The interplay between African protected savannas and their surrounding pastoral rangelands

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Contents


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Chapter 1

General introduction

Nina Bhola

PROTECTED AREAS: ORIGIN, DEFINITION AND FUNCTION

Human societies have long set aside vast areas of land to conserve nature in the form of hunting reserves, religious forests, and common grounds (Chape et al. 2008). The current concept of national parks evolved in the mid-1800s as European colonists were converting native landscapes to farms, ranches, and cities (Hansen and DeFries 2007). During this period the key goal in Africa was usually the protection of wildlife for hunting opportunities, not so much for nature conservation. However, during the 20th century, the key goal was the protection of nature. By minimizing the influence of humans, natural ecosystems were expected to continue to maintain ecological processes and native species. As a result, protected areas became a cornerstone of the global conservation strategy. More than 100,000 terrestrial protected areas have been established covering some 16.8 million km^2 of the world's land surface area of which Africa contributes an impressive 4.2 million km^2 (Chape et al. 2005).

PROTECTED AREA SIZE, HABITAT HETEROGENEITY AND PRODUCTIVITY

Protected areas often host diverse communities of wildlife, with many species usually able to coexist in particular areas (Newmark 1996). Yet, despite the high level of protection and expansion of national parks and reserves, protected areas are not always functioning as originally envisioned (Hansen and DeFries 2007). Declining wildlife populations and local extinctions remain a growing concern (Brashares et al. 2001, Owen-Smith and Mills 2006, Ogutu et al. 2009, Ogutu et al. 2011), although significantly high levels of protection has slowed declines and in some species reversed the trends (McNaughton and Georgiadis 1986, Thirgood et al. 2004). The theory of Island Biogeography (IBT) has been extensively used in explaining species richness patterns in island systems and other insular communities such as protected areas (MacArthur and Wilson 1967). According to this theory there is a positive association between reserve size and the number of species it can support; a relationship considered sufficiently strong to reliably predict rates of species loss (Soulé et al. 1979). Large areas gain more species through immigration and support larger populations that are therefore less prone to stochastic extinction. Furthermore, large areas often contain more habitat types and hence offer more opportunities for niche differentiation (Ricklefs and Lovette 1999). In contrast, small reserves contain small populations and are more likely to lose species than are large ones as a result due to stochastic population fluctuations (MacArthur and Wilson 1967, Rosenzweig 1995). Small reserves thus provide opportunities for fewer species than larger reserves because they contain lower diversity of habitat types and therefore offer fewer opportunities for niche differentiation. Furthermore, species extinctions within small reserves are more likely due to low population densities and greater vulnerability to ecological catastrophes.

Despite the generality and popularity of the Island Biogeography Theory, several studies have reported richness patterns that are inconsistent with its predictions

(Lomolino and Weiser 2001, Jonsson et al. 2011). This is neither satisfactory nor surprising given that many small reserves are situated in unique habitats in which the diversity of habitats, landscape heterogeneity or vegetation productivity is sufficiently high to support rich species assemblages despite their small sizes (Báldi 2008). This discrepancy can be explained at least in part by an alternative theory of species richness patterns, known as the species–energy theory, which predicts that species richness should reflect the total amount of available energy (Wright 1983) or the habitat heterogeneity hypothesis (Rosenzweig 1995). Yet, despite the wide recognition that area *per se*, heterogeneity and productivity each can explain a part of the variation in species richness among protected areas, it is surprising that very few studies have examined their relative importance (Ricklefs and Lovette 1999, Rensburg et al. 2002). This raises fundamental questions about how area, heterogeneity and productivity might interact to shape species richness patterns in protected areas, particularly given area might influence species richness indirectly via its correlation with other factors. Furthermore, several studies have shown that most parks and reserves do not encompass the full range of resource gradients, migratory corridors and seasonal habitats necessary for the maintenance of a diverse array of wildlife populations (Fynn and Bonyongo 2010). This is of great significance to conservation because it is well known that the nature of landscapes around reserves and reserve boundaries markedly affect ecological processes operating within and between reserves and their surroundings, hence affecting the number of species reserves can sustain (Murray 1995, Belovsky 1997, Hansen and DeFries 2007). Processes such as expanding human settlements, cultivation, fencing and other land transformations in regions neighbouring reserves, together with incursions of domestic livestock into supposedly protected areas soften reserve boundaries and reduce their effective sizes by interfering with vital ecosystem processes such as breeding, escape from predation, access to critical resources via movements etc., thereby increasing the risk of localized species extirpations (Woodroffe and Ginsberg 1998, Parks and Harcourt 2002, Newmark 2008). Thus, to minimize species losses or extreme population fluctuations, protected areas must be either sufficiently large to accommodate large-scale migrations along resource gradients, or if they are small, must be sufficiently heterogeneous or productive (Baldi, 2008), and experience minimal to moderate disturbances from their surrounding land use matrix (Hansen and DeFries 2007).

Accordingly, one aim of this thesis is to attempt to disentangle the effects of area, heterogeneity and productivity on species richness using 300 different-sized protected areas distributed across the entire African continent (Chapter 2). Patterns of plant diversity and richness also vary along environmental gradients, however, the explanation for this variation is relatively unclear. I therefore, investigate the differential plant responses to disturbance by fire and browsing as causes of changing woodland composition among sites along a rainfall gradient, given their importance to large mammals (Chapter 3). Furthermore, I describe the distributional patterns of that result from seasonal movements of large carnivores and herbivores between protected areas and their surrounding human-dominated landscape (Chapter 4 & 5). I further attempt to explain the ecological processes underlying these patterns (Chapter 6) using data from the Mara-Serengeti ecosystem in east Africa as a case study.

THE SAVANNA BIOME

The African savanna biome is characterized by a continuous understorey of grasses, scattered closed thickets of a diverse range of shrubs and dense Acacia/Commiphera woodlands and is found in climates with strongly seasonal rainfall patterns (Walker 1987). This biome supports a higher diversity of ungulates than any other terrestrial biome or continent (Du Toit and Cumming 1999). Some 46 species of ungulates are endemic to the African savanna biome. The present distribution of both ungulate and carnivore diversity across the African continent is associated with the high spatial heterogeneity within the savanna biome. A particularly high concentration of species is evident in the topographically diverse Rift Valley region of the East African savanna (McNaughton and Georgiadis 1986). More specifically, (Du Toit and Cumming 1999, Olff et al. 2002) have shown that the high ungulate and carnivore diversity in African savannas is directly linked to variation in soil fertility and rainfall. Rainfall, is highly spatially, seasonally and inter-annually variable (Owen-Smith and Ogutu 2003, Ogutu et al. 2008). The large variability in rainfall, coupled with high spatial heterogeneity in soils, geomorphology and water availability enables the coexistence of diverse large herbivore assemblages (Olff et al. 2002).

THE MAASAI MARA ECOSYSTEM – RESEARCH SITE

The Maasai Mara ecosystem is located in southwestern Kenya and borders the Serengeti National Park in Tanzania to the south (Fig. 1.1). It is a semi-arid savanna encompassing 1530 km^2 of the protected Maasai Mara National Reserve (MMNR) in which only wildlife conservation and tourism are permitted, as well as about 4000 km2 of the adjoining pastoral ranches in which traditional pastoralism by the Maasai people and pastoral settlements, some cultivation and wildlife tourism constitute the major forms of land use. The adjacent Maasai pastoral ranches, including Koyiaki, Siana, Ol Kinyei, Lemek and Ol Chorro Oiroua support large herds of livestock and diverse assemblages of resident herbivores. During the wet season resident herbivore move from the protected reserve and its adjoining pastoral lands (Stellfox et al. 1986). The ecosystem is characterized by the annual migration which brings over one million wildebeest (*Connochaetes taurinus*), 0.2 million zebra (*Equus burchelli*) and 0.4 million Thomson's gazelle (*Gazella thomsoni*) from the Serengeti Plains to the south and Loita Plains to the northeast of the MMNR from July to October at least (Talbot and Talbot 1963, Pennycuick and Norton-Griffiths 1976, Maddock 1979, Sinclair and Norton-Griffiths 1979).

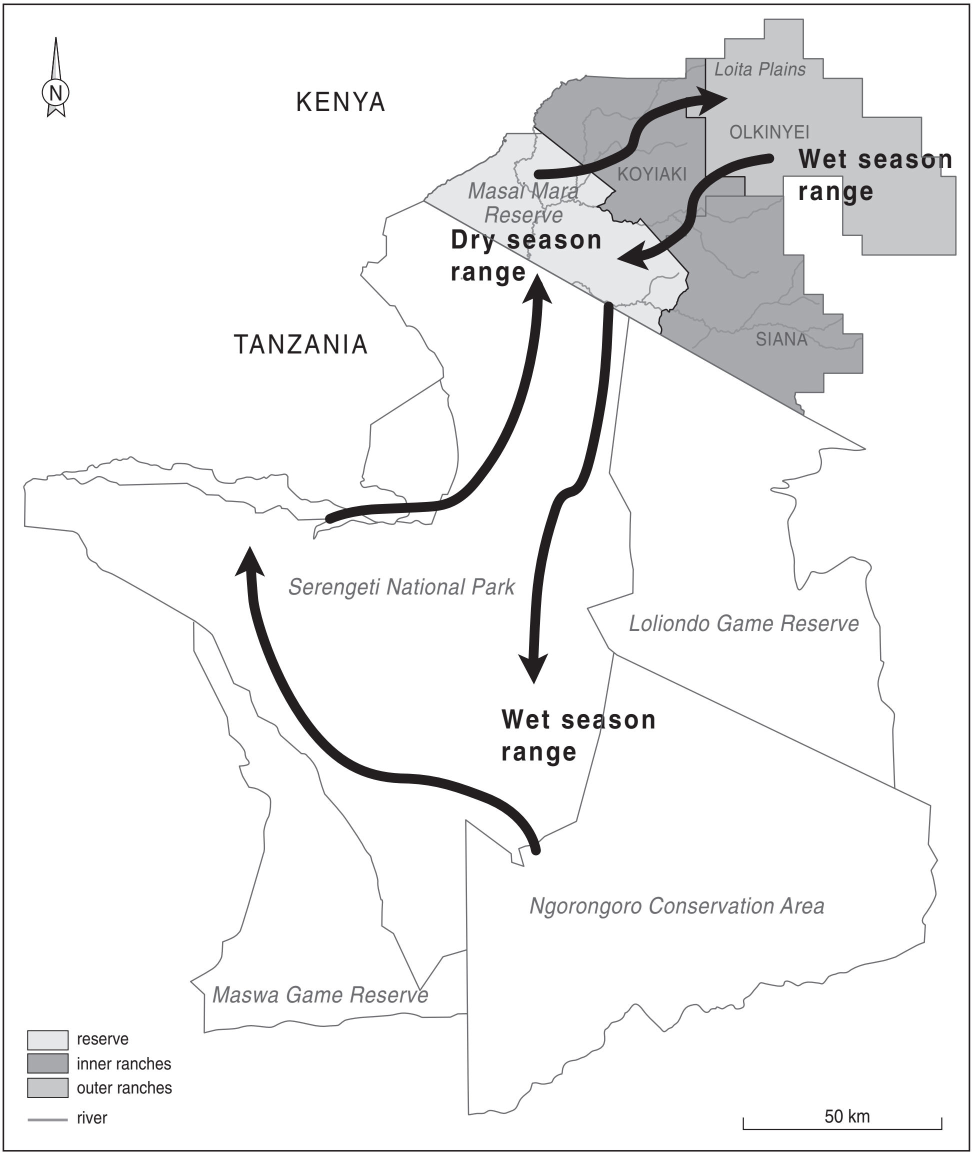

Figure 1.1 The Mara-Serengeti ecosystem showing the wildebeest migration from their wet season range in the south northwards into the dry season range in the Maasai Mara National Reserve and its adjoining pastoral ranches. Besides the Serengeti migration, the Loita population uses the Loita plains during the wet season together with resident herbivores and move into the Maasai Mara National Reserve in the dry season.

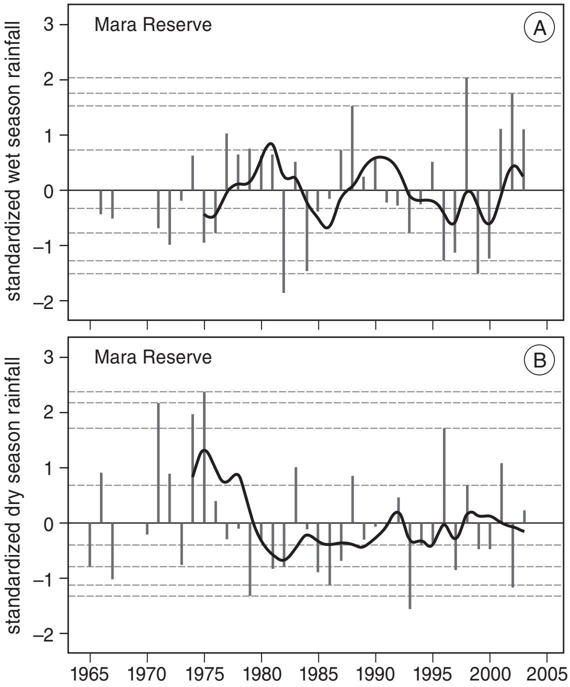

Figure 1.2 Fluctuations in rainfall in the Maasai Mara National Reserve based on areal averages over sixteen stations, standardized relative to the long-term mean and standard deviation. Needles indicate the standardized records and solid lines the 5-year running means. Dashed horizontal grey lines are the 5, 10, 25, 40, 50, 60, 75, 90, 95 and 100th percentiles of the frequency distribution of each rainfall component. The percentiles are used to assess the degree of departure of standardized rainfall components from their respective long-term means (Ogutu et al. 2007).

