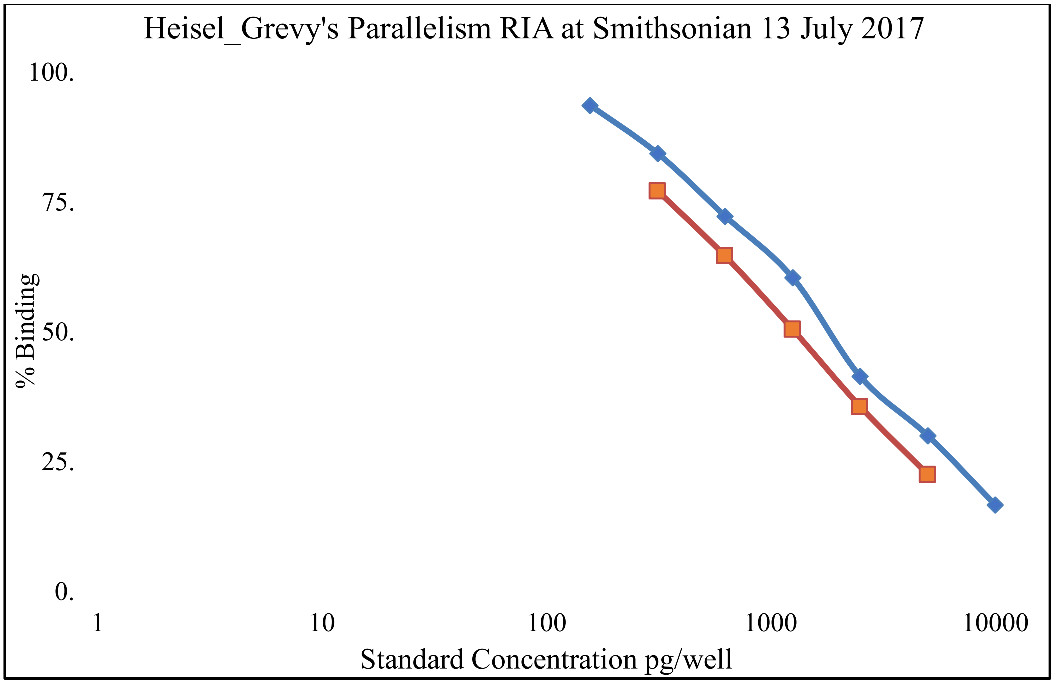


From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). *Preferred Reporting Items for Systematic Reviews and Meta-Analyses*: The PRISMA Statement. PLoS Med 6(7): e1000097. doi:10.1371/journal.pmed1000097

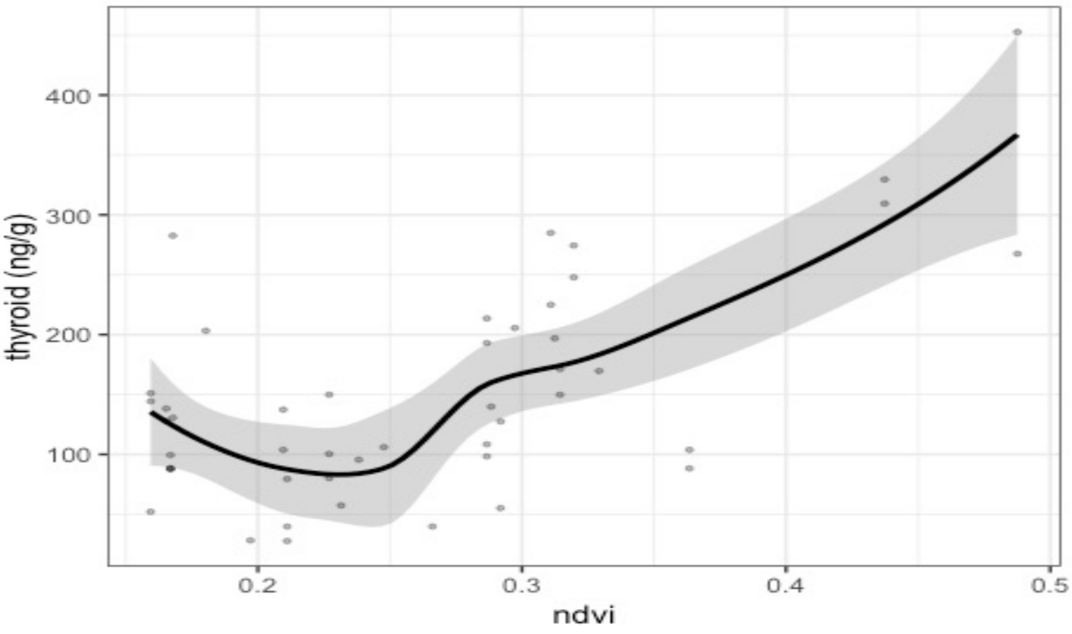
For more information, visit www.prisma-statement.org.

