ANTHROPOGENIC DISTURBANCE, ECOLOGICAL CHANGE, AND WILDLIFE CONSERVATION AT THE EDGE OF THE MARA-SERENGETI ECOSYSTEM

By

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ABSTRACT

ANTHROPOGENIC DISTURBANCE, ECOLOGICAL CHANGE, AND WILDLIFE CONSERVATION AT THE EDGE OF THE MARA-SERENGETI ECOSYSTEM

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Biodiversity has been steadily declining in most ecosystems due to the direct and indirect effects of a growing human population. Large carnivores are particularly threatened by the negative effects of human population growth due to their slow life histories, wide-ranging behavior, and conflict with people over livestock depredation. The Maasai Mara National Reserve (henceforth, the Reserve) is located at the edge of the Mara-Serengeti ecosystem in southwestern Kenya, and is a stronghold for large carnivore conservation in East Africa. The Reserve has traditionally supported a great density and diversity of herbivores and large carnivore species year-round. However, current research indicates that anthropogenic activities immediately outside Reserve boundaries may be having negative effects on wildlife within the Reserve itself.

My research investigates the short- and long-term effects of anthropogenic disturbance around the edges of the Reserve on wildlife populations within Reserve boundaries. First, I document longitudinal trends in the ecological and anthropogenic threats to wildlife. Next, I analyze the effects these threats have on herbivore and carnivore populations. I then test the hypothesis that spotted hyenas can serve as an indicator species in this ecosystem. Finally, management authorities play critical roles in conserving wildlife in the Reserve, so in my last dissertation chapter, I work to clarify the effects of prescribed burn management on African mammals.

My research indicates that there have been declines in mammalian herbivore abundance and diversity from 1989-2013 in the Talek region of the Reserve. In this same region and time period, I document significant increases in temperature, the number of pastoralist settlements, the number of livestock grazing inside the Reserve, and the number of tourist lodges. Of all these threats to wildlife, livestock inside the Reserve had the largest negative effect on native herbivores. Also, the frequency of lion sightings in the Talek region have declined by 55 % between 2004-2008 and 2009-2013, while the sympatric population of spotted hyenas has undergone rapid growth. These changes appear to be due to the indirect effects of a growing human population.

The speed of movement exhibited by spotted hyenas was affected by the turning angle of their trajectory, the animal's proximity to anthropogenic disturbance, the time of day, the ambient temperature, the amount of rainfall, the amount of moonlight, and interactions between anthropogenic disturbance and social rank and anthropogenic disturbance and the time of day. The tortuosity of the paths of movement by spotted hyenas was affected by the speed of their movement, time of day, their proximity to anthropogenic disturbance, and the amount of rainfall. The speed at which spotted hyenas moved correlated with the diversity and abundance of resident herbivores up to 26 and 14 weeks into the future, respectively, and with the abundance of carnivores and migratory herbivores up to 20 weeks into the future; these results suggest spotted hyenas might be useful as in indicator species in this ecosystem. Prescribed burns affected the numbers of resident herbivores for 120 days, of small carnivores for 365 days, and of large carnivores for 120 days following the burning event.

This dissertation is dedicated to Jean and Sanford Green and Edith and David Friedman.

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running carnivore monitoring projects in the world, but also to analyze a portion of her long-term data that was collected well before I joined the project. For her to place this trust in me, I am extremely honored. Dr. Holekamp has also provided me with the opportunity of a lifetime to spend more than three and a half years living and working in one of the most enchanting places in the world.

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CHAPTER 1:

General introduction

Introduction

The conservation outlook for much of the world's wildlife is currently very grim. Of the more than 7.5 million estimated species of animals on the planet (Mora et al. 2011), the International Union for the Conservation of Nature (IUCN) currently lists over 20% of those that have been described as threatened with extinction (IUCN 2015). Although the background rate of extinction is estimated to be two species per 10,000 species per 100 years, some researchers estimate that we may currently be experiencing rates of extinctions up to 100 times greater than this (Dirzo et al. 2014; Ceballos et al. 2015). The world is in the midst of a mass extinction event, the sixth in the history of the planet, and one that is being caused primarily by effects associated with human population growth (McKee et al. 2003; Butchart et al. 2010; IUCN 2015). Of the wildlife species that are most threatened with extinction in our lifetimes, large mammalian carnivores are a particularly sensitive group given their slow life histories, wide ranging behavior, and conflict with people over personal safety and livestock depredation.

The reduction or complete extirpation of large mammalian carnivores can have ecosystem-wide consequences due to the reduction or removal of the top-down control many large carnivores exert over species at lower trophic levels in natural ecosystems (Estes et al. 2011; Ripple et al. 2014). The direct threats of human population growth on large mammalian carnivores often stem from conflict over livestock depredation, and can result in the mortality of large carnivores (Woodroffe 2001; Woodroffe & Frank 2005; Ripple et al. 2014; Ogada 2014). The indirect threats of a growing human population to mammalian carnivore populations have been harder to elucidate because they may take years to manifest. However, they can include decreased numbers of prey from overharvesting, increased levels of vigilance behavior (e.g., Pangle & Holekamp 2010), shifts in activity patterns (e.g., Van Dyke et al. 1986; Frank & Woodroffe 2001; Carter et al. 2012; Rasmussen & Macdonald 2012), and altered stress physiology (e.g., Creel et al. 2002; Van Meter et al. 2009; Creel et al. 2013b; Bhattacharjee et al. 2015). Whereas management and conservation efforts have been implemented to curb and halt the direct effects of a growing human population on carnivores, both its indirect effects and techniques to manage these effects remain poorly understood.

The Mara-Serengeti ecosystem in East Africa is a stronghold for the conservation of large carnivores (Riggio et al. 2013), it is an important source of foreign exchange for local and national economies (Karanja 2003; Norton-Griffiths et al. 2008; Polasky et al. 2008), and it is a challenging area to manage because of its myriad stakeholders. The northernmost portion of the Mara-Serengeti ecosystem is the Maasai Mara National Reserve (henceforth, the Reserve). The Reserve is referred to as the “Jewel in Kenya’s crown” because of its spectacular wildlife viewing (Walpole et al. 2003); the Reserve is host to a remarkable density and diversity of herbivore and carnivore species throughout the year. These resident species are joined seasonally by an estimated 1.2 million wildebeest (*Connochaetes taurinus*) and hundreds of thousands of zebra (*Equus quagga*; Bell 1971; Maddock 1979; Sinclair & Arcese 1995).

Unfortunately, there are various threats to wildlife in the Reserve. Habitat change and livestock grazing inside and outside of the Reserve may be responsible for the widespread declines in herbivore populations within the Reserve (Ottichilo et al. 2000; Ogutu & Owen-Smith 2005; Ogutu et al. 2005; 2009; 2011). Anthropogenic disturbance inside the Reserve has also been closely associated with behavioral (Boydston et al.

2003a; Kolowski et al. 2007; Kolowski & Holekamp 2009; Pangle & Holekamp 2010), physiological (Van Meter et al. 2009), and demographic changes in spotted hyenas (*Crocuta crocuta*; Watts & Holekamp 2009; Pangle & Holekamp 2010), the most abundant large mammalian carnivore in this ecosystem. Limited information is available on how anthropogenic disturbance may be affecting other large carnivores in this ecosystem, such as lions (*Panthera leo*; but see Ogutu et al. 2005).

In the Reserve, we are presented with a unique situation that allows us to further understand how human activities are affecting wildlife populations. The eastern portion of the Reserve is managed by the Narok County Government. Wildlife species in this region are exposed to anthropogenic disturbance by livestock grazing inside the Reserve, direct conflicts with people over livestock losses, and an unregulated tourism industry. In contrast to the east, the western portion of the Reserve has been under strict management by the Mara Conservancy since the early 2000's (Walpole & Leader-Williams 2001). The Mara Conservancy restricts livestock grazing, limits tourism development, and maintains a relatively pristine environment for wildlife.

This range of human activity within the same ecosystem creates the rare opportunity for a natural experiment to investigate the effects of anthropogenic disturbance on wildlife. In my dissertation, I use this naturally-occurring variation in anthropogenic disturbance to inquire how herbivore and carnivore populations within the Reserve are faring across time and space. I also investigate ways in which conservation and management organizations can best conserve the populations of wildlife that are declining. This research represents a significant contribution to conservation and management efforts in the region.

Summary of this dissertation

In 1988, Drs. Kay Holekamp and Laura Smale began an intensive study of the behavioral ecology of spotted hyenas in the Reserve (the Mara Hyena Project). From 1988 to the present (27 years), The Mara Hyena Project has monitored the behavior, demography, and physiology of up to 6 clans of spotted hyenas, the abundance and diversity of mammalian herbivores, the numbers and spatial distributions of sympatric carnivore species in the Reserve, and the ecological and anthropogenic factors that may be affecting local wildlife populations (e.g., daily temperature and rainfall, numbers of livestock grazing within Reserve boundaries). Long-term datasets like these are imperative for asking questions related to population trends over time. I utilize this long-term dataset, as well as new data I collected, to investigate how anthropogenic disturbance and ecological change are affecting wildlife populations in both the short- and long-term within the Reserve.

I begin my dissertation, in Chapter 2, by characterizing the long-term effects of human population growth and anthropogenic disturbance on herbivore populations in the Reserve. In Chapter 3, I investigate the long-term effects of anthropogenic disturbance on the populations and behavior of large carnivores inside the Reserve. In Chapter 4, I inquire whether the behavior of spotted hyenas can predict declines in populations of sympatric wildlife. In my final chapter, Chapter 5, I attempt to clarify the temporal responses of African mammals to grassland management by prescribed burning.

The overarching goal of my dissertation is to clarify the effects of anthropogenic disturbance around the Reserve on wildlife communities living within Reserve boundaries. My dissertation presents an integrative approach that incorporates behavioral and demographic data to understand the effects of human population growth on wildlife in an important protected area in Kenya. The results from my dissertation provide information critical for understanding the long-term effects of anthropogenic disturbance on wildlife populations.

Writing style of this dissertation

My dissertation is the culmination of work done for many years before I started my own research, and collaborations with other scientists. I am extremely grateful for all of their contributions to this dissertation, and they will co-author all publications with me presenting the work described here; I will therefore use the first person plural throughout the remainder of this dissertation to recognize their contributions.

CHAPTER 2:

Long-term ecological change in the eastern Maasai Mara National Reserve

Introduction

Worldwide human population growth is a major threat to biological diversity (McKee et al. 2003; Butchart et al. 2010). Protected Areas (PAs) represent an important mechanism for wildlife conservation, particularly in developing nations, and numbers of PAs have been increasing over time (Butchart et al. 2010). In sub-Saharan Africa, the fragmentation of wildlife habitat in an expanding matrix of agriculture and urbanization has only amplified the importance of PAs for conserving critical habitat (Newmark 2008). However, intensive anthropogenic activity near PAs may exacerbate threats to biodiversity within PA boundaries (Woodroffe & Ginsberg 1998; Wittemyer et al. 2008; Newmark 2008; Craigie et al. 2010). There is now a critical need to understand exactly how anthropogenic activity around the edges of PAs affects wildlife populations within park boundaries. Unfortunately, these effects are difficult to document because they may take many years to emerge, and long-term ecological datasets are challenging and expensive to generate and maintain.

One of the most important PAs in East Africa in terms of its extraordinary biodiversity, the observability of its wildlife, and its ability to attract both tourists and foreign exchange, is the Maasai Mara National Reserve (henceforth, the Reserve) in southwestern Kenya. The Reserve, situated in the northernmost portion of the Mara-Serengeti ecosystem, is host to a remarkable diversity of wildlife. In addition to supporting high densities of resident herbivores and carnivores, it also serves as the northernmost destination for the annual migrations of wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) from Serengeti National Park (Bell 1971; Maddock 1979; Sinclair & Arcese 1995). The Reserve is contiguous with the Serengeti National

Park to the south, but flanked by expanding populations of Maasai pastoralists along all of its other borders. Since the 1950s, rapid human population growth along the edges of the Reserve has led to loss of habitat suitable for wildlife, increased levels of mechanized agriculture, and heightened grazing pressure from livestock (Serneels et al. 2001; Thompson & Homewood 2002; Ogutu et al. 2005; 2009). It has been hypothesized that these changes in habitat might be contributing to declines in numbers of many resident herbivores within and around the Reserve (Ottichilo et al. 2000; Serneels & Lambin 2001; Lamprey & Reid 2004; Ogutu et al. 2005; 2009; 2011). Monitoring efforts started in 1960 have documented declines in resident wild herbivores at levels exceeding 50 % for some species, both inside and outside Reserve boundaries (Ottichilo et al. 2000; Homewood et al. 2001; Serneels & Lambin 2001; Ottichilo et al. 2001; Ogutu et al. 2011). Numbers of migrant herbivores visiting the Reserve have also been declining; since 1984, there has been a 35 % decrease in the numbers of migratory wildebeest that visit the Reserve each year (Norton-Griffiths et al. 2008).

Conflict between people and wildlife in and around the Reserve is a complex issue compounded by the changing lifestyles of the local Maasai pastoralists. Once nomadic, Maasai pastoralists around the Reserve have become sedentary in recent decades (Ogutu et al. 2009), and are investing in agriculture and livestock production around Reserve boundaries (Homewood et al. 2001; Thompson & Homewood 2002; Thompson et al. 2002; Norton-Griffiths et al. 2008). The presence of increasing numbers of pastoralists around Reserve boundaries may also be influencing wildlife populations. Overall numbers of livestock in the region are poorly documented, but are believed to be stable or to have increased since the 1970s (Norton-Griffiths et al. 2008;

Ogutu et al. 2011), with their numbers only declining in years of drought (Ottichilo et al. 2000). Furthermore, the subdivision of communally-owned lands around the Reserve and lax regulation of Reserve rules have encouraged pastoralists to rely on illegally grazing livestock within park boundaries year-round (Boydston et al. 2003a; Kolowski & Holekamp 2009; Ogutu et al. 2009; Butt 2014), especially during drought years.

In addition to livestock grazing, a poorly regulated tourism industry may also be having adverse effects on resident wildlife near Reserve boundaries. Hundreds of thousands of tourists visit the Reserve each year. General disregard for a formal moratorium on the construction of new tourist facilities has resulted in many new lodges being built along the edges of the Reserve in recent years (Karanja 2003; Reid et al. 2003). Whether the presence of these tourist lodges affects nearby wildlife is unknown.

Using data collected from 1988-2013, our goal was to investigate the effects of anthropogenic disturbance and ecological change on wild mammalian herbivores in the Talek region of the Reserve. To do this, we documented long-term trends in herbivore diversity and abundance, and simultaneously monitored natural ecological and anthropogenic variables that might be affecting these measures. We then used hierarchical models to test hypotheses suggesting several possible explanations for observed temporal patterns in herbivore abundance and diversity. These hypotheses suggest that herbivore abundance and diversity might be affected by rainfall patterns, increasing temperature, increasing numbers of pastoralists living near Reserve borders, the expansion of tourist facilities along Reserve boundaries, numbers of livestock grazing within Reserve boundaries, and the interaction between livestock grazing and rainfall. Although previous researchers have documented declines in wild herbivore populations in the Reserve (Ottichilo et al. 2000; Ogutu et al. 2009; 2011), none have yet to investigate trends in overall biodiversity, or explicitly test hypotheses invoking relationships between ecological and anthropogenic effects on herbivores simultaneously (but see Ogutu et al. 2009).

Methods

Study area

The Reserve is primarily comprised of open grassland interspersed with riparian areas. It has traditionally supported large herds of resident and seasonally migrant herbivores alongside populations of small and large carnivores throughout the year (Bell 1971; Sinclair & Norton-Griffiths 1979; Stelfox et al. 1986; Craft et al. 2015). Rainfall patterns are bimodal, with most rain falling in November-December and March-May. Because the study site is less than 2 degrees south of the equator, there is limited seasonal variation in temperature. Our study took place in the Talek region (henceforth, Talek), located in the northeastern portion of the Reserve (Figure 2.1). The Talek region is approximately 143 km^2 in size, and is characterized by a flourishing tourism industry and exponential human population growth along the edges of the Reserve (Figure 2.1a,b; Reid et al. 2003; Lamprey & Reid 2004).

Data collection

Herbivore data

Two 4-km line-transects were surveyed biweekly in Talek starting in October 1988; further detail on methods used for counting herbivores can be found in previous publications (Holekamp et al. 1999; Boydston et al. 2003a; Van Meter et al. 2009). The northernmost transect was located in short-grass habitat, while the southernmost transect was located in long-grass habitat (Figure 2.1c). Resident herbivores monitored in the current study were impala *(Aepyceros melampus)*, topi (*Damaliscus korrigum jimela),* Coke's hartebeest (*Alcelaphus buselaphus cokii),* warthog (*Phacochoerus aethiopicus*), Grant's gazelle (*Gazella granti*), cape buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*), Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), eland (*Taurotragus oryx*), duiker (*Sylvicapra grimmia*), African elephant (*Loxodonta africana*), oribi (*Raphicerus campestris*), reedbuck (*Redunca redunca*), waterbuck (*Kobus ellipsiprymnus*), bushbuck (*Tragelaphus scriptus*), and Thomson's gazelle (*Eudorcas thomsoni*). Thomson's gazelle in Talek are non-migratory and present year-round; here they were considered to be residents in all analyses. The migrant herbivores we monitored were wildebeest and zebra. We also analyzed two metrics to investigate trends in mammalian herbivore biodiversity: species richness and Shannon's diversity index of evenness (henceforth, evenness). We did this to look at both the total biodiversity in Talek (richness), as well as the weighted abundance of each species in the herbivore community (evenness). We calculated species richness as the total number of different herbivore species sighted on each transect, and evenness was calculated for all transects on which more than one species were seen.

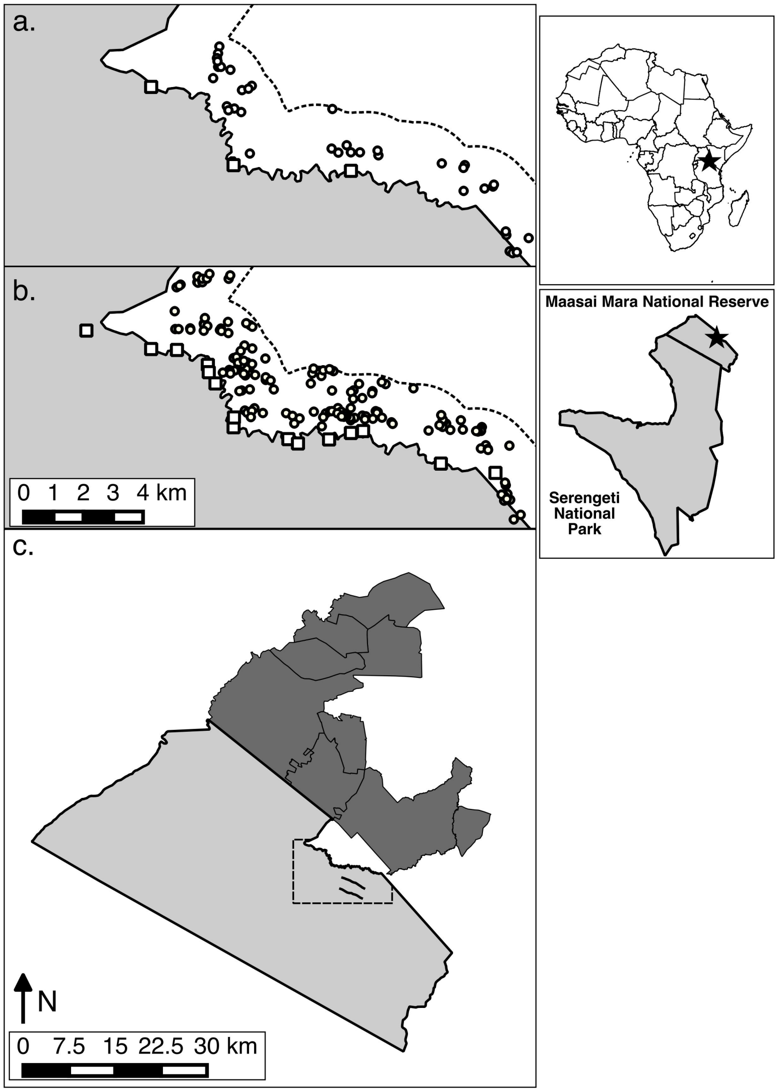


Figure 2.1. The Talek region of the Maasai Mara National Reserve in southwestern Kenya. The locations of pastoralist settlements (**o**) and permanent tourist lodges and camps (□) in (a) 1991 and (b) 2012 within 2 km of the Reserve border in the Talek region. The solid line is the boundary of the Reserve, and the shaded area lies within Reserve boundaries. All pastoralist settlements within 2 km of the Reserve boundary (dotted line) are noted. (c) The location of the Talek region in the Maasai Mara National Reserve (dashed lines) and the community conservancies north of the Reserve (dark shaded regions).

Figure 2.1 cont'd. The two 4-km transects along which we monitored herbivores at biweekly intervals in the current study are noted with solid lines.

Meteorological data

Daily precipitation was monitored from a weather station in Talek. The effect of rainfall on herbivore numbers in this ecosystem is complex (Runyoro et al. 1995; Ogutu et al. 2008; 2009); however, years of extreme droughts may negatively influence herbivore numbers and the activity of pastoralists grazing their livestock. We calculated a drought index for each year as the total amount of rainfall in mm subtracted from the average of all years, divided by the standard deviation. Thus, a drought index value less than zero in any given year indicates below-average rainfall during that year. We acquired mean monthly minimum and maximum temperatures from the Narok meteorological station (~72 km northeast of the Reserve) for the years 1989 to 2011. No temperature data were available for 2004 or 2005.

Number of pastoralist settlements

The communities around the Reserve are predominantly comprised of Maasai pastoralists living in traditional circular, fenced villages, called "bomas" (Lamprey & Reid 2004; Kolowski & Holekamp 2006). To investigate the rate of human population growth in Talek, we identified all bomas within 2 km of the Reserve boundary in 1991, 2000, 2004, and 2012, using aerial photography, field surveys, and satellite imagery (Boydston et al. 2003a; 2003b; Kolowski & Holekamp 2006).

Livestock

No livestock were seen grazing on the open plains within Reserve borders in the Talek region from 1988-1991. To estimate the numbers of livestock grazing inside the Reserve in Talek in later years, starting in 2000 we regularly drove throughout the Talek region and counted all sheep, goats, and cattle within Reserve boundaries (Kolowski & Holekamp 2009). Counts occurred up to twice daily between 2000-2008, and were performed between 0500-1000 h and 1600-2000 h to account for variation in daily livestock grazing behavior. Starting in May 2008, all counts occurred between 1600-2000 h and were only performed up to twice per month with one count taking place in the first half of the month, and one count taking place in the second half. For longitudinal analyses, we only included counts that occurred between 1600-2000 h. Goats and sheep were combined (called "shoats") due to difficulties distinguishing between them in the field. "Livestock" included the total numbers of shoats and cattle in all analyses.

Tourism

We counted tourist lodges and interviewed lodge managers at all tourist facilities within 2 km of the Reserve boundary in the Talek region to document changes between 1988 and 2013 with respect to the total number of lodges and beds available to tourists.

Statistical analyses

All statistical analyses were performed in a Bayesian framework and conducted in R v. with JAGS (R Core Team 2015). We analyzed temporal trends in the drought index, average monthly minimum and maximum temperatures, and the number of bomas, tourist lodges, and beds available to tourists along the edge of the Reserve in the Talek region using general linear models. The climatic variables were modeled with a normal distribution and an identity link, and the number of bomas, tourist lodges, and beds available to tourists were modeled with a Poisson distribution and a log link. We modeled the climatic variables of drought and temperature, and the number of tourist lodges and beds for tourists, as a function of year, and the number of bomas as a function of year and $year^2$. Counts of livestock were overdispersed, so we analyzed them using a negative binomial distribution and a logit link. We modeled the number of livestock seen grazing inside park boundaries as a function of year, $year^2$, and $year^3$; in all analyses, we included $year^2$ and $year^3$ to investigate non-linear trends in these parameters. To account for seasonal variation in temperature and livestock grazing, we fit month as a random effect.

We developed hierarchical models in a Bayesian framework to examine trends in herbivore abundance and diversity in the Talek region, and to test predictions of hypotheses forwarded to explain this variation. To examine trends over time, we first used data from 1989-2013 (25 years; 1989 was the first complete year of herbivore data) to model the total number of resident and migrant herbivores counted, species richness, and evenness, as a function of year, with transect identity coded as a fixed effect. Evenness was modeled using a log-normal distribution with an identity link, but the total number of resident and migrant herbivores and species richness were zero-inflated and overdispersed. We therefore modeled them with a zero-inflated negative binomial distribution with a log-link following Zipkin et al. (2010). In this parameterization, we defined $y_{i,t,k,j}$ as the dependent variable $_i$ in year $_t$ during biweekly interval $_k$ on transect $_j$. Biweekly intervals ranged from 1-24, and corresponded to the two-week long period during that year when the count took place (e.g., days 1-15 in January = biweekly interval 1). The mean of $y_{i,t,k,j}$ is $\mu_{i,t,k,j} = \lambda_{i,t,k,j} \bullet z_{i,t,k,j}$, where $z_{i,t,k,j}$ is a Bernoulli distributed random variable that determines whether or not a count is included in the model and is a function of an intercept (β0) and transect identity (β1). When $z_{i,t,k,j} = 1$, the counts were modeled with a negative binomial distribution. Month of the survey was included as a random effect to account for the annual movements of wildlife within the Reserve.

Next, using data from 2000-2013 (14 years) we ran a second analysis to test hypotheses that might explain variation in herbivore abundance and diversity over time. This subset of data was selected because it encompassed the period during which we systematically monitored livestock inside Reserve boundaries, and therefore had near complete datasets for all of our covariates. Using the same distributions as in the previous analysis, we modeled total numbers of resident and migrant herbivores counted, species richness, and evenness, as a function of the ecological and anthropogenic influences of the drought index, the minimum and maximum temperatures, the number of tourist lodges in the Talek region, the number of pastoralist settlements outside Reserve boundaries, the number of livestock grazing inside the Reserve in the Talek region, and an interaction between this last variable and drought. For years in which no data were available for bomas, we extracted the predicted numbers from our generalized linear models. Missing data for the minimum and maximum temperatures of 2004, 2005, and 2012 were defined as the temperatures in the year preceding each missing year. We tested for the collinearity of covariates using

Pearson's correlation coefficients. The number of bomas and lodges in the Talek region between 2000-2013 were highly correlated (Spearman's correlation coefficient $r = 0.97$); to investigate the effects of tourist lodges and human population growth in the Talek region, we averaged the two values and created a new covariate ("development"). There were no significant correlations between any other covariates (Spearman's correlation coefficient $r < 0.7$).

We evaluated the effects on our dependent variables of each independent variable during the 2 years prior to the count. All covariates were mean-standardized by 2-year average to examine the relative impact of each independent variable on our dependent variables. Thus, we modeled the estimated mean herbivore count or diversity measure per sample ($\lambda_{i,t,k,j}$) with the function:

$$\lambda_{i,t,k,j} = \alpha 0[\text{month}]_i + \alpha 1_i \bullet \text{drought}_{t-2} + \alpha 2_i \bullet \text{tmin}_{t-2} + \alpha 3_i \bullet \text{tmax}_{t-2} + \alpha 4_i \bullet \text{development}_{t-2}$$
$$+ \alpha 5_i \bullet \text{livestock}_{t-2} + \alpha 6_i \bullet (\text{livestock}_{t-2} \bullet \text{drought}_{t-2}) + \alpha 7_i \bullet \text{transect}_j$$

where $\lambda_{i,t,k,j}$ is a function of the intercept (α0) and ecological and anthropogenic covariates (α1 through α7).

Each model was fit separately by MCMC. We used uninformative priors for all of our covariates, and each model was run with 3 chains, for 100,000 iterations, with a 50,000 burn-in. Chains were thinned by 10, and $\hat{R}$ values were examined to ensure model fit (Gelman & Hill 2007). Posterior parameter estimates with 95 % credible intervals (CIs) that did not overlap zero were considered to be statistically significant. In all analyses, year was coded as a time-series variable so that each year indicated an increase of one time step.