Rainfall in this region is bimodal with the 'short rains' falling in November-December and the 'long rains' in March–June, with the dry season covering July-October. Rainfall increases regionally from about 500 mm in the southeast to over 1200 mm per year in the northwest (Pennycuick and Norton-Griffiths 1976). Analysis of the El Niño-Southern Oscillation (ENSO), temperature, rainfall (Fig. 1.2) and Normalized Difference Vegetation Index (NDVI) time series data covering a large part of our study period produced many results relevant to this thesis (Ogutu et al. 2007). Here I summarize only the findings most pertinent to this study. (1) The longest (1990-95) and the strongest (1997-98) recorded ENSO events both occurred during the monitoring period (1977-2010). (2) Furthermore, the period during 1989–2003 was among the hottest recorded since the 1960's. (3) Severe droughts occurred in 1993 and 1999-2000, implicating marked deficits in soil moisture but moderate droughts were also evident in 1991 and 1994. (4) The wet season rainfall component showed quasi-periodic oscillations with a cycle-period of about 5 years. (5) The dry season rainfall was unusually higher than average during the mid to late 1970s and fell below average thereafter. The marked climatic variation was thus a major factor during this study.

THE INFLUENCE OF HUMANS IN THE MARA-SERENGETI

As early as ca. 2000 years ago, in the Neolithic period, an area stretching from the Narok district (present day Narok and Trans Mara Counties) in Kenya to the Simanjiro and Kiteto districts in Tanzania was occupied by advanced pastoralists, who managed their cattle, sheep and goat herds for maximized production and who did not hunt wildlife (Lamprey and Reid 2004). However, only in the last 300 years, have the Maasai pastoralists (the largest pastoralist group in the area) occupied the Mara-Serengeti ecosystem (Olff and Hopcraft 2008). The pastoral way of life has coexisted with wildlife in these savannas for thousands of years, keeping the woodlands open by regular use of fire and controlling bush encroachment by keeping sheep and goats (Lamprey and Reid 2004). However, over the course of the last 60 years, cultivation of large tracts of grazing land adjacent to the core protected areas Mara-Serengeti ecosystem, rapid human population growth, a transition from a semi-nomadic to a sedentary life style and sub-division of formerly communally owned group ranches have led to a manifold increase in settlements (Lambin et al. 2003). These new land tenure systems tend to fragment ecosystems into disjunct parcels (Buckland et al. 2001, Serneels et al. 2001). The conversion and alienation of land previously used by wildlife has resulted in changes in ecosystem size (Fig. 1.3). Such changes may disrupt fundamental ecological processes (Hansen and DeFries 2007), including, trophic structure (Hopcraft et al. 2010), ecological flows into and out of reserves (Hansen and DeFries 2007), shrinking of crucial habitats for seasonal and migration movements and altered population source/sink dynamics (Serneels et al. 2001), as well increasing exposure of wildlife to deleterious human activities (e.g. illicit human harvests) or to exotic species and diseases (Packer et al. 1999). This means that, although protected areas may not

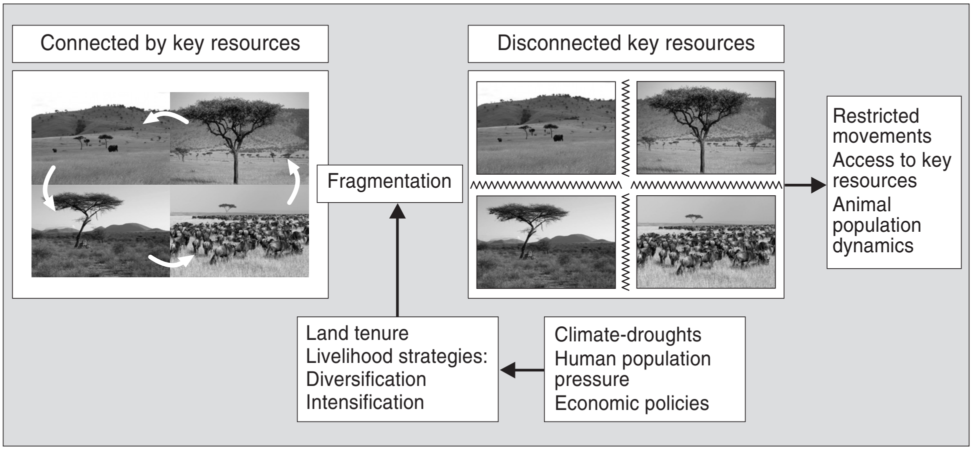

Figure 1.3 Conceptual model of forces operating over different temporal scales. Fragmentation leads to short-term effects on the mobility of wildlife necessary to exploit heterogeneity in resources, which eventually causes declines in wildlife (modified from Galvin et al. 2008).

contain the full suite of habitats required by organisms to meet all their annual life-history requirements, seasonally important habitats often lie outside the boundaries of protected areas. Thus, increasing habitat fragmentation precludes the potential for species to move to future climatically suitable habitats (Ogutu et al. 2007) threatening the future viability of wildlife populations.

TRENDS IN WILDLIFE POPULATION DYNAMICS

Over the last two centuries, ungulate movements have been severely disrupted by human activities (Bolger et al. 2008, Harris et al. 2008). For example, wildebeest numbers in Kruger National Park declined substantially from 6,000 individuals in 1965 to around 1,500 individuals by 1987 after the erection of a fence in 1961 (Ben-Shahar 1993). In the Athi-Kaputiei plains in Kenya, losses of wildebeest from around 30,000 to about 5,000 individuals have been recorded (Reid et al. 2008b). Not only has Africa experienced losses of migrations but also substantial declines of resident populations (Caro and Scholte 2007, Western et al. 2009 , Craigie et al. 2010). A most noteworthy example of such losses is in the Mara portion of the Mara-Serengeti ecosystem since 1977, where populations of almost all wildlife species have declined to a third or less of their former abundance both in the protected Maasai Mara National Reserve and in the adjoining pastoral ranches (Ogutu et al. 2009, Ogutu et al. 2011). As with wildlife populations vegetation dynamics have undergone dramatic changes in the Mara-Serengeti ecosystem.

VEGETATION DYNAMICS IN THE MARA-SERENGETI

The history of vegetative changes in the Mara-Serengeti has been well documented (Thuiller et al. 2005). The dynamics of savanna woodlands have experienced cycles or transitions between stable states following ecological perturbations, with shifts from open grassland to dense woodland and back to grasslands. Figure 1.4 highlights and summarizes the major perturbations and the consequences on vegetation dynamics across the ecosystem.

During the rinderpest outbreak in 1888–1889 herds of livestock, wildebeest, buffalo and people were decimated. Only ruminants were affected because they are closely related to livestock. During this period, humans abandoned large parts of the Serengeti as the increase in the thickets and woodlands allowed the spread of tsetse from the Serengeti outward into previously cultivated areas. The reduction in human and wild herbivore numbers reduced the incidence of fire and so allowed the escape of tree seedlings in the 1890's (Sinclair et al. 2008a). The woody vegetation was reduced by the increase in burning when the human population returned in the 1930's and a campaign to control tsetse flies was launched. This involved burning and active reduction of trees, leading to a rapid decline in tree densities and abundance and an increase in

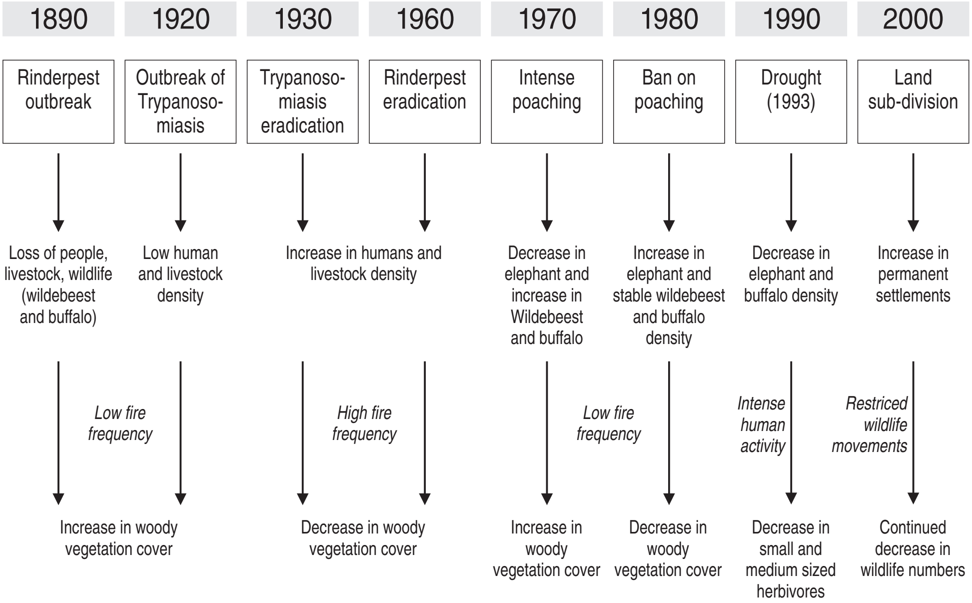

Figure 1.4 Summary of the major events in the Mara since 1800s.

people and livestock. In 1951, the Serengeti National Park in Tanzania was created and in 1961 the Maasai Mara Reserve in Kenya was established. In the 1960's a campaign to eradicate rinderpest saw the consequent rise of both livestock and wildebeest and buffalo populations (1963-1977).

Following this period severe poaching activities decimated the rhino and elephant populations. Some 50% of the population disappeared during 1984-1986 (Dublin and Douglas-Hamilton 1987). But the wildebeest population increased following the eradication of the rinderpest in the 1960s and reduced the dry grass serving as fuel for fires. Consequently, tree seedlings that had previously been unable to escape from fire were now able to grow. After the 1970's a rapid increase in woody vegetation emerged consisting of a different composition of species. By 1989 a ban on ivory trade was placed and elephant population densities increased. By the 1990s elephant densities increased in the Mara which caused a loss woody cover by the removal of seedlings and regenerating rootstocks. Until today, the Mara is maintained in a predominately grassland state (Dublin and Douglas-Hamilton 1987, Dublin et al. 1990b), with sparsely distributed *Acacia* and *Croton* woodland thickets. The sustained decline in woody vegetation may threaten the biodiversity that depends on it, leading to increased browser competition for the few remaining resources (Walpole et al. 2004). It is therefore important to understand the causes of changing woodland composition given their importance as a source for niche separation in animal communities (Silvertown 2004).

RAINFALL AND VEGETATION QUANTITY AND QUALITY

Rainfall patterns influence livestock and wildlife biomass (Coe et al. 1976, East 1984, Fritz and Duncan 1994), abundance (Ogutu et al. 2008), distribution (Western 1975), demography and population dynamics (Owen-Smith and Mills 2006), through its influence on vegetation (both quantity and quality), habitat suitability and availability of surface water. The standing grass biomass in the herb layer of east African grasslands varies dramatically during the course of a year in response to seasonal rainfall (Boutton et al. 1988b). These large fluctuations in vegetation standing biomass are extremely important in determining feeding styles (East 1984) and movement patterns (Talbot and Talbot 1963, Maddock 1979) by large mammalian herbivores. Concomitant with the seasonal variability in plant biomass are equally important changes in nutrient content and digestibility. At the onset of the wet season in the Maasai Mara National Reserve, grasses are high in digestibility and nutrient concentrations, such as nitrogen and phosphorous (Sinclair 1975). During this period of early growth, concentrations of crude protein in grass leaves are approximately 8-20%. As the grass grows taller, its nutritional quality declines as a result of increases in structural carbohydrates, so that both nutrient concentration and digestibility decrease (Boutton et al. 1988b). During the dry season, in contrast, vegetation quantity is low but of higher quality (Fritz and Duncan 1994).

HERBIVORE BODY SIZE AND FOOD QUANTITY AND QUALITY

In addition to influencing their response to seasonal rainfall variation, body size also influences the choice of habitats by herbivores. Small-bodied herbivores have narrow dietary tolerances because they have small rumens and can retain ingesta in the rumen for only short periods of time (Kerr and Packer 1997). They thus tend to select the most easily digestible and nutritious plant matter (Kerr and Packer 1997, Du Toit and Cumming 1999). In contrast, larger-bodied herbivores are relatively unconstrained by the quality of forage because of their large digestive tracts and are therefore able to extract sufficient energy from coarse forage (Illius and Gordon 1992, Kleynhans et al. 2011).

BODY SIZE AND PREDATION RISK

Predation risk is tightly linked to herbivore body size (Hopcraft et al. 2011). Larger herbivores are less vulnerable to predation because they are more difficult to capture and handle by predators due to their large body-size (Sinclair et al. 2003). Tall and dense vegetation cover generally conceals predators thereby increasing their efficiency in catching prey (Hopcraft et al. 2005, Riginos and Grace 2008). Thus it can be expected that predation risk should be higher during the wet season when grass height is relatively taller compared to the dry season. Furthermore, such landscape features as rivers and valleys also conceal predators and enhance predation risk. As a result, small and medium-sized herbivores that are more susceptible to a broader spectrum of predators than are larger ones avoid these areas and tend to concentrate instead in areas of shorter grass cover where visibility of potential predators is higher.

THE MARA REGION AS A RESEARCH AREA

In African savannas the distribution of herbivores has been relatively well studied within protected areas, such as the Mara-Serengeti ecosystem of Kenya and Tanzania (McNaughton 1988, McNaughton 1990, Anderson et al. 2010), but are much less well understood in human–dominated pastoral systems, such as the pastoral ranches of the Mara region in Kenya. Even fewer studies have considered how functional differences among herbivores owing to variation in body size and feeding style, rainfall seasonality and predominant land use shapes herbivore distributions, through their effect on the quality and quantity of food and predation risk (Sensenig et al. 2010, Hopcraft et al. 2011, Kleynhans et al. 2011).

Understanding the consequences of human activities in human-dominated rangelands bordering protected areas on the density, demography and persistence of large herbivores over relatively long periods of time requires an intact ecological baseline area or benchmark that is relatively free of human impact (Sinclair et al. 2002). Therefore, the Mara-Serengeti ecosystem is an ideal benchmark for assessing how changes in human and livestock-dominated systems influence wildlife in pastoral systems over time. Importantly, wildlife has been monitored by the Department for Remote Sensing and Resource Survey (DRSRS) continually for 41 years in the Mara region of Kenya, producing 50 independent aerial surveys conducted using the same counting technique during 1977-2010. This increases our confidence in and ability to separate the impacts on wildlife distributions of livestock and human use of the pastoral ranches of the Mara despite the lack of true replication, which is extremely difficult, if not impossible to achieve in practice at landscape scales.

SPECIFIC RESEARCH QUESTIONS:

How do area, heterogeneity and productivity interact to shape species richness patterns?