CHAPTER 3: SUPPLEMENTAL FIGURES

ENVIRONMENTAL AND DEMOGRAPHIC CORRELATES OF STRESS AND INFECTION IN THE ENDANGERED GREVY'S ZEBRA



Supplemental Figure 3.1: Six serial dilutions (1:4, 1:8, 1:16, 1:32, 1:64; orange line) of fecal extracts yielded a displacement curve parallel to the standard curve (P= 0.002; R2 = 0.986; blue line). This indicates that for this radioimmunoassay of fecal glucocorticoid metabolites from Grevy's zebra, the antibody was recognizing the fecal metabolites proportionally to the synthetic standard curve. The x-axis values represent the concentration of standards from 1 to 10,000. The y-axis represents the percent antibody bound at each standard concentration.



Supplemental Figure 3.2: Effect of NDVI on thyroid hormone for a subset of individuals (n=47). Data points are shown with a loess smoother (solid line) and standard error in grey.

SUPPLEMENTARY DOCUMENTS

CHAPTER 2: SUPPLEMENTAL DOCUMENTS

IS IT TIME TO MOVE WILDLIFE STUDIES INTO THE GENOMIC ERA?: A META-ANALYSIS ON GENOMIC VARIATION-DISEASE ASSOCIATION

Supplementary Document 2.1: Systematic search for genetic variation-disease meta-analysis

We used the following string of search terms:
(genetic diversity* OR heterozygosity OR inbreed* OR candidate gene*) AND (disease* OR infect* OR 103aptive103*) AND (wild* OR natural) NOT (plant*) NOT (human*) NOT (domestic*) NOT (invert*) NOT (insect*) NOT (103aptive*)

Search in Web of Science and EBSCO databases on January 20, 2017.
Web of Science produced 4404 results and EBSCO Database (includes: MEDLINE, CAB Abstracts, Environment Complete, Wildlife & Ecology Studies Worldwide, Agricola) produced 1743 results, for a total of 6147 records from our database search. Additionally, we identified 17 new studies through new literature updates and bibliographies or figures in original set of articles. This resulted in a total of 6164 records.

Removed 866 duplicates (n=5298)
We first screened titles and abstracts for basic inclusion criteria: the study had to have quantified genetic diversity and a disease response in wildlife (exclusive to managed, captive, and zoo animals), and disease could not be an experimental infection. This initial screening process removed an additional 5233 studies, resulting in 65 studies that were examined within the full text.

Guidelines for exclusion:

1. We did not include any reports of non-infectious disease. For example, some papers also tested for carcinoma, toxins, or trauma (Acevedo-Whitehouse et al 2003) and heterozygosity). Because this paper focused, solely on infectious disease and its relationship to genetic variation, we left these reports out of our data collection.

2. We excluded studies if they included experimental infection or treatment of disease or if the host species was a domestic or captive.

3. We excluded studies if the sample size (i.e. number of animals in the study) was less than 4 (for calculation of sampling variance).

4. Lastly, if effect size was not reported or impossible to calculate from reported data, or if the directionality of effect (positive or negative relationship between genetic diversity and disease) was not given, we excluded the study.