Results

Herbivore abundance and diversity

From January 1989 through December 2013, we sampled the abundance, diversity, and evenness of mammalian herbivores in Talek biweekly, a total of 1104 times (mean ± standard error replicates per transect = 552.0 ± 6). Species richness and evenness values were available for 902 and 773 of these samples, respectively. Counts of herbivore abundance and diversity varied among months, with a distinctive trough in the number of resident herbivores counted during months when migrant herbivores were present (Figure 2.2).

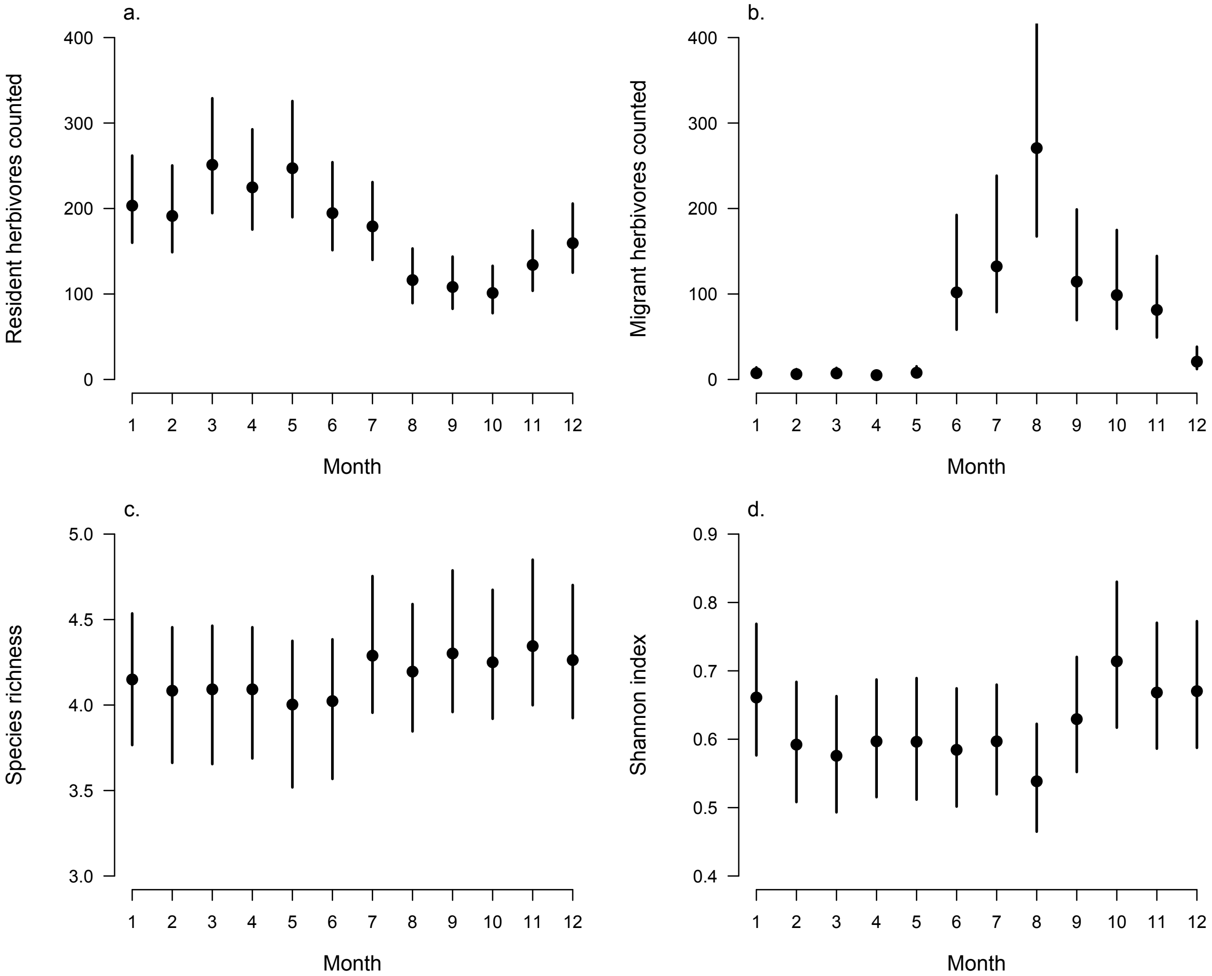


Figure 2.2. Temporal trends in the modeled counts of (a) resident and (b) migrant herbivores, (c) species richness, and (d) the Shannon index in the Talek region by month between 1989-2013. Mean ± 95 % credible intervals are displayed.

We found evidence for significant declines in the total number of resident and migrant herbivores counted, species richness, and evenness in Talek over time (Table 2.1, Figure 2.3). The numbers of resident and migrant herbivores counted and species richness varied with transect identity (Table 2.1, Figure 2.3); the transect located in long-grass habitat had significantly fewer resident herbivores and lower species diversity, but a larger number of migrant herbivores, than did the transect in short-grass habitat (Table 2.1, Figure 2.3). Species evenness did not vary with transect identity (Table 2.1). Transect identity had a significant effect on the inclusion parameter $z_{i,t,k,j}$ for all dependent variables, indicating that species richness and herbivore numbers were more likely to be greater than zero on the transect in short-grass habitat (expected mean posterior [95 % CI] residents: intercept = 6.78 [4.65, 9.6], transect = -5.69 [-8.5, -3.54]; migrants: intercept = 4.22 [1.94, 8.35], transect = -3.47 [-7.48, -1.38]; species richness: intercept = 6.93 [4.7, 10.66], transect = -5.69 [-9.4, -3.44]).

Table 2.1. Mean posterior parameter estimates (and 95 % credible intervals) of random and fixed effects from the hierarchical models that investigated trends in the numbers of resident and migrant herbivores, richness, and evenness from 1989-2013 in the Talek region of the Maasai Mara National Reserve. Significant posterior estimates, not including the intercept, are indicated in bold font (95 % credible intervals not overlapping zero). Month of the year was modeled as a random effect on the intercept; here we present the average for all 12 months. Parameter estimates are for the transect located in long-grass habitat.

Parameter	Residents	Migrants	Richness	Shannon
Intercept	5.13 (4.87, 5.39)	3.45 (2.91, 4.06)	1.43 (1.33, 1.52)	-0.48 (-0.63, -0.34)
Trend	**-0.01** **(-0.02, 0)**	**-0.05** **(-0.07, -0.02)**	**-0.02** **(-0.02, -0.01)**	**-0.01** **(-0.02, 0)**
Transect	**-1.33** **(-1.49, -1.16)**	**0.56** **(0.22, 0.91)**	**-0.34** **(-0.42, -0.26)**	0 (-0.1, 0.1)

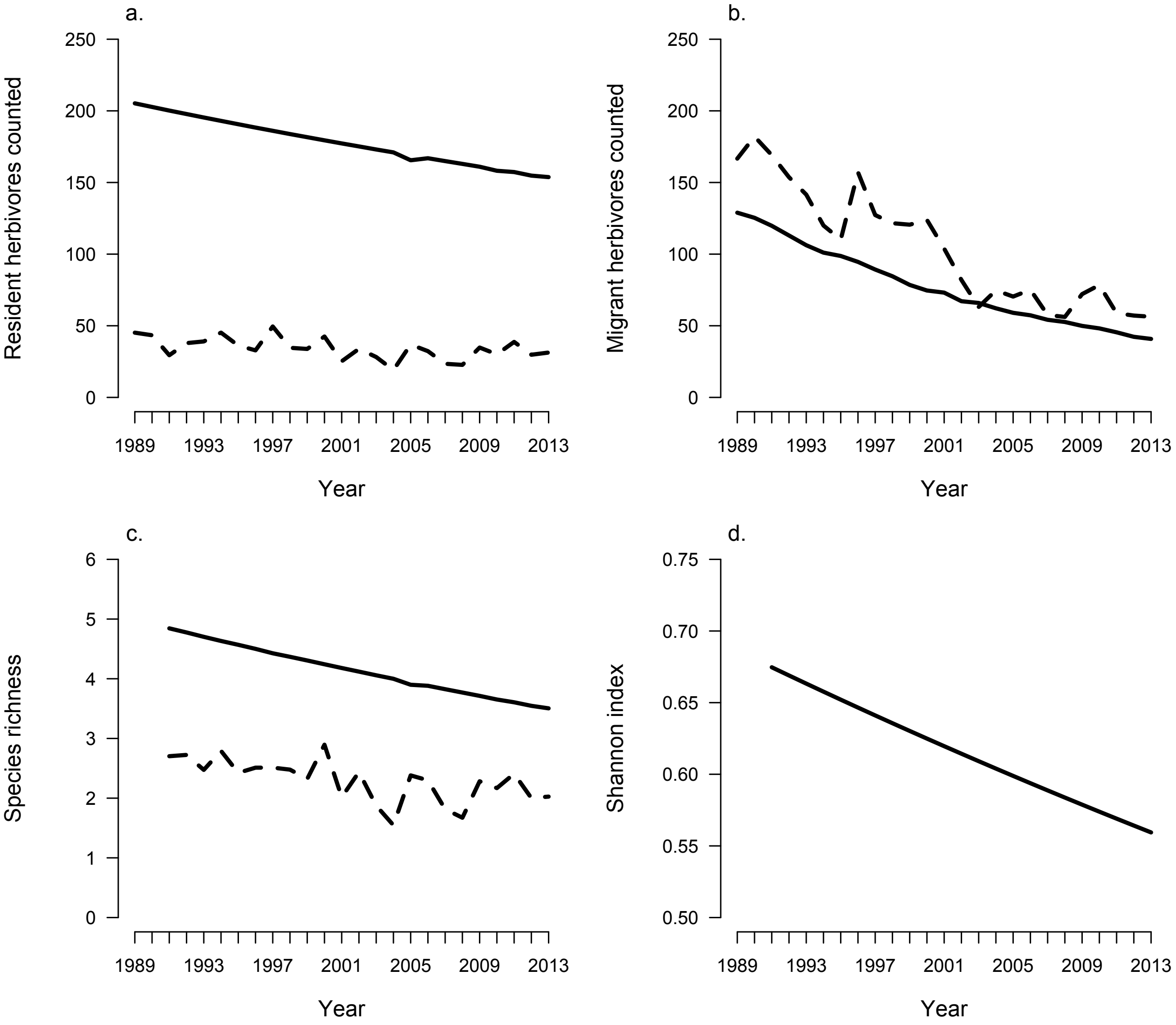


Figure 2.3. Temporal trends in the mean expected yearly count of (a) resident and (b) migrant herbivores, (c) species richness, and (d) the Shannon index in the Talek region between 1989-2013. The transect in short grass habitat is indicated with solid lines and the transect in long grass habitat is indicated with dashed lines (a-c). We present the average for both transects because there was no statistical difference in the Shannon index between transects (d). All declining trends were significant (95 % credible intervals did not overlap zero for the parameter of trend over time*)*.

Meteorological data

Drought index values < 0 were recorded for nearly half of the study years, but did not increase in frequency over time (Table 2.2, Figure 2.4). Both yearly mean minimum and maximum temperatures recorded in Narok between 1989-2011 increased over time (Table 2.2, Figure 2.4). Mean minimum temperatures increased by 2.6 ºC and mean maximum temperatures increased by 1.4 ºC.

Table 2.2. Mean posterior parameter estimates and 95 % Credible Intervals (95 % CI) of the models investigating the temporal trends in ecological and anthropogenic factors in the Talek region. A negative binomial distribution with a logit link was used for livestock, and a Poisson distribution with a log link was used for the number of bomas, tourist lodges, and beds for tourists; all other analyses were performed using a normal distribution and an identity link. All posterior parameter estimates are presented on the normal scale. The parameter Year indicates the amount of change in each subsequent year. Significant posterior parameters are indicated in bold font (95 % CI not overlapping 0).

Parameter	Estimate	95 % CI
Drought		
Intercept	0	(-0.428, 0.42)
Year	0.024	(-0.035, 0.082)
Max. temperature		
Intercept	24.832	(24.39, 25.276)
Year	**0.032**	**(0.013, 0.051)**
Min. temperature		
Intercept	10.272	(9.786, 10.755)
Year	**0.074**	**(0.054, 0.095)**
Bomas		
Intercept	60.039	(49.949, 71.593)
Year	**4.036**	**(2.399, 6.292)**
Year^2	0.064	(-0.002, 0.003)
Livestock		
Intercept	512.816	(418.287, 632.017)
Year	18.646	(-0.8, 50.419)
Year^2	**-20.949**	**(-19.643, -23.643)**
Year^3	**2.049**	**(1.595, 3.311)**
Tourist lodges		
Intercept	5.641	(4.735, 6.659)
Year	**0.409**	**(0.238, 0.649)**
Beds for tourists		
Intercept	468.717	(460.356, 477.231)
Year	**26.502**	**(25.057, 28.498)**

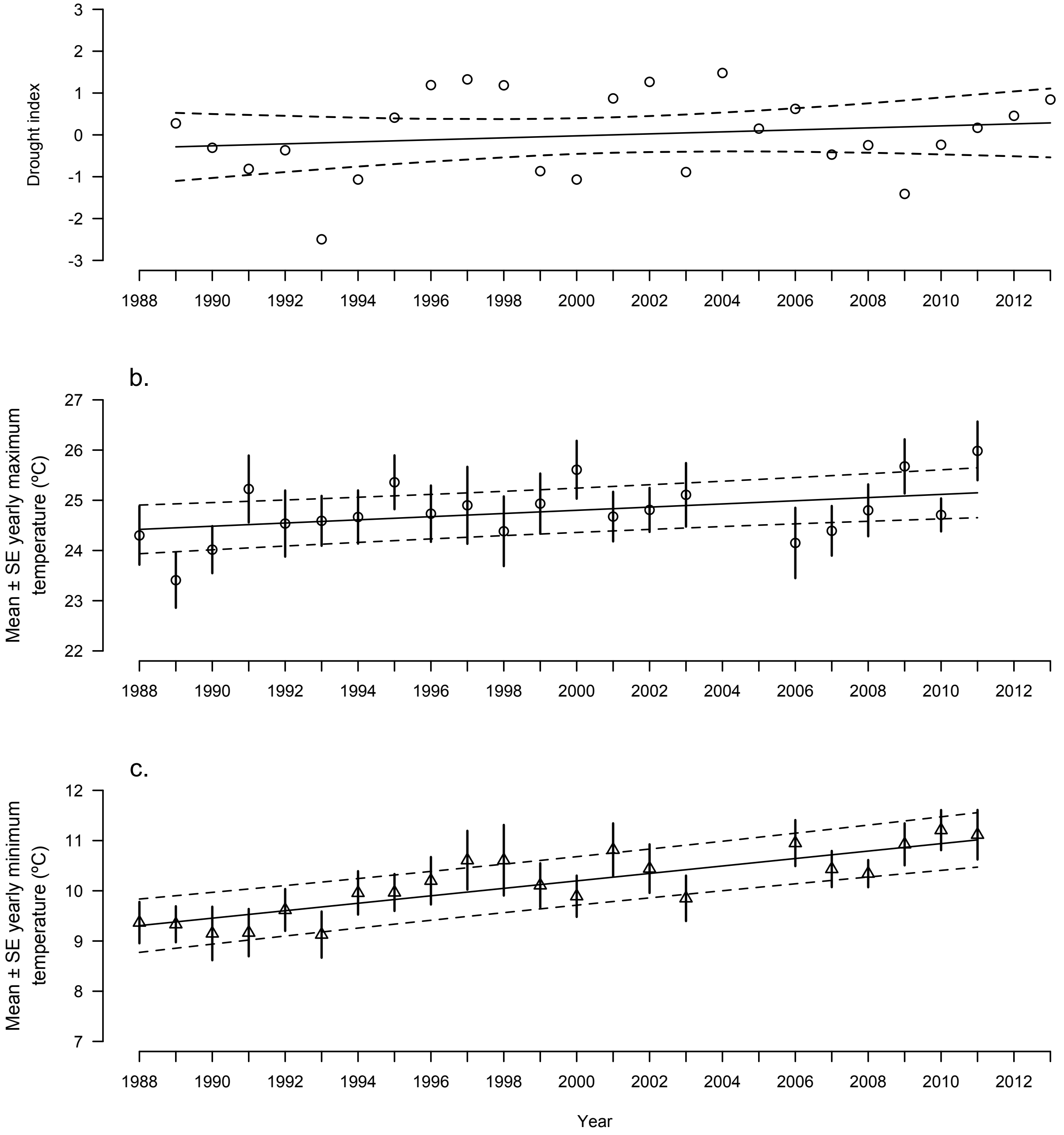


Figure 2.4. Yearly temporal trends in (a) the drought index in the Talek region of the Maasai Mara National Reserve, and (b) mean ± standard error (SE) maximum and (c) minimum temperatures in Narok, Kenya.

Figure 2.4 cont'd. Solid lines are the polynomial equations fit to the data using general linear and generalized linear mixed-effects models in R, and dashed lines indicate the 95 % credible interval around this equation.The drought index is the number of standard deviations from the mean precipitation for the entire study where a given year's precipitation was observed to fall.

Number of pastoralist settlements

The human population along the Reserve boundary increased from 1991 to 2012 (Table 2.2, Figures 2.1 & 2.4). This represents growth in the local Maasai community by over 406 % during the course of this study.

Livestock

The average number of livestock counted grazing daily inside the Reserve in the Talek region increased from 0 in 1988, to 2,218.85 in 2013 (Table 2.2, Figure 2.5). Furthermore, the number of shoats seen grazing inside park boundaries increased over time. Whereas cattle represented 85.0 % of all livestock counted in 2000, they represented only 66.7 % in 2013.

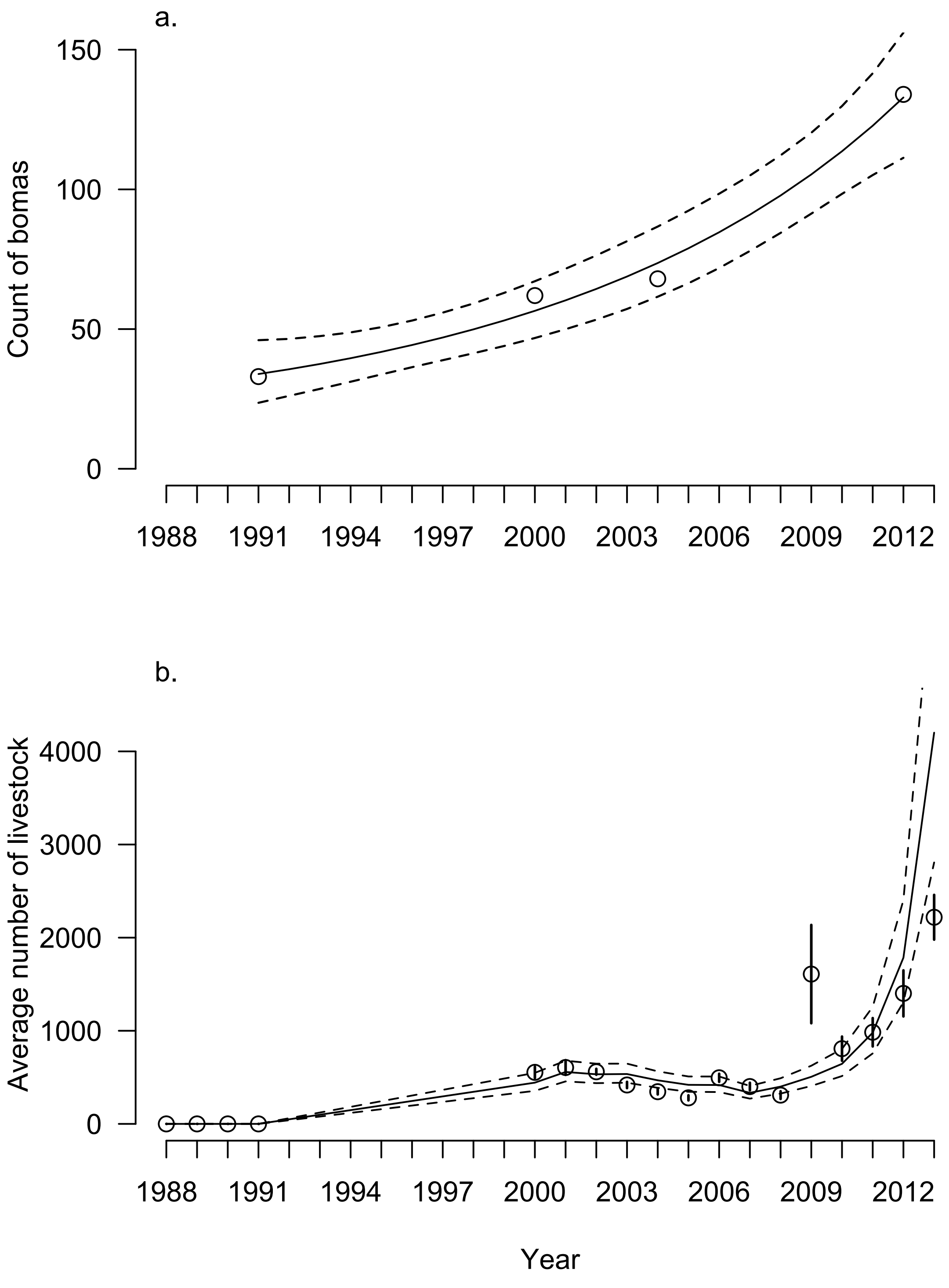


Figure 2.5. Temporal trends in the (a) total number of pastoralist settlements along the edge of, and (b) mean numbers (± standard error) of livestock grazing daily inside, Reserve boundaries in the Talek region between 1988-2013.

Figure 2.5 cont'd. Solid lines represent the polynomial equations fit to the data using general linear and generalized linear mixed-effects models in R, and dashed lines indicate the 95 % credible interval around this equation.

Tourism

The number of tourist facilities and beds available for tourists increased between 1988 and 2013 (Table 2.2, Figure 2.6), representing increases of 500 % and 366.4 %, respectively. These increases started in 1997 and continue to the present (Figure 2.6).

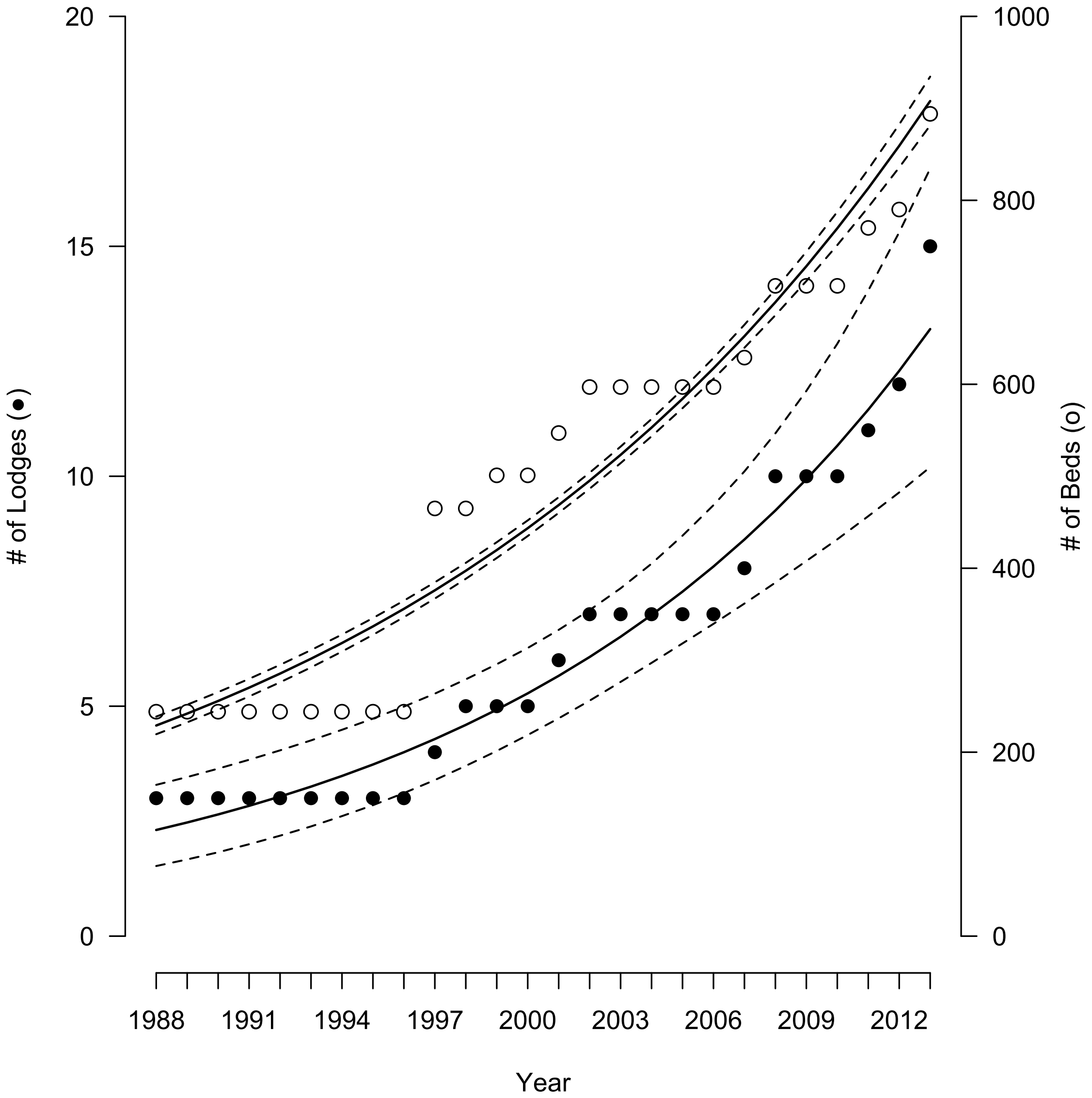


Figure 2.6. Temporal trends in the number of tourist lodges (●) and beds available to tourists (**o**) in the Talek region of the Maasai Mara National Reserve, Kenya, between 1988-2013. Solid lines represent the polynomial equations fit to the data using general linear models in R, and dashed lines indicate the 95 % credible interval around this equation.

Hypothesis testing

We modeled variation in the abundance, diversity, and evenness of mammalian herbivores in the Talek region between 2000 and 2013 as a function of the ecological and anthropogenic factors monitored there during the 2 years before each herbivore count. In this subset of data, transect identity significantly predicted species richness and the number of resident herbivores on transects, but not any other measure; species richness was higher, and there were more resident herbivores counted, on the transect in short-grass habitat than on the transect in long-grass habitat (Table 2.3). Transect identity also had a significant effect on the inclusion parameter $z_{i,t,k,j}$ for the abundance of resident herbivores and species richness, but not for the number of migrant herbivores (expected mean posterior [95 % CI] residents: intercept = 5.79 [3.60, 9.91], transect = -4.83 [-8.94, -2.62]; species richness: intercept = 5.89 [3.80, 5.64], transect = -4.58, [-8.03, -2.47]; migrants: intercept = 4.25 [1.50, 8.46], transect = -2.92 [-7.17, 0.64]).

Although none of our ecological or anthropogenic factors predicted variation in the numbers of migrant herbivores or species evenness, many factors were important in predicting resident herbivore abundance and species richness. The habitual grazing of livestock inside the Reserve and increased rainfall had significant negative effects on both the abundance of resident herbivores and species richness (Table 2.3), yet the interaction between these two factors had no effect (Table 2.3). Increases in minimum and maximum temperatures also positively affected species richness and the numbers of resident herbivores on transects (Table 2.3). Surprisingly, the documented increase in development of tourist facilities and the number of pastoralist settlements along the edge of the Talek region had no effect on any of our dependent variables. Of our independent variables, livestock grazing had the largest, significant negative effect on the abundance of resident herbivores and species richness (Figure 2.7).

Table 2.3. Mean posterior parameter estimates (and 95 % credible intervals) from the hierarchical models that tested hypotheses to explain the variation in herbivore diversity and abundance in the Talek region. Statistically significant parameter estimates are highlighted in bold font (95 % credible intervals that did not overlap zero). Month of the year was modeled as a random effect on the intercept; here we present the average for all 12 months. Parameter estimates are for the transect located in long-grass habitat.