In **Chapter 2**, I explore if the effects of reduced area on species richness can be substituted with or compensated for to some extent by increasing landscape heterogeneity or productivity. I explore this hypothesis by analyzing the relative importance of area, heterogeneity and productivity in shaping species richness across 300 protected areas in continental Africa.

Having explored these relationships inside protected areas on a continental scale, I then investigate the processes structuring community assembly of woodlands and seasonal movements of large mammal communities in the Maasai Mara National

Reserve and its surrounding rangelands. Thus, I address the following specific additional questions:

What are the ecological processes which maintain richness, composition and stability within tree communities in African savannas?

The woodland communities in the Maasai Mara National Reserve represent important and reliable habitats for many browsing herbivores, especially during dry periods (Oloo et al. 1994, Dublin 1995). Understanding the processes that maintain the assembly of woodland communities across space in African savanna tree communities is often unknown. Three generic types of assembly processes have been proposed. (1) competition (Tilman 1994) (2) habitat filtering (Wilson and Keddy 1986, Callaway 1995) and (3) stochastic processes (Hubbell 2001). In **Chapter 3**, I asses the importance of these process in shaping assembly of tree communities arrayed along a rainfall gradient. I use nestedness of community composition, and the relations between rainfall and diversity, rainfall and stability, and diversity and stability as indicators of the relative importance of different community assembly processes. If competitive interactions are important in structuring these communities, diversity should decrease with increasing rainfall due to competitive replacement, but stability should increase with diversity. Alternatively, if diversity increases with rainfall, competitive processes are apparently not important. Instead, either habitat filtering or stochastic processes determine the community assembly. Strong nestedness in the community structure could result from complex interactions between species determined by a species' ability to cope with stresses or disturbances or by to ecological drift. I use a long term dataset based on biennial vegetation monitoring data collected by the Masai Mara Ecological Monitoring program over a 15-year period spanning 1989–2003 in Kenya's Maasai Mara National Reserve (MMNR) to test these predictions.

How do pastoralism and protection influence the distribution and abundance of large carnivores in the Mara region of Kenya?

The overlap of large carnivores, livestock and people can create conflicts that often threaten the future viability of carnivore populations in the pastoral systems of Africa. As the natural prey-base for carnivores declines, carnivores are threatened by local extinction. The patterns of predation are also likely to vary among seasons because of related changes in prey vulnerability. In **Chapter 4**, I examine how pastoralism and protection influence carnivore density and distribution by: (1) estimating the density and population size of lions, spotted hyenas and jackals; (2) characterizing their spatial distribution inside and outside the reserve; and (3) establishing the extent to which land management influences carnivore population levels and spatial distribution by controlling for the effects of grass height, elevation and prey biomass density.

How do agro-pastoralism and protection influence the abundance and demography of large herbivores in the Mara region of Kenya?

Wild herbivores often move seasonally across landscapes and conservation boundaries to obtain essential resources. These seasonal movements are constrained by herbivore body size through its influence on food quantity and quality as well as vulnerability to predation. Large herbivores can tolerate more fibrous and lower-quality diets than can small herbivores because of their larger gastrointestinal tracts and lower specific metabolic requirements (Owen-Smith 1988, Ritchie and Olff 1999, Hopcraft et al. 2010). In addition, large herbivores are much more difficult for predators to capture so that a smaller fraction of large herbivores die from predation than do small herbivores (Sinclair et al. 2003). Thus, it may be expected that large herbivores should concentrate inside the reserve where forage availability is sufficiently high all year-round owing to the absence of livestock grazing, whereas small herbivores can be expected to concentrate in the human-dominated pastoral landscapes, where vegetation is kept in a short and active growth stage by livestock, thereby minimizing predation risk because of lower densities and high visibility of potential predators. Thus, herbivore body size can be expected to control their responses to seasonal disparities in forage quantity and quality and predation risk between protected and pastoral landscapes. In **Chapter 5**, I test these hypotheses by comparing and contrasting the density and demography of 13 wild and three domestic herbivore species of varying body sizes (15-1725Kg) and between the Maasai Mara National Reserve and its adjoining pastoral ranches using aerial surveys conducted in the wet and dry seasons during 1977-2010.

Which factors influence the spatial distribution of hotspots of large herbivore abundance in the Mara region of Kenya?

Food availability and quality and predation risk have all been identified as key determinants of herbivore hotspots in savannas. Hotspots are defined as locations of high densities of (often multiple species of) wild herbivores that persist for extended periods of time. The long-term persistence of hotspots depends upon the stability, predictability and sufficiency of forage despite variability mediated through rainfall seasonality (Fryxell et al. 2005). This raises fundamental questions about the extent to which ecological factors and processes shaping distributions of hotspots in protected areas can be extrapolated to human-dominated systems, such as the pastoral ranches of the Mara region. In **Chapter 6**, I investigate the relative effects of multiple environmental and anthropogenic factors on spatial distributions of herbivore hotspots both inside and outside the protected area on different landscapes dominated by livestock and cultivation. I propose a metric for characterizing hotspots based on quantile regression analysis which I then apply to assess how herbivore hotspots change over time and space and what environmental and anthropogenic factors determine the presence of hotspots of herbivores in the Mara using the 10 most abundant species within the protected reserve and its adjoining pastoral landscapes.

Finally, in **Chapter 7**, I integrate and synthesize the key findings of the different chapters and discuss some characteristics that may influence the vulnerability of protected areas in relation to ongoing land use and climate changes and highlight the implications of this study in the wider context of global conservation efforts.


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Chapter 2

Dissecting the interplay between area, landscape heterogeneity and productivity in shaping species richness in African protected areas

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ABSTRACT

We investigated the influences of landscape heterogeneity and primary productivity relative to that of protected area size on species richness of large African mammals in 300 protected areas distributed throughout Africa. Landscape heterogeneity was quantified using a multidimensional composite index encompassing spatial variation in NDVI, elevation and habitat types whereas primary productivity using the spatial mean of NDVI. Species richness for carnivores, ungulates and primates was calculated using distribution data derived from the African Mammal Databank. Carnivore species richness responded positively to increasing spatial heterogeneity but not area or productivity, whereas ungulate and primate species richness responded positively to increasing spatial heterogeneity and primary productivity gradients but less sensitively to variation in protected area size. Although significantly positively correlated with species richness, protected area size became insignificant after factoring out the effect of landscape heterogeneity and productivity, suggesting that area captures only part of the variance explained by these two factors. Hence heterogeneity and productivity can be viewed as two proximate determinants of species richness beyond the contribution of area. The variance explained by area was largely due to variation in landscape heterogeneity and productivity and became insignificant after accounting for variation in the latter two factors. These findings have three significant implications for biodiversity conservation. First, conservation efforts should be directed at preserving or promoting heterogeneity in protected areas of all sizes to ensure the continued coexistence of their complement of multiple species assemblages. Second, strategically positioning small protected areas in more heterogeneous and productive landscapes will enhance the biodiversity they can conserve. Lastly, large protected areas are essential not only for hosting (large) source populations for small areas but also for ensuring long-term viability of wide-ranging species.

INTRODUCTION

Terrestrial protected areas cover 16.8 million km^2 (11%) of the world's land surface area (West et al. 2006) of which Africa contributes 4.2 million km^2. However, the effective ecosystem size and species' home ranges often extend well beyond the designated boundaries of most protected areas. As a result, degradation, fragmentation and loss of natural habitats around protected areas progressively reduce their conservation capacity (Harcourt et al. 2001) and hence species richness, especially for small protected areas (Parks and Harcourt 2002). Besides the loss of surrounding natural habitats, high human population densities pressing against protected area boundaries further reduce their effective sizes and wildlife dispersal movements, thus increasing the risk of localized species extirpations (Parks and Harcourt 2002, Newmark 2008). If protected areas function as habitat islands as predicted by the classic island biogeographic theory (MacArthur and Wilson 1967, Schoener 1976), then we should expect a positive relationship between protected area size and species richness. A common mechanism underlying such relationships is a dynamic equilibrium between immigration and extinction rates that buffer large populations against the risk of extinctions (MacArthur and Wilson 1967, Pimm et al. 1988). Furthermore, large areas are generally better buffered from external pressures because they have shorter perimeters relative to their surface areas (Vézina 1985). The size of a protected area might also influence its species richness indirectly via other factors. Large areas are more likely to contain a higher diversity of habitats than smaller ones and the resultant high spatial heterogeneity can enhance species richness by offering more opportunities for niche differentiation (MacArthur and Wilson 1967, Schoener 1976). This promotes greater specialization and coexistence of many species, whilst lessening the effects of catastrophic events (Ricklefs and Lovette 1999). The species-energy hypothesis is yet another complementary theory that attempts to explain patterns of species richness beyond that explained by area. It predicts a positive relationship between species richness and available energy to higher trophic levels, with net primary productivity (NPP) often used as a proxy for energy availability (Wright 1983, Currie 1991, Kerr et al. 2001). A common explanation for this relationship is that areas with greater food supply support more individuals, and hence the resultant communities support more species at a given population size (Wright et al. 1993, Kaspari et al. 2000). Another plausible explanation of this relationship is that areas with higher primary productivity are less seasonally variable (Kay et al. 1997) and therefore have more abundant supply of resources throughout most of the year. This promotes the coexistence of many species (DeAngelis 1994, Srivastava and Lawton 1998).

Since area *per se*, heterogeneity and productivity each can explain only part of the variation in species richness among protected areas, it is surprising that very few studies have examined their relative importance (Ricklefs and Lovette 1999, Rensburg et al. 2002). This raises fundamental questions about how area, heterogeneity and productivity might interact to shape species richness patterns. There are three main mechanisms through which area, habitat heterogeneity and productivity may interactively determine species richness. First, many small protected areas are situated in unique habitats in which the structural diversity of vegetation or landscape heterogeneity is sufficiently high to support rich species assemblages (Báldi 2008). Such locally unique conditions are often the main reason for selecting the locations of the protected areas in the first place. Hence, small areas may deviate from the expected species-area relationship for the species groups they support making species richness appear independent of area size even if it is not (Lomolino and Weiser 2001, Triantis et al. 2003). Second, in analogy to the theory of how multiple resources limit the growth of single plant species (Tilman 1982), area, heterogeneity and productivity can be viewed as different factors limiting species richness. Multiple outcomes are then possible from their combinatory effects, with an increase in a currently limiting factor leading to an increase in species richness, while an increase in the other non-limiting factors having little effect on richness. As an example, a small park which is highly heterogeneous will contain a high diversity of habitats but because its small area size is a limiting factor, population sizes will be small and the species it supports will be more vulnerable to extinction. Thus, an increase in area would decrease extinction risk, thereby increasing richness, while an increase in heterogeneity would not increase richness due to high extinction rates. However, if a park is large, while heterogeneity is low then an increase in park size alone would increase the population size but only an increase in heterogeneity will increase the diversity of habitat types and therefore species richness (Fig. 2.1A). The same argument applies to the combined effects of area and productivity and heterogeneity and productivity in the case where area does not explain much of the variation in species richness. In either case, the operations of the three factors resemble that of essential limiting resources (Tilman 1982). The limiting factor hypothesis may be more generally applicable to a range of factors beyond those we consider here (Kerr and Packer 1997). Third, the effects of area and heterogeneity or productivity on species richness may be substitutable to some extent such that the effect of reduced area on species richness can be compensated for by increasing landscape heterogeneity or productivity (Fig. 2.1B). Heterogeneity and productivity may also operate in a similarly substitutable way. In both cases, the three factors may determine species richness similarly to substitutable limiting resources (Tilman 1982).

The aim of this study is to dissect and understand the interplay between area, heterogeneity and productivity in shaping patterns of mammalian species richness across 300 African protected areas. In particular, we tested if these three factors operate as essential or substitutable factors in determining species richness, and explored how their effects vary among three major mammalian taxa (carnivores, ungulates and primates). Protected areas in Africa provide a rare opportunity for studying the role of these three factors on variation in species richness because they tend to be relatively small in size with most ranging in area between 10 and 100 km_ and only a few exceeding 10,000 km_ (Chape et al. 2008). Furthermore, these areas have widely varying habitat types, productivities and topographies. For this study we collated data on species richness from distribution data for 75 carnivores, 95 ungulate and 57 primate species. Habitat heterogeneity was assessed using a linear combination of

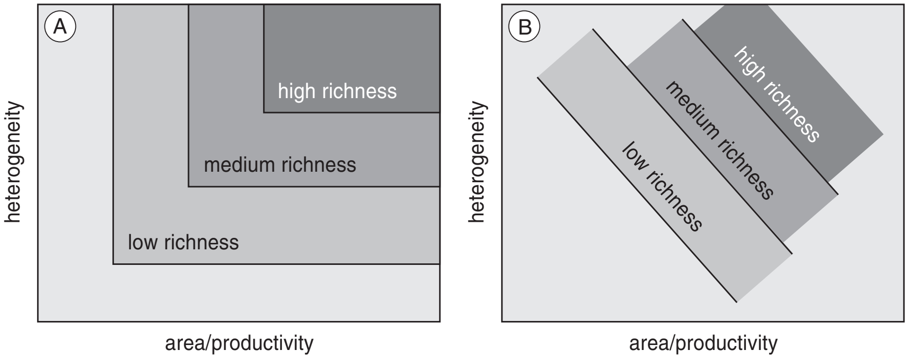

Figure 2.1 Theoretical predictions of the relative importance of both area and heterogeneity in determining species richness. A) An increase in one limiting factor leads to an increase in species richness, while an increase in the other non-limiting factor has little effect on richness. B) The effect of reduced area on species richness can be compensated for by increasing landscape heterogeneity.

spatial variability in NDVI averaged over a 5-year window to minimize temporal variance, elevation and habitat types. We used the spatial mean of NDVI as a proxy for primary productivity. These variables were selected because they have been measured at high spatial resolutions over the entire African continent and have been widely used previously to predict patterns of species richness (Rahbek and Graves 2001, Jetz and Rahbek 2002, Kerr and Ostrovsky 2003).