5. The final number of studies used for out meta-analysis was 36 unique studies.

6. This captured data from 28 unique mammal host species (Supp. Fig 2).

CHAPTER 4: SUPPLEMENTAL DOCUMENTS

KNOWLEDGE PERCEPTIONS, LOCUS OF CONTROL, AND MOTIVATIONS REGARDING WILDLIFE AND WILDLIFE CONSERVATION IN SAMBURU, KENYA

Supplementary Document 4.1: Interview questions

Each question is coded to indicate which research theme it addresses:

(E = Ecological knowledge)

(L = Locus of control)

(M = motivations & values)

Interview script and protocol:

Interviewer:

Translator:

Gender:

Conservancy:

Village:

Date:

Start Time:

End Time:

DEMOGRAPHIC QUESTIONS

Q1 (D) What age set do you identify with?

Q2 (D) Do you have any job in wildlife conservation? Or do your immediate family members?

Q3 (D) What is your level of formal education?

WILDLIFE TRENDS ACTIVITIES AND ASSOCIATED QUESTIONS:

Activity 1: Overall abundance of wildlife over an individual's lifetime.

Materials: Table with age sets written as column headings (Figure 4.1), 10 pebbles

Instructions:

- Identify which age set you belong to.
- Ask to distribute the 10 pebbles between Age Sets, beginning with their own age set and continuing thru current time period, to represent **overall abundance of wildlife** throughout their lifetime.

Q4 (E): Over your **lifetime**, the overall **abundance** trend was increasing/decreasing/stable/fluctuating?

Q5 (E) Within just the **current** age set, do you think wildlife **abundance** is increasing, decreasing, or stable?

Q6 (L) What do you believe are the primary reasons for changes in the **abundance** of wildlife over your **lifetime**?"

Q7 (L) What do you believe are the primary reasons for the **current** trends in wildlife **abundance**?

Activity 2: Diversity of wildlife species associated with age sets.

Materials: Table with age sets written as column headings (Figure 4.1), 10 pebbles.

Instructions:

- Identify which age set you belong to.
- Ask to distribute the 10 pebbles between Age Sets, beginning with their own age set and continuing thru current time period, to represent **overall diversity of wildlife** throughout their lifetime.

Q8 (E): The overall **diversity** trend was increasing/decreasing/stable/fluctuating?

Lkimaniki (1947-58)	Lkishili (1959-74)	Lkuroro (1975-1898)	Lmolli (1990-2005)	Lkidaru (2006-)

Activity 3: Global geographic distribution of wildlife

Materials: Photos of 9 wildlife species, global map with continents (Figure 4.2), 7 pebbles

Instructions:

- Introduce the wildlife species, global map and continents, and explain the activity.
- Assess willingness to do the activity
- If willing,
    - Go one species at a time, discuss the species, then ask to distribute the 7 pebbles on continents where they believe the animals occur.
    - Repeat for remaining species

Activity 4: National geographic distribution of wildlife

Materials: Photos of 9 wildlife species, national map with regions (Figure 4.2), 10 pebbles

Instructions:

- Introduce the national map, and explain the activity.
- Assess willingness to do the activity
- If willing,
    - Go one species at a time, discuss the species, then ask to distribute all 10 pebbles on regions of Kenya where they believe the animals occur, distributing pebbles according to perceived abundance.
    - Repeat for remaining species.

PERCEPTIONS REGARDING EXTINCTION :

Q9 (E). If a species (such as any of those in the photos) only exists in this region, do you think it's possible that it could go extinct? Extinction means there would be no more left in the world.

DOES RARITY MOTIVATE CONSERVATION:

Q10 (M). If we told you that a species were only found in this region and nowhere else in the world, would that change the way you think about it and behave towards it? Would it make you care for that animal more?

Q11 (M). What factors or reasons would motivate you to conserve a species of wildlife?

DO PERSONAL ACTIONS IMPACT CONSERVATION?

Q12 (L) What personal actions that you do, can have an impact on the ability of a wildlife species to survive here? Are those impacts positive or negative, or mixed?

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