Parameter	**Residents**	**Migrants**	**Richness**	**Shannon**
Intercept	4.73 (4.33, 5.15)	2.84 (1.88, 3.94)	1.26 (1.12, 1.4)	-0.55 (-0.71, -0.39)
Drought	**-0.93** **(-1.26, -0.6)**	0.16 (-0.63, 0.94)	**-0.28** **(-0.44, -0.13)**	-0.03 (-0.21, 0.15)
Development	-0.1 (-0.4, 0.2)	0.36 (-0.41, 1.09)	-0.05 (-0.19, 0.09)	0.03 (-0.14, 0.2)
Minimum temperature	**0.98** **(0.22, 1.76)**	-0.18 (-1.87, 1.59)	**0.33** **(0.02, 0.64)**	0.11 (-0.28, 0.48)
Maximum temperature	**0.81** **(0.13, 1.52)**	-0.85 (-2.42, 0.76)	**0.32** **(0.02, 0.63)**	0.16 (-0.2, 0.51)
Livestock	**-1.36** **(-2.47, -0.31)**	0.94 (-1.55, 3.39)	**-0.53** **(-0.99, -0.06)**	-0.31 (-0.85, 0.24)
Livestock x Drought	-0.38 (-0.83, 0.07)	-0.1 (-1.15, 0.93)	-0.14 (-0.34, 0.07)	0.03 (-0.21, 0.26)
Transect	**-1.34** **(-1.6, -1.08)**	-0.18 (-0.86, 0.48)	**-0.37** **(-0.49, -0.25)**	0.05 (-0.09, 0.18)

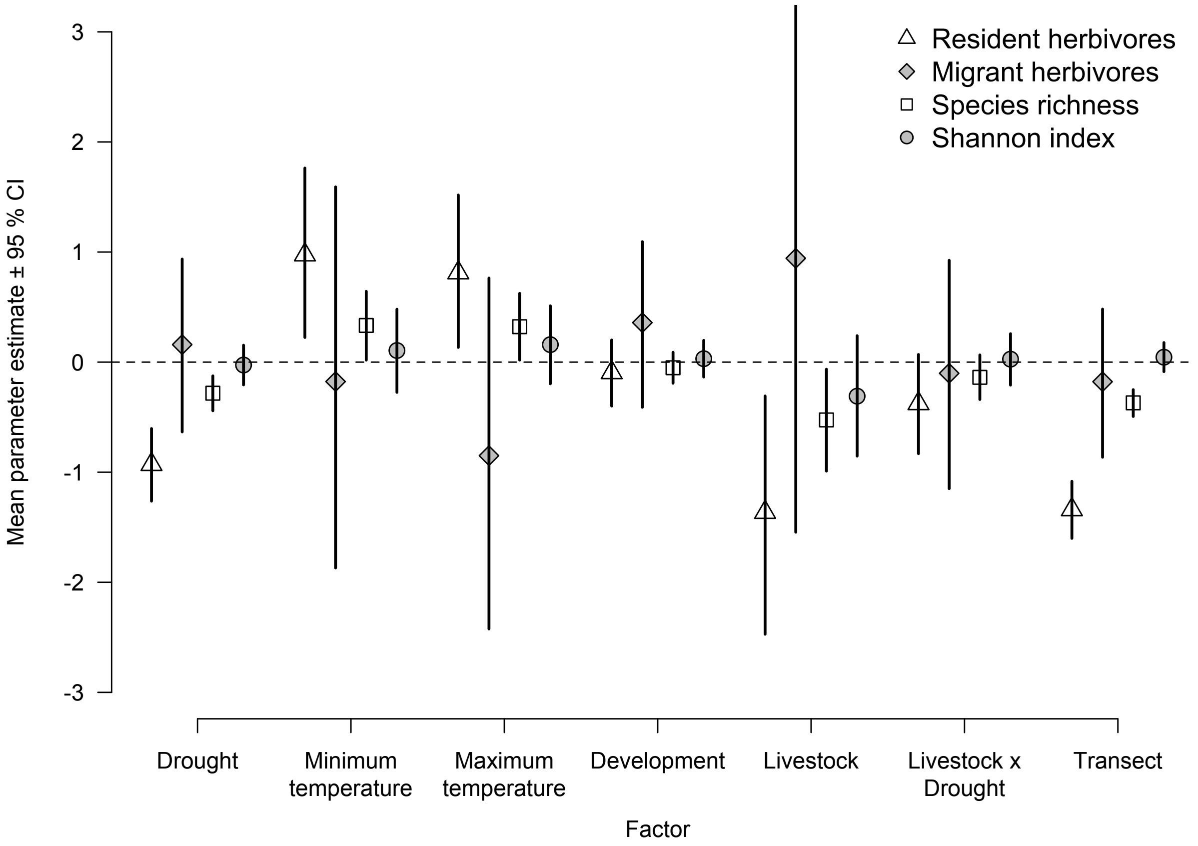


Figure 2.7. The relative importance of the ecological and anthropogenic variables affecting the abundance of resident and migrant herbivores, species richness, and Shannon index. Mean posterior estimates and 95 % Credible Intervals (CIs) are shown.

Discussion

This study presents new and important data documenting trends in overall mammalian herbivore diversity in the Talek region of the Maasai Mara National Reserve. Species richness, species evenness, and the numbers of resident and migrant herbivores declined significantly during the course of this study. Although collected completely independently and using different methods from those of earlier studies, our data are consistent with results from previous research on temporal changes in herbivore numbers in the Reserve (Ottichilo et al. 2000; Ogutu et al. 2005; Norton-Griffiths et al. 2008; Ogutu et al. 2009; 2011).

In the current study, we tested specific hypotheses that might explain changes in herbivore diversity and abundance in the Talek region. Although none of our ecological or anthropogenic factors predicted the numbers of migrant herbivores or species evenness, many of our covariates were important in predicting the abundance of resident herbivores and species richness. Increases in minimum and maximum temperatures positively affected the abundance of resident herbivores and species richness. The Talek region is primarily covered with C_4 grasses (McNaughton 1983), and higher local temperatures are likely to increase their nutrient concentrations over time (Ritchie 2008). Thus, in the short-term, increased local temperatures may provide a small benefit to wild herbivores. Species richness and the number of resident herbivores in our study were negatively affected by rainfall. The relationship between rainfall and herbivore abundance in the Reserve is complex, and it varies among species and herbivore age classes (Ogutu et al. 2008; 2009). Our results add to these previous findings, but are not straightforward. We do not yet know the mechanism for the negative effect of rainfall in the current study, but possible explanations may include the susceptibility of wildlife to disease during wet years, or a negative interaction between localized habitat degradation and extremely wet years. Further research is needed to shed more light on this.

The number of livestock grazing in the Reserve had the strongest negative effect on species richness and on numbers of resident herbivores in Talek (Figure 2.7).

Although illegal since the Reserve was established (Talbot & Olindo 1990), livestock grazing has always been a part of this ecosystem (Reid 2012). Small numbers of livestock were present inside the Reserve in Talek before 1992, but herders grazed them surreptitiously in thickets along the northern border. Thus, livestock grazing inside the park went from being low-intensity and restricted in distribution on the open plains of Talek from 1988-1991, to an average of more than 2,000 livestock counted in open plain regions daily twenty years later in 2013. One recent livestock count in early 2015 revealed 20,800 livestock grazing inside the Reserve in the Talek area in a single day, so livestock grazing within Reserve borders still appears to be increasing. Identifying the exact mechanism for the negative effect of livestock on wildlife populations in the Reserve will demand further research, but might stem from competition between livestock and wildlife for nutrients (Prins 1992; Veblen 2008; Riginos et al. 2012), the compaction of soils in heavily grazed regions (Figure 2.8), and/or distinctive changes in vegetation and habitat due to overgrazing (Homewood & Rodgers 1988; Kiage 2013). Regardless of the specific mechanism, livestock grazing most likely affects important food resources and other habitat features salient for wild ungulates.

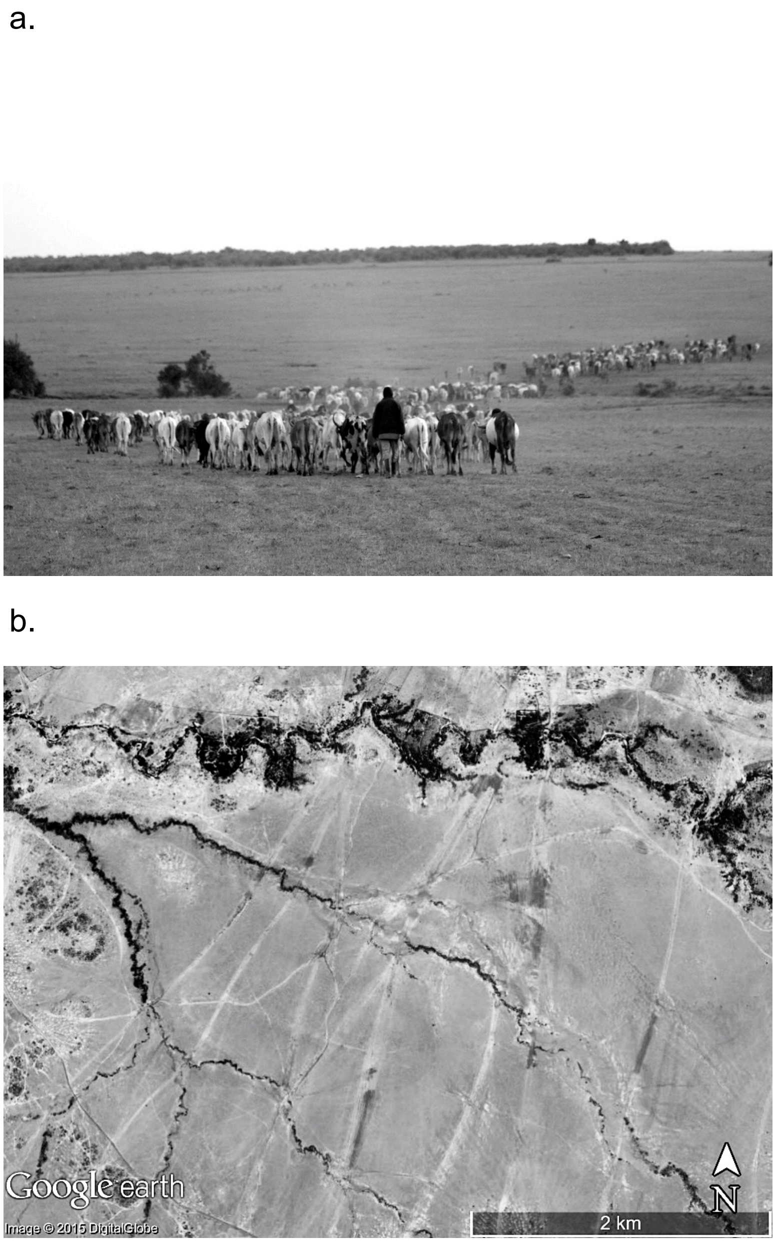


Figure 2.8. The intensive grazing taking place in the Talek region. (a) Multiple herds like this graze inside the Reserve daily. (b) The effects of intensive, sustained grazing in the Talek region on vegetation and soils, as seen from a satellite orbiting the earth in space (Photo credit: Google Earth).

Figure 2.8 cont'd. The near-vertical swaths across this landscape are the tracks left by large cattle herds moving back and forth into the Reserve from bomas situated outside the northern Reserve boundary, indicated here by the jagged line of riverine vegetation.

Although our analyses suggest the number of tourist lodges and pastoralist settlements did not significantly predict declines of resident and migratory herbivore populations and diversity in Talek, habitat change and degradation north of the Reserve were believed to contribute to wildlife declines in earlier studies (Ottichilo et al. 2000; Serneels et al. 2001; Serneels & Lambin 2001; Ogutu & Dublin 2002; Ogutu et al. 2009; 2011). Many resident herbivores regularly use pastures outside of the Reserve due to displacement by migratory animals, to gain access to better forage, or for wet season dispersal ranges (Stelfox et al. 1986; Bhola et al. 2012a; 2012b). The rapid habitat changes due to tourism and human population growth in and around Talek, including fencing, may ultimately restrict important wildlife corridors, and prevent these seasonal movements from occurring. Furthermore, there are likely to be other negative indirect effects from the increase in pastoralist settlements and tourism infrastructure along the Talek River. The Talek River is the northern boundary of the Reserve in the Talek region, and the only semi-permanent watercourse in this area (Figures 2.1 and 2.8). Habitat changes associated with an increase in the numbers of pastoralist settlements and tourist lodges along its banks may ultimately trigger broad ecological changes due, for example, to declining water quality. Future research should investigate the indirect effects this habitat change might have on wildlife.

The results from the current study are representative of what is occurring in the Talek region, but not throughout the Reserve as a whole. The Talek and Sekenani regions have rapidly expanding human populations along Reserve boundaries (Reid et al. 2003; Lamprey & Reid 2004). However, other parts of the greater Mara ecosystem remain pristine because they are much less strongly affected by people, including the entire area of the Reserve lying west of the Mara River, which is managed by a nonprofit organization called the Mara Conservancy (Walpole & Leader-Williams 2001). When the Mara Conservancy initially took over management of the western portion of the Reserve in 2001, the environment was degraded due to lax control of livestock grazing and poaching of wild ungulates (Ogutu et al. 2009). After initiating strict limits on grazing within Reserve boundaries and increasing anti-poaching patrols, this portion of the Reserve is now remarkably unaffected by anthropogenic disturbances aside from visitation by tourists. Areas north of the Reserve made similar changes with the establishment of several private conservancies starting in 2005 (Figure 2.1). The merging of these rangelands has transformed ~ 938 km^2 of area once open for livestock grazing into heavily managed wildlife preserves (Figure 2.1). The long-term effects of these conservancies on wildlife within the Reserve have yet to be elucidated. However, it is possible that the development of these restricted-grazing regions might actually be causing Maasai pastoralists to graze their livestock within the Reserve more frequently than they did before establishment of these conservancies .

Local wildlife management authorities have no control over abiotic factors such as rainfall or temperature; however, they can and should control the frequency and intensity of livestock grazing within Reserve boundaries. Prior to the creation of the

Reserve, livestock were an integral part of the Mara ecosystem (Homewood & Rodgers 1991; Reid 2012), and they are unlikely to disappear from it any time soon. At decreased levels, there is a possibility for mutual benefits from shared grazing by livestock and native ungulates (Prins 2000; Arsenault & Owen-Smith 2002; Riginos et al. 2012). Livestock grazing at moderate levels and rotational grazing patterns can enrich savanna ecosystems through habitat modification (Adler et al. 2001; Augustine et al. 2011). Yet, without strict management, enforcement, and compliance, habitual and intensive grazing of livestock has the potential to competitively suppress wild herbivore populations (Prins 1992; 2000; Butt & Turner 2012), and can lead to long-term declines in the abundance and diversity of native wildlife (Reid 2012; Riginos et al. 2012).

There are many important and unanswered questions emerging from the current research that future study of variation in management regimes could potentially address. These include understanding 1) what effects the private conservancies are having on the intensity of livestock grazing within Reserve boundaries, 2) whether wildlife numbers and diversity will recover if livestock grazing is controlled in the Reserve, and 3) what long-term effects the development of tourism infrastructure are having on wildlife populations and ecosystem function. In other regions of Kenya, maintenance of the traditional nomadic lifestyle of pastoralists helps mitigate conflicts between livestock and carnivores (Schuette et al. 2013b), and reduces the probability of long-term changes in herbivore numbers and diversity. Research is desperately needed in the Mara ecosystem to understand how traditional Maasai pastoralists and their livestock can best coexist with native wildlife, and how tourism practices can work to have a minimal impact on resident wildlife. However, without the rapid collection of data to address these questions and the enactment of management reforms that limit or alleviate some of the grazing pressure and tourism development in Talek, numbers and diversity of wild ungulates are likely to continue to decline in the eastern Maasai Mara.

CHAPTER 3:

Effects of anthropogenic disturbance on long-term trends in the demography and behavior of lions and spotted hyenas in the Maasai Mara National Reserve, Kenya

Introduction

The conservation outlook is currently grim for large carnivores throughout the world. Their populations have been declining in most ecosystems as a result of habitat change, direct conflicts over livestock, utilization of their body parts for subsistence and trade, and depletion of their prey (Ripple et al. 2014). Although there have been many recent examples of the potential for coexistence between carnivores and people in human-dominated landscapes (Carter et al. 2012; Schuette et al. 2013b; Yirga et al. 2013; Dorresteijn et al. 2014), and although some carnivore populations may actually be rebounding in the face of growing human populations (Chapron et al. 2014), most carnivore species known to be critical for maintaining ecosystem function have undergone major declines or range contractions in recent decades (Ripple et al. 2014).

The reduction or complete extirpation of large carnivores can have ecosystem-wide consequences due to the lessening or removal of the top-down control many of them exert over species at lower trophic levels in natural ecosystems (Estes et al. 2011; Ripple et al. 2014). One common example of the restructuring of natural ecosystems that occurs when apex predators decline is a specific type of trophic cascade called a mesopredator release (Crooks & Soulé 1999); this involves an increase in numbers of smaller carnivores that are ordinarily limited by the apex predators. In addition to mesopredator releases, the removal of large carnivores can trigger predator-mediated trophic cascades in other sympatric wildlife populations (Hebblewhite et al. 2005; Johnson et al. 2007; Berger et al. 2008). The effects of these trophic cascades have been well documented in many parts of the world, and can include declines in bird populations, altered vegetation structure, and potentially even climate change (Estes & Palmisano 1974; Beschta & Ripple 2009; Wilmers et al. 2012).

In many developing nations, Protected Areas (PAs) play a crucial role in the conservation of large carnivores (Woodroffe & Ginsberg 1998; Packer et al. 2013). However, rapid human population growth around PAs has the capacity to intensify anthropogenic threats to wildlife within reserve boundaries (Wittemyer et al. 2008; Newmark 2008; Craigie et al. 2010). Large carnivore populations are extremely vulnerable to these types of threats due to their expansive home ranges, slow life histories, and large energy demands (Ripple et al. 2014; Woodroffe and Ginsberg 1998). Thus, it is critical to understand how anthropogenic disturbances around existing PAs might be affecting carnivore populations within PA borders.

The Mara-Serengeti ecosystem is a stronghold for the conservation of large carnivores in east Africa (Ogutu & Dublin 2002; Riggio et al. 2013), and revenues from tourists hoping to see large carnivores there represent a key source of foreign exchange for local and national economies (Karanja 2003; Norton-Griffiths et al. 2008; Polasky et al. 2008). The Maasai Mara National Reserve (henceforth, the Reserve) comprises the northernmost portion of the Mara-Serengeti ecosystem, and has historically contained some of the highest densities of large carnivores in the world due to abundant prey throughout the year (Ogutu & Dublin 2002; Craft et al. 2015). However, activity associated with recent human population growth outside of the Reserve has been affecting wildlife populations within Reserve boundaries. Starting in the 1960s, habitat change and livestock grazing inside and outside of the Reserve have been implicated in the widespread declines in herbivore populations within the Reserve (Ottichilo et al.

2000; Ogutu et al. 2009; 2011; see also Chapter 2 of this dissertation), and have been closely associated with behavioral (Boydston et al. 2003a; Kolowski et al. 2007; Kolowski & Holekamp 2009), physiological (Van Meter et al. 2009), and demographic changes in spotted hyenas (*Crocuta crocuta*; Watts & Holekamp 2009; Pangle & Holekamp 2010), the most abundant large predator in this ecosystem. Limited information is available on how anthropogenic disturbance may be affecting other large carnivores in this ecosystem, such as lions (*Panthera leo*; but see Ogutu et al. 2005)*,* and this is an important area for research.

The Reserve is a good place in which to study effects of anthropogenic disturbance on large carnivore populations within PAs due to its high densities of lions and spotted hyenas and the rapid human population growth around its borders (Ogutu & Dublin 2002; Lamprey & Reid 2004; Ogutu et al. 2005; Watts & Holekamp 2009). Throughout their range, lions and hyenas exhibit a high degree of dietary and spatial overlap (Hayward & Kerley 2005; Hayward 2006; Périquet et al. 2014), resulting in intense interference and exploitation competition and intraguild predation (Kruuk 1972; Cooper 1991; Watts & Holekamp 2008; 2009; Périquet et al. 2014). Lions have historically represented the greatest natural source of mortality to spotted hyenas (Kruuk 1972; Watts & Holekamp 2008; 2009; Périquet et al. 2014). Conflict between lions and people can result in declines in lion population numbers (Woodroffe 2001; Woodroffe & Frank 2005), and in areas where lion numbers have declined significantly, spotted hyenas can more easily maintain possession of their kills and kleptoparasitize food from lions (Watts & Holekamp 2008). This in turn enhances their reproductive success by permitting younger weaning ages of cubs and shorter inter-birth intervals

(Watts & Holekamp 2008). This suggests that the short-term effects of people on populations of large carnivores in the Reserve may be negative for lions, but might indirectly be positive for hyenas.

In addition to changing population sizes, one other way in which lions and spotted hyenas may respond to anthropogenic disturbance in the Reserve is through their space-use. Although it is affected by many factors, including patterns of rainfall, prey availability and moonlight (e.g., Stratford & Stratford 2011; Cozzi et al. 2012; Oriol-Cotterill et al. 2015), the space-use of large carnivores can also be affected by anthropogenic disturbance. For example, large carnivores in areas of high anthropogenic activity may shift their activity patterns to be more nocturnal to avoid conflict with humans (e.g., Van Dyke et al. 1986; Frank & Woodroffe 2001; Carter et al. 2012; Rasmussen & Macdonald 2012), or alter their space-use to completely avoid areas of intense anthropogenic activity (e.g., Van Dyke et al. 1986; Schuette et al. 2013b; 2013a). Previous research in the Reserve has shown spotted hyenas modify their behavior in areas of intensive livestock grazing. Spotted hyenas whose group territory was used daily for livestock grazing were more likely to be active at night than during day-light hours (Boydston et al. 2003a; Kolowski et al. 2007), and were found more often in or near dense vegetation than were conspecifics whose territory was not grazed by livestock (Boydston et al. 2003a; Kolowski & Holekamp 2009). Unfortunately, no research exists on how lions may be affected by increases in livestock grazing in the Reserve, but previous research has shown that lions shift their temporal patterns of activity to avoid encountering people (Schuette et al. 2013b; Oriol-Cotterill et al. 2015). Lions and hyenas may respond to the effects of anthropogenic disturbances within and around the Reserve by moving farther away from its boundaries, effectively diminishing the size of the PA for them. As the numbers of livestock grazing in the Reserve continue to increase (Boydston et al. 2003a; Kolowski & Holekamp 2009; Chapter 2 of this dissertation), and habitat change outside of the Reserve accelerates (Lamprey & Reid 2004; Norton-Griffiths et al. 2008), it is critical to understand how lions and hyenas are affected by disturbances along Reserve boundaries.

Our goals were to investigate trends in the population sizes of spotted hyenas and the number of lions sighted within the Reserve, determine how these trends varied in areas characterized by varying amount of anthropogenic disturbance, and examine how the space-use of these large carnivores inside the Reserve is affected by anthropogenic disturbance inside and outside Reserve boundaries. To do this we used data collected since 1988, and exploited naturally-occurring variation in the exposure of these large carnivores to anthropogenic disturbance within Reserve boundaries.

The effects on carnivores inside the Reserve of anthropogenic activity associated with human populations living immediately outside Reserve borders are expected to increase with the carnivores' proximity to Reserve boundaries. Therefore the distances at which lions and hyenas are found from Reserve borders can be used as a proxy to assess their respective sensitivities to anthropogenic disturbance. Because spotted hyenas exhibit great behavioral flexibility (Holekamp & Dloniak 2010), we predicted that their numbers would be less strongly affected by anthropogenic disturbance than would numbers of lions. Given that lions exhibit less flexible behavior, have a larger body size, and have slower life histories, we anticipated their numbers might decline in disturbed areas (Woodroffe 2001; González-Suárez & Revilla 2013). Over time we expected this would result in declines in the population sizes of lions in areas of comparatively high anthropogenic disturbance. We also predicted that, in areas of more intensive anthropogenic activity, spotted hyenas and lions would both be more likely to be found deeper in the Reserve and thus farther away from people. Here we present, to our knowledge, the first study documenting how anthropogenic disturbances along the edge of a PA can influence the numbers and space-use of sympatric lions and hyenas concurrently, and how the differential sensitivities of these large carnivores to this disturbance may be manifested.

Methods

Study site

The Reserve is primarily comprised of open grassland interspersed with riparian areas. It has traditionally supported large herds of resident and seasonally migratory herbivores, together with populations of small and large carnivores that are present year-round (Bell 1971; Sinclair & Norton-Griffiths 1979; Stelfox et al. 1986; Craft et al. 2015). Rainfall patterns in the Reserve are bimodal, with most rain falling in November-December and March-May.

There is considerable naturally-occurring variation in the exposure of carnivores to anthropogenic disturbance within park boundaries stemming from differences in management regimes and proximity to the edge of the Reserve. The eastern side of the Reserve is managed by the Narok County Government. Within this portion of the Reserve (Figure 3.1), the Talek region in particular is an area near the Reserve border that in recent decades has undergone enormous change involving increases in the number of human settlements and tourist facilities outside the Reserve, as well as an exponential increase in livestock grazing inside Reserve boundaries (Boydston et al. 2003a; Lamprey & Reid 2004; Kolowski & Holekamp 2009; Chapter 2 of this dissertation). In contrast to the Talek area, other portions of the Reserve are far less affected by anthropogenic activity. In particular, the portion of the Reserve west of the Mara River, called “the Mara Triangle,” is remarkably pristine (Figure 3.1). In 2001, management of The Mara Triangle was assigned to the Mara Conservancy, and the wildlife in this part of the Reserve experience virtually no anthropogenic activity at all aside from visitation by tour vehicles. Here we were able to exploit these differences in anthropogenic activity to test hypotheses suggesting how large carnivores within Reserve boundaries are being affected by anthropogenic disturbance.

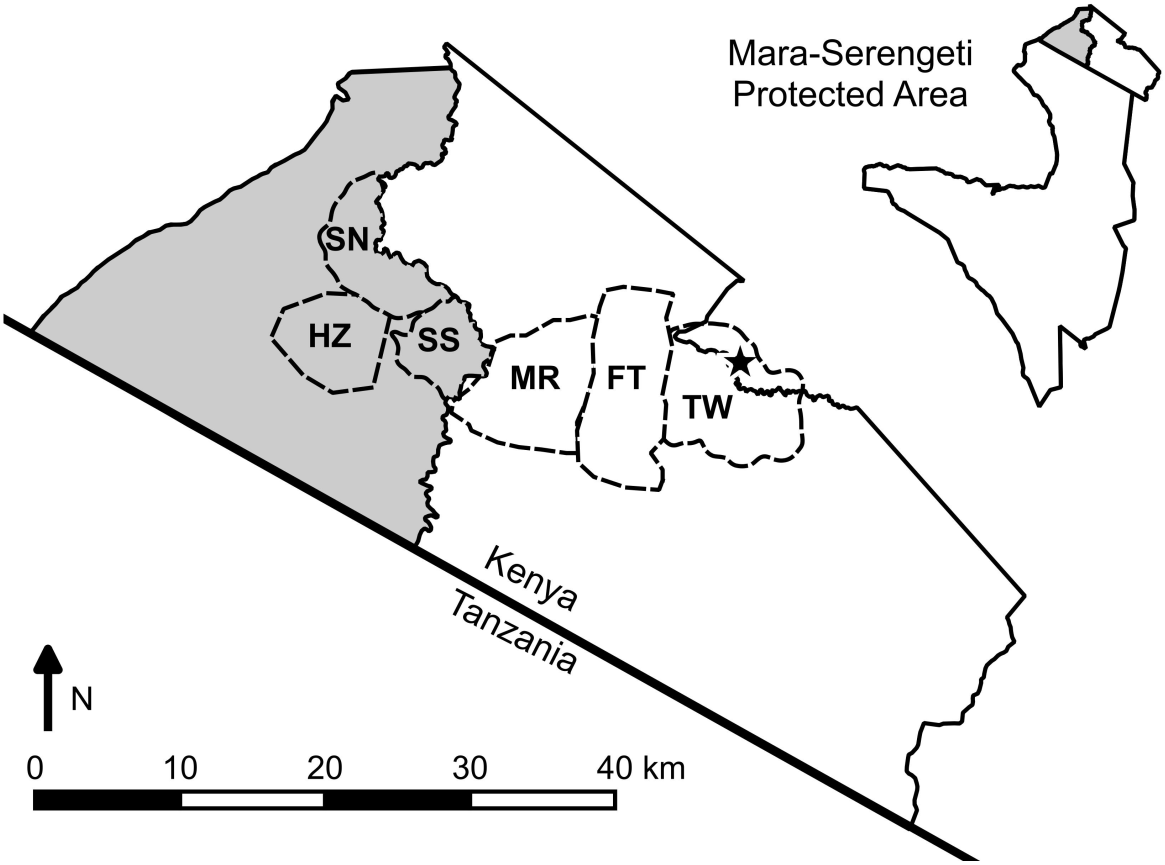


Figure 3.1. Sites of carnivore monitoring in the Maasai Mara National Reserve, Kenya. The approximate boundaries of the six territories defended by members of our study hyena clans are indicated with dashed lines. Study clans in the Mara Triangle (shaded region), which is managed by the Mara Conservancy, are Serena North (SN), Serena South (SS), and Happy Zebra (HZ). Clans in regions managed by the Narok County Government (no shading) are Talek West (TW), Fig Tree (FT), and Mara River (MR). The TW clan is located in the Talek region of the Reserve. The star (★) indicates the closest town bordering the Talek region (the town of Talek).