MATERIALS AND METHODS

Selection of Protected Areas

We selected 300 African protected areas from the World Database on Protected Areas (WDPA 2006) prepared by a consortium of various organizations (Fig. 2.2). The database contains information derived from governmental agencies with direct responsibility for protected areas and includes the site name, national designation, location, size, International Union for Conservation of Nature (IUCN) management category, date of designation, whether the protected area is marine or terrestrial and a biogeographic code. We selected only terrestrial protected areas designated in accordance with the IUCN management categories and measuring at least 20 km^2 in size. Protected areas of this size are large enough to potentially include several different habitat types, with varying habitat structures and elevations (Seiferling et al. 2011). In many countries, there were overlaps between adjacent protected areas, with strict nature reserves lying within boundaries of national parks or other protected area categories. Furthermore, several different protected areas were sometimes situated adjacent to one another and hence functioned as one larger, ecological protected unit. We therefore, merged or embedded such adjacent protected areas together in ArcGis 9.3 (ESRI 2009) and re-calculated the total area of the entire cluster of protected areas. For

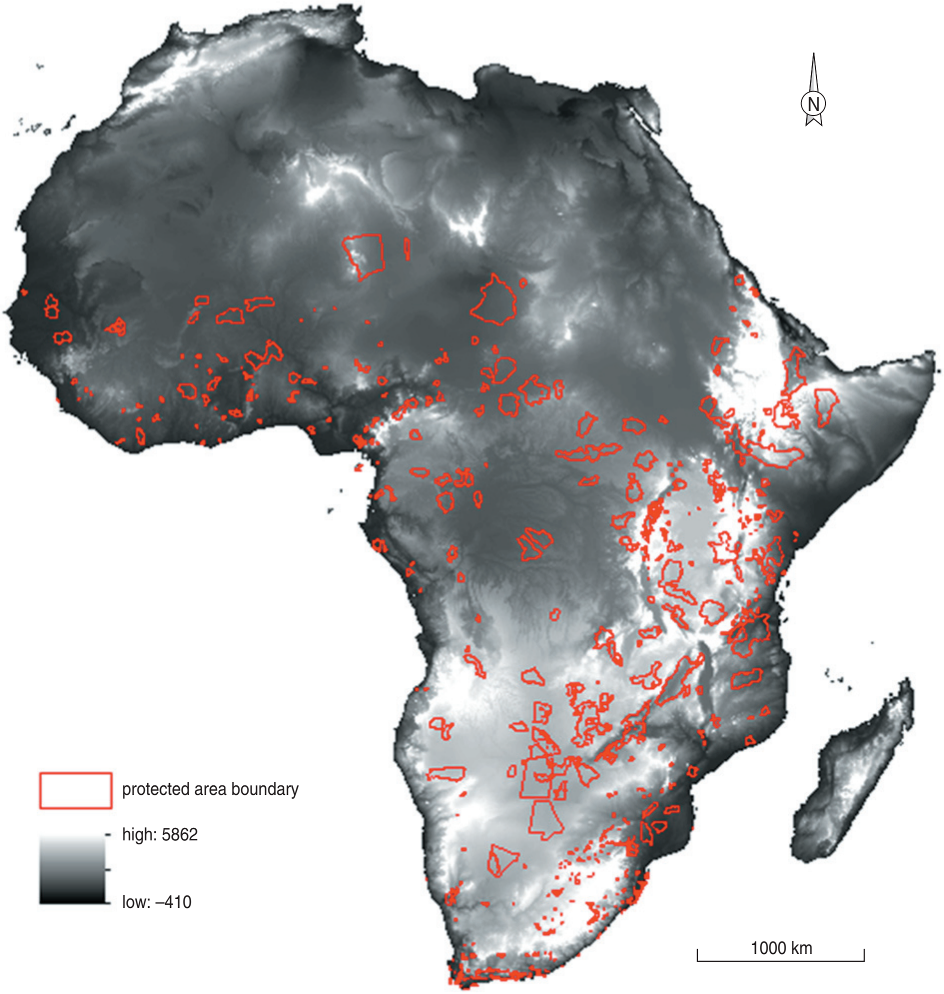

Figure 2.2 The 300 protected areas considered in this study overlaid on the SRTM (Shuttle Radar Topography Mission) world digital elevation. Elevation ranges from a minimum of -410 m below sea level (black) to a maximum of 5862 m above sea level (white).

example, we merged the Tanzanian Serengeti National Park and Ngorongoro Conservation Area and the Kenyan Maasai Mara National Reserve into one larger cluster of protected areas representing the Serengeti-Mara ecosystem straddling the Kenya-Tanzania international boundary. The merging operations reduced the total number of protected areas from the initial 657 to 300, ranging between 20 -11,0844 km^2.

Data on large African mammals

We selected large mammal species with well-known distributions in Africa from the African Mammal Databank compiled by a consortium of 12 international organiza-

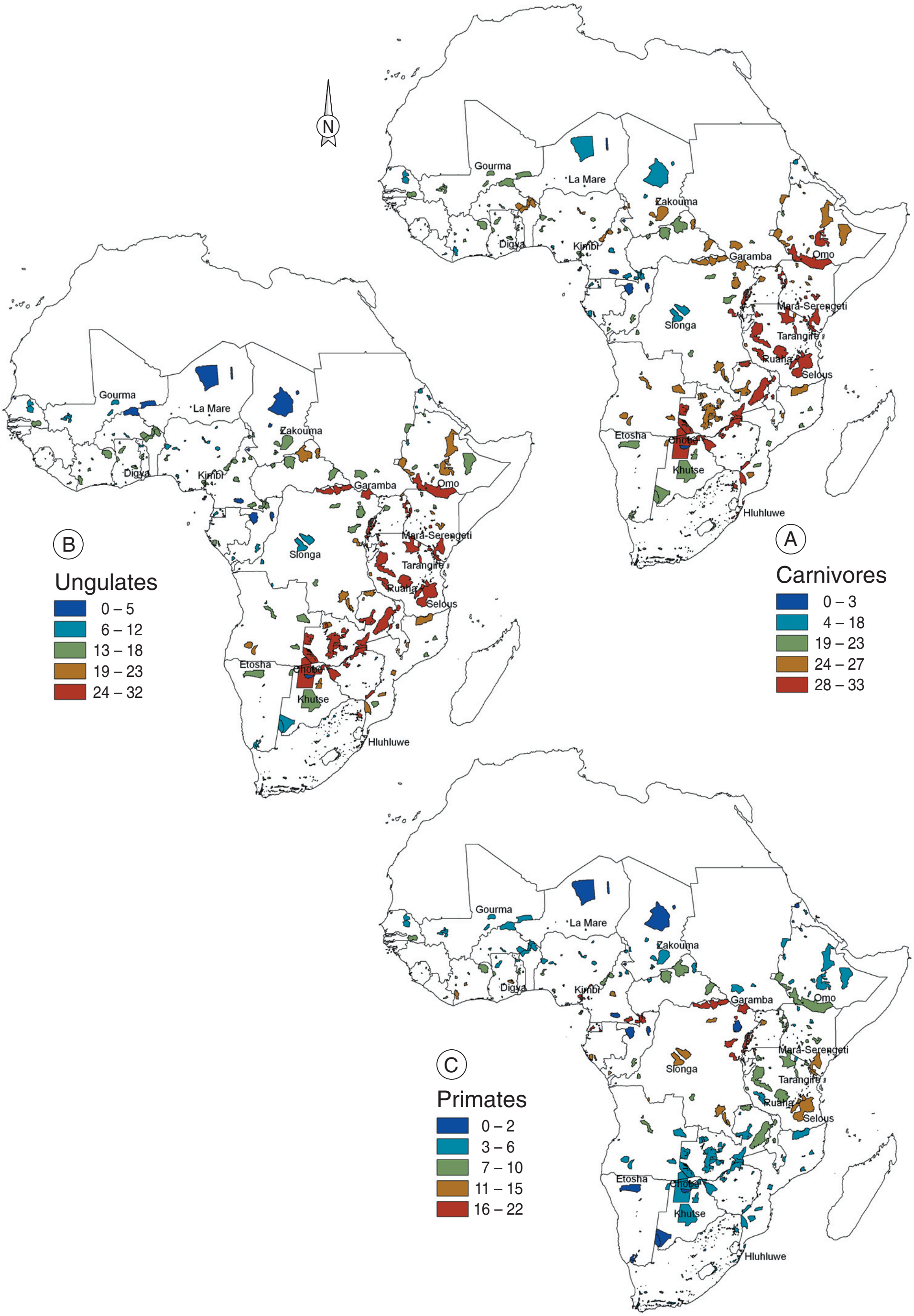

Figure 2.3 Species richness in each protected areas across Africa for each taxa A) carnivore, B) ungulate C) primate.

tions (International Union for Conservation of Nature, World Conservation Monitoring Centre, Birdlife, Conservation International, The Nature Conservancy, etc.), drawing together a network of more than 7000 experts around the world. Boitani et al.(1998) provide complete details of the methods used to determine the distribution, ecology and conservation status for each species in Africa. The database includes information on all species belonging to the orders Primates, Carnivora, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla, and Pholidota and a full range of geo-referenced information on the distributions of the species. In summary, the data bank currently includes a total of 281 species, belonging to 7 orders and 28 families. We selected only species weighing more than 1 kg and belonging to three major taxa, namely carnivores (Canivora $n = 75$ species), ungulates (Artiodactyla and Perissodactyla, $n = 95$) and primates ($n = 57$). The presence or absence of each of these species was recorded in each of the selected protected areas. We then calculated species richness as the total number of different species coexisting in each protected area. Figure 2.3 shows the distribution of species richness within each taxa in each protected area.

Environmental data

Remotely sensed vegetation data

We used a remotely sensed vegetation index, the Normalized Difference Vegetation Index (NDVI) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS–TERRA) data set (2000 – 2005) subsetted for Africa. NDVI is derived from the near infrared (NIR) and visible red bands of a satellite image. The red and NIR light reflected from plants is a function of the photosynthetically active compounds present, which is related to Net Primary Productivity (NPP), (Tucker and Sellers 1986). Data on NDVI originally acquired at 250×250 m^2 resolution were resampled to 1×1 km^2 using ArcGis 9.3 (ESRI 2009) and a WGS84 Geographic Coordinate System (GCS). The NDVI data were averaged into a long-term mean annual NDVI for each grid cell within each protected area. We then used these data to estimate the spatial mean as a measure of primary productivity (NDVIMEAN) and variance (NDVIVAR, a component of heterogeneity) of NDVI across all grid cells within each protected area.

Variation in Elevation

Shuttle Radar Topography Mission (SRTM) data on elevation were acquired from 1-degree digital elevation model (DEM) tiles from the Consortium for Spatial Information (CGIAR-CSI) of the Consultative Group for International Agricultural Research (CGIAR). We used the new version of the original SRTM dataset, which omits single pixel errors. We first imported and merged the 1-degree tiles into continuous elevational surfaces in an ArcGRID format (Jarvis et al. 2008). Data from the DEM originally acquired at 90×90 m^2 resolution were then resampled to 1×1 km^2 in ArcGIS 9.3 (ESRI 2009) using WGS84 as a GCS. We used the data to measure spatial variation in elevation (EVAR) within each protected area, as a second component of spatial heterogeneity.

Habitat Diversity

Measurements of habitat types were derived from the Global Land Cover 2000 dataset, developed based on regional expertise. It uses a globally consistent legend based on the FAO Land Cover Classification System (FAO 2000) and 1 km resolution SPOT imagery (Mayaux et al. 2004). A total of 27 habitat categories have been documented. We defined habitat variety (HVAR) as the number of different natural land-cover classes in a protected area and used it as the third component of spatial heterogeneity.

STATISTICAL ANALYSES

Measurement of heterogeneity

Each of the candidate variables measures some aspect of landscape heterogeneity and productivity in protected areas. Thus, we expected protected areas with a large variety of habitat types and a high variance in elevation and NDVI to have high landscape heterogeneity, whereas, areas with lower variability in these factors to have correspondingly lower landscape heterogeneity. A good index of landscape heterogeneity should reflect the multiple potential niches or habitats that different species can occupy. We first evaluated the extent to which using the three candidate variables representing landscape heterogeneity, i.e., NDVIVAR, EVAR and HVAR performed better than using a single multivariate composite index of landscape heterogeneity derived from a principal components analysis (PCA). All the three variables were standardized to zero mean and unit variance prior to the analysis to minimize the effect of differences in measurement scale on their relative contributions to explaining variation in species richness. Since the first principal component (PC1) was correlated positively with all the three variables and explained most (66%, Table 2.1) of the total sample variance, we used the resulting factor loadings of PC1 instead of the individual variables as a composite index of landscape heterogeneity see, e.g. (August 1983).

We used multiple linear regression analyses to relate species richness to landscape heterogeneity (PC1), standardized mean primary productivity (NDVIMEAN) and the logarithm of area (LOGAREA) and their interactions, separately for each taxon. Linearity of the relationship between species richness and area was achieved through a logarithmic transformation of area. The models were fit using ordinary least squares and models of varying complexities compared using the corrected Akaike Information

Table 2.1 Factor loadings for the first principal component (PC1) from the principal component analysis. The first component explained 66% of the overall variance.

Variables	PC1
NDVIVAR	0.595
EVAR	0.571
HVAR	0.531

Criterion (Burnham and Anderson 2002) in R version 2.12.0 (R Development Core Team 2010). To establish if LOGAREA still influenced species richness after accounting for heterogeneity and/ or productivity, since both indices may be correlated with area, we calculated partial correlation coefficients between the species richness for each taxon and LOGAREA while partialling out heterogeneity or productivity.

RESULTS

The average species richness for the 300 African protected areas was highest for carnivores (22.9 ±2.0), intermediate for ungulates (14.6 ±5.1) and primates (6.7 ±2.6). Models containing all the three original variables used to calculate the composite index of heterogeneity (NDVIVAR, EVAR and HVAR) explained smaller variances in species richness for all taxa than using PC1 itself (Supplementary material Tables S1 and S1-S3). We therefore used PC1 to index landscape heterogeneity instead of using all its three original constituent variables. The partial correlation analyses (Table 2.2A) suggested that both area and heterogeneity are important predictors of species rich-

Table 2.2A Pearson correlation coefficients between the logarithm of protected area size and landscape heterogeneity (PC1) and species richness for carnivores, ungulates and primates.

	Carnivores†	Ungulates	Primates
Correlations			
Area	0.14 **	0.26 **	0.18 **
PC1	0.45 **	0.52 **	0.42 **
Partial correlations			
Area	-0.02 ns	0.07 ns	0.06 ns
PC1	0.43 ***	0.47 ***	0.39 ***

†** $P < 0.05$, ***$P < 0.01$

Table 2.2B Pearson correlation coefficients between the logarithm of protected area size and productivity (MEANNDVI) for carnivores, ungulates and primates.

	Carnivores†	Ungulates	Primates
Correlations			
Area	0.22 **	0.14 ns	0.19 ns
NDVI	0.30 **	0.21 **	0.53 **
Partial correlations			
Area	0.2**	0.11 ns	0.19 ns
NDVI	0.28**	0.15 **	0.39**

†** $P < 0.05$, ***$P < 0.01$

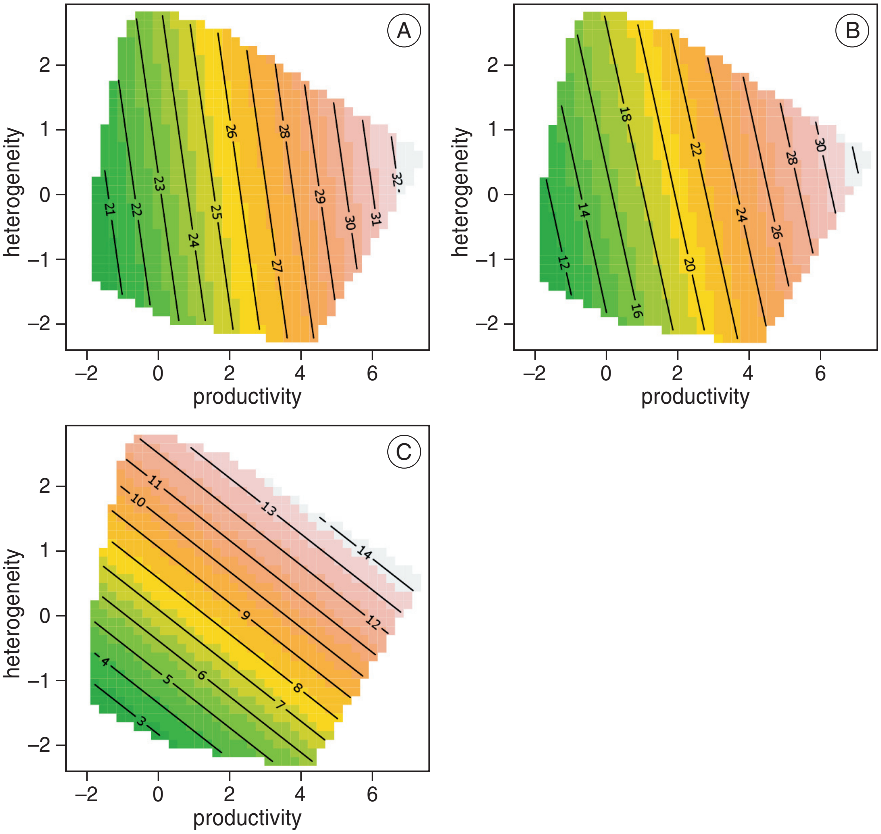

Figure 2.4 Bivariate linear interpolation plots showing the relationships between A) carnivore, B) ungulate and C) primate species richness and landscape heterogeneity (PC1) and primary productivity (NDVIMEAN) gradients for 300 African protected areas. Contour lines represent varying levels of species richness.

ness for all the three taxa, but that the correlations with log area were much smaller than those with PC1 or MEANNDVI (Table 2.2B). After factoring out the effects of heterogeneity (i.e. PC1) or productivity, protected area size accounted for only a minor and non-significant variation in species richness (Table 2.2A and B). In contrast, heterogeneity and productivity were both significantly correlated with species richness even after factoring out the effect of area.

From the multiple regression analyses, the AICc-selected best models for predicting species richness included gradients in landscape heterogeneity and primary productivity for all the three taxa (Supplementary material Tables S2-S4). Protected area size did not explain any additional variation in species richness beyond that explained by heterogeneity and productivity for any of the three taxa. Specifically, carnivore richness increased significantly only with increasing landscape heterogeneity (Table 2.3, Fig. 2.4A) whereas ungulates and primate richness increased significantly with both

Table 2.3 Multiple linear regression coefficients (estimate), their standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits for the AICc-selected best approximating models relating carnivore, ungulate and primate species richness to landscape heterogeneity gradient (PC1) and primary productivity gradient (NDVIMEAN) for 300 African protected areas.

Taxa	Effect	Estimate	SE	LCL	UCL	T	P>lTl
Carnivores	Intercept	22.9	0.266	22.37	23.42	86	0.0003
	PC1	1.35	0.188	0.98	1.72	7.2	0.0004
	NDVI	0.34	0.261	0.17	0.85	1.3	0.189
Ungulates	Intercept	15.64	0.336	14.97	16.3	14.9	0.0007
	PC1	2.3	0.237	1.83	2.76	1.8	0.0005
	NDVI	0.9	0.33	0.25	1.55	0.2	0.0073
Primates	Intercept	6.7	0.192	6.32	7.08	6.3	0.0007
	PC1	0.9	0.135	0.63	1.16	0.6	0.0007
	NDVI	2.08	0.188	1.71	2.45	1.7	0.0004

increasing heterogeneity and productivity (Table 2.3, Figs 2.4B and C). A unit change in landscape heterogeneity was associated with a larger change in species richness than a similar change in productivity for ungulates but primate species richness showed the opposite pattern (Table 2.3, Fig. 2.4C, Supplementary material Tables S2-S4). For primates, primary productivity and heterogeneity acted in apparently substitutable ways (Fig. 2.4C), such that areas of high landscape heterogeneity but low productivity supported high species richness. There was little support for quadratic relationships between species richness and any of the three predictor variables or their interactions for all the three taxa (Table 2.3, Figs 2.4 A-C).

DISCUSSION

The classic island biogeographic theory (MacArthur and Wilson 1967) predicts relationships expected between species richness, area and colonization rates, and postulates that larger areas should support more species and larger populations by providing more opportunities for niche differentiation and dispersal (Ricklefs and Lovette 1999). Habitat diversity, which often correlates with area, is well known to affect species richness independently of area *per se* (Rosenzweig 1995), such that, all else being equal, the more habitats an area has, the more species it can support. The amount of primary productivity is also positively related to species richness (Wright et al. 1993). We thus tested the effects on species richness of (*i*) the size of a protected area, which affects immigration and extinction rates, with large populations having low risks of extinction, (*ii*) landscape heterogeneity, necessary for niche differentiation and coexistence of multiple species and, (*iii*) mean primary productivity, indexing the availability of temporally stable resources or more individuals.

The contributions of the three different factors to explaining variation in species richness differed among the three mammalian taxa. Carnivore species richness was sensitive to habitat heterogeneity but not area or productivity. This is surprising because carnivores are wide-ranging species requiring large home-ranges (Ruggiero and Kitzberger 2004) able to support large prey populations through greater resource supply and hence reduce vulnerability to extinctions. Our findings suggest that the influence of area on carnivore species richness can be captured through the effect of heterogeneity thus making heterogeneity an essential predictor of carnivore species richness over and above that of area. Carnivore richness was higher in more heterogeneous areas suggesting that coexistence of multiple carnivore species is enabled by a greater niche differentiation that promotes greater resource partitioning among carnivores and their prey species (Vézina 1985).

For ungulate richness, habitat heterogeneity accounted for markedly more variation than primary productivity or area did. Ungulates species richness was positively correlated with habitat heterogeneity, with primary productivity making a statistically significant but marginal additive contribution, suggesting that, like carnivores, ungulates also tend to exploit their environments in different ways. Several factors, including mouth and gut morphology and body size underpin interspecific differences among ungulates with respect to diet (Bell 1970, Jarman 1974, Kerr and Packer 1997). Cromsigt et al. (2009) also found that landscape heterogeneity facilitated ungulate diversity in savanna ecosystems independently of area at more local scales. This is consistent with the notion that high spatial heterogeneity promotes species richness because limiting resources can be more readily shared in complex habitats (Ruggiero and Kitzberger 2004). It is likely that high habitat heterogeneity supports correspondingly high ungulate species richness by promoting greater specialization and coexistence of a large number of species (Srivastava and Lawton 1998). Additionally, the population of certain ungulate species may also be locally high, resulting in a marginally significant relationship with productivity, if the amount of productivity in a system provides better opportunities for supporting more individuals or a broader resource base necessary for more species to coexist (Kaspari et al. 2000). Our results thus provide some support for the limiting resource hypothesis that states that heterogeneity, and, to some extent productivity, are essential factors in determining ungulate species richness.

For primates, we found that both productivity and heterogeneity have strong effects on species richness, suggesting that they may operate in a substitutable way. This means that the constraint imposed on primate species richness by low landscape heterogeneity can be compensated for by high productivity. This is likely because primates generally span a narrower range of energy variation, indexed by primary productivity (mainly tropical rainforests), than the other taxa (Ruggiero and Kitzberger 2004). We found no significant effect of area on primate species richness after accounting for heterogeneity and productivity. Kay et al. (1997) found a similar pattern for primates in South America, suggesting that habitats with the highest plant productivity are also less seasonally variable, and therefore, support many primate species by providing an abundant supply of food sources all year-round.

Although these findings reveal interesting patterns in the relationships established between mammal species richness, area, heterogeneity and productivity, some caveats should be kept in mind when interpreting the patterns. First, even though our results suggest that a small park which is highly heterogeneous should support high species richness, the relationship between area and heterogeneity may be confounded with that of intensive management in small parks. Such management may involve the promotion of landscape heterogeneity (e.g. through fire management), manipulation of diversity through species reintroductions, translocations and culling operations. Species reintroductions are a common practice in Africa, especially in smaller southern African parks (Hayward et al. 2007). In the absence of such managerial interventions, small parks would probably contain fewer species than larger ones due to local extinctions, as predicted by the island biogeographic theory. However, where management interventions are largely absent, area and heterogeneity may be substitutable to some extent in their effects on species richness such that the effect of reduced area on species richness can be compensated for by increasing landscape heterogeneity as hypothesized in Fig. 2.2B. It can thus be argued that intensive management aimed at promoting functional heterogeneity may compensate to some degree for the effect of small area size in small parks (Du Toit et al. 2003).

Second, another possible explanation for the lack of a strong species-area relationship is that conservation reserves are not yet really true islands in Africa (Newmark 1995). The officially gazetted size of an unfenced game reserve is often less than the area actually used by some species. Only when game reserves are either completely fenced, or become effectively isolated by surrounding development will most species be completely unable to disperse beyond the reserves and remain confined to habitats available within the reserves. Until such isolation occurs, the effective size of a reserve will be greater than its nominal size. This disparity between nominal and effective reserve area available for species was the case for many reserves in our sample of 300 African protected areas, allowing many species to range beyond designated reserve boundaries.

These findings suggest that while the size of an area is significant in determining mammalian species richness, its dominant role may be mediated through variation in habitat heterogeneity and primary productivity (Wright 1983, Hurlbert 2006, Kalmar and Currie 2006). Our results have important implications for biodiversity conservation and conservation planning strategies (see e.g. Báldi 2008). New conservation reserves should ideally be strategically situated in productive areas with high habitat diversity to reduce threats to biodiversity and promote long-term viability of species assemblages. This will often not be possible, however, because rapid human population expansion and the associated pressure for more productive land to support the populations will usually make the excision of such areas for reserves difficult.

Acknowledgements

We thank the consortia that produced the World Database on Protected Areas, Global Land Cover 2000, and African Mammal Databank for making their data freely available.

SUPPLEMENTARY MATERIAL

Table S1 Multiple linear regression coefficients (estimate), their standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits and AICc values for all the three original variables used to calculate the composite index of heterogeneity (NDVIVAR, EVAR and HVAR) for 300 African protected areas. r^2 is the amount of variance explained by each model expressed as a percentage.

Species	Effect	Estimate	SE	LCL	UCL	T	P>ITI	AICc	r^2
Carnivores	Intercept	19.7	0.579	18.56	20.84	34.1	0.000	1704.9	14. 7
	NDVIVAR	34.22	16.499	1.74	66.69	2.1	0.039		
	EVAR	0.01	0.002	0	0.01	2.2	0.031		
	HVAR	0.31	0.112	0.09	0.53	2.8	0.005		
Ungulates	Intercept	10.06	0.742	8.6	11.52	13.6	0.0005	1849.2	22.9
	NDVIVAR	84.78	21.177	43.1	126.47	4	0.014		
	EVAR	0.06	0.031	0	0.012	1.9	0.0006		
	HVAR	0.46	0.144	0.017	0.74	3.2	0.00002		
Primates	Intercept	4.83	0.493	3.85	5.79	9.8	0.000	1612.1	11.5
	NDVIVAR	70.09	14.054	42.43	97.75	4.9	0.000		
	EVAR	0.001	0.002	0.001	0.002	0.5	0.626		
	HVAR	-0.08	0.096	-0.27	0.1	-0.9	0.385		

Table S2 Multiple linear regression coefficients (estimate), their standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits and the corrected Akaike Information Criterion (AICc) for the 10 models relating carnivore species richness to landscape heterogeneity gradient (PC1), primary productivity gradient (NDVI) and the logarithm of area for 300 African protected areas. The selected best model is highlighted in bold face. r^2 is the amount of variance explained by each model expressed as a percentage.