Data collection

Demography and behavior of spotted hyenas

Spotted hyenas live throughout sub-Saharan Africa in social groups, called clans, containing an average of 29 individuals (Holekamp & Dloniak 2010). Clans are comprised of adult females and their juvenile offspring, and several immigrant males. Males usually disperse after reaching sexual maturity, which occurs at approximately 24 months of age (Smale et al. 1997; van Horn et al. 2003; Boydston et al. 2005), but females are philopatric except in cases of rare clan fission events, when groups of females split off from the parent clan to form entirely new clans (Holekamp et al. 1993; Frank et al. 1995; Hofer & East 2003; Boydston et al. 2005; Höner et al. 2007). Each clan is structured by a linear matrilineal dominance hierarchy in which natal animals dominate immigrant males; immigrant males hold ranks based on their tenure in the clan (Smale et al. 1997; East & Hofer 2001).

Clans of spotted hyenas have been monitored in the Maasai Mara National Reserve as part of a longitudinal study that began in 1979 (Frank 1986). Here we monitored six different clans between 1988 and 2013 throughout the Reserve, in areas characterized by varying levels of anthropogenic activity. We studied five clans exposed to low levels of anthropogenic disturbance (Serena North, Serena South, Happy Zebra, Mara River, Fig Tree), and one clan exposed to a significantly higher level in the Talek region (Talek West; Figure 3.1). Wild animals in the Talek region are exposed to thousands of livestock grazing daily inside the Reserve (Boydston et al. 2003a; Kolowski & Holekamp 2009; Chapter 2 of this dissertation), and because they live near the edge of the Reserve, they are experiencing rapid human population growth and rapid development of tourism infrastructure (Chapter 2 of this dissertation).

We observed hyenas daily in each clan during morning (0500-1000 h) and evening (1600-2100 h) observation periods. During these two periods of observation, we drove 1-2 vehicles systematically throughout the territories of one or more study clans, recording the GPS locations of all hyenas encountered. In 2013, size of the clan territories monitored ranged from 28.29 to 77.04 km^2 (Figure 3.1). All hyenas in each study clan were individually recognized based on their unique spot patterns, scarring, and ear damage. When a natal animal was seen for the first time, its birthdate was estimated to ± 7 days (Holekamp et al. 1996), and it was sexed based on the morphology of its erect phallus (Frank et al. 1990). Immigrant males were assigned clan membership after being present for at least 6 months. With our intensive, year-round monitoring, individuals were considered dead or missing if they were not seen for six continuous months. Their date last seen then became their death or disappearance date. To assess demographic change throughout the study, mean monthly clan size was calculated as the total number of individuals in all age classes present during each month in which a particular clan was observed.

In addition to non-invasively monitoring clan demography and the locations of hyenas via daily observations, starting in 1991 multiple individuals were immobilized with Telazol (6.5 mg/kg) administered in a plastic dart fired from a CO_2 powered rifle (Telinject Inc., Saugus, California), and fitted with VHF (Telonics Inc., Mesa, AZ, USA) or GPS radio collars with VHF functionality (Vectronic Aerospace, Berlin, Germany). We utilized radio telemetry to assist in locating hyenas in the Talek region, and recorded the location, composition, and group sizes of hyenas when individuals were located. A visual confirmation was not always possible, and in these cases, the location was triangulated and localized to within 200 m^2.

Estimating lion abundance and documenting their use of space

We used two different metrics to investigate trends in lion abundance in the Reserve because records were not maintained on individual lions as they were for spotted hyenas. First, between 1988 and 2013, we monitored the number of times lions were found < 200 m from spotted hyenas each month within the boundaries of the territory defended by the Talek West clan of spotted hyenas. Second, we also recorded the GPS locations of all lions seen during morning and evening observation periods described above within the territories of four of our hyena study clans regardless of whether or not spotted hyenas were also present with the lions. This additional sampling occurred between 2004-2013 in the territory defended by the Talek West clan of spotted hyenas, and between 2009-2013 in the territories defended by the Serena North, Serena South, and Happy Zebra clans of spotted hyenas.

Monitoring of ecological and anthropogenic variables

To distinguish between anthropogenic and natural ecological influences on the distances from the Reserve boundary at which lions and hyenas were sighted, in the Talek region we calculated the mean number of herbivore prey present in the territory of the Talek West clan every month, the amount of rainfall, and the mean number of livestock grazing in the territory of the Talek west clan. Three 4-km line-transects were sampled biweekly in Talek on which all mammalian herbivores were counted within 100 m of each transect centerline. Further information on our methods can be found in previous publications (e.g., Holekamp et al. 1999; Boydston et al. 2003a; Van Meter et al. 2009). We calculated the monthly average of the total numbers of herbivores counted in Talek on all three transects. In each month, we also calculated the total amount of rain that fell at a weather station in the Talek region. Starting in 2000, we performed livestock counts to estimate the total number of livestock grazing in the Talek region of the Reserve. Observers systematically drove throughout the Talek West territory and recorded the numbers of cattle, sheep, and goats grazing within park boundaries. Counts occurred up to twice daily between 2000-2008, and were performed between 0500-1000 h and 1600-2000 h. Starting in May 2008, all counts occurred between 1600-2000 h and were only performed up to twice per month, with one count taking place in the first half of the month and one count taking place in the second half. No livestock were present in the territory of any other study clan. We mean-standardized the monthly estimates of herbivore abundance, the amount of rainfall, and the number of livestock recorded in Talek for use in subsequent analyses.

Statistical analyses

All analyses were conducted with generalized linear and generalized linear mixed-effects models (see parameterizations below). We fit all of our models using MCMC analyses in R with JAGS (R Core Team 2015). For all analyses, we used uninformative priors, ran our models with three chains for 20,000 iterations with a 10,000 burn-in, and thinned by 10. We examined $\hat{R}$ values for all parameters to ensure model fit (Gelman & Hill 2007). For all analyses, we present posterior parameter estimates and credible intervals (CIs) on the normal scale. Parameter estimates for which the 95 % CI did not overlap zero were considered to be statistically significant.

Longitudinal trends in size of the Talek West clan and comparisons with other clans in the Reserve

We analyzed mean monthly clan sizes to determine how the clan size of spotted hyenas in the Talek region has changed over time. Our goals here were twofold: 1) to investigate whether clan size in this region has changed over time, and 2) to determine whether the Talek West clan was significantly different in size from the other clans in the Reserve. To do this, we first conducted a longitudinal analysis of Talek West, the clan exposed to high levels of anthropogenic disturbance in the Talek region, by investigating trends in clan size from 1988-2013 with year coded as a time-series variable. We then compared mean monthly clan sizes in Talek West to all other clans for which we had data in concurrent years. Mean monthly clan size data were available starting in 2002 for Mara River, 2007 for Fig Tree, and 2008 for Happy Zebra, Serena South, and Serena North. In both analyses, mean monthly clan sizes were overdispersed, so we utilized a negative binomial distribution.

Trends in lion interactions with hyenas and lion sightings

We performed longitudinal analyses to investigate temporal trends in lion numbers in the Talek region, and cross-sectional analyses to investigate differences among clans within the Reserve. We first modeled temporal trends in the monthly frequency of the number of sightings when both lions and hyenas were present together to determine whether this changed significantly between 1988 and 2013. We modeled the number of hyena locations per month where lions were also present as a function of year coded as a time-series variable. We mean standardized the total number of locations at which hyenas were observed each month, and included this as an offset. Here we fit the model with a zero-inflation adjustment following Zipkin et al. (2010), where the probability of inclusion of a month when no lions were sighted was modeled as a random variable. Second, we compared the mean monthly numbers of lions sighted in Talek during two five-year periods, 2004-2008 and 2009-2013. We also compared the numbers of lions sighted in Talek in 2009-2013 with the numbers of lions sighted in the territories defended by the Serena North, Serena South, and Happy Zebra clans of spotted hyenas during this same time period to identify differences that may be stemming from anthropogenic disturbance. To account for variation in the total amount of search effort invested in each territory, the number of hours each month during which observers were searching for carnivores within territory boundaries was mean-standardized and included as an offset. In both analyses, we utilized a negative binomial distribution because our counts were overdispersed.

Spatial analysis of hyena and lion locations

We modeled the distances at which lions and hyenas were found from the Reserve boundary in the Talek region as a function of hour and year coded as time series variables, prey abundance, rainfall, and the number of livestock grazing in the Talek region during that month. We also included quadratic terms for each of these covariates to investigate the possibility of nonlinear relationships. Year and hour were included to investigate long-term trends and short-term daily patterns in these distances, respectively. For both models 1700 h was set as hour = 1. Locations at dens were not included in this analysis due to concerns regarding autocorrelation. These models were fit with a log-normal distribution.

Results

Temporal trends in the clan sizes of spotted hyenas

Monthly clan sizes in the Reserve ranged from 22 to 126 individuals, with a mean ± SE of 55.26 ± 0.87 (Figure 3.2). The Talek West clan was consistently the largest study clan; it also increased significantly in size over time (Table 3.1) and underwent two clan fission events, in each of which the clan split from one parent clan into two discrete daughter clans (Figure 3.2; also see Holekamp et al. 1993). These two fission events were completed by 1990 and 2001, respectively, and both resulted in declines in overall clan size. Starting in 2008 the Talek West clan underwent rapid growth while sizes of the other clans studied in the Reserve remained relatively stable. The Talek West clan was significantly larger than the other study clans during nearly all years when concurrent data were available (2002-2013; Table 3.1).

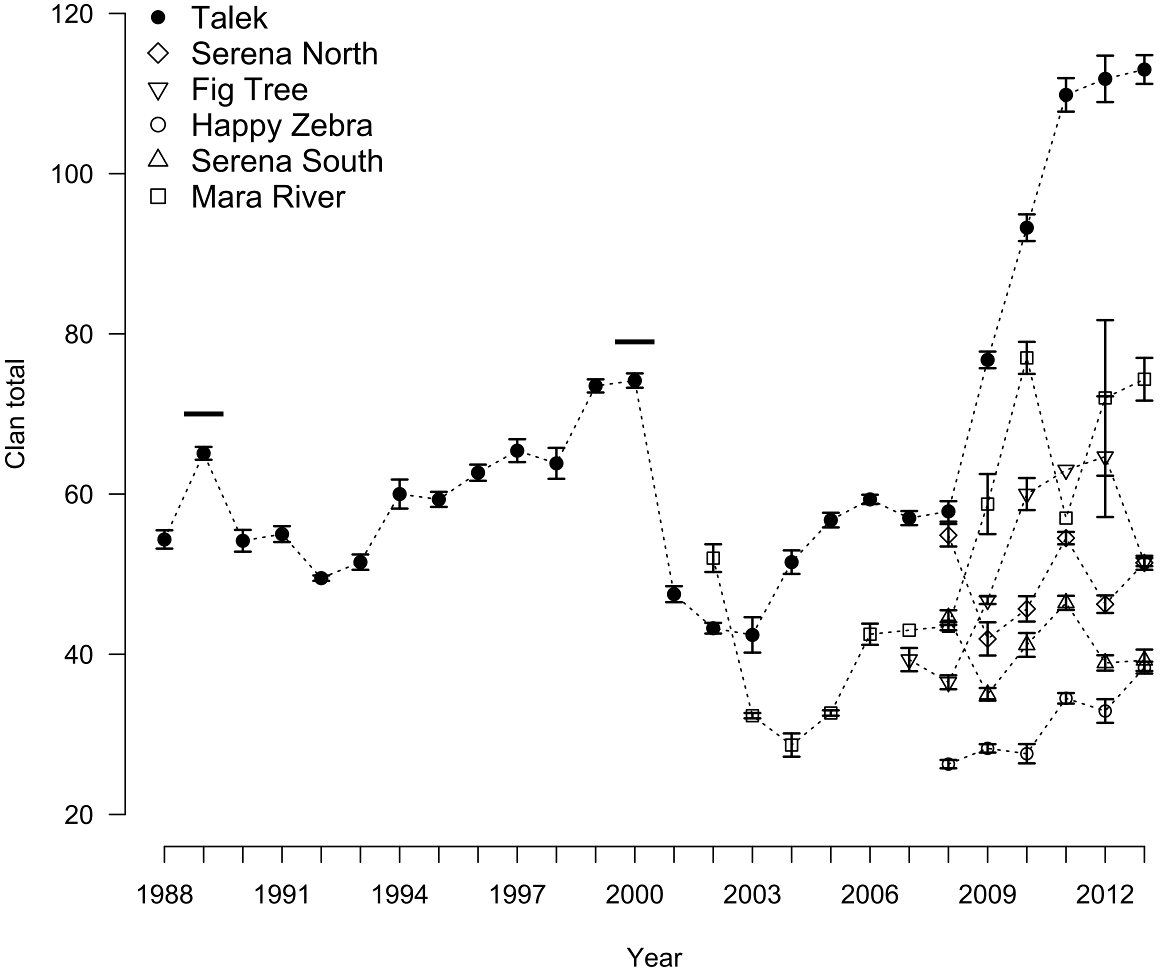


Figure 3.2. Trends in the sizes of spotted hyena clans in the Maasai Mara National Reserve, Kenya. The yearly mean ± standard error (SE) clan sizes are presented for the Talek West (1988-2013), Fig Tree (2007-2013), Mara River (2002-2013), Serena North (2008-2013), Serena South (2008-2013), and Happy Zebra clans (2008-2013). Years without SE bars did not have multiple censuses. The two documented clan fission events in Talek West that occurred in 1989 and 2000 are indicated with horizontal lines.

Table 3.1. Summary of the mean posterior parameter estimates and 95 % Credible Intervals (CIs) for longitudinal trends in size of the Talek West clan of spotted hyenas (1988-2013), and cross comparisons between the Talek West clan and other clans in the Reserve between 2002 and 2013. The Talek West clan has increased significantly over time, and was significantly larger than all other study clans. Significant posterior parameter estimates are indicated in bold font (95% CIs that did not overlap with zero). The parameter Year indicates the amount of change in each subsequent year.

Parameter	Mean posterior estimate (95% CI)
Longitudinal trends in clan size of Talek West (1988-2013)	
Mean monthly clan size	74.8 (72.3, 77.37)
Year	**1.7 (1.4, 2.02)**
Cross-comparisons of clan sizes of spotted hyenas	
Talek West (2002-2013)	72.74 (69.59, 75.97)
Mara River (2002-2013)	**50.73 (41.66, 59.95)**
Fig Tree (2007-2013)	**49.02 (39.44, 59.61)**
Serena North (2008-2013)	**48.71 (41.06, 56.57)**
Serena South (2008-2013)	**40.6 (33.37, 47.92)**
Happy Zebra (2008-2013)	**31.77 (24.88, 39.06)**

Trends in lion interactions with hyenas and lion sightings

Between 1988 and 2013, we recorded a total of 87,734 locations of spotted hyenas in the Talek region, and lions were also present at 1,188 of them. The number of interactions between lions and hyenas per month ranged from 0 to 18, with a mean ± SE of 3.92 ± 0.23. The frequency of interactions between lions and hyenas in Talek has significantly declined since 1988 (intercept and [95% CI]: 1.2 [0.1, 1.41]; change per year mean posterior estimate and [CI]: -0.03 [-0.04, -0.007]). We performed 315 monthly counts of lions within the territories of 4 study clans between 2004 and 2013.

The total number of lions sighted ranged from 0 to 233 per clan territory per month, with a mean ± SE of 29.21 ± 2.08. There were significant differences in the mean numbers of lions sighted per clan (Figure 3.3). The number of lions sighted in the territory of the Talek West clan decreased significantly between 2004-2008 (expected mean posterior [95% CI] = 34.92 [26.8, 46.39]) and 2009-2013 (15.85 [12.002, 20.74]), to a level lower than that in Serena North (46.36 [35.3, 60.58]), but not different from those in Serena South or Happy Zebra (13.02 [9.63, 17.38] and 18.75 [14.13, 23.98], respectively).

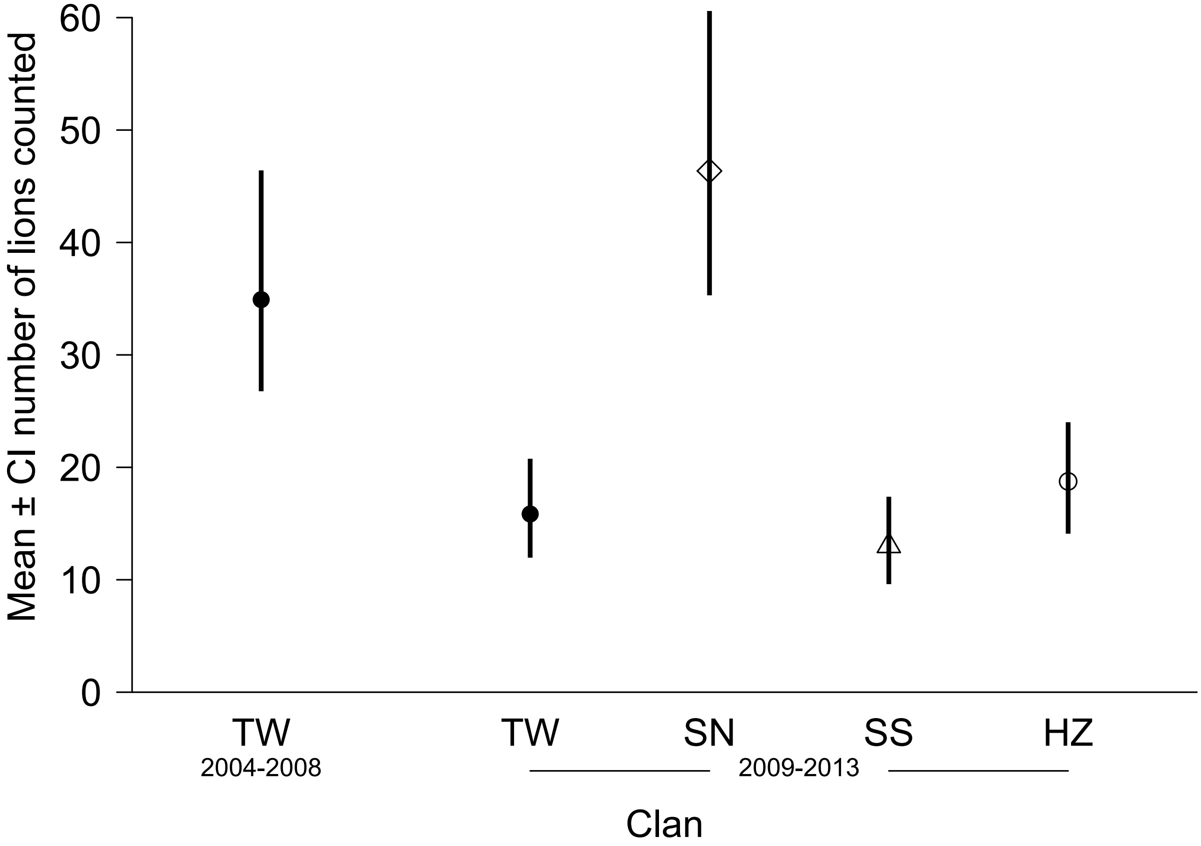


Figure 3.3. The expected mean number of lions sighted per month per clan of hyenas ± 95 % credible interval (CI) between 2004-2008 and 2009-2013. The territory of the Talek West clan (TW) is located in the Talek region, and the territories of the Serena North (SN), Serena South (SS), and Happy Zebra (HZ) clans are located in the Mara Triangle. The expected mean count in TW significantly declined between 2004-2008 and 2009-2013 (posterior parameter estimates 95 % CIs did not overlap with one another). The expected mean monthly count of lions in TW in 2009-2013 was significantly lower than SN, but no different than SS or HZ, during the same time period.

Spatial analysis of hyena and lion locations

Between 2004 and 2013, we recorded the locations of individual and groups of hyenas in the Talek West territory when the hyenas were not at dens a total of 23,470 times (mean ± SE locations per year: 2,347 ± 179.27), and recorded 1,161 locations of lions (mean ± SE locations per year: 116.1 ± 17.79). The distances at which hyenas and lions were found from the Reserve boundary changed significantly over time and were influenced by current ecological conditions (Table 3.2). We observed significant increases in distances from the Reserve boundary over the course of this study among both lions and hyenas. The quadratic effect of year was also significant for lions and hyenas (Table 3.2), indicating that both species may have been decreasing their distances to the Reserve boundary in recent years. Lions and hyenas were more likely to be farther away from the edge of the Reserve during daylight observation hours than during the dark hours of observation before sunrise or after sunset (Figure 3.4), and also when prey were more abundant (Table 3.2). The distances at which hyenas were found from the Reserve boundary were significantly predicted by the linear effects of rainfall and livestock; hyenas were more likely to be closer to the boundary during times of higher than average rainfall, and farther away when livestock were grazing at higher numbers within the Reserve (Table 3.2). Lions were more likely to be farther from the boundary of the Reserve when rainfall was higher than average, but this was also a nonlinear relationship. The effect of livestock was not significant in predicting the distances at which lions were found from the Reserve boundary (Table 3.2).

Table 3.2. Mean posterior summaries and 95 % Credible Intervals (CIs) for variables explaining the distances in meters at which spotted hyenas and lions were found from the Reserve boundary over time in the Talek region of the Maasai Mara National Reserve, Kenya. Locations of hyenas and lions considered here were recorded from 2004-2013. Variables are listed in descending order of importance following year and hour based on the weights of their untransformed posterior parameter estimates. Statistically significant posterior parameter estimates are indicated in bold font (95% CIs that did not overlap with zero).

Parameter	**Mean posterior estimate (95% CI)**
Hyenas	
Intercept	669.16 (644.78, 693.44)
Year	**61.88 (56.91, 66.75)**
Year^2	**-15.91 (-17.21, -14.56)**
Hour	**98.91 (94.85, 103.01)**
Hour^2	**12.79 (12.35, 13.23)**
Prey	**-48.62 (-58.25, -39.15)**
Livestock	**25.44 (8.37, 42.96)**
Prey^2	**13.91 (7.91, 19.85)**
Rain	**-10.78 (-19.18, -1.94)**
Rain^2	-2.36 (-7.65, 2.73)
Livestock^2	-1.61 (-6.26, 3.24)
Lions	
Intercept	709.0 (592.08, 835.27)
Year	**37.87 (22.66, 55.0)**
Year^2	**-5.11 (-10.79, -0.17)**
Hour	**32.22 (26.76, 37.84)**
Hour^2	**11.98 (10.71, 13.29)**
Prey^2	**69.1 (40.78, 101.63)**
Prey	**-57.10 (-100.69, -14.23)**
Rain	**51.08 (7.56, 98.37)**
Rain^2	**-33.53 (-64.48, -5.53)**
Livestock	54.19 (-20.64, 147.53)
Livestock^2	-5.06 (-28.11, 16.73)

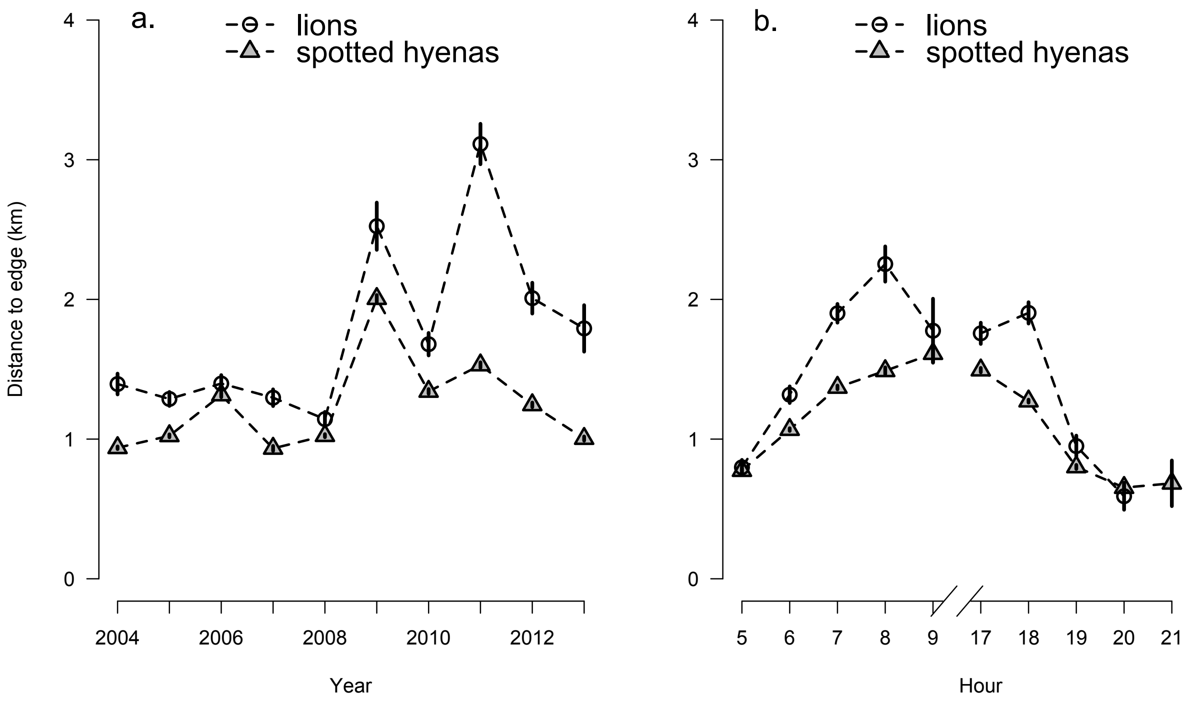


Figure 3.4. Mean ± standard error (SE) distances at which spotted hyenas and lions were found from the Reserve boundary (a) over years of the study, and (b) over hours of the day during which we monitored lions and spotted hyenas.

Discussion

Our research presents new and important data documenting concurrent long-term trends in the populations of two long-lived species of large carnivores in the Maasai Mara National Reserve. The Reserve has long been seen as a stronghold for the conservation of large carnivores in east Africa (Ogutu & Dublin 2002; Riggio et al. 2013), yet our work suggests that the large carnivores inside this PA may not be adequately buffered from the anthropogenic activity occurring immediately outside the boundaries of the Reserve. In the Talek region at the edge of the Reserve, where thousands of livestock graze daily inside the park, and rapid habitat change is occurring immediately outside of Reserve boundaries, the local population of spotted hyenas has undergone rapid growth during the same period in which we observed a significant decline in the frequency of lion sightings. Two systematic assessments based on individual lion identities documenting the total number of lions inside the Reserve were conducted by Ogutu et al. (2002) and by Dloniak (2006). Dloniak's (2006) work indicated that the lion population had declined by 40% since Ogutu et al. (2002) estimated the lion population size 13 years earlier. Our research indicates these downward population trends in lions are likely to be continuing in the Reserve, at least in the Talek area.

Although we do not have information on the total number or density of lions in the Talek region, both the total number of lions sighted in Talek, and the frequency of their interactions with hyenas, declined significantly over time. These declines were concomitant with an increase in the size of the local clan of spotted hyenas. Thus, the effects of anthropogenic disturbance along the edge of the Reserve appear to be affecting lions and hyenas in radically different ways. However, in areas of the Reserve experiencing significantly less anthropogenic disturbance than the Talek region, such as the Mara Triangle, the patterns in clan sizes of spotted hyenas and lion sightings varied among clan territories. The Serena North territory had the largest clan size in the Mara Triangle, but also had the most lions sighted of all the clans studied there. Furthermore, it was in the territories of the smallest clans we monitored in the Mara Triangle where we observed numbers of lions sighted similar to those in Talek. Therefore, local ecological conditions also play a significant role in determining the numbers of these large carnivores (e.g., prey availability).