Models	Effect	Estimate	SE	LCL	UCL	T	P>|T|	AICc	r^2
1	Intercept	20.740	0.917	18.940	22.540	22.600	0.001	1740.700	2.100
	Log Area	0.320	0.131	0.070	0.580	2.400	0.014		
2	Intercept	22.900	0.267	22.380	23.430	85.900	0.001	1697.600	15.700
	PC1	1.372	0.188	1.000	1.740	7.300	0.000		
3	Intercept	22.900	0.289	22.330	23.470	79.200	0.001	1744.400	0.800
	NDVI	0.440	0.283	-0.120	1.000	1.500	0.121		
4	**Intercept**	**22.900**	**0.266**	**22.380**	**23.430**	**86.000**	**0.000**	**1697.200**	**16.200**
	PC1	**1.350**	**0.188**	**0.990**	**1.730**	**7.200**	**0.000**		
	NDVI	**0.340**	**0.261**	**-0.170**	**0.860**	**1.300**	**0.189**		
5	Intercept	23.200	0.926	21.380	25.030	25.000	0.000	1699.500	15.700
	Log Area	-0.040	0.134	-0.310	0.220	-0.300	0.735		
	PC1	1.460	0.206	0.990	1.810	6.700	0.000		
6	Intercept	20.530	0.919	22.380	23.430	22.300	0.001	1739.100	3.300
	Log Area	0.350	0.131	0.100	0.610	2.700	0.007		
	NDVI	0.530	0.282	-0.020	1.090	1.800	0.060		
7	Intercept	23.020	0.936	21.180	24.870	24.600	0.000	1699.800	16.100
	Log Area	-0.010	0.135	-0.280	0.250	-0.100	0.893		
	PC1	1.370	0.207	0.960	1.780	6.600	0.001		
	NDVI	0.330	0.265	0.000	1.090	1.200	0.202		
8	Intercept	23.220	0.951	21.360	25.100	24.400	0.000		
	Log Area	-0.040	0.134	-0.310	0.220	-0.300	0.728	1701.500	15.800
	PC1	1.480	0.730	0.050	2.930	2.000	0.042		
	Log Area x PC1	-0.010	0.094	-0.200	0.170	-0.100	0.900		
9	Intercept	20.850	0.914	19.060	22.660	22.800	0.000	1732.800	6.100
	Log Area	0.290	0.132	0.030	0.550	2.200	0.027		
	NDVI	3.010	0.905	1.240	4.800	3.300	0.000		
	Log Area x NDVI	-0.350	0.123	-0.600	-0.110	-2.800	0.000		
10	Intercept	22.880	0.267	22.360	23.410	85.800	0.000	1700.700	15.300
	PC1	1.400	0.192	1.020	1.780	7.300	0.000		
	NDVI	0.290	0.265	-0.230	0.820	1.100	0.264		
	PC1 x NDVI	0.200	0.194	-0.170	0.590	1.000	0.284		

Table S3 Multiple linear regression coefficients (estimate), their standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits and the corrected Akaike Information Criterion (AICc) for the 10 models relating ungulate species richness to landscape heterogeneity gradient (PC1), primary productivity gradient (NDVIMEAN) and the logarithm of area for 300 African protected areas. The selected best model is highlighted in bold face. r^2 is the amount of variance explained by each model expressed as a percentage.

Models	Effect	Estimate	SE	LCL	UCL	T	P>ITI	AICc	r^2
1	Intercept	10.410	1.209	8.030	12.780	8.600	0.000	1900.300	6.700
	Log Area	0.780	0.173	0.440	1.120	4.500	0.001		
2	Intercept	15.640	0.343	14.970	16.300	4.600	0.000	1838.000	24.800
	PC1	2.330	0.244	1.860	2.800	9.700	0.001		
3	Intercept	15.640	0.387	14.870	16.400	40.400	0.000	1912.700	2.600
	NDVI	1.060	0.379	0.310	1.810	2.800	0.005		
4	**Intercept**	**15.640**	**0.336**	**14.970**	**16.300**	**46.500**	**0.001**	**1832.600**	**28.700**
	PC1	**2.350**	**0.237**	**1.830**	**2.760**	**9.600**	**0.001**		
	NDVI	**0.900**	**0.336**	**0.250**	**1.550**	**2.700**	**0.007**		
5	Intercept	14.280	1.179	11.960	16.600	12.100	0.000	1838.600	25.200
	Log Area	0.200	0.174	-0.130	0.530	1.100	0.232		
	PC1	2.200	0.262	1.680	2.720	8.400	0.000		
6	Intercept	14.280	1.178	11.960	16.600	12.100	0.000	1890.100	10.600
	Log Area	0.200	0.169	-0.130	0.530	1.100	0.232		
	PC1	2.200	0.262	1.680	2.720	8.400	0.000		
7	Intercept	13.760	1.176	11.450	16.060	11.700	0.000	1832.800	27.400
	Log Area	0.280	0.173	-0.050	0.610	1.600	0.097		
	PC1	2.110	0.261	1.600	2.630	8.100	0.000		
	NDVI	0.980	0.333	0.330	1.640	2.900	0.003		
8	Intercept	14.350	1.209	11.970	16.730	11.800	0.000	1840.500	25.200
	Log Area	0.280	0.171	-0.130	0.530	1.100	0.244		
	PC1	2.410	0.929	0.590	4.240	2.600	0.010		
	Log Area x PC1	-0.020	0.123	-0.260	0.200	-0.200	0.810		
9	Intercept	10.290	1.191	7.950	12.640	8.600	0.000	1885.400	12.600
	Log Area	0.780	0.171	0.450	1.120	4.500	0.001		
	NDVI	4.170	1.178	1.850	6.490	3.500	0.000		
	Log Area x NDVI	-0.410	0.167	-0.720	-0.090	-2.500	0.011		
10	Intercept	15.650	0.337	14.980	16.310	46.400	0.000	1834.200	24.100
	PC1	2.260	0.243	1.790	2.740	9.300	0.000		
	NDVI	0.930	0.335	0.270	1.590	2.800	0.005		
	PC1 x NDVI	-0.150	0.245	-0.630	0.320	-0.600	0.529		

Table S4 Multiple linear regression coefficients (estimate), their standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits and the corrected Akaike Information Criterion (AICc) for the 10 models relating primate species richness to landscape heterogeneity gradient (PC1), primary productivity gradient (NDVIMEAN) and the logarithm of area for 300 African protected areas. The selected best model is highlighted in bold face. r^2 is the amount of variance explained by each model expressed as a percentage.

Models	Effect	Estimate	SE	LCL	UCL	T	P>|T|	AICc	r^2
1	Intercept	4.240	0.768	2.750	5.740	5.600	0.000	1632.200	3.800
	Log Area	0.370	0.109	0.160	0.580	3.400	0.001		
2	Intercept	6.700	0.229	6.260	7.160	29.300	0.023	1608.700	11.400
	PC1	0.970	0.161	0.660	1.300	6.100	0.343		
3	Intercept	6.700	0.206	6.300	7.110	32.600	0.342	1547.400	28.300
	NDVI	2.140	0.201	1.750	2.540	10.700	0.008		
4	**Intercept**	**6.700**	**0.192**	**6.330**	**7.080**	**35.000**	**0.000**	**1507.500**	**38.000**
	PC1	**0.900**	**0.135**	**0.640**	**1.170**	**6.700**	**0.000**		
	NDVI	**2.080**	**0.188**	**1.710**	**2.450**	**11.100**	**0.000**		
5	Intercept	5.810	0.793	4.260	7.380	7.300	0.002	1609.300	11.800
	Log Area	0.130	0.114	-0.090	0.360	1.200	0.243		
	PC1	0.890	0.176	0.550	1.240	5.100	0.001		
6	Intercept	5.820	0.793	4.260	7.380	7.300	0.007	1519.800	35.300
	Log Area	0.130	0.114	-0.090	0.360	1.200	0.243		
	PC1	0.900	0.177	0.550	1.240	5.100	0.002		
7	Intercept	4.670	0.661	3.370	5.970	7.100	0.000	1539.200	30.100
	Log Area	0.310	0.095	0.120	0.500	3.200	0.001		
	PC1	0.710	0.147	0.420	0.990	4.800	0.000		
	NDVI	2.180	0.187	1.810	2.550	11.600	0.000		
8	Intercept	6.190	0.807	4.600	7.780	7.700	0.000	1606.800	13.100
	Log Area	0.110	0.114	-0.110	0.340	1.000	0.335		
	PC1	2.150	0.620	0.930	3.370	3.500	0.001		
	Log Area x PC1	-0.170	0.080	-0.330	-0.010	-2.100	0.036		
9	Intercept	3.240	0.630	2.000	4.480	5.100	0.000	1517.900	36.100
	Log Area	0.530	0.091	0.350	0.710	5.800	0.081		
	NDVI	1.100	0.624	-0.130	2.330	1.800	0.078		
	Log Area x NDVI	0.170	0.085	0.000	0.330	2.000	0.049		
10	Intercept	6.730	0.191	6.350	7.100	35.300	0.000	1508.300	45.400
	PC1	0.850	0.137	0.580	1.120	6.200	0.001		
	Ndvi	2.150	0.190	1.770	2.520	11.300	0.000		
	PC1 x NDVI	-0.280	0.139	-0.560	-0.010	-2.000	0.042		


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Chapter 3

Community assembly processes in savanna woodlands in relation to rainfall

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ABSTRACT

Community assembly processes shape the diversity and composition of ecological communities. Three proposed generic types of assembly processes are competition, habitat filtering, and stochastic processes. Although the relative importance in shaping communities is likely to vary both spatially and temporally, little work has examined this variation in natural communities. Depending on their relative importance the three generic processes are expected to result in different relationships between rainfall and (*i*) community biomass, (*ii*) diversity, (*iii*) stability and (*iv*) composition. Using woodland community data from eight plots arrayed along an East-West rainfall gradient in the Masai Mara National Reserve of Kenya and monitored for 15 years, (1989-2003) we analyze relationships between spatial variation in rainfall and (*i*) community biomass, (*ii*) diversity, (*iii*) stability and (*iv*) composition and use them as proxies for establishing the relative importance of the three generic processes in the assembly of the savanna woodland communities along the rainfall gradient. Our results show that community biomass and species richness increased with increasing rainfall. Biomass decreased whereas richness and evenness hardly varied over time. Both rare and common species occurred in more diverse communities, prevalent at locations of high rainfall, suggesting strong nestedness patterns in community composition. Moreover, community stability and diversity were unrelated. Better conditions for tree establishment and better protection from browsers apparently enable rare species to successfully establish, leading to higher species diversity at high rainfall. Habitat filtering apparently limits species richness mostly in drier areas, whereas light competition apparently plays a limited role in the assembly of savanna woodland communities. If climate change further increases the frequency and severity of droughts and thereby lowers soil moisture, the intensity of browsing will increase reducing recruitment, especially of rare, stress-sensitive species, and hence the overall species diversity.

INTRODUCTION

Tropical savannas rank among the most widespread terrestrial biomes, covering some 20% of the earth's land surface area (Chape et al. 2008). Of this, Africa contributes more than a half and supports substantial human, livestock and wildlife populations. Besides their importance to supporting human wellbeing, only a minor part of African savannas is formally protected to preserve their high diversity and abundance of wildlife (Chape et al. 2008). Savannas are characterized by a continuous grass layer, scattered closed thickets of a diverse range of shrubs and dense *Acacia/Commiphora* woodlands and occur in climates with strongly seasonal rainfall patterns (Walker 1987).

Savannas consist of diverse habitat types. Of these habitat types, the closed thickets often occur in riparian areas and on hilltops, consisting of diverse and dense patches of woody species. They add spatial heterogeneity to the ecosystem by adding taller and longer lived landscape elements (Belsky 1994). These woody thickets represent important and reliable habitats for many browsing herbivores, especially during extreme dry periods (Oloo et al. 1994, Dublin 1995). They are functionally important even for grazing herbivores because they protect grass leaves from direct solar radiation and hence prolong the retention of green grass and the quality of forage for herbivores, especially during dry periods (Treydte et al. 2009). As a result, thickets contribute significantly to biodiversity and spatial heterogeneity in savannas.

Rainfall is the primary climatic variable controlling the productivity of savannas (Sinclair et al. 2008b). Increasing rainfall generally leads to higher primary productivity, and hence to greater plant biomass if this is not consumed. Spatial and temporal rainfall patterns may therefore explain not only variation in productivity, but also in diversity, composition and stability patterns of savanna woodland communities. A trend of rising temperatures, recurrent severe droughts and other environmental stresses (e.g., more frequent fires, increased herbivory and habitat loss) in African savanna ecosystems suggests that the survival prospects of species in particular communities, given the increasing severity of their physical environments expected as a consequence of these changes, will depend most strongly on their relative abilities for competition, resisting disturbances or dispersal (MacDougall 2005). Although the relative importance of these processes in shaping communities is likely to vary both spatially and temporally, relatively little work has examined this variation in tropical African savannas (Ozinga et al. 2005; Adler & Levine 2007)

Proposed processes of community assembly fall into three broad categories: (1) those that emphasize the fundamental role of niche differentiation mediated by competitive interactions (Tilman 1987, Loreau and Hector 2001) , (2) those that focus on environmental disturbance and stress, resulting in habitat filtering (e.g., extreme climatic events, fire, or herbivory (Liancourt et al. 2005), and (3) those that focus on a speciation-extinction dynamic equilibrium mediated by demographic stochasticity (Hubbell 2005). Here, we attempt to elucidate the relative importance of three generic assembly processes using long term monitoring data on tree biomass, diversity, composition and stability patterns in woodlands arranged along a rainfall gradient in a premier African savanna, namely, the Mara-Serengeti ecosystem. The data were collected biennially by the Masai Mara Ecological Monitoring Program over a 15-year period spanning 1989–2003 in Kenya's Masai Mara National Reserve (MMNR). Specifically, we analyze the spatial relationships between rainfall and (*i*) tree community biomass, (*ii*) species richness, (*iii*) evenness, (*iv*) stability and (*v*) composition. We use the resultant insights to infer and interpret savanna woodland community assembly processes.

Increasing rainfall generally leads to higher biomass and dominance of particular species, resulting in differential competitive exclusion, if competition for light enables species with stronger competitive abilities to outperform (i.e. become taller than) less competitive species (Grime 1973). Stronger competition for light generally reduces the diversity of plant communities (Tilman, 1982). So, if diversity indeed declines towards higher rainfall, this can be interpreted as the effect of more competition for light. But if diversity increases towards higher rainfall, competition for light is unlikely to be important in structuring these communities and alternative processes, such as habitat filtering or stochastic processes, would be at play (Bond et al. 2001, Hubbell 2001, Liancourt et al. 2005). Habitat filtering can occur where stressful conditions restrict the establishment and/or survival of species imposed by the abiotic environment (Cornwell and Ackerly 2009). If the stability of communities increase with diversity, as ecological theory predicts (Tilman and Downing 1994, Tilman et al. 2006), this could be interpreted as suggesting an important role for competition mediated by niche differentiation (Silvertown 2004). Under changing environmental conditions the loss of one species can be compensated for by other co-existing species (Tilman 1996). Alternatively, if diversity and stability are unrelated, this can be viewed as signaling habitat filtering or stochastic processes. A high nestedness in community structure has been shown in extinction dominated systems (Wright and Reeves 1992). In such systems, we would expect rare species to be more likely to become locally extinct first, resulting in a decrease in diversity over time. Also, high nestedness has been viewed as a sign of more complex interactions between species (Bascompte et al. 2003), for example due to facilitation or mutualisms expected to predominate at higher rainfall, thereby minimizing competitive pressure and increasing diversity over time. We test predictions of the following three hypotheses relating to the regulation of community assembly. (H1) If competition is more important in maintaining highly diverse communities (Fig. S1A), we expect community (*i*) biomass to increase with rainfall, (*ii*) species richness to decrease with increasing rainfall, (*iii*) species evenness to decrease with increasing rainfall, (*iv*) stability to increase with increasing richness, and (*v*) species composition (i.e., nestedness) to vary spatially such that dry areas will have both weak and strong competitors whereas wet areas will have only strong competitors (species poor communities). (H2) If habitat filtering is more important (Fig. S1B), then we expect (*i*) community biomass to increase with rainfall, (*ii*) species richness to increase with rainfall, (*iii*) species evenness to be spread evenly across the rainfall gradient, (*iv*) community stability to be low and unrelated to diversity, and (*v*) species composition of communities to vary with rainfall such that wet areas will have both common and rare species but dry areas will have only common species that are able to establish and/or survive under stressful conditions (eg. drought or disturbance), as resulting in communities to exhibiting significant nestedness. (H3) If demographic stochasticity is more important in determining community structure (Fig. S1C), then we expect (*i*) community biomass to increase with rainfall, (*ii*) species richness to increase with increasing rainfall, (*iii*) species evenness to be constant over the whole rainfall gradient, (*iv*) community stability to be high over the whole rainfall gradient but unrelated to diversity, and (*v*) species composition of communities to also show nonrandom patterns (i.e., nestedness).

METHODS

Study Area

The study was conducted in the Masai Mara National Reserve (MMNR), a premier protected area covering some 1530 km^2 in south-western Kenya and the northernmost section of the Mara-Serengeti ecosystem. The ecosystem is delineated by annual migratory movements of wildebeest (*Connochaetes taurinus*), zebra (*Equus burcheli*) and Thomson's gazelle (*Gazella thomsoni*) from the Serengeti plains in the south and Masai pastoral ranches to the north-east. The reserve is a dry season refuge for both migratory and resident herbivores (Dublin et al. 1990a), whereas the pastoral ranches support vasts herds of livestock and a diverse assemblage of resident large wild herbivores (Stellfox et al. 1986). The MMNR and its neighbouring pastoral ranches constitute the Mara region. Rainfall in the Mara region is bimodal with "short" rains falling during November–December and "long" rains during March–June. The dry season spans July–October but January-February is also often dry. Rainfall in the Mara-Serengeti ecosystem increases along a southeast-northwest gradient and with increasing altitude and averages less than 600 mm in the South East in Tanzania and over 1200 mm in the northwest in the Mara region (Pennycuick & Norton-Griffiths 1976). Mean temperature levels have been rising in the Mara region in recent decades, a rise associated with progressive habitat desiccation (Ogutu et al. 2007). The MMNR also experiences recurrent severe droughts, the most noteworthy during the study period (1989–2003) being in 1993 and 1999-2000 (Ogutu et al. 2007).

Sampling design and monitoring

The Masai Mara Ecological Monitoring Program (MMEMP) established four pairs of *Croton* thicket plots in the MMNR in 1989 (Dublin 1991). The dominant species in *Croton* thickets consist of the fire-tolerant shrubs *Croton dichogamus*, *Euclea divinorum*, *Grewia similis* and *Tarenna graviolens* interspersed with *Acacia* species such as *A. gerradii* and 53 relatively rare species (Table S1). Each paired plot was sampled every two years during 1989–2003, except in 1994, 1996, 1997, 1999, 2000 and 2001 when insufficient funding precluded vegetation sampling. As a result, each plot was sampled approxi-

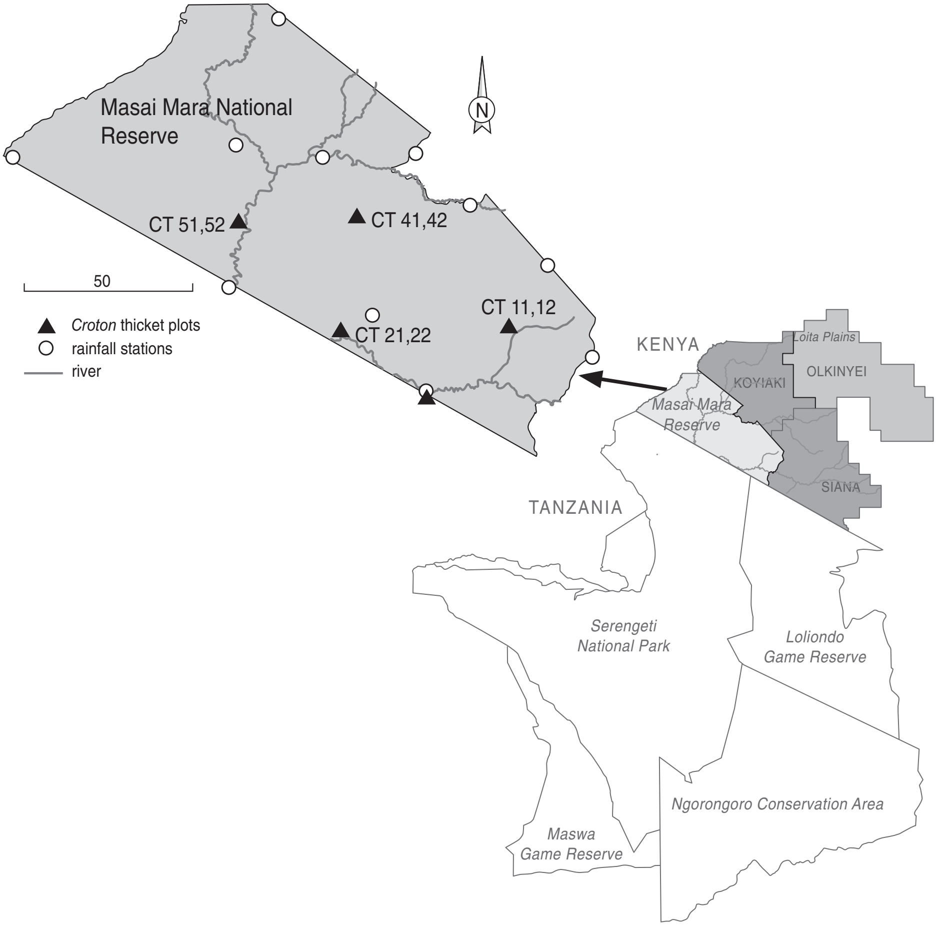


Figure 3.1 Distribution of four pairs of *Croton* thicket plots across the Maasai Mara National Reserve.

mately eight times on average during the monitoring period. Sampling in each plot took a month to complete, on average, with a sampling day starting at 0700-0730 h and ending at 1700 h. The paired plots each measuring 20 × 100 m were selected to represent the dominant woodland habitats, and were arrayed along a rainfall gradient covering the full length and breadth of the MMNR (Fig. 3.1). Each pair of plots was located 50 m apart and oriented along a southeast-northwest gradient. Metal rods driven into the ground were used to mark the boundaries of each plot. The plots were accessed by vehicle, or on foot, using a global positioning system (GPS). Plots were not fenced and hence were open to all grazers and browsers. Over the course of the monitoring period, four field staff carried out the same sampling procedure in each plot to ensure comparability of the long-term vegetation samples. All the field staff were thoroughly trained in vegetation sampling, identification of plant species and data recording before carrying out field sampling to ensure consistency. All trees and shrubs with stem diameters 10 cm or larger were measured using a standard diameter tape and identified following (Beentje 1994). Measurements of stem diameter were taken at 10 cm above the ground, rather than at breast height because of the diminutive stature of most of the trees in the woodland communities. Additional measurements recorded for each tree and used in this study were height, degree of browsing and extent of damage by fire as detailed below for each attribute.

Height

Tree height (in cm) was assumed to be the height of the main tree crown and was measured using a regular measuring tape. Individual plants of the five major dominant species within each plot were measured and assigned to one of three height classes: seedlings < 0.6 m, saplings > 0.6 but < 1.50 m and adults > 1.50 m. These height classes overlap the mean browsing heights for the common large browsing species in the study area (Dublin, Sinclair & McGlade 1990). The sapling height category represents the mean browsing height of resident antelope browsers primarily involved in woodland dynamics in the Serengeti-Mara, including impala, dikdik (*Rhynchotragus kirki*), Grant's gazelle (*Gazella granti*) and impala (*Aepyceros melampus*) (Dublin 1991). Elephants and giraffes (*Giraffa camelopardalis*) largely browse on trees taller than 1.5 m in both Croton thickets and *Acacia* woodlands, whereas fires affect all trees shorter than 3 m (Dublin et al. 1990).

Browsing and fire damage

Individual trees were categorized into seven damage classes encompassing "no damage" (0) to "severe damage" (7) using combinations of browsing characteristics, such as bark striping, branch clipping, branch breakage and branch toppling. To calculate the proportion of young plants damaged by browsers we amalgamated the seven damage classes into either "damaged" or "not damaged". The numbers of individual plants damaged by fire were categorized similarly visually using fire scars on the barks or branches of trees. From 1991 to 2003, burning by the MMNR management was largely restricted to the short dry season (January-February), when grass biomass and combustibility is low due to high moisture content, making fires less damaging. Therefore, fire scars became extremely rare in the *Croton* woodlands and had little influence on this study.

Community biomass index and stability

We estimated the basal area (in m^2) as $\pi d^2/4$, where d is the stem diameter. We then estimated the parabolic volume (in m^3) of the individual trees as the basal area × height/2. We then averaged the parabolic volume over all individuals within each plot in each year to obtain an index for total community biomass. We also calculated a community-level stability index (S), as the standard deviation divided by the mean community biomass (coefficient of variation) for each plot over the entire monitoring period as well as for each year across all the plots. A community is regarded as "stable" if S is equal to 1 and unstable if S is equal to 0 (Pimm 1984).

Species richness, evenness and nestedness

Species richness was determined by the total number of different species whereas species evenness (Pielou, 1977) was calculated as the diversity/*ln* (richness), where diversity is derived using the Shannon-Wiener Diversity index *H′* (Shannon & Weaver, 1949). We estimated an index of nestedness (N) for the species presence/absence matrix as a measure of community composition (Wright & Reeves 1992).

Rainfall measurements

Monthly rainfall data were collected from a network of 58 rain gauges distributed over the entire Mara-Serengeti ecosystem by the Serengeti Ecological Monitoring Program and the Masai Mara Ecological Monitoring Program during 1985–2003 (Coughenour 2006). Forty three of these 58 gauges were located in the Serengeti whereas the remaining 15 were located in the Mara Reserve. We used spatially interpolated monthly mean and annual precipitation over the entire ecosystem at a spatial resolution of 1 × 1 km^2 using the PPTMAP computer program described in detail by Reed et al. (2009). We associated each vegetation sampling plot in the MMNR with the interpolated monthly rainfall for the grid cell in which the plot fell based on the 1985-2003 rainfall measurements. Rainfall was summarized into wet (November-June) and dry (July-October) season and annual (November-October) components. We derived seasonal and annual rainfall lags and moving averages spanning periods of 1 to 5 years before the sampling year to evaluate the influence of delayed and cumulative past rainfall on seedling and sapling recruitment dynamics. The five-year period was selected to match the 5-year quasi-periodic oscillation evident in the regional rainfall and the associated changes in vegetation state (Ogutu et al. 2007). Table 3.1 summarizes the specific rainfall components, lagged and moving averages that we considered.

Table 3.1 Rainfall components, the months covered by each component, moving averages and lags computed for each component

Rainfall component	Months	Moving averages	Lagged rainfall
Wet season	Nov-Jun	Mavwet1-Mavwet5	Lagwet1-Lagwet5
Dry season	Jul-Oct	Mavdry1-Mavdry5	Lagdry1-Lagdry5
Annual	Nov-Oct	Mavannual1- Mavannual5	Lagannual1-Lagannual5

STATISTICAL ANALYSIS

Temporal variation in community biomass

We calculated the total community biomass of all trees averaged over all plots in each year. We then analyzed temporal trends in community biomass using linear regression analyses. The biomass was the response variable whereas the year of vegetation sampling was incorporated in the models as a fixed effect. To assess changes in community biomass in response to rainfall, we regressed the total community biomass of all trees over all plots on each of the total of 30 rainfall components assuming normal errors and an identity link. We used AICc in R version 2. 12. 0 (R Development Core Team 2010), to select both the best model and rainfall component most strongly correlated with biomass (Table S2). We tested for temporal trends in species richness and evenness using the same statistical approach as for biomass and regressed these against the various rainfall components.

Spatial variation in species diversity, stability and nestedness

To characterize the spatial patterns in species richness and evenness we summed the total number of different coexisting species and calculated the relative abundance of each species to the total abundance in each plot and averaged them over the monitoring period. We evaluated spatial patterns in species richness (the number of species) and evenness (a measure of the equitability of the proportional abundances of species) in each plot by averaging them over the monitoring period. The relationships between species richness and evenness and rainfall were analyzed using standard linear regressions. Again, AICc was used to identify the best model and the rainfall component having the strongest correlation with richness and evenness (Table S2). The models were also fit using a linear regression assuming normality of errors and an identity link.

We determined community stability using all the data collected biennially on woody vegetation biomass within each plot during 1989-2003. To evaluate the relationship between community stability and richness, we calculated stability in community biomass (S) as $S = j/m$ (i.e., coefficient of variation) where j is the standard deviation and m is the mean biomass in a given plot during 1989-2003. We used linear regression analyses to evaluate temporal variation in community-level stability between plots of varying richness. The models, incorporating richness as a continuous covariate, were also fit assuming normality and an identity link.