The decline in the number of lion sightings over time in the Talek region is unlikely to be due to decreased detectability of lions in our study area. Lions and hyenas regularly occupy the same regions of the Reserve (Ogutu et al. 2005; Watts & Holekamp 2008; 2009), and also show a high degree of spatial overlap throughout sub-Saharan Africa in environments where they both still occur (Creel & Creel 1996; Périquet et al. 2014). Based on searching for lions and hyenas during both hours of daylight and darkness during all years of this study, we infer that the apparent trends in lion sightings are real.

Given the decline in lion sightings over time in the Talek region and the concurrent increase in the clan size of sympatric spotted hyenas, it appears that the anthropogenic activities around Talek may be having a negative effect on lions and a positive effect on hyenas. In the current study we cannot infer causation between the increase in the size of the spotted hyena clan in Talek and the reduced frequency at which we sighted lions, but it is possible that this may represent a case of mesopredator release. On the other hand, there are certain characteristics here that distinguish this from other documented cases of mesopredator release. For example, in contrast to most pairs of apex and meso-predators, lions and hyenas both prey primarily on medium- and large-bodied herbivores, and historically these species have exhibited a high degree of geographic overlap (Hayward & Kerley 2005; Hayward 2006; Périquet et al. 2014). It could thus be argued that they offer similar ecosystem services through top-down controls, which would distinguish them from the species pairs in other cases of mesopredator release. The long-term effects are currently unknown of a carnivore community in the Reserve that is made up of more spotted hyenas and fewer lions. To our knowledge, no previous work describes a mesopredator release within a PA containing multiple large carnivore species living at high densities like we have here.

Interestingly, the amount of rainfall and numbers of livestock grazing in Talek appear to be having different effects on the space-use of hyenas and lions. Whereas hyenas increased their distances from the boundary when higher than average numbers of livestock were grazing in this region, lions were not affected. Whereas higher than average rainfall increased the distance to the Reserve boundary for lions, it decreased this distance for hyenas. Heavy rainfall can cause prey to disperse, and bring carnivores into closer proximity to people, and thus ultimately increase rates of conflict (Kolowski & Holekamp 2006; Kissui 2008; Sogbohossou et al. 2011; Lyamuya et al. 2014). In the current research, responses to rainfall appear to be bringing hyenas closer to regions of conflict, while lions are moving farther away. The effects of prey were the same for lions and hyenas; an increase in prey availability decreased the distances at which both species were found from the Reserve boundary.

Of the hours we sampled, both lions and hyenas were more likely to be closer to the boundary of the Reserve during hours of darkness than daylight in Talek (Figure 3.4). This is a novel finding for spotted hyenas, and supplements earlier evidence that lions prefer to be closer to areas containing dense human populations when human activity is expected to be the lowest (Schuette et al. 2013b; Oriol-Cotterill et al. 2015). In contrast to previous research, our results show that this change is occurring inside Reserve boundaries. Our observation that both lions and hyenas were approaching Reserve boundaries more closely during hours of darkness than hours of daylight suggests that lions and hyenas might often be leaving the Reserve at night and moving into the surrounding community lands where they may be preying upon livestock. GPS collar data from spotted hyenas and lions in Talek will be needed to test this hypothesis. However, conflict stemming from large carnivores leaving PAs to prey on livestock in community lands is a serious source of declining large carnivore populations worldwide, as it often results in retaliatory spearing, poisonings, and poaching (Woodroffe 2001; Woodroffe & Frank 2005; Ripple et al. 2014; Ogada 2014). In the current study, these types of conflict may be responsible for the apparent decline in the Talek lion population.

Above all, our research indicates that the carnivore populations within the Maasai Mara National Reserve are changing. If we wish to maintain this iconic Reserve as a stronghold for large carnivore populations, we need to perform a rapid assessment of the actual population size of lions, investigate in more detail the changes that are occurring within the carnivore community and their underlying causal factors, and assess the effects of this altered carnivore guild on the ecosystem. PAs in sub-Saharan Africa are quickly becoming islands surrounded by degraded rangelands and exponentially growing human populations (Newmark 2008). For large carnivores in particular, their future conservation relies on the efficacy of these sanctuaries to protect species, like lions, that may be particularly sensitive to habitat degradation and at high risk for conflicts with people (Packer et al. 2013; but see Creel et al. 2013a). Successful community conservation work can help to mitigate conflicts outside of PAs (Hazzah et al. 2014), and is integral to long-term conservation of large carnivores. However, if sensitive species continue to decline within PAs, even the best conservation efforts in community lands may not be able to sustain their populations into the future.

CHAPTER 4:

Early warning signals of environmental degradation: Do the movements of spotted hyenas indicate the diversity and abundance of sympatric wildlife?

Introduction

Worldwide human population growth has become a major threat to global biodiversity (McKee et al. 2003; Butchart et al. 2010). The direct (e.g., bushmeat consumption) and indirect (e.g., climate change, competition for resources) effects of human population growth on native wildlife occur in nearly all ecosystems, and have led to many long-term declines in wildlife populations. One mechanism to help understand ecological changes associated with human population growth is the use of indicator species, which can be used as proxies to reveal ecosystem trends, offer insight into appropriate conservation strategies, and vastly improve conservation and management decisions (Landres et al. 1988; Caro & O'Doherty 1999; Caro 2010). Indicator species have been used in the past as proxies to assess changing environmental conditions in many ecosystems (Landres et al. 1988; Caro & O'Doherty 1999; Caro 2010). Whereas use of indicator species was hailed early on as an important surrogate measure to assist in wildlife conservation, recent research has cast doubt on their utility (Fleishman & Murphy 2009; Kessler et al. 2011).

When selecting an indicator species to understand broad ecological trends, the chosen species should occur throughout a wide geographic range, be available for continuous assessment, be cost-effective and relatively easy to measure, have a well-understood natural history, and respond quickly to ecological change (Noss 1990; McGeoch & Chown 1998). Other recommendations are that indicator species should be large-bodied, have large home ranges, and occupy high trophic positions so they can reflect ecological change at multiple trophic levels (Caro & O'Doherty 1999). Nevertheless, many organisms previously classified as indicator species lack some or all of these qualities (Hilty & Merenlender 2000). Furthermore, indicator species have traditionally been used on a presence/absence basis to assess the effects of environmental change on other sympatric species. That is, if the indicator species is present in an ecosystem, then you are likely to find other sympatric species there as well (Fleishman et al. 2005; Caro 2010). Thus traditional indicator species have been selected for their sensitivity to specific types of environmental change. For example, common farmland birds in Europe have been proposed as indicator species for the effects of agriculture on the biodiversity of sympatric wildlife because of their sensitivity to agricultural production (Gregory et al. 2005). If these birds are absent or declining, this indicates other wild birds in Europe are also likely to be declining. However, long-lasting damage may occur before this type of an indicator species can be identified and monitored. Additionally, by the time these sensitive species are eradicated, long-lasting damage may already have been done to sympatric wildlife populations. Therefore, it would be useful to find an indicator species that can indicate impending changes to populations of sympatric species through more labile metrics (Caro 2010), such as behavioral measures. Behavioral changes in one species could then be used to better understand trends in sympatric wildlife. Here we inquired whether the movement patterns of spotted hyena (*Crocuta crocuta*) could indicate changes in populations of sympatric mammals. Spotted hyenas exhibit many of the traits sought in idealized indicator species as described above (e.g., wide distribution, well-understood natural history, high trophic position, respond quickly to ecological change, etc.). Having an indicator species that can indicate the abundance and diversity of sympatric species before any changes become apparent would potentially be extremely useful for wildlife managers and conservationists throughout the African continent.

The spotted hyena has a remarkably high degree of intraspecific variation in behavior and occurs over a broad geographic range (Holekamp & Dloniak 2010). Spotted hyenas are extremely adaptable carnivores that can survive by scavenging on carrion, but they are also very efficient hunters of live prey. In contrast to most other African animals occupying similar trophic positions, spotted hyenas thrive on a wide diversity of prey species (Kruuk 1972; Cooper et al. 1999; Hayward 2006), breed year round (Holekamp et al. 1996), and can be active either day or night (Kruuk 1972; Kolowski et al. 2007; Stratford & Stratford 2011). Also, spotted hyenas can persist at high densities even in areas of intensive human activity (e.g., Ethiopia) where all of their natural prey have been extirpated (Yirga et al. 2012; 2013).

The space-use behaviors of spotted hyenas exhibit a number of important characteristics that may allow them to inform us about deteriorating ecosystems while there is still time to repair damage inflicted by anthropogenic activity. Previous research suggested that the behavior of hyenas changes in response to anthropogenic activity roughly 5 years before any changes become apparent in their population dynamics (Kolowski & Holekamp 2009). Thus, these animals emit early warning signals about their own future welfare. Here our goal was to determine whether the behavior of spotted hyenas might also correlate with certain characteristics of sympatric wildlife.

We tested the hypothesis that the spotted hyena can serve as an indicator species in the northernmost portion of the Mara-Serengeti ecosystem, within the Maasai Mara National Reserve (henceforth, the Reserve), in southwestern Kenya. Specifically, we were interested in examining how the behaviors of spotted hyenas may correlate with numbers and diversity of sympatric wildlife. The Reserve has historically supported a great abundance and diversity of carnivores, resident and migrant herbivores, and many species vulnerable to extinction including black rhinos (*Diceros bicornis*) and African elephants (*Loxodonta africana*). However, some areas of the Reserve are currently undergoing massive ecological changes associated with increasing anthropogenic activity along Reserve borders. Human population growth around the Reserve has increased exponentially since 1950 (Lamprey & Reid 2004; see also Chapter 2 of this dissertation), resulting in habitat degradation due to mechanized agriculture (Serneels et al. 2001; Lamprey & Reid 2004; Ogutu et al. 2009), urbanization, and the intensive grazing of livestock by pastoralist communities (Thompson & Homewood 2002; Ogutu et al. 2005). Evidence suggests that these threats may be responsible for long-term declines in populations of resident and migrant herbivores (Ottichilo et al. 2000; Homewood et al. 2001; Serneels & Lambin 2001; Ottichilo et al. 2001; Ogutu et al. 2005; Norton-Griffiths et al. 2008; Ogutu et al. 2009; 2011; Chapter 2 of this dissertation), behavioral and physiological changes in spotted hyenas (Boydston et al. 2003a; Kolowski et al. 2007; Kolowski & Holekamp 2009; Van Meter et al. 2009), and altered population sizes of resident carnivores within Reserve boundaries (Ogutu et al. 2005; Dloniak 2006; Chapter 3 of this dissertation). By using naturally-occurring variation in ecological change stemming from proximity to anthropogenic disturbance, we inquired whether the movements of spotted hyenas were correlated with the abundance and diversity of sympatric wildlife populations, and if so, how far in advance. Examining the effects of anthropogenic disturbance and ecological change in a complex system like the Mara-Serengeti is quite challenging; an indicator species might assist conservation and management officials in understanding how this ecosystem may be faring over time.

To test our hypothesis, we monitored the fine-scale movement parameters of speed and the tortuosity of paths taken by spotted hyenas fitted with GPS collars, and combined these measurements with in-depth sampling of sympatric herbivore and carnivore populations within the Reserve. The speed of movement and turning angle of large carnivores are known to be influenced by anthropogenic and ecological factors (e.g., lions (*Panthera leo*); Oriol-Cotterill et al. 2015). Thus, we predicted that these movement parameters of spotted hyenas would also be influenced by current ecology, and most importantly, and that they might also be able to serve as an indicator of the abundance and diversity of sympatric wildlife. By using the naturally-occurring variation in anthropogenic disturbance and ecological conditions within the Reserve, we first investigated the ecological and anthropogenic factors that influence the speed and tortuosity of travel by collared spotted hyenas. We then asked to what extent these movement patterns of spotted hyenas correlate with the abundance and diversity of sympatric species at future time points.

Methods

Study site

The Reserve is comprised primarily of open grassland interspersed with riparian habitat along seasonal watercourses. The Reserve has traditionally supported many resident herbivore and carnivore species year-round, and is also visited seasonally by migrating wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), and Thomson's gazelle (*Eudorcas thomsonii)* populations from the Serengeti National Park to the south (Bell 1971; Sinclair & Norton-Griffiths 1979), and the Loita Plains to the northeast (Stelfox et al. 1986). The only permanent river in this ecosystem, the Mara River, serves as the boundary between two different management agencies (Figure 4.1).

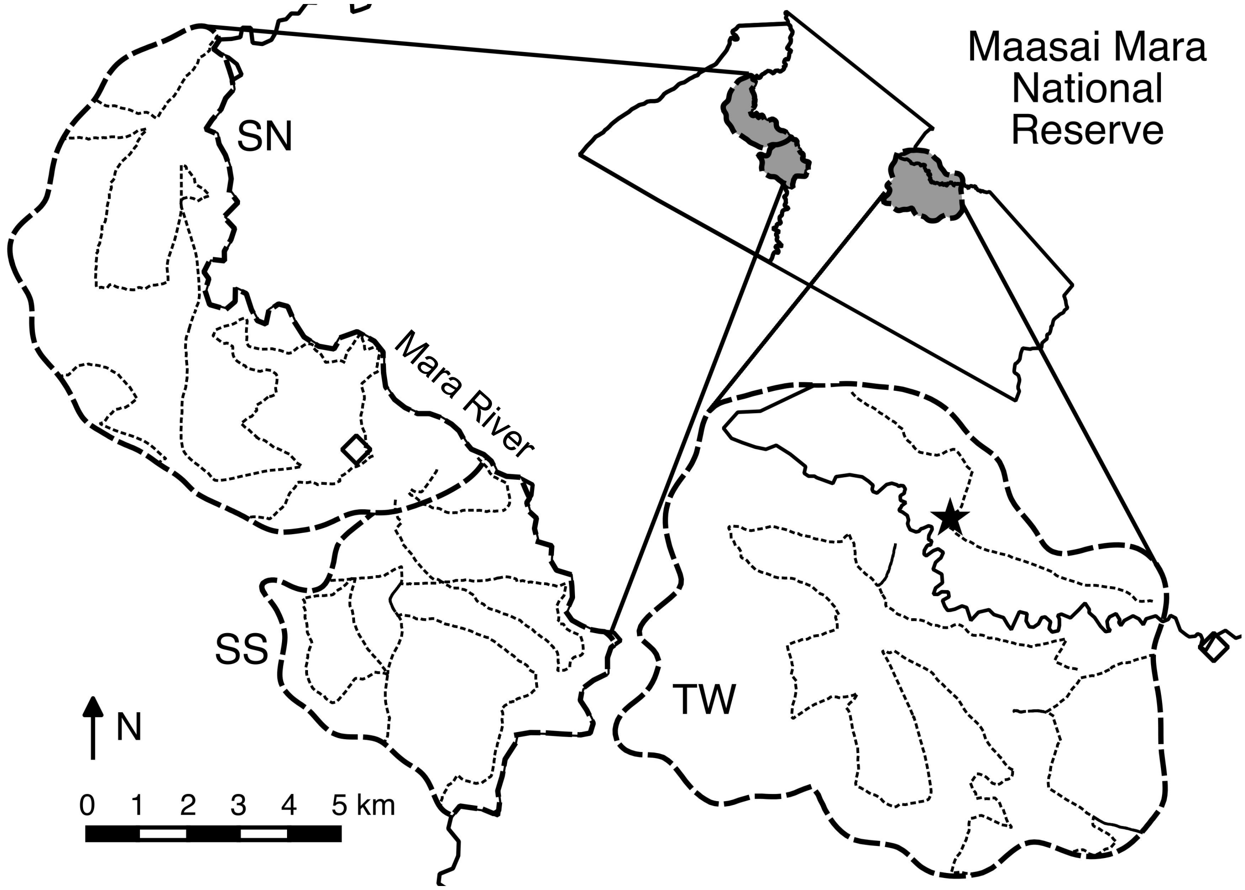


Figure 4.1. Locations of the study clans and loops (dotted lines) run to sample sympatric wildlife in the Maasai Mara National Reserve, Kenya. The clans in areas managed by the Mara Conservancy are Serena North (SN) and Serena South (SS). The clan of hyenas in the region exposed to severe anthropogenic disturbance, and managed by the Narok County Government, is the Talek West clan (TW). Talek West is located in the Talek region of the Reserve. Territory boundaries are indicated with thick dashed lines. The locations of the weather stations (◇) and the town (★) closest to the TW territory (Talek) are also noted.

The Narok County Government (NCG) manages the eastern side of the Reserve. Within this portion of the Reserve (Figure 4.1), the Talek region, in particular, is an area near the Reserve border that in recent decades has been subjected to a great deal of anthropogenic disturbance. This disturbance includes increases in the number of human settlements and tourist facilities outside the Reserve, as well as an exponential increase in numbers of livestock grazing inside Reserve boundaries (Boydston et al. 2003a; Lamprey & Reid 2004; Kolowski & Holekamp 2009; Chapter 2 of this dissertation); here we refer to these effects collectively as “anthropogenic disturbance.” In contrast to the Talek region, other portions of the Reserve are far less affected by anthropogenic disturbance. In particular, the portion of the Reserve west of the Mara River, called “the Mara Triangle,” is remarkably pristine. The Mara Conservancy (TMC) manages The Mara Triangle, and the wildlife in this area encounters virtually no anthropogenic activity at all aside from visitation by tour vehicles. We were able to exploit this naturally-occurring variation in anthropogenic disturbance to investigate the ecological and anthropogenic influences on behavior by spotted hyenas, and determine whether and how the behavior of spotted hyenas might correlate with numbers of sympatric wildlife in both disturbed and undisturbed areas.

Monitoring the movements by spotted hyenas

Spotted hyenas are gregarious, large carnivores that live in social groups called clans. Each clan is comprised of immature juveniles, adult females, and immigrant males. Females are philopatric except in the rare cases of clan fission events (Holekamp et al. 1993). Males emigrate from their natal clan upon reaching sexual maturity (van Horn et al. 2003). On average, clans of spotted hyenas are comprised of 29 individuals throughout sub-Saharan Africa (Holekamp & Dloniak 2010), and clan members defend a communal territory by scent marking and sparring with neighboring clans (Kruuk 1972; Mills 1990b; Henschel & Skinner 1991; Boydston et al. 2001). Each clan is structured by a linear matrilineal dominance hierarchy in which natal animals dominate immigrant males; immigrant males hold ranks relative to one another based on their tenure in the clan.

The space-use of spotted hyenas can be influenced by many factors, including rainfall, prey availability, social rank, time of day, and indirect effects stemming from anthropogenic disturbance by cattle grazing (Kruuk 1972; Mills 1990b; Boydston et al. 2003a; 2003b; Kolowski et al. 2007; Kolowski & Holekamp 2009; Stratford & Stratford 2011). In areas where prey are relatively abundant, spotted hyenas travel an average of 11 km per day (Kruuk 1972; Kolowski et al. 2007), but have been documented to travel up to 75 km per day in areas with fewer prey (Henschel & Skinner 1987; Mills 1990a; Hofer & East 1993). Spotted hyenas in the Reserve are capable of crossing their entire territory (~10km) in < 1 hour (Boydston et al. 2003a).

We studied three clans of spotted hyenas to investigate ecological and anthropogenic influences on their movements (Table 4.1), and to see if the movements exhibited by individual group members were correlated with the future abundance and diversity of sympatric wildlife. Two clans were located in the relatively undisturbed Mara Triangle, managed by TMC (“Serena North” and “Serena South”), and one was located in the highly disturbed Talek region on the eastern side of the Reserve, managed by NCG (“Talek West”; Figure 4.1). Animals were individually identified by their spot patterns, ear damage and other unique features. Standardized ranks were calculated for all natal clan members ranging from 1 to -1 based on outcomes of dyadic aggressive interactions (Holekamp & Smale 1993); a value of 1 was assigned to the highest-ranking female in the clan and a value of -1 to the lowest.

Table 4.1. Salient characteristics of the Talek West, Serena North, and Serena South clans of spotted hyenas monitored in the current study in 2013. Standard errors are presented in parentheses. The number of tourists per territory was estimated as the number of vehicles counted biweekly during counts by Mara Hyena Project personnel.

Parameter	**Talek West**	**Serena North**	**Serena South**
Clan size (no. hyenas)	113.00 (1.80)	51.42 (0.87)	39.25 (1.34)
Territory size (km^2)	77.04	42.67	28.29
Mean density of hyenas	1.47 / km^2	1.21 / km^2	1.39 / km^2
Tourists (no. encountered)	8.18 (1.79)	13.28 (1.76)	1.89 (0.64)
Livestock (no. inside territory)	2218.85 (240.35)	0	0

We anesthetized 6-8 spotted hyenas in each clan with Telazol (6.5 mg/kg) administered in a plastic dart fired from a CO_2 powered rifle (Telinject Inc., Saugus, California), and fitted them with GPS radio collars (Vectronic Aerospace, Berlin, Germany) to monitor fine-scale movement behaviors. Collars were deployed on parous females of low- and high-ranks (i.e., only in the lowest and highest thirds of the rank hierarchy for that clan, respectively). We set the collars to record GPS locations of the hyenas and the ambient temperature at hourly intervals from 1600 h to 1000 h, and once again at 1300 h. Speeds and turning angles (indicating the degree of tortuosity) were calculated between successive hourly locations in the movement paths of the hyenas with the package ‘adehabitatLT’ in R (Calenge 2006; R Core Team 2015). For all analyses, we used the absolute value of the turning angle as a measure of tortuosity, regardless of the directionality of each hyenas’ trajectory.

Sampling the abundance of sympatric wildlife

A grid of 200 x 200 m cells was delineated on a map of each hyena territory, and we calculated the estimated abundance of each of the following animals within each 200 x 200 m grid cell (henceforth, cell) every 4-6 weeks between July 2012-March 2014: olive baboon (*Papio anubis*), banded mongoose (*Mungos mungo*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus scriptus*), caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*), Kirk’s dik dik (*Madoqua kirkii),* eland (*Taurotragus oryx*), African elephant, Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), Grant’s gazelle (*Nanger granti*), hartebeest (*Alcelaphus buselaphus*), hippo (*Hippopotamus amphibius*), spotted hyena, impala (*Aepyceros melampus*), leopard (*Panthera pardus*), lion (*Panthera leo*), oribi (*Ourebia ourebi*), ostrich (*Struthio camelus)*, bohor reedbuck (*Redunca redunca)*, black rhino, serval (*Leptailurus serval*), side-striped jackal (*Canis adustus*), slender mongoose (*Galerella sanguinea*), Thomson’s gazelle, topi (*Damaliscus korrigum jimela)*, vervet monkey (*Chlorocebus pygerythrus*), warthog (*Phacochoerus africanus*), wildebeest, and zebra.

To estimate the number of animals in each cell, we employed a novel sampling technique that exploits the easy observability of animals in the Reserve’s open grassland habitat. We first defined sampling loops (henceforth, “loops”) within each territory to allow for maximum coverage and minimal opportunities for double counting wildlife (Figure 4.1). All efforts were made to include > 500 m of track in each square kilometer of each territory, and resulted in 35.28–44.52 km of loop in each of the three territories we monitored. Part of the territory of the Talek West clan extends outside Reserve boundaries; we also included a separate 8.95 km loop in this region (Figure 4.1). All loops were sampled on preexisting roads and tracks. Loops were sampled on each of three consecutive days (each of these three days was called a “replicate”) in each territory every four to six weeks (each three-day sampling period was called a “sample”), unless limited by weather.

We randomly chose three starting locations on each loop equidistant from one another. Each replicate in a sample started at a different location in an attempt to capture any temporal variation in herbivore movement throughout the day. Observers (1-3) started each loop per sample at first light by driving our vehicle along the loop’s centerline. Upon first detecting an animal or group of animals, we recorded the GPS location of our vehicle, the distance to the animal(s) from the vehicle using a laser rangefinder (Nikon Laser 1200), and the bearing to the animal(s) from the vehicle. Using these data, we projected the GPS location of the animal(s). Animals of the same species that were separated by < 200 m were considered to be part of the same grouping, and were assigned to one location at the center of the group.

To account for effects of sampling error due to variation in the observability of wildlife, we calculated species-specific detection probabilities using the package ‘unmarked’ in R v. 3.2.0 (Fiske & Chandler 2011). Detection probabilities were assumed to decay as a function of the distance from the centerline of the loop (Buckland et al. 2001). For all species with > 100 locations, we modeled the probability of detection as a function of vehicle type (small or large) in which the replicate was performed to account for variation in detection due to grass height, and the number of observers in the vehicle (1 or > 1). We used hazard functions because they had the lowest AIC values in fitting our data (Buckland et al. 2001). Using the models with the best fit, we determined the distance for each species at which its detection probability equaled or exceeded 90 %. The average ± standard error 90 % detection distances for herbivores and carnivores with more than 100 sightings were 393.61 ± 38.27 and 140.02 ± 14.51 m, respectively. The 90 % detection probability of species with fewer than 100 locations was assumed to be 100 m from the centerline of the loop. We then buffered the loops by each of these species-specific detection distances to create a detection region for each species in each replicate. Locations of animals we sighted during replicates that fell within these detection regions were then assigned to the cell in which they were located, within that replicate of that sample, and were used in all analyses. Observer effort per cell per species was defined as the number of square meters in which the detection region for that species overlapped with the cell.

Statistical analyses

Predictors of movement patterns by spotted hyenas

To investigate the ecological and anthropogenic influences on the movement patterns of spotted hyenas, we used linear mixed-effects models fit by maximum likelihood in the ‘nlme’ package in R v. 3.2.0 (R Core Team 2015). We modeled the turning angle and speed between successive locations of spotted hyenas as a function of clan membership, rank (high or low), whether or not the location was inside or outside of the Reserve, and both hour and hour^2 fit as time-series variables. We hypothesized that the speed between successive locations of spotted hyenas would be a function of their turning angles, and similarly, that the turning angles between successive locations would be a function of their speeds; we included each of these predictor variables in our models to investigate the interactions between these movement parameters. We also hypothesized that intra-clan competition and time of day would influence the movement behaviors of spotted hyenas, and that these effects would vary among clans. Low-ranking hyenas could alter their movement behaviors to avoid conflict with high-ranking conspecifics, for example, by moving faster than high-ranking hyenas or by moving during different hours of the day. Movement behaviors of spotted hyenas were also hypothesized to vary with exposure to anthropogenic disturbance; we predicted that spotted hyenas in the Talek West clan would move faster than Serena North or Serena South hyenas to avoid conflicts with livestock herders, and that low-ranking hyenas would be more strongly affected than high-ranking hyenas. Therefore, we fit interactions between clan and rank, clan and hour, and hour and rank in our models. Rainfall, ambient temperature, and moonlight were also hypothesized to influence the movement patterns of spotted hyenas and were therefore included in our models.

The GPS collars recorded ambient temperature hourly. The amount of daily rainfall in mm was collected at two weather stations in the Reserve (Figure 4.1). Precipitation was recorded daily at 0500 h; we modeled the speed and turning angles of hyenas during any given night (1600 h to 1000 h) as a function of data from the following morning at 0500 h. We assigned a value representing the proportion of the moon that was illuminated for movement behaviors that occurred after sunset and moonrise, but before moonset or sunrise. All moons visible between these hours were assigned a value between 0 and 1 corresponding to the proportion of the moon that was illuminated on that night (i.e., full moon = 1, new moon = 0). We assigned a moon value of 0 to hours in which the moon was not present, or if the movement value was calculated before moonrise on that day. The percentage of moon illuminated each night was obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php). To account for any variation in the speed of movement or path tortuosity among the spotted hyenas monitored in this study not explained by our other covariates, we nested each night's identity in hyena identity, and coded it as a random effect. This nesting also accounted for any additional interactions between the day on which the movement parameters were collected and hyena identity. Temporal serial autocorrelation was accounted for by fitting both models with first-order autoregressive covariance structures. Speed between successive points was log-transformed to achieve normality, but turning angles were normally distributed. We ran one full model with all parameters included, separately, for both speed and turning angle.

Spotted hyenas as an indicator species

We analyzed the movements of spotted hyenas to investigate whether and how they might correlate with the local abundances of sympatric wildlife within Reserve boundaries in the future. To do this, we used the 'glmmADMB' package in R v. 3.2.0

(Bolker et al. 2012; R Core Team 2015). We calculated the total number of resident herbivores, migrant herbivores, carnivores, and the value of species richness in each 200 x 200 m cell per sample. The abundance and diversity of wildlife in each cell were then modeled as a function of the speeds and turning angles exhibited by spotted hyenas in that same cell before the sampling event. We investigated how the movement of hyenas over a course of two weeks might correlate with the abundance and diversity of sympatric wildlife in our samples at five time points: 2, 8, 14, 20, and 26 weeks later. We did not investigate time periods beyond 26 weeks due to the high degree of seasonality in herbivore movements and weather patterns in this environment. All turning angles and speeds of movement were mean-standardized. We also included social rank to investigate how movements of low- and high-ranking hyenas might correlate differently with the abundance and diversity of sympatric wildlife. We expected the movements of spotted hyenas in pastoralist community lands to be influenced by additional factors which might alter the relationship between their movements and the populations of sympatric wildlife (e.g., threats of conflict, range contraction, habitat change; Ogutu et al. 2011; Elliot et al. 2014; Oriol-Cotterill et al. 2015). Therefore, we only used locations of spotted hyenas within Reserve boundaries for the indicator species analyses to avoid these confounding factors. The total amount of observer effort in each square meter within each cell per sample was mean-standardized and included as an offset. All of our dependent variables were zero-inflated and overdispersed; we fit these models with a negative binomial distribution and a constant zero-inflation parameter. Models for each time point were run separately for each dependent variable. Thus, for each time-point we ran one full model with speed, angle, and rank. The first model in the series of time-points in which a behavior emitted by monitored hyenas failed to significantly correlate with the abundance or diversity of sympatric wildlife was considered to be the cessation of any relationship between the movements of hyenas and that ecological factor. Subsequent models were then run with that behavior removed. We present results from the models in which a hyena movement behavior significantly correlated with species richness or mammalian herbivore or carnivore abundance ($P < 0.05$).

Results

Predictors of the movement patterns by spotted hyenas

From 22 adult female hyenas we collected a total of 138,751 locations that were separated by one hour (mean number of locations ± SE per hyena: 6306.86 ± 619.40) on 953 nights (mean number of nights ± SE per hyena: 498.41 ± 38.45) between April 2012 and November 2014. There was no significant difference between Serena North and Serena South clans in our models ($P > 0.10$), so we combined data from these two clans in all subsequent analyses and created the variable “Management agency” to contrast NCG with TMC.

Turning angles of spotted hyenas were predicted by the speed at which spotted hyenas traveled, the time of day, whether or not the hyena was located inside or outside Reserve boundaries, and daily rainfall (Table 4.2). None of our other model parameters significantly predicted the turning angles of spotted hyenas ($P > 0.05$, Table 4.2). The speed at which spotted hyenas traveled between locations was significantly predicted by turning angle, time of day, ambient temperature, daily rainfall, social rank, management agency, whether or not hyenas were located inside or outside the Reserve*,* moonlight, an interaction between management agency and time of day, and an interaction between management agency and the social rank of the hyena (Figure 4.2, Table 4.2). Post-hoc tests indicated the differences in management agency, and the interactions between management agency and rank and management agency and time of day, were significant even when only looking at locations of spotted hyenas within Reserve boundaries (management agency within Reserve: estimate ± SE = -0.744 ± 0.114; $P \leq 0.001$; Mara Conservancy x low rank within Reserve: estimate ± SE = 0.44 ± 0.17; $P = 0.019$; Mara Conservancy x hour within Reserve: estimate ± SE = -0.024 ± 0.004; $P \leq 0.001$). The interaction between social rank and hour had no effect on the speed of movement by hyenas ($P > 0.05$; Table 4.2).

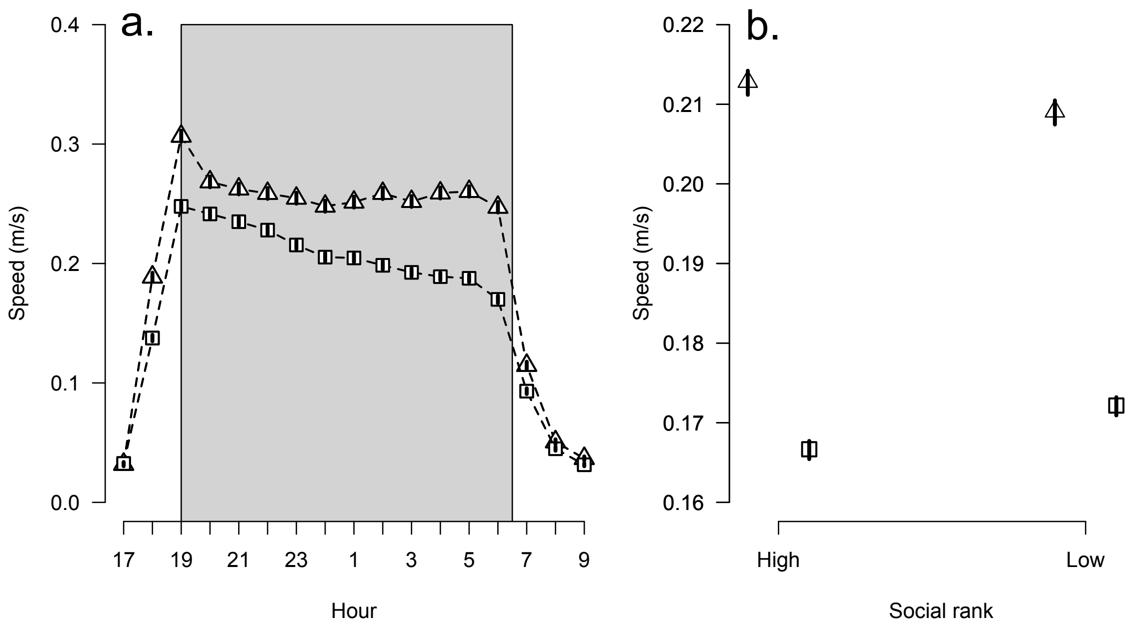


Figure 4.2. Speeds of movement by spotted hyenas inside Reserve boundaries of the Maasai Mara National Reserve, Kenya, in areas managed by the Narok County Government (△) and the Mara Conservancy (□). (a) Mean ± standard error (SE) speeds by individuals throughout the night. Hours of darkness are shaded in grey. (b) Mean ± SE speed of movement by spotted hyenas by rank and management agency.

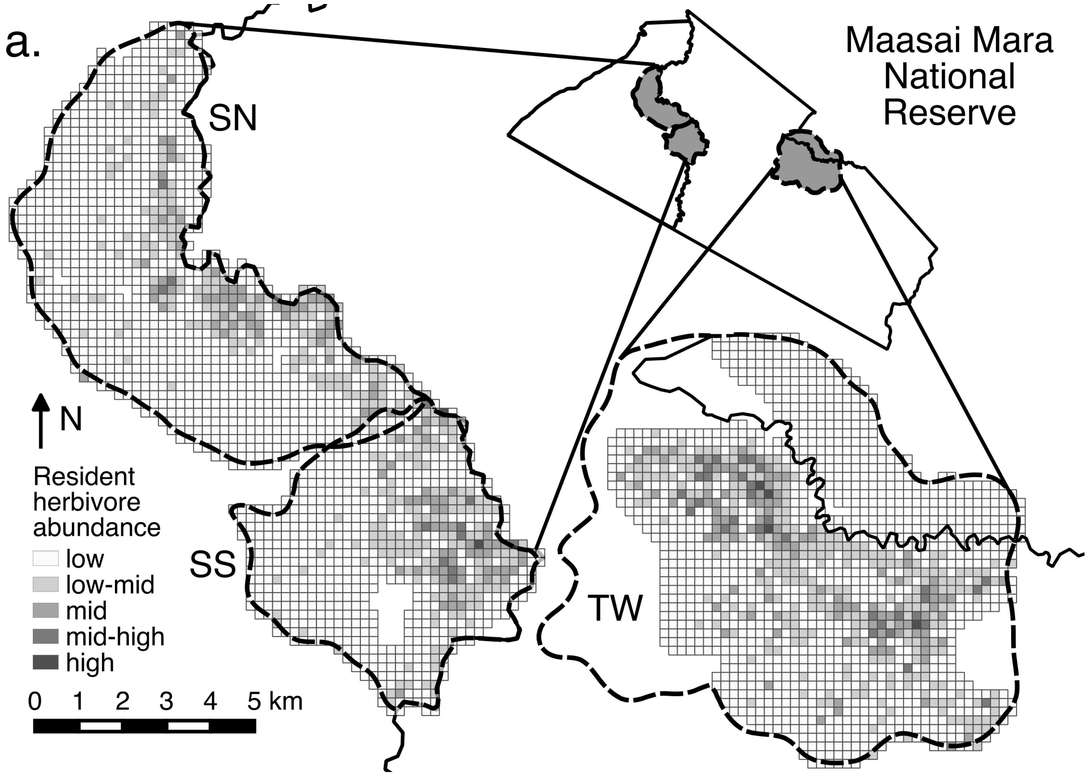
Table 4.2. Results from the generalized linear mixed-effects models that predicted the speed and turning angles of spotted hyenas between successive locations separated by one hour inside and around the Maasai Mara National Reserve, Kenya. Parameter estimates, Standard Errors (SEs), Degrees of Freedom (DF), *T*-, and *P*-values are displayed. Significant parameter estimates are indicated in bold font ($P < 0.05$).

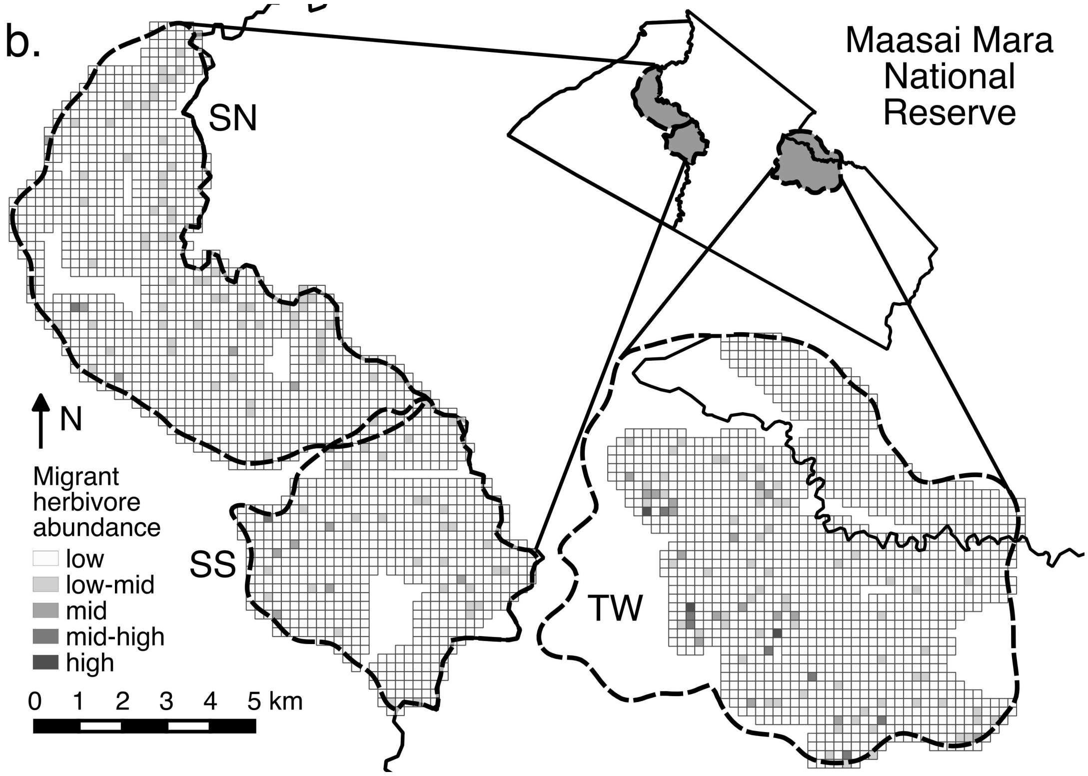
Parameter	Value (SE)	*DF*	*T*	*P*-value
Speed				
Intercept	-2.197 (0.1)	126529	-22.068	< 0.001
Turning angle	**-0.266 (0.006)**	**126529**	**-45.13**	**< 0.001**
Management agency (TMC)	**-0.686 (0.114)**	**18**	**-6.026**	**< 0.001**
Rank (Low)	**-0.321 (0.134)**	**18**	**-2.397**	**0.0276**
Hour	**-0.257 (0.004)**	**126529**	**-61.705**	**< 0.001**
Hour^2	**-0.031 (0.001)**	**126529**	**-59.378**	**< 0.001**
Reserve (Inside)	**-0.314 (0.034)**	**126529**	**-9.16**	**< 0.001**
Temperature	**-0.207 (0.01)**	**126529**	**-19.866**	**< 0.001**
Rain	**0.019 (0.009)**	**126529**	**2.062**	**0.0392**
Moonlight	**0.14 (0.024)**	**126529**	**5.765**	**< 0.001**
Management agency x Hour	**-0.021 (0.004)**	**126529**	**-5.826**	**< 0.001**
Management agency x Rank	**0.431 (0.17)**	**18**	**2.533**	**0.0208**
Rank x Hour	0.005 (0.004)	126529	1.301	0.1934
Turning angle				
Intercept	1.712 (0.025)	126529	69.424	< 0.001
Speed	**-0.669 (0.011)**	**126529**	**-59.484**	**< 0.001**
Management agency (TMC)	0.005 (0.027)	18	0.171	0.8663
Rank (Low)	-0.06 (0.032)	18	-1.904	0.073
Hour	**0.005 (0.001)**	**126529**	**3.801**	**< 0.001**
Hour^2	**0.001 (0.001)**	**126529**	**2.087**	**0.0369**
Reserve (Inside)	**-0.079 (0.012)**	**126529**	**-6.752**	**< 0.001**
Temperature	-0.006 (0.004)	126529	-1.68	0.0929
Rain	**0.006 (0.003)**	**126529**	**2.102**	**0.036**
Moonlight	0.003 (0.008)	126529	0.42	0.674
Management agency x Hour	0.001 (0.001)	126529	-0.388	0.698
Management agency x Rank	0.03 (0.04)	18	0.75	0.463
Rank x Hour	-0.002 (0.001)	126529	-1.448	0.148

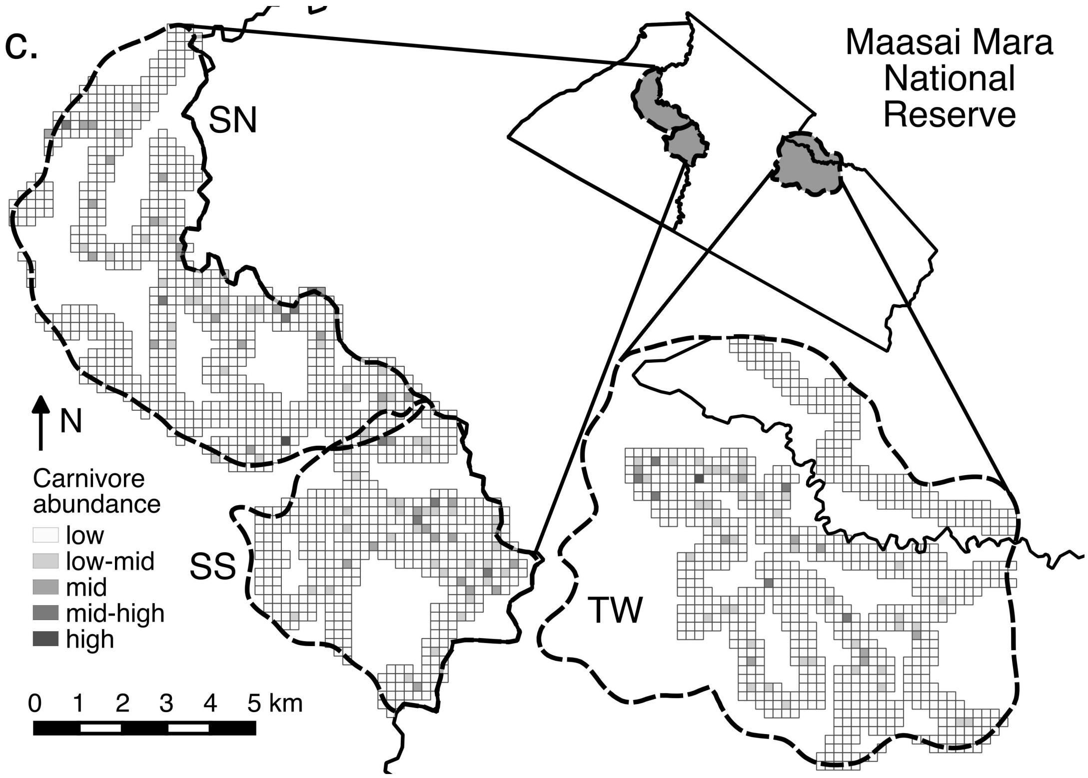
Spotted hyenas as an indicator species

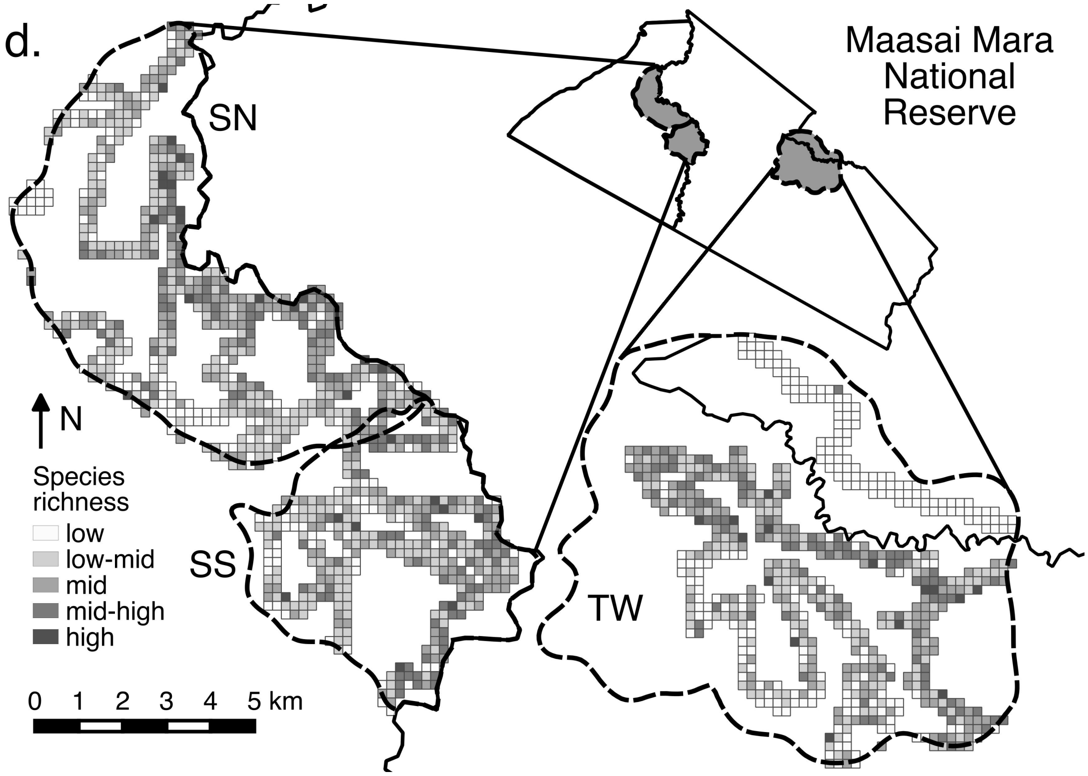
We conducted 16 samples of the abundance and diversity of herbivores and carnivores in the Talek West, Serena North, and Serena South territories between July 2012 and March 2014. This sampling resulted in a total count of 364,905 individual animals with a mean ± SE of 4.956 ± 0.269 per cell. Estimated counts of wildlife were calculated in 5,039 cells inside and outside of the Reserve (Figure 4.3). The average ± SE numbers of resident and migrant herbivores, and carnivores counted per grid cell were 2.334 ± 0.087, 2.933 ± 0.277, and 0.037 ± 0.003, respectively. This varied depending on whether sampling was done inside or outside the Reserve (resident herbivores inside: 2.507 ± 0.093; resident herbivores outside 0.001 ± 0.001; migrant herbivores inside: 3.133 ± 0.296; migrant herbivores outside: 0.001 ± 0.001; carnivores inside: 0.039 ± 0.003; carnivores outside: 0.001 ± 0.001). Average ± SE number of species found per cell was 0.411 ± 0.012, which also differed depending on whether sampling was done inside or outside of the Reserve (species richness inside: 0.434 ± 0.012; species richness outside: 0.001 ± 0.001). Sample sizes for speeds of movement and tortuosity values of hyenas within cells for which sympatric wildlife information was available varied among 2-, 8-, 14-, 20-, and 26-week time points (2-week *n* = 39,966, 8-week *n* = 35,122, 14-week *n* = 33,010, 20-week *n* = 29,830, 26-week *n* = 26,961).

Figure 4.3. Variation in the abundance and distribution of (a) resident (b) and migrant herbivores, (c) carnivores, and (d) species richness within the Serena North (SN), Serena South (SS), and Talek West (TW) territories in the Maasai Mara National Reserve, Kenya. Darker shades indicate a comparatively greater abundance (a-c), or diversity (d) in that 200m x 200m grid cell than in lighter cells during this study, accounting for effort. Open areas within territory boundaries indicate regions with no sampling effort.




b.
Maasai Mara
National
Reserve
SN
SS
TW
N
Migrant
herbivore
abundance
low
low-mid
mid
mid-high
high
0 1 2 3 4 5 km


c.
Maasai Mara
National
Reserve
SN
SS
TW
N
Carnivore
abundance
low
low-mid
mid
mid-high
high
0 1 2 3 4 5 km



Cells in which spotted hyenas moved faster were correlated with fewer carnivores and herbivores, and with lower species richness at future time points. This significant trend occurred at the 2-, 8-, and 14- week time-points for resident herbivores, the 2-, 8-, 14-, 20-, and 26-week time-points for species richness, and at the 2-, 8-, 14-, and 20-week time-points for carnivores and migrant herbivores ($P < 0.05$; Table 4.3). Turning angle was a significant negative predictor of resident herbivore abundance 2 weeks later, and species richness 2, 8, 14, 20, and 26 weeks later. Turning angle was a significant positive predictor of migrant herbivore abundance 2 and 8 weeks later, and of carnivore numbers 2 weeks later ($P < 0.05$; Table 4.3). Rank of the hyenas was a significant predictor of species richness and the numbers of sympatric wildlife. Cells in which hyenas of low rank were more likely to be found had higher numbers of resident and migrant herbivores, and greater species richness (*P* < 0.05), but fewer carnivores (*P* < 0.05), than did cells in which hyenas of high rank were found (Table 4.3).

Table 4.3. Results from the generalized linear mixed-effects models that predicted herbivore and carnivore abundance, and species richness, as a function of the speed, turning angles, and rank of spotted hyenas in the same area previous to the count. The behaviors of spotted hyenas significantly predicted the numbers of resident herbivores 2, 8, and 14 weeks before the sample, species richness 2, 8, 14, 20, and 26 weeks before the sample, and numbers of migrant herbivores and carnivores 2, 8, 14, and 20 weeks before the sample. Significant parameter estimates are indicated in bold font (*P* < 0.05).

Parameter	**Estimate (SE)**	***Z***	***P***
Resident herbivores			
2 weeks			
Intercept	1.13 (0.019)	59.680	≤ 0.001
Speed	**-0.034 (0.009)**	**-3.600**	**≤ 0.001**
Angle	**-0.044 (0.01)**	**-4.450**	**≤ 0.001**
Rank (low)	**0.218 (0.019)**	**11.630**	**≤ 0.001**
8 weeks			
Intercept	1.164 (0.021)	56.160	≤ 0.001
Speed	**-0.055 (0.01)**	**-5.340**	**≤ 0.001**
Angle	-0.02 (0.011)	-1.860	0.062
Rank (low)	**0.167 (0.02)**	**8.170**	**≤ 0.001**
14 weeks			
Intercept	1.112 (0.021)	52.980	≤ 0.001
Speed	**-0.049 (0.01)**	**-4.660**	**≤ 0.001**
Rank (low)	**0.104 (0.021)**	**4.940**	**≤ 0.001**
Species richness			
2 weeks			
Intercept	-1.295 (0.011)	-115.450	≤ 0.001
Speed	**-0.057 (0.008)**	**-6.740**	**≤ 0.001**
Angle	**-0.032 (0.009)**	**-3.680**	**≤ 0.001**
Rank (low)	**0.138 (0.017)**	**8.250**	**≤ 0.001**
8 weeks			
Intercept	-1.361 (0.013)	-105.770	≤ 0.001

Table 4.3 cont'd

Speed	**-0.054 (0.009)**	**-5.730**	**≤ 0.001**
Angle	**-0.024 (0.01)**	**-2.420**	**0.016**
Rank (low)	**0.174 (0.019)**	**9.280**	**≤ 0.001**
14 weeks			
Intercept	-1.325 (0.013)	-100.300	≤ 0.001
Speed	**-0.062 (0.01)**	**-6.300**	**≤ 0.001**
Angle	**-0.026 (0.01)**	**-2.590**	**0.010**
Rank (low)	**0.089 (0.019)**	**4.550**	**≤ 0.001**
20 weeks			
Intercept	-1.427 (0.015)	-95.250	≤ 0.001
Speed	-0.012 (0.011)	-1.090	0.274
Angle	**-0.043 (0.011)**	**-3.840**	**≤ 0.001**
Rank (low)	**0.117 (0.022)**	**5.450**	**≤ 0.001**
26 weeks			
Intercept	-1.395 (0.016)	-87.050	≤ 0.001
Angle	**-0.073 (0.012)**	**-6.110**	**≤ 0.001**
Rank (low)	**0.08 (0.023)**	**3.440**	**≤ 0.001**
Carnivores			
2 weeks			
Intercept	-2.388 (0.046)	-52.330	≤ 0.001
Speed	**-0.386 (0.036)**	**-10.790**	**≤ 0.001**
Angle	**0.094 (0.029)**	**3.290**	**0.001**
Rank (low)	**-0.75 (0.064)**	**-11.680**	**≤ 0.001**
8 weeks			
Intercept	-3.491 (0.066)	-53.000	≤ 0.001
Speed	**-0.158 (0.043)**	**-3.660**	**≤ 0.001**
Angle	-0.012 (0.042)	-0.300	0.767
Rank (low)	-0.122 (0.082)	-1.480	0.140
14 weeks			
Intercept	-3.356 (0.063)	-53.690	≤ 0.001
Speed	**-0.258 (0.047)**	**-5.560**	**≤ 0.001**
Rank (low)	**-0.736 (0.093)**	**-7.920**	**≤ 0.001**
20 weeks			
Intercept	-3.477 (0.073)	-47.460	≤ 0.001
Speed	**-0.138 (0.047)**	**-2.960**	**0.003**
Rank (low)	**-0.219 (0.091)**	**-2.400**	**0.016**
Migrant herbivores			
2 weeks			
Intercept	0.493 (0.042)	11.610	≤ 0.001
Speed	**-0.114 (0.019)**	**-5.960**	**≤ 0.001**
Angle	**0.042 (0.018)**	**2.320**	**0.020**

Table 4.3 cont'd

Rank (low)	**0.531 (0.035)**	**15.340**	**≤ 0.001**
8 weeks			
Intercept	0.682 (0.047)	14.590	≤ 0.001
Speed	**-0.146 (0.022)**	**-6.820**	**≤ 0.001**
Angle	**0.085 (0.02)**	**4.330**	**≤ 0.001**
Rank (low)	**0.412 (0.038)**	**10.970**	**≤ 0.001**
14 weeks			
Intercept	0.81 (0.046)	17.550	≤ 0.001
Speed	**-0.086 (0.021)**	**-4.160**	**≤ 0.001**
Angle	0.028 (0.02)	1.400	0.160
Rank (low)	**0.182 (0.038)**	**4.760**	**≤ 0.001**
20 weeks			
Intercept	0.696 (0.054)	12.860	≤ 0.001
Speed	**-0.07 (0.023)**	**-3.020**	**0.003**
Rank (low)	**0.141 (0.044)**	**3.200**	**0.001**

Discussion

Here we present results showing that the movement patterns of spotted hyenas correlate with the future abundance and diversity of sympatric wildlife. Previous research suggested the space-use behaviors and stress physiology of spotted hyenas can be used to indicate the hyenas' own future welfare (Kolowski & Holekamp 2009; Van Meter et al. 2009). The results from our study show that the movement patterns of spotted hyenas also correlate with the abundances and diversity of sympatric wildlife. Many wildlife populations in the Reserve are currently in decline (Ottichilo et al. 2000; Ogutu & Owen-Smith 2005; Ogutu et al. 2009; 2011; Chapters 2 and 3 of this dissertation), and our findings reveal that spotted hyenas might be a useful tool in predicting these declines. Armed with this information, conservation biologists and wildlife management officials can study the behavior of spotted hyenas to understand how the effects of changing environments may manifest in other wildlife. Furthermore, by recognizing the regions in which the movement behaviors of spotted hyenas are changing, it may be possible to identify and halt the disturbances that may be responsible.

In the current research, a complex set of ecological and anthropogenic factors influenced the movements of spotted hyenas. The daily activity pattern of spotted hyenas in the Reserve is crepuscular and nocturnal, with no clear peaks throughout the night (Kolowski et al. 2007). Our research adds to these earlier findings, but is the first to report that ambient temperature and amount of moonlight can also have an effect on the speed of movement of hyenas in the Reserve. The daily minimum and maximum temperatures near the Reserve have increased by 2.6 ºC and 1.4 ºC, respectively, from 1988 to 2011 (Chapter 2 of this dissertation), and daily temperatures are expected to continue to rise based on climate change models (Ritchie 2008). In the current research, spotted hyenas traveled faster on nights with more moonlight, which is in contrast to previous research (Cozzi et al. 2012). This is also different from previous research on lions (*Panthera leo)*, which found that lions moved slower in areas of high anthropogenic activity on nights with more moonlight (Oriol-Cotterill et al. 2015). Future research should investigate how the amount of moonlight may be interacting with anthropogenic activities within and around the Reserve to affect hyena behavior, and how this in turn might affect the probability of conflict with people. More rainfall also led to faster movements by spotted hyenas. Previous research has documented slower movement rates by spotted hyenas during wet than dry seasons in other areas of Africa (Stratford & Stratford 2011), but none has yet to document the effects of fine-scale rainfall patterns on the movements of spotted hyenas like we have here.

Using different methods, but consistent with previous research (Kolowski et al. 2007; Kolowski & Holekamp 2009), we found that spotted hyenas living in regions of high anthropogenic disturbance consistently moved faster than did animals in more pristine areas. Interestingly, the speed of movement also differed between inside and outside of Reserve boundaries, and was predicted by social rank. Previous research in the Reserve did not find a correlation between rates of hyena activity and social rank (Kolowski et al. 2007). Yet, the results from our study show animals of low social rank exhibiting faster movement in undisturbed regions than did high-ranking animals in the same areas. The space-use of spotted hyenas has previously been shown to vary with social rank; adult females of low social rank tend to range more widely when not limited by den-dwelling cubs, probably to avoid intra-specific competition while foraging (Boydston et al. 2003b). However, the effects of anthropogenic activity inside the Talek region and outside of the Reserve may be affecting this relationship. Low-ranking hyenas in Talek moved at slower speeds than did high-ranking animals in the same areas, whereas we found the opposite relationship between low- and high-ranking hyenas in TMC (Figure 4.2). Talek is the region of the Reserve with the highest levels of anthropogenic disturbance; thus, the influences of people on the speed of movement by hyenas appear to be stronger than the effects of certain natural intra-specific interactions.

The tortuosity of the paths of spotted hyenas was predicted by the time of day, the amount of rainfall, and whether the animals were moving inside or outside of the Reserve (Table 4.2). Spotted hyenas inside of the Reserve had smaller turning angles than did those outside of the Reserve, indicating that hyenas were more likely to display less straightforward movements in the community lands. The area immediately outside of the Reserve contains an expanding population of Maasai pastoralists (Lamprey & Reid 2004; Chapter 2 of this dissertation). Many of these pastoralists keep much of their wealth in livestock. In recent years, these communities have become reliant on grazing their livestock within the Reserve both day and night (Butt 2014; see also Chapter 2 of this dissertation). Thus, the potential for conflict between large carnivores and people is now high both inside and outside of the Reserve. Although no previous research exists on effects of proximity to human settlements on the space-use or movement behaviors of spotted hyenas with GPS collars, research on lions has indicated variation in turning angles as a function of proximity to people. In areas where lions are more likely to come into conflict with people, turning angles are significantly lower than where the probability of conflict is lower (Oriol-Cotterill et al. 2015). Using the same calculation for turning angle, but in contrast to Oriol-Cotterill et al's (2015) findings, we found that spotted hyenas exhibit more directed movements in areas inside of the Reserve boundaries than outside its borders. This may indicate that spotted hyenas in community lands display more erratic behaviors and are more disrupted than animals within the Reserve.

The fact that the rates of movement by spotted hyenas correlated with the local abundance of sympatric wildlife up to 26 weeks later could be helpful to wildlife managers. Although this relationship may only assist in understanding short-term threats to wildlife in the environment, it can serve as another tool for wildlife managers to assess the status of this ecosystem. Monitoring herbivore and carnivore population trends over time is costly, and many years of data are often needed to appropriately determine the status of wildlife populations. Furthermore, a general assessment of wildlife abundance and diversity needs to occur well before it is possible to understand what ecological or anthropogenic influences may be causing any perceived changes. Research like ours represents at least an initial step in finding ways for indicator species not only to reflect current ecological conditions, but also to estimate future conditions. It remains to be seen whether the movements of hyenas will correlate with the abundance or diversity of sympatric wildlife in other areas of sub-Saharan Africa.

Spotted hyenas are one of the few species in this region of Kenya in which population sizes appear to be increasing in areas of intensive anthropogenic disturbance (Chapter 3 of this dissertation). However, the changes in their movement behaviors and space-use to cope with these disturbances, like those documented here and in previous studies (Boydston et al. 2003a; Kolowski et al. 2007; Kolowski & Holekamp 2009), are likely to be costly in the long-term and could ultimately lead to population declines. For example, we could start to see populations of spotted hyenas decline in the future if faster movements increase the probability of conflicts with people. Above all, when one of the most adaptive and plastic species in this environment is showing changes in its behavior, we can expect sympatric wildlife, which may be more limited in their abilities to adapt to changing environments, to be faring considerably worse.

CHAPTER 5:

Temporal dynamics of the responses by African mammals to prescribed fire

Introduction

Fire plays a significant role in structuring ecosystems in sub-Saharan Africa, both as a natural occurrence and as a management technique for increasing vegetation biomass, vegetation palatability, and biodiversity (Norton-Griffiths 1979; Archibald 2008; Driscoll et al. 2010). Fire is an important tool commonly used by wildlife managers to maintain grassland vigor (Dublin 1986; Bond et al. 2005; Govender et al. 2006). Fires clear nutrient-deficient biomass (Van de Vijver et al. 1999), and in conjunction with appropriately timed precipitation, may enhance primary productivity and foraging opportunities for herbivores (Moe et al. 1990; Van de Vijver et al. 1999). However, deliberate burning by wildlife managers can interfere with the maintenance of natural ecological processes if prescribed fire regimes do not mimic naturally occurring fires (Parr & Andersen 2006; Van Wilgen et al. 2007; Van Wilgen & Biggs 2011; Van Wilgen et al. 2011). Deliberate burning may also have long-term effects on arthropods, birds, and small mammals (Salvatori et al. 2001; Yarnell et al. 2007; Little et al. 2013), making it particularly important to understand the ecological consequences of burning. Even though the management practice of burning has been used for decades in sub-Saharan Africa, relatively little is known about the temporal dynamics of herbivore responses to prescribed burns (de Ronde et al. 2004; but see Sensenig et al. 2010; Driscoll et al. 2010).

Wildlife managers have long used prescribed burning as a tool to achieve a variety of short- (< 1 year) and long-term (≥ 1 year) goals. Although the primary short-term goal is to create new foraging opportunities for herbivores during dry seasons by increasing primary productivity (e.g., Hobbs & Spowart 1984; Moe et al. 1990; Vermeire et al. 2004; Geldenhuys et al. 2004; Everson et al. 2004), short-term effects of burns might include making carnivores easier for ecotourists to see and photograph. Long-term goals include improving habitat quality to increase the carrying capacity of an area for one or more herbivore species (e.g., Parrini & Owen-Smith 2010), preventing grassland areas from becoming woodlands (e.g., Norton-Griffiths 1979; Dublin 1986), and increasing carnivore population sizes by enhancing abundance of their prey (e.g., Dees et al. 2001). Burning is also often undertaken by wildlife managers in hopes of inducing both short- and long-term increases in native plant and animal species diversity in a particular area (Hobbs & Spowart 1984; Moe et al. 1990; Vermeire et al. 2004; Geldenhuys et al. 2004; Everson et al. 2004; Parrini & Owen-Smith 2010), and by pastoralists as a means to control ectoparasites (Riginos et al. 2012).

New vegetative growth after fire is utilized by some herbivores, and may temporarily alter regional species abundance (Wilsey 1996; Dees et al. 2001; Klop & Prins 2008). Previous research has found that large mammalian herbivores in sub-Saharan Africa respond to burning in 3 ways: 1) utilizing immediate post-fire conditions (< 30 days post-burn), 2) exploiting post-fire re-growth of vegetation (≥ 30-365 days post-burn), and 3) using burned habitat after considerable re-growth has occurred (> 365 days post-burn; reviewed by de Ronde et al. (2004). Although many wildlife species use burned areas at some point during vegetation re-establishment, not all species respond similarly (de Ronde et al. 2004). In some regions of Africa interspecific variation in post-fire utilization by herbivores can be explained in part by body size; that is, a negative allometric relationship exists between body mass and tendency to use burned sites (Wilsey 1996; Sensenig et al. 2010). However this relationship varies among geographic regions of sub-Saharan Africa (Tomor & Owen-Smith 2002; Klop et al. 2007), and is further complicated by interspecific variation in mode of digestion, with ruminants showing stronger preferences for post-burn vegetation than non-ruminants (Sensenig et al. 2010).

Most research to date has focused on responses of African herbivores to prescribed burning, and virtually nothing is currently known about responses by African carnivores (but see Eby et al. 2013). Burned areas should attract carnivores if prey are more common and more readily accessible there than in unburned areas. However, the clearing of vegetation may also decrease capture success of ambush-style hunters that require adequate cover to capture prey. In North America, Florida panthers (*Puma concolor coryi*) utilized burned areas for up to 1 year after burning, presumably because of increased prey abundance in burned regions (Dees et al. 2001). Based on their results, Dees et al. (2001) suggested that burned areas may support larger panther populations, and thus facilitate their conservation.

Here we monitored wildlife use of 4 areas in the Mara-Serengeti ecosystem, both before and after burning, to document responses of indigenous mammals to prescribed fire. Our objectives were to determine which species responded positively to burning, and to quantify the duration of those responses. Specifically, we were interested in determining which of 8 herbivore species were more likely to be seen on burned than unburned patches, which of these species were seen on burned patches in higher densities than on unburned patches, and for those that were seen in higher densities, how long these effects lasted. Additionally, we wanted to quantify how prescribed burning might enhance visibility of small and large carnivores to ecotourists in this ecosystem. We used line-transect sampling in a repeated measures experimental design and generalized linear models to quantify wildlife response to burning while simultaneously accounting for annual patterns of precipitation, season, and movements of migratory herbivores. Wildlife managers and conservationists can use the results from our study to improve the efficacy of prescribed fire regimes in grassland ecosystems in sub-Saharan Africa.

Study area

Our study was conducted from 2008 to 2011 in the Mara Triangle region of the Maasai Mara National Reserve (henceforth, the Reserve), Kenya, at 1° 25' 41.20"S, 34° 57' 35.14"E (Figure 5.1). The Mara Triangle, which is managed by The Mara Conservancy, encompasses approximately 500 km^2, and is bounded by the Siria Escarpment, the Mara River, and the international border with Tanzania (Figure 5.1). The Mara Triangle is primarily open, rolling grassland savannah interspersed with bush-covered inselbergs, and riparian vegetation along seasonal and permanent watercourses. Daily minimum and maximum temperatures averaged 15.5 °C ± 0.4 °C (SE) and 29.5 °C ± 0.5 °C (SE), respectively, with little seasonal variation. Precipitation varies seasonally, with most falling during long (March-May) and short (November-December) rainy periods each year, resulting in significant seasonal variation in local biomass and nutrient content of grasses (Boutton et al. 1988a; 1988b). Dominant grasses available to herbivores included *Themeda triandra* during the dry seasons, and *Digitaria macroblephara, Hyparrhenia filipendula, Pennisetum mezianum,* and *Setaria sphacelata* after the long rains (Sinclair 1979; Dublin 1986). The standing biomass, comprised mainly of *T. triandra* during the dry seasons, serves as fuel for fires (Anderson & Talbot 1965; McNaughton & Banyikwa 1995; Everson et al. 2004). The Reserve supports large herbivore and carnivore populations year-round, and also supports large herds of migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) from both the Serengeti to the south and the Loita region to the northeast; these herds are usually present during the dry season from July to October each year (Bell 1971; Maddock 1979; Sinclair & Norton-Griffiths 1979; Stelfox et al. 1986). Migratory populations of Thomson's gazelle *(Eudorcas thomsoni)* that reside north of the Reserve also move into the Reserve during the dry season (Stelfox et al. 1986). The large migratory herbivores (i.e. wildebeest, zebra) reduce standing grass biomass, and this change in vegetation also affects local gazelle distributions and abundances (Bell 1971; Maddock 1979). For example, in the Serengeti National Park, Thomson's gazelle follow localized movements of wildebeest and zebra, capitalizing on new vegetative growth that is stimulated by removal of the standing biomass (Bell 1971).

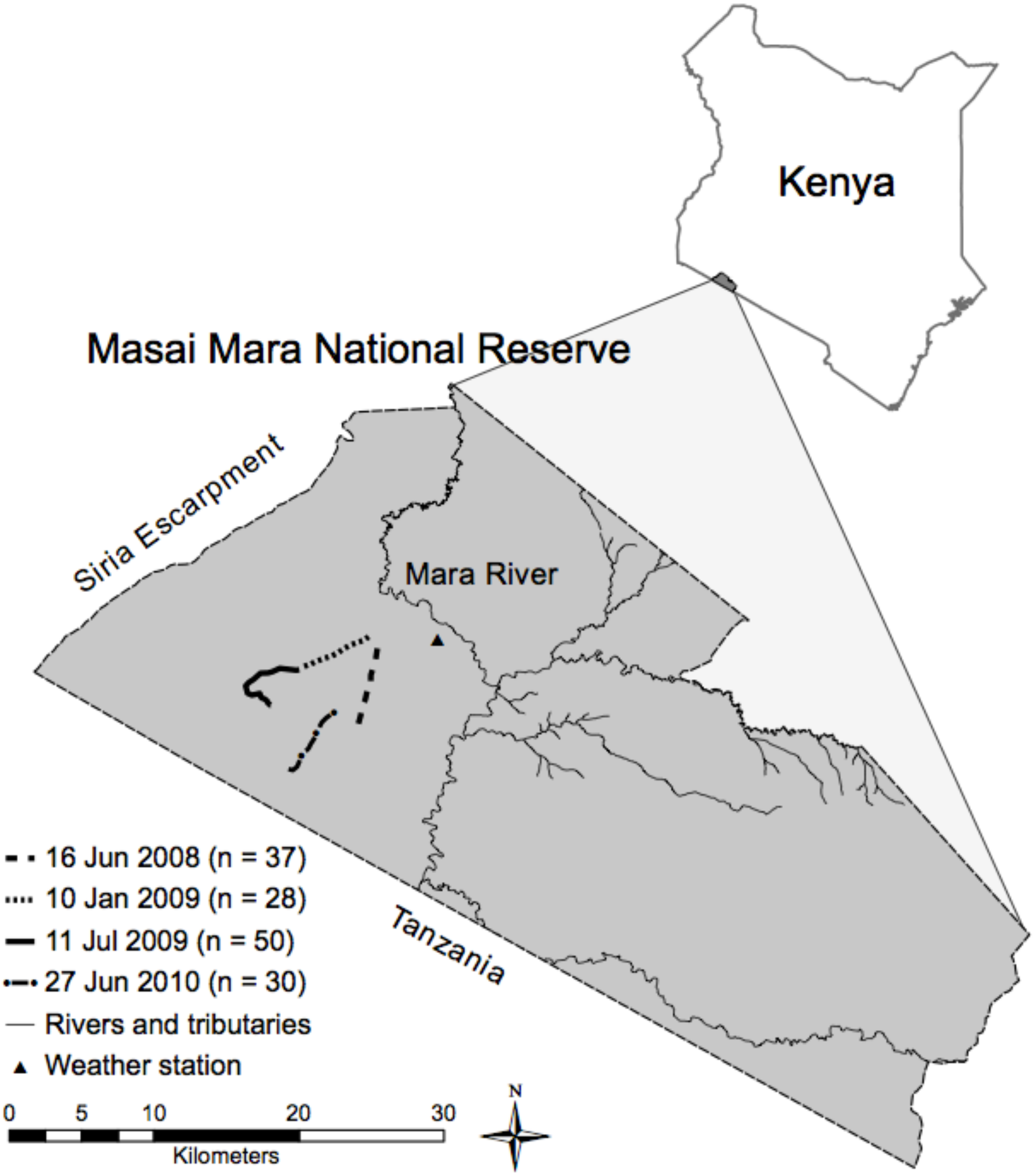


Figure 5.1. Herbivore and carnivore survey transect locations in the Maasai Mara National Reserve, southwestern Kenya, 2008-2011. The four burn transects monitored in the Reserve are shown with the dates on which burns were initiated and the sample size representing the total number of times each transect was sampled. The dark triangle indicates the location of our weather station.

Methods

Line-transect sampling

From 2 August 2008 through 20 July 2011, we sampled abundance of common savannah mammals along 4 permanent transects (Figure 5.1), each 5-7 km long, before and after a single burn was initiated in each region. Burns took place on 16 June 2008, 10 January 2009, 11 July 2009, and 27 June 2010, and ranged from 29.8 to 49.8 km^2 in total area. Each transect (Figure 5.1) was surveyed twice per month, once during the first half of the month (days 1-15), and once during the second half (days 16-31). Observers (1 or 2) sampled mammal abundance between 0700 and 1000 hours by driving transects at 15-20 km/hr and recording all mammals within 100 m of the transect centerline, creating a 200 m-wide detection area. During a subset of surveys taken June-August 2011 ($n = 55$), we used a rangefinder and distance sampling to estimate detection functions for the herbivores monitored here with the program ‘unmarked’ in R (Buckland et al. 2001, Fiske and Chandler 2011). We did this in both burned and unburned areas, and estimated that detection probability was ≥ 90 % for all sampled species within 100 m of the transect centerline under both conditions (Figure 5.2). Although we were only counting animals within 100 m of the transect centerline, our inability to estimate detection probabilities repeatedly during our study to account for variation due to year, season or transect location may have resulted in incomplete detection, and therefore, underestimates of herbivore numbers on transects. However, this was most likely the case in unburned areas with thick vegetation, and particularly for the smaller animals counted.

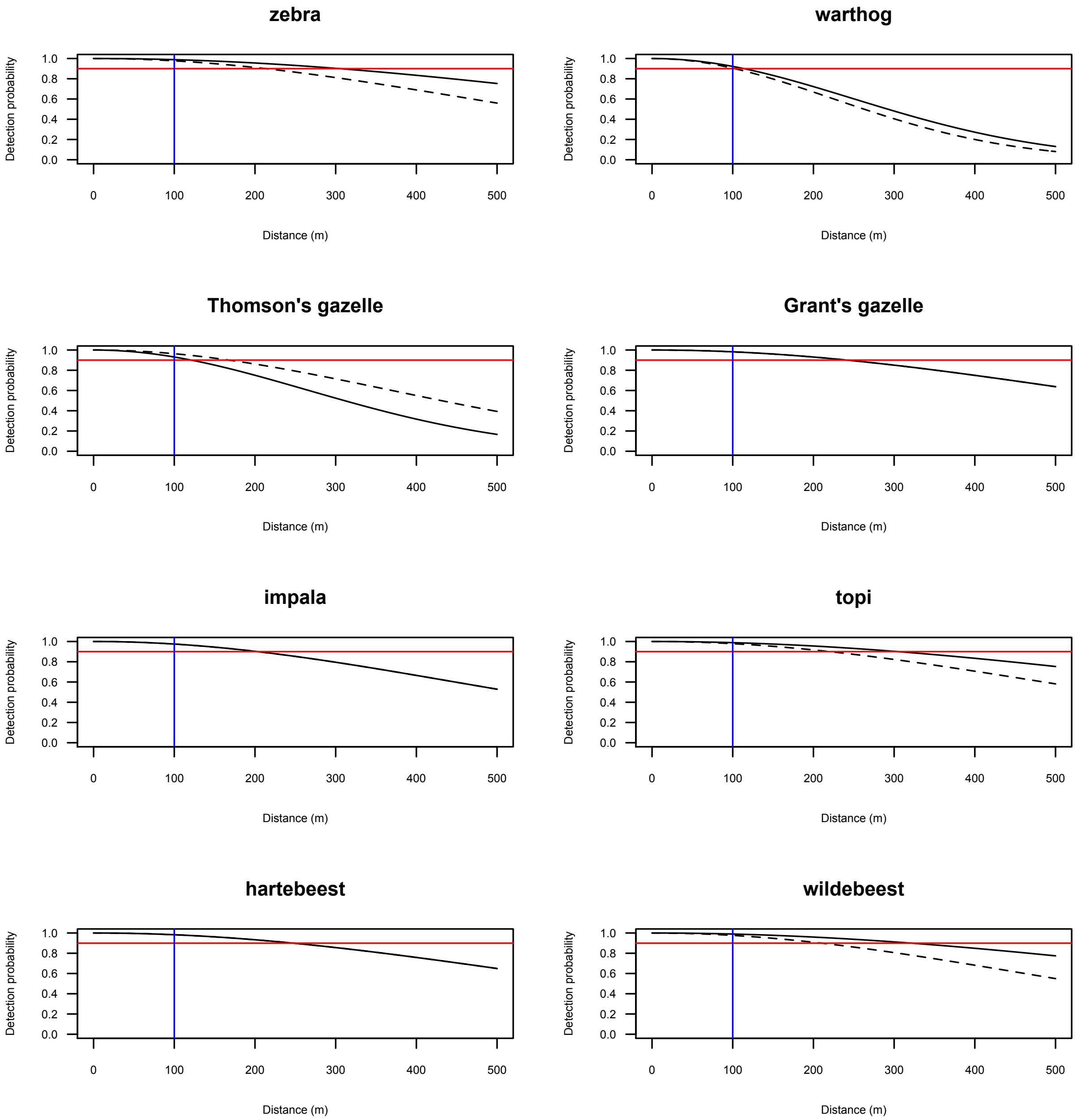


Figure 5.2. Detection probabilities for the 8 herbivore species monitored in this study based on unpublished data from D. S. Green. Detection distances were calculated using a rangefinder during June-August of 2011. Solid lines indicate the detection function for animals in burned areas, whereas dashed lines indicate the detection function for animals seen in non-burned areas.

Figure 5.2 cont'd. Figures with only one line indicate no differences between detection distances as a function of burned status. The vertical line indicates the maximum distance for which animals were recorded in the study, and the horizontal line indicates the 90 % detection probabilities in burned and unburned areas.

The herbivore species recorded on each transect included zebra, warthog (*Phacochoerus africanus*), Thomson's gazelle, Grant's gazelle (*Nanger granti)*, impala *(Aepyceros melampus)*, topi (*Damaliscus lunatus jimela),* Coke's hartebeest (*Alcelaphus buselaphus cokei)*, and wildebeest. For each individual herbivore detected along any transect, we categorized it as present in either a burned or unburned area to generate animal densities (count per km^2) for each species. Animal density was used because transect lengths varied. Along some portions of transects, a mosaic of burned and unburned patches occurred. Such areas were only categorized as burned when > 50 % of the detection area was burned. Small carnivores recorded on transects included black-backed jackals (*Canis mesomelas*), side-striped jackals (*Canis adustus*), bat-eared foxes (*Otocyon megalotis*), and banded mongoose (*Mungos mungo*). Large carnivore species recorded were African lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and cheetahs (*Acinonyx jubatus*).

Statistical analyses of herbivore data

We quantified herbivore selection of burned areas using generalized linear modeling with the glm package in R (R Core Team 2015). The model estimated herbivore density for each species based on season, burn status, precipitation, and transect identity. Every transect survey in each 2-week interval was the statistical replicate for analyses, with one replicate per transect for densities of animals found in both burned and unburned areas. Species for which we found that burn status was a significant parameter were considered to be selecting burned over unburned areas (ANOVA *F* test; $P < 0.05$).

Burn status was coded as a binary variable (burned or unburned). We accounted for seasonal variation in vegetation, the annual movements of wildebeest, zebra, and Thomson's gazelle, and the timing of burns by coding each density with a categorical variable (season) inclusive of the month during which each transect was sampled; November-February was considered the early wet season, March-June was considered the late wet season, and July-October was considered the dry season. July-October was also considered to be the period during which migratory herbivores were present in our study area. Due to large effects of seasonality on herbivore densities in the Reserve, we investigated impacts of burning on herbivores ≤ 365 Days Since Burn (DSB) such that each season was represented only once in the data set for each transect. We obtained daily precipitation from a local weather station (Figure 5.1) and summarized precipitation amounts (in mm) for the 2-week period corresponding to each survey, in addition to coding a quadratic term to investigate non-linear effects of rainfall (precipitation^2). To account for potential effects of spatial autocorrelation, or the impact of burn location on herbivore density, transect identity (ID) was included as a fixed effect. We also included interaction terms in our models between total precipitation and burn status, and between burn status and season, to account for variation in local vegetation and presence or absence of migratory herbivores. Animal densities were

$\log_e$(density + 1) transformed to achieve normality. Hence, our global model for each herbivore species was:

$$\log_e(\text{density} + 1) \sim 1 + \text{season} + \text{burn status} + \text{transect} + \text{precipitation} + \text{precipitation}^2 + (\text{burn status} \times \text{precipitation}) + (\text{burn status} \times \text{season}) + (\text{burn status} \times \text{precipitation}^2)$$

We determined the significance of these factors with an ANOVA *F*-test of the glm global model. A type II error structure was utilized because precipitation is a large driver of seasonality in our study system, and this ensured that each main effect was fit against all other terms when evaluating significance. We evaluated the global model for each herbivore species separately and used influence plots of residuals in R to ensure fit and identify any overly influential data points. Residuals were normally distributed, and no outliers were detected.

To determine how long animals occurred in greater densities on burned than unburned sites, we compared density estimates between burned and unburned sites along transects during several 30-day intervals following initiation of each burn. DSB = 0 on the date of the burning event. We ran an analysis of variance (ANOVA) across 30 day blocks to determine which species yielded significant *F* ratios ($P < 0.05$; Crawley 2007), before performing multiple linear comparisons on these groupings using a Tukey adjustment to discern in which 30 day blocks statistically different animal density estimates occurred between burned and unburned areas ($P < 0.05$).

Impact of prescribed burning on carnivore visibility

Carnivores were observed too infrequently to use a generalized linear modeling framework, so we tested the duration of carnivore responses to burning by using a Pearson’s chi-squared test of independence with Yates’ correction. We recorded all carnivores seen on transects, but whether they were seen in a burned or unburned patch was not noted due to sampling constraints; therefore carnivore numbers were only compared between pre- and post-burn. We compared the numbers of carnivores sighted during four time intervals: preburn, 1-120 DSB, 121-365 DSB, and 366-748 DSB. Data for small and large carnivores were analyzed separately.

Estimating vegetation recovery with the Normalized Difference Vegetation Index (NDVI)

The Normalized Difference Vegetation Index (NDVI) is a reliable indicator of the amount and quality of biomass in a particular region (reviewed in Pettorelli et al. 2005). In the current study, monthly averages of NDVI were obtained from the National Oceanic and Atmospheric Administration (NOAA) from the Moderate Resolution Imaging Spectroradiometer (MODIS) at a resolution of ~ 5 x 5 km. To investigate the rate of vegetation recovery and its relationship to herbivore numbers and carnivore visibility on burn transects, we extracted NDVI values for the grid cells in which > 60 % of the transect was located for the burns that occurred 11 July 2009 and 27 June 2010. We then divided these values by 10,000 to restore them to a -1 to 1 range. Using NDVI, we estimated when vegetation biomass returned to pre-burn levels, how herbivore numbers varied over time in relation to vegetation recovery, and determined whether variation in visibility of carnivores was spurious or instead corresponded to the clearing of local vegetation.

Results

Four different transects were surveyed a minimum of 28 times each (see legend for Fig 1), resulting in a total of 145 counts of large mammals on all transects between 2 August 2008 and 20 July 2011, documenting effects of 4 prescribed burns (Figure 5.1). Data were collected up to 136 days before burns, and up to 748 days after burns occurred. Herbivores were seen during 73.1 % of the surveys and small and large carnivores were observed during 13.8 % and 11.0 %, respectively.

Effects of season, transect location, and precipitation on herbivore densities

As expected, season was a strong predictor of density for zebra ($F_{2,168} = 18.224$, $P \leq 0.001$), Thomson's gazelle ($F_{2,168} = 5.217$, $P = 0.006$), and wildebeest ($F_{2,168} = 55.859$, $P \leq 0.001$). Interestingly, it was also a strong predictor for warthog ($F_{2,168} = 3.532$, $P = 0.031$) and impala ($F_{2,168} = 3.181$, $P = 0.0441$), but not for other species ($P > 0.05$). Transect ID was an important predictor for densities of Grant's gazelle ($F_{3,168} = 3.122$, $P = 0.027$), impala ($F_{3,168} = 10.492$, $P \leq 0.001$), and topi ($F_{3,168} = 5.926$, $P \leq 0.001$), but not for any other species ($P > 0.05$). The fixed effects of total precipitation and precipitation^2 were significant only for impala ($F_{1,168} = 4.964$, $P = 0.027$ and $F_{1,168} = 4.956$, $P = 0.027$). Results from each global model are presented in Table 5.1.

Table 5.1. The results from the ANOVA *F*-test and probabilities derived from generalized linear models that predicted herbivore densities based on ecological factors for 8 herbivore species in the Mara-Serengeti ecosystem, southwest Kenya, 2008-2011. Bolded *P* values indicate statistically significant effects. Denominator df = 168 in all global models.

Species	***F***	**df**	***p-value***
zebra			
season	18.224	2	**≤ 0.001**
status	19.568	1	**≤ 0.001**
transect	2.072	3	0.106
precipitation	0.046	1	0.831
precipitation^2	0.005	1	0.946
status:precipitation	0.010	1	0.920
status:season	0.251	2	0.779
status:precipitation^2	0.057	1	0.812
warthog			
season	3.532	2	**0.031**
status	34.563	1	**≤ 0.001**
transect	1.775	3	0.154
precipitation	0.990	1	0.321
precipitation^2	1.708	1	0.193
status:precipitation	0.259	1	0.611
status:season	0.312	2	0.733
status:precipitation^2	0.207	1	0.650
Thomson's gazelle			
season	5.217	2	**0.006**
status	83.472	1	**≤ 0.001**
transect	1.392	3	0.247
precipitation	0.254	1	0.615
precipitation^2	0.143	1	0.706
status:precipitation	0.196	1	0.659
status:season	0.644	2	0.527
status:precipitation^2	0.086	1	0.770
Grant's gazelle			

Table 5.1 cont’d

season	0.253	2	0.7764
status	14.755	1	**≤ 0.001**
transect	3.122	3	**0.027**
precipitation	0.813	1	0.369
precipitation^2	1.469	1	0.227
status:precipitation	0.236	1	0.628
status:season	0.160	2	0.852
status:precipitation^2	0.398	1	0.529
impala			
season	3.181	2	**0.044**
status	3.275	1	0.072
transect	10.492	3	**≤ 0.001**
precipitation	4.964	1	**0.027**
precipitation^2	4.956	1	**0.027**
status:precipitation	0.163	1	0.687
status:season	1.984	2	0.141
status:precipitation^2	0.402	1	0.527
topi			
season	1.851	2	0.160
status	51.309	1	**≤ 0.001**
transect	5.926	3	**≤ 0.001**
precipitation	0.071	1	0.790
precipitation^2	0.208	1	0.649
status:precipitation	0.407	1	0.525
status:season	3.146	2	**0.046**
status:precipitation^2	1.099	1	0.296
hartebeest			
season	0.223	2	0.800
status	0.318	1	0.574
transect	1.149	3	0.331
precipitation	1.076	1	0.301
precipitation^2	0.756	1	0.386
status:precipitation	0.005	1	0.944
status:season	1.142	2	0.322
status:precipitation^2	0.109	1	0.742
wildebeest			

Table 5.1 cont'd

season	55.859	2	**≤ 0.001**
status	2.944	1	0.088
transect	0.911	3	0.437
precipitation	2.279	1	0.133
precipitation^2	1.245	1	0.266
status:precipitation	0.053	1	0.818
status:season	1.196	2	0.305
status:precipitation^2	0.077	1	0.781

Effects of burning on herbivores

Wildlife response to burning was species-specific, with zebra, warthog, Thomson's gazelle, Grant's gazelle, and topi occurring in larger numbers in burned than unburned areas ($P < 0.05$; Table 5.2). Densities of impala and wildebeest showed trends towards selecting burned areas ($P = 0.072$ and $P = 0.088$, respectively*)*, but hartebeest showed no response to burn status ($P > 0.10$). The interaction between season and burned status was significant only for topi ($F_{2,168} = 3.146$, $P = 0.046$). The interaction between burned status and precipitation was not significant for any species ($P > 0.05$).

Table 5.2. Results from the ANOVA *F*-test and probabilities derived from generalized linear models that predicted herbivore densities based on burn status in the Mara-Serengeti ecosystem, southwest Kenya, 2008-2011. df = 1,168 in all comparisons.

Species	***F***	***P-value***
zebra	19.568	≤ 0.001
warthog	34.563	≤ 0.001
Thomson's gazelle	83.472	≤ 0.001
Grant's gazelle	14.755	≤ 0.001
impala	3.275	0.072
topi	51.309	≤ 0.001
hartebeest	0.318	0.574
wildebeest	2.944	0.088

Temporal dynamics of burn effects on herbivores

Using only those species for which burn status was a predictor of density, we next assessed the temporal dynamics of these responses. ANOVA *F*-tests indicated significant differences ($P < 0.05$) between numbers of animals seen on burned areas compared to unburned areas of transects over time for Thomson’s gazelle ($F_{11,156} = 2.044$, $P = 0.028$) and topi ($F_{11,156} = 2.070$, $P = 0.026$), but not for zebra ($F_{11,156} = 1.073$, $P = 0.387$), Grant’s gazelle ($F_{11,156} = 0.890$, $P = 0.552$), warthog ($F_{11,156} = 0.696$, $P = 0.741$), or wildebeest ($F_{11,156} = 0.730$, $P = 0.709$). The direct effects of burning on Thomson’s gazelle lasted up to 120 DSB, and we observed a significant increase in topi densities on transects from 181-240 DSB (Figure 5.3).

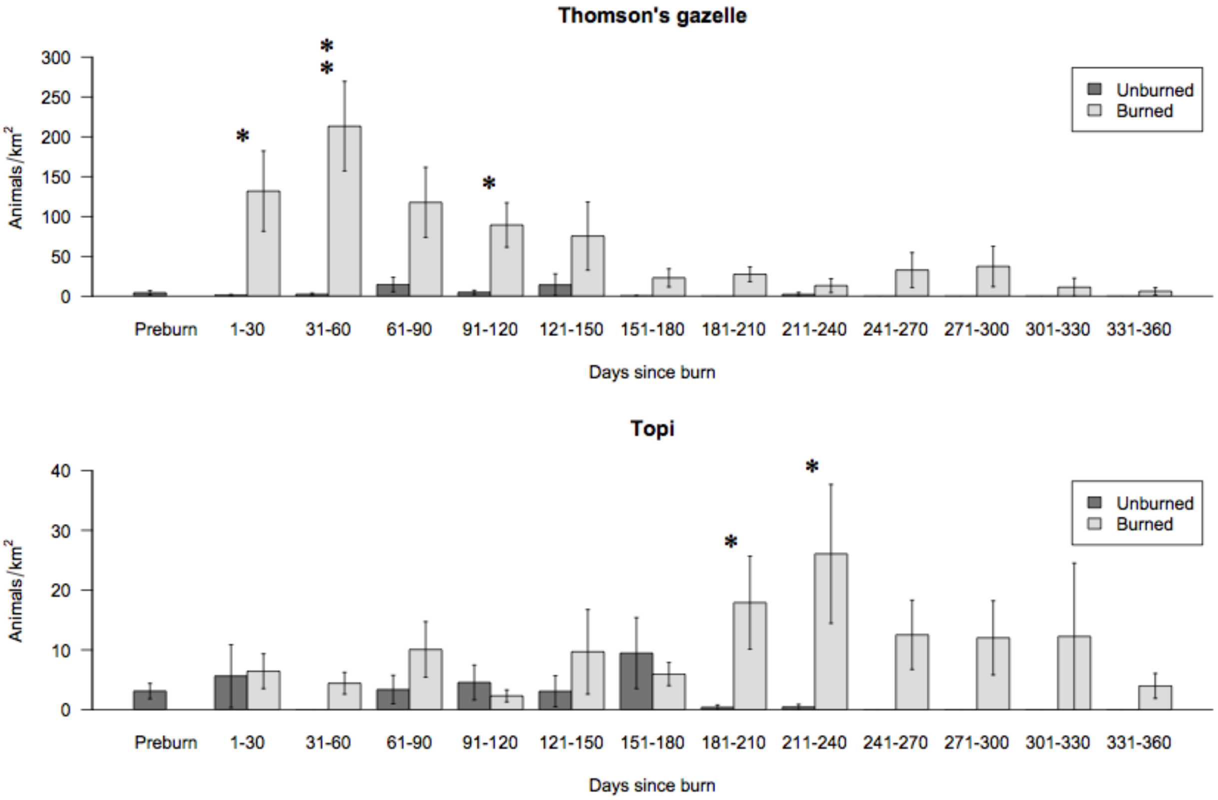


Figure 5.3. Density of Thomson's gazelle and topi on burned and unburned areas, relative to the time of the fire, in the Maasai Mara National Reserve. "Preburn" includes averaged data collected prior to the burn. Each subsequent interval on the x-axis represents a 30-day block of time after the burn. Error bars represent 95% confidence intervals around the means. Two asterisks indicate significant differences between densities on burned vs. unburned areas at $P \leq 0.001$; one asterisk indicates significant differences at $P < 0.05$.

Impact of burning on carnivore visibility

Burning appeared to increase numbers of both small and large carnivores seen on transects (Figure 5.4). Compared to pre-burn sightings, large carnivores were observed in higher numbers up to 120 days after burns ($\chi_1^2 = 23.193$, $P \leq 0.001$), but not during later time blocks (121-365 DSB: χ_1^2= 3.698, *P* = 0.104 and 366-748 DSB: χ_1^2 = 2.647, *P* = 0.186). Small carnivores were observed more frequently after than before burns for up to 365 days after burning (1-120 DSB: χ_1^2 = 15.510, $P \leq 0.001$ and 121-365 DSB: χ_1^2 = 8.254, *P* = 0.006), but not more than one year after burning events (366-748 DSB; χ_1^2 = 1.0714, *P* = 0.575).

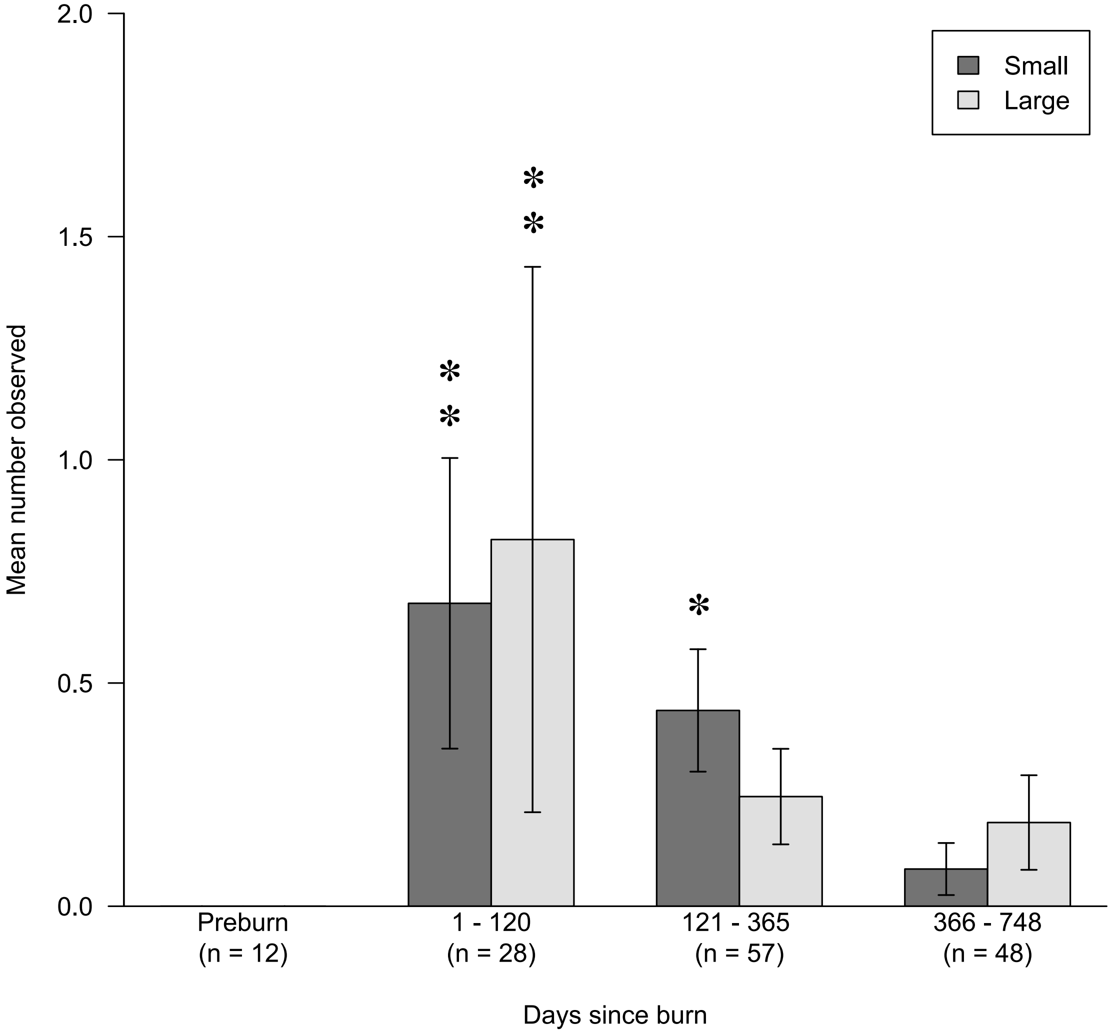


Figure 5.4. Carnivore abundance in burned areas, relative to the time of the fire, in the Maasai Mara National Reserve. Two asterisks indicate significant differences from preburn abundances at $P \leq 0.001$; a single asterisk indicates significant differences from preburn abundances at $P < 0.05$ (χ^2 test of independence with Yates' correction). Error bars represent 95% confidence intervals around the means. Sample sizes for each grouping, representing the number of transects run, appear below the bars.

Vegetation recovery with NDVI

Reduction of local vegetation biomass following the burns was clearly visible using NDVI (Figure 5.5). Levels of vegetation decreased by nearly half following the burns, remained at these levels for approximately 120 days, and returned to pre-burn levels by 180-210 days after burning (Figure 5.5).

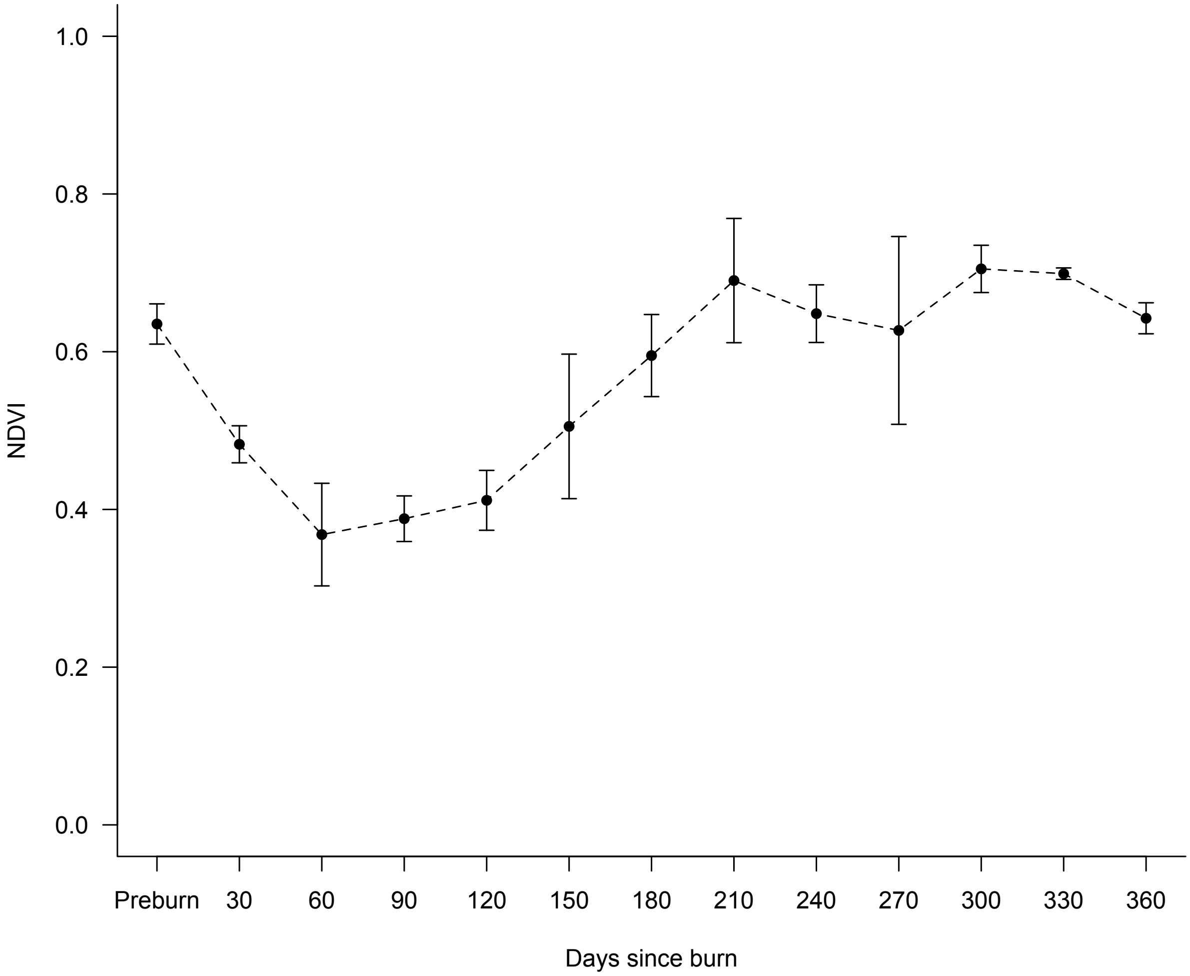


Figure 5.5. The response of local vegetation to prescribed burning assessed using the Normalized Difference Vegetation Index (NDVI).

Figure 5.5 cont'd. The values represented here are the averaged monthly values for the 2 ~ 5 x 5 km grid cells in which > 60% of the burn transects fell for the prescribed burns taking place on 11 Jul 2009 and 27 Jun 2010. Values were grouped by their Days Since Burn (DSB), and "Preburn" indicates the 30-day interval before burning was initiated. Error bars indicate 95% confidence intervals around the means.

Discussion

Although prescribed burns in the current study increased local abundances of some herbivore species (zebra, warthog, Thomson's gazelle, Grant's gazelle, topi), these effects were surprisingly short-lived and variable, with significant differences in abundance between burned and unburned patches found only for Thomson's gazelle and topi. Our results indicate that herbivore response to burning is influenced by complex relationships among species, season, location, precipitation, and time since burn. For many years, wildlife managers have viewed prescribed burning in sub-Saharan African savannahs as important for creating new foraging opportunities for wildlife during dry seasons (Norton-Griffiths 1979; Archibald 2008; Driscoll et al. 2010). New vegetative growth stimulated by burning is utilized by certain wildlife (Van de Vijver et al. 1999; de Ronde et al. 2004; Sensenig et al. 2010), and may contribute to population growth over the long-term. However, here we found that burn effects did not last more than four months for any species including Thomson's gazelles, which exhibited stronger and more immediate responses than any other herbivore monitored. We found that zebra, warthog, Thomson's gazelle, Grant's gazelle, and topi responded favorably to burning, as was also found in some earlier studies (Moe et al. 1990; Wilsey

1996; Gureja & Owen-Smith 2002; de Ronde et al. 2004). Our results suggest that zebra, warthogs, Grant’s gazelle, and topi may utilize burned areas that occur within their normal home ranges, but that these species do not congregate in large numbers on burned areas. Furthermore, because transect was also a strong predictor of density for topi abundance, the differences between burned and unburned patches 181-240 DSB should be viewed with caution, although others have also observed that topis select post-fire regrowth (Gureja & Owen-Smith 2002). Overall, our data suggest that long-range movements to use burned habitats are probably uncommon among zebra, warthogs, Grant’s gazelle, and topi.

Numbers of Thomson’s gazelle in burned areas remained elevated for ≤ 120 days (Figure 5.3). This finding is consistent with that from Wilsey (1996) who also found that Thomson’s gazelle utilize freshly burned areas. The immediate response of Thomson’s gazelle to burning is likely caused by enhanced nutrient availability and reduced cellulose content in forage shortly after burns. Sensenig et al. (2010) found that nutrient content of vegetation increases within 30 days of the initial burn, but that enhanced nutrient content only persists for ≤ 90 days. This change in vegetation associated with increases in Thomson’s gazelle numbers is consistent with our NDVI data; bulk forage decreased immediately after burns, allowing for the stimulation of new growth. Gazelles have highly tactile lips and narrow muzzles that allow for preferential feeding on isolated patches of protein-rich foliage, an adaptation that facilitates foraging on new growth in burned patches (Bell 1971; Maddock 1979; Estes 1991). During the seasonal migration of wildebeest and zebra in the Serengeti ecosystem, Thomson’s gazelle follow wildebeest and zebra herds that have stimulated growth of protein rich, cellulose-poor grass shoots by their grazing activity (Bell 1971; Maddock 1979). Our data suggest that prescribed burning has a similar effect. However, once the biomass of vegetation returns to approximately half its pre-burn values, 120 days after burning, Thomson's gazelles no longer appear to select burned over unburned areas, so the effects of burning on this species are short-lived.

Topi occurred in significantly higher numbers in burned areas 181-240 days after the fire, affirming their preference for post-fire regrowth (Gureja & Owen-Smith 2002; de Ronde et al. 2004). This also coincides with the interval after burns in which NDVI data show a return to pre-burn levels (Figure 5.5). Transect identity and the interaction between burn status and season also influenced the presence of topi in burned areas (Table 5.1). In some parts of the Reserve topi are known to defend traditional territories, and in other areas they defend small territories on leks during the breeding season (Bro-Jørgensen & Durant 2003); the significant effects of transect identity and the interaction between burn status and season on topi numbers observed here may reflect variation in territory quality for topis and the seasonality of their lekking behavior in the Reserve. Previous research in South Africa found that topi selected post-fire growth around 4 weeks after burning (Gureja & Owen-Smith 2002), indicating that those topi exploited burns earlier than did the topi observed in our study. In that earlier study, a small population of topi was investigated (n = 23, compared to 4675 in the Reserve, as described by Ogutu et al. 2011), and their patterns of territory use were unknown in South Africa. Perhaps lower salience of territory quality for topis in southern Africa than the Reserve affects the timing of their use of burned areas, and allows them to respond faster to the availability of burned patches.

Transect location also affected responses of impala and Grant's gazelle to prescribed burning. Unfortunately, however, Grant's gazelle and impala were seldom seen on transects, being present on only 6.8 % and 14.4 %, respectively, of all transects sampled. Our infrequent sightings of impala and Grant's gazelles on transects, together with limited information about their territorial behavior in the Reserve, make interpretation of these results difficult. Responses of impala to prescribed burning were also affected by precipitation, whereas responses of other herbivores were not.

Season was a strong predictor of density for zebra, Thomson's gazelle, and wildebeest, as was expected based on previous research and their known migratory patterns in the Reserve (Stelfox et al. 1986). Interestingly, season was also a strong predictor for warthog and impala, indicating that these species might also benefit more at some times of year than others from the modification of local vegetation. The high degree of seasonality in the Reserve may have driven ephemeral responses to burning by herbivores in the current study. Other savannah ecosystems that have less extreme seasonality with respect to both rainfall and large movements of herbivores than in the current study may see greater effects of burning on herbivore populations than those documented here.

Little information exists on how prescribed burning affects African carnivores or the implications of burning for carnivore management. Although results from the current study are preliminary, they provide a starting point for understanding how prescribed burning in sub-Saharan African grasslands can be expected to affect indigenous carnivores. In our study, prescribed burning appeared to increase numbers of both small and large carnivores, but our results must be cautiously viewed because we were unable to account for detection probability. No carnivores were observed on transects before the burns occurred. It is reasonable to assume that carnivores might utilize burned areas as prey become locally abundant and accessible. However, it is also plausible that removal of tall grass by burning might simply improve detection probability. We were unable to distinguish between these two hypotheses.

Our data on large carnivores are consistent with both of these hypotheses because increases in numbers of large carnivores coincided with enhanced abundance of Thomson’s gazelles during the first 120 days after burning, and because the recovery of vegetation following the burn event was complete by 210 days after burning. A study by Eby et al. (2013) found African lions were more likely to be tracked during daylight hours in unburned areas, suggesting that they were avoiding burned habitat. This result is contrary to our findings, and further underscores the need for future research on the impacts of prescribed burning on carnivore populations. However, our data for small carnivores are more difficult to interpret. If larger numbers of these carnivores were due to our enhanced ability to detect them, we would not expect to see numbers of small carnivores differing significantly from pre-burn numbers ≥ 210 days post-burn, when vegetation biomass returned to pre-burn values. Our data show significant increases over preburn numbers of small carnivores to persist until one year after a burn. We emphasize that the numbers of small carnivores seen were small, so our result for this group should be interpreted with caution. We would expect the effects of burning on the prey of small carnivores to be more likely negative than positive. The likely costs of prescribed burning to small carnivores include at least temporary reductions in numbers of small mammals, ground-nesting birds, insects, reptiles, and amphibians. Such prey animals are vulnerable to prescribed burning, and burns are known from earlier research to have negative direct and indirect effects on their current and future population sizes (Russell et al. 1999; Salvatori et al. 2001; Archibald et al. 2005; Yarnell et al. 2007; Little et al. 2013).

Management implications

Creating new foraging opportunities for herbivores during dry seasons is an important reason given by wildlife managers for prescribed burning in sub-Saharan Africa (Hobbs & Spowart 1984; Moe et al. 1990; Vermeire et al. 2004; Geldenhuys et al. 2004; Everson et al. 2004). Although the impacts of burning on local and migratory herbivore populations were surprisingly short-lived in the current study, even slight improvements in forage quality and quantity in the region may assist these populations during the dry seasons. Moreover, even small increases in herbivore population sizes due to enhanced forage quality after burning might have important positive implications for endangered carnivore populations (e.g., cheetah, lions) that depend on these herbivores as a food source. However, it is also important to note that large resident herbivores, such as elephants and buffalos (not addressed in this study), may require considerable bulk forage year round, and burning large areas may therefore have long-term detrimental effects on them. Herbivore population sizes may not necessarily increase due to burning, because all that can be observed in short-term studies of burn effects, including ours, is the redistribution of herbivores across the landscape. We do not yet know enough about longer-term effects of burning on population dynamics of

African wildlife, so these should be studied further. Prescribed burns may also interfere with practices in place to preserve natural ecology if burns are incorrectly timed, occur too frequently, or are inappropriately intense (Van Wilgen et al. 2007). Because of the known and potential ecological costs of burning (Russell et al. 1999; Salvatori et al. 2001; Yarnell et al. 2007; Little et al. 2013), we recommend that managers understand the limitations of prescribed burns, clearly weigh the benefits of burning against its potential costs, and formulate clear objectives before initiating a program of prescribed burning.

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