We estimated an index of nestedness of the species presence/absence matrix using the ‘binmatnest’ algorithm of (Rodríguez-Gironés & Santamaría 2006), implemented in the ‘bipartite’ R package (Dormann, Gruber & Freund 2008) to characterize how species are distributed among all the plots. The tree data from all survey years (1989–2003) were used to construct a species presence-absence matrix. This procedure followed a three step process: first, the matrix is reorganized by arranging rows (plots) and columns (species) from full (species presence) to empty (species absence) cells. Second, to maximize nestedness the full cells are mainly located in the upper-left corner and empty cells are mainly located in the lower right corner. An isocline for this matrix of perfect nestedness is calculated. Third, for the reorganized, presence-absence matrix, full cells above the isocline and empty cells below the isocline were identified and a normalized sum of their distances to the isocline calculated, in such a way that it ranged from 0 (no deviation and therefore perfect nestedness) to 100 (maximum deviation and therefore perfect ‘un-nestedness’). This normalized deviation measure of an observed matrix from a perfectly nested matrix is called the ‘nestedness temperature’ with low values indicating high nestedness. More details on this procedure can be found in Rodríguez-Gironés & Santamaría (2006). To test whether the observed nestedness was higher or lower than that expected by chance, we used a null model developed for a permutation test by Bascompte et al. (2003). The test involves creating new matrices of the same size as the observed matrix. The probability of each cell in these matrices being filled is the average of the probability of filling each of its associated rows ($n = 8$) and columns ($n = 70$). This type of null model is relatively conservative, but is less vulnerable to type II errors (Cottenie 2005; Rodríguez-Gironés & Santamaría 2006). We ran the null model with 1000 permutations as implemented in the 'bipartite' package.

RESULTS

Temporal trends in rainfall and temperature

The period 1989–2003 was one of the hottest recorded since the 1960's (Ogutu et al. 2007), therefore climatic variation was likely a major factor during this study. In particular, this period was characterized by recurrent severe droughts (1993, 1997 and 1999–2000), mild droughts during 1991 and 1994, and exceptional floods associated with the longest (1990–1995) and strongest (1997–1998) ENSO episodes on instru-

Table 3.2 Linear regression coefficients for the relationships between community biomass, richness, evenness and stability averaged across all plots in each year and across all years for each plot. r^2 is the proportion of variance explained by each model

Variable	Scale	Effect	Estimate	SE	T	P>|T|	r^2
Community biomass	Temporal	Intercept	10669.08	4256.537	2.507	0.046	0.42
		Year	-5.206	2.103	-2.475	**0.048**	
Community biomass	Temporal	Intercept	12.324	46.193	0.267	0.799	0.46
		Mavdry2	0.77	0.289	2.671	**0.037**	
Richness	Temporal	Intercept	-698.955	426.14	-1.64	0.152	0.21
		Year	0.36	0.214	1.687	0.142	
Evenness	Temporal	Intercept	1.441	4.531	0.318	0.761	0.16
		Year	0	0.002	-0.179	0.864	
Stability	Temporal	Intercept	32.522	26.067	1.248	0.259	0.068
		Year	-0.016	0.013	-1.23	0.265	
Community biomass	Spatial	Intercept	425.24	392.59	1.083	0.32	0.06
		Dry4	-1.924	2.518	-0.764	0.474	
Richness	Spatial	Intercept	-177.832	80.353	-2.213	0.069	0.42
		Mavdry2	0.272	0.11	2.464	**0.049**	
Evenness	Spatial	Intercept	0.326	0.188	1.736	0.133	0.18
		Mavdry2	0.002	0.001	1.614	0.158	
Community stability	Spatial	Intercept	-0.168	0.653	-0.258	0.805	-0.04
		Richness	0.027	0.032	0.847	0.43	

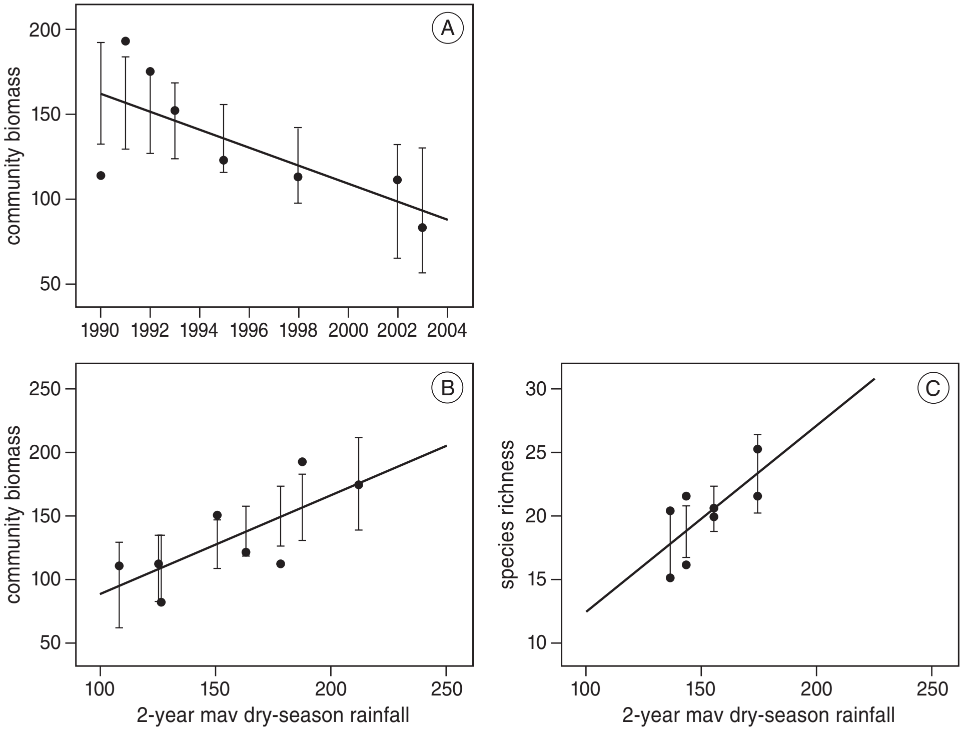


Figure 3.2 (A) Year-to-year changes in woody biomass averaged over 8 paired plots, (B) the relationships between 2-year cumulative dry season rainfall and woody biomass averaged over 8 paired plots and (C) the relationships between 2-year cumulative dry season rainfall and species richness for each plot averaged across all years in the Masai Mara National Reserve during 1989–2003.

mental record. The cumulative dry season rainfall component was largely below average from 1980s to 2003 implying reduced vegetation production and quality in the savanna grasslands (Ogutu et al. 2007). Detailed descriptions of the temporal climatic patterns are presented elsewhere (Ogutu et al. 2007).

Temporal variation in community biomass, richness, evenness and stability

Community biomass over the entire landscape declined consistently over the monitoring period (Fig. 3.2A) but increased linearly with the 2-year cumulative moving average of the dry season rainfall (Table 3.2, Fig. 3.2B). However, species richness and evenness and community stability were apparently temporally invariant (Table 3.2).

Spatial variation in community biomass, richness, evenness, stability and nestedness

Average woody biomass per plot did not vary significantly with any rainfall component. However, species richness per plot increased up the rainfall gradient and also increased strongly with the 2-year cumulative moving average of the dry season rainfall (Table 3.2, Fig. 3.2C). In contrast, the average species evenness per plot was not

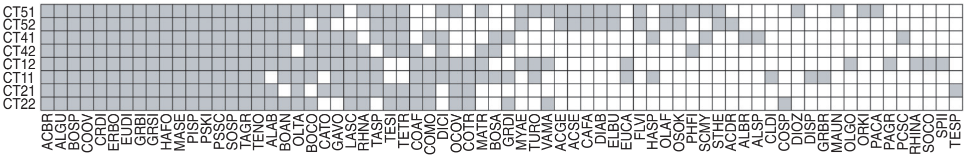


Figure 3.3 Maximally packed species presence–absence matrix (where species and sites are ordered according to incidence and species richness) for samples from woody vegetation plant communities arrayed across the Masai Mara National Reserve, Kenya. Filled cells indicate presences, white cells indicate absences. The measure of nestedness varies from 0 (no nestedness) to 100 (perfect nestedness). Nrows and Ncolumns are the sum of the nestedness introduced by rows (sites) and columns (species), representing the independent contributions of sites and species to total nestedness. The matrix is significantly nested under the constrained null model ($P < 0.05$).

significantly related to rainfall (Table 3.2). The coefficient of variation of biomass (stability index) for each plot was not significantly correlated with richness (Table 3.2). The average ($\overline{N}$ ± 1SE) "nestedness temperature" of the randomized communities was 49.254 ±11.325. The observed nestedness temperature was 34.50 and was significantly ($P < 0.05$) lower than that expected for randomly assembled communities, indicating that species composition was significantly more nested than expected by chance alone (Fig. 3.3).

DISCUSSION

Biomass and rainfall

As predicted, community biomass across the entire landscape was influenced most strongly by the 2-year cumulative moving average of the dry season rainfall. The relationship reflects tree responses to delayed or carry-over effects of prior dry-season conditions rather than to immediate habitat conditions. Furthermore the greater importance of the dry season rainfall relative to the other rainfall components suggests that woody vegetation biomass is limited more strongly by variation in the dry-season rainfall. The significant effect of cumulative past rainfall on woody vegetation biomass suggests that woody species allocate and store more resources through their deep taproots and re-use the stored resources to increase biomass in years of high rainfall.

Species richness and rainfall

If competition for light were the main process governing the structural organization of these woodland communities we would expect a decrease in species richness with increasing rainfall as predicted by (H1). However, our results show that species richness in each plot increased with increasing rainfall in each plot. This suggests apparently that competition for light is apparently not the main mechanism controlling the structure of these communities.

Species evenness and rainfall

If competition were the main process governing community assembly we would expect to find a negative relationship between evenness and rainfall in which only a few species are competitively dominant and relatively abundance in wetter areas or a positive relationship as a result of strong below-ground competition for water and nutrients (Nijs and Roy 2000). In contrast, we found a positive, albeit insignificant relationship between evenness and rainfall thus providing no evidence for increasing importance of competition for light in wetter areas. Also, we found consistently high value of evenness along the rainfall gradient (0.8) suggesting species complementarity resulting from facilitation or the co-dominance of both common and rare species (Aarssen 1983, Loreau and Hector 2001). One may therefore assume that uncommon species may not be negatively affected by the presence of common species due to little niche overlap (Smith and Knapp 2003), as predicted by H2. If higher-productivity sites had more individuals than lower-productivity sites, one possible explanation for the increased species richness observed in the high-productivity sites could be due to positive interactions between species due to facilitation or mutualisms (Bascompte et al. 2003).

Species composition/nestedness and rainfall

Our results show a strong nested pattern in community structure such that common species are present in both low and high rainfall areas whereas rare species are present only in the wetter areas. Bastolla et al. (2009) also showed that nestedness reduces effective interspecific competition and enhances the number of coexisting species, providing evidence that competition is not likely the main process shaping these communities. Instead, this nestedness pattern can provide pathways for rare species to persist (Jordano 1987) via facilitative or mutualistic interactions. However, the lack of a theory that takes into account the structure of interactions limits further assessment of the implications of such network patterns for biodiversity (Bastolla et al. 2009).

Species richness and community stability

It has long been debated whether diverse ecological systems are more or less stable than those with fewer species (McNaughton 1977, Tilman 1996). We expected a negative relationship between the community stability and species richness if competitive mechanisms were the main force structuring community assembly, since in diverse communities the loss of one species can be compensated for by the gain of a competing species (Tilman and Downing 1994). These predictions were however not supported. Instead, our results show no significant relationship between stability and richness along the rainfall gradient implying that a loss of a species harmed by a disturbance will not necessarily be compensated for by a superior competitor. Hence, this further supports the evidence for minimal competition and a more important role for habitat filtering or stochastic processes in explaining compositional stability patterns across the woodland communities of the Masai Mara.

In savanna systems, it is well known that during high rainfall plant biomass increases and provides fuel for hot fires (Trollope 1984, Scholes et al. 2002). Thus, whereas the drier areas with less grass fuel experience fewer, less intense fires, the wetter areas contain higher biomass, and likely experience more and intense fires. Fire limits both recruitment and the progression of individuals from the sapling stage to adults (Higgins et al. 2000). Therefore, while a positive relationship exists between community biomass and rainfall, suggesting that these communities contain fire-tolerant species that have the potential to proliferate after burning (Bond and Van Wilgen 1996), it does not explain why species richness would increase with rainfall. Instead, fire may have led to dominance of certain fire-tolerant species at higher rainfall sites which in turn may have led to facilitative interactions with woody species and increases in richness.

Herbivory might also account for increased habitat filtering in low rainfall areas. Drier areas have more soil nutrients due to less leaching than wet areas. Combined with adjustments in the plant carbon/nutrient balance, dry areas support some of the richest assemblages of herbivores (Sinclair 1995, Ritchie and Olff 1999). It is likely that herbivores have a greater impact on trees in drier areas because they consist of highly palatable species owing to the high nutrient availability in the soils (Anderson and Briske 1995), compared to wetter areas. Furthermore, the higher root to shoot ratio below ground makes these plant species tolerant to herbivory because more resources are stored underground. As a result, the few grazing-tolerant plant species that persist in such areas allocate more nitrogen to their leaves, making them more palatable but able to regrow quickly (Bond, Smythe and Balfour, 2001). This has been observed in South African savannas (Owen-Smith and Cooper 1987, Bond et al. 2001). As a result, the high densities of grazers impose considerably high mortality rates on tree species that are less tolerant to grazing (Olff and Ritchie 1998). Trees suffer less due to herbivory in wetter areas because they store relatively more carbohydrates above ground so that the above ground green leaves are high in indigestible carbon. Consequently, low densities of herbivores potentially allow the rare species to co-exist with the common species in areas of high rainfall (Olff and Ritchie, 1998).

In the high rainfall areas, we surprisingly did not find evidence that light competition structures these tree communities. Competition is considered a major structuring force in many systems. In savannas in particular, competition occurs between grass and tree seedlings-because the grass layer shades the establishing woody seedlings and both grasses and tree seedlings compete for water and nutrients (Knoop and Walker 1985, Skarpe 1992, Scholes and Archer 1997). In most cases, these patterns have been found in pot experiments under controlled conditions. However, we found relatively weak evidence that competitive mechanisms were structuring these communities, thus suggesting that stress-tolerance or stochastic processes are probably more important in shaping local distribution patterns. Communities that are structured by such processes are likely to be found only in open savanna ecosystems where the high light availability reduces the need for tall stature. For data collected near rivers in even wetter areas, we expect the vegetation to be denser and competition for light to be more important in structuring these woodland communities (Brenes-Arguedas et al. 2011) and the stability of the woodlands to be highly dependent on species diversity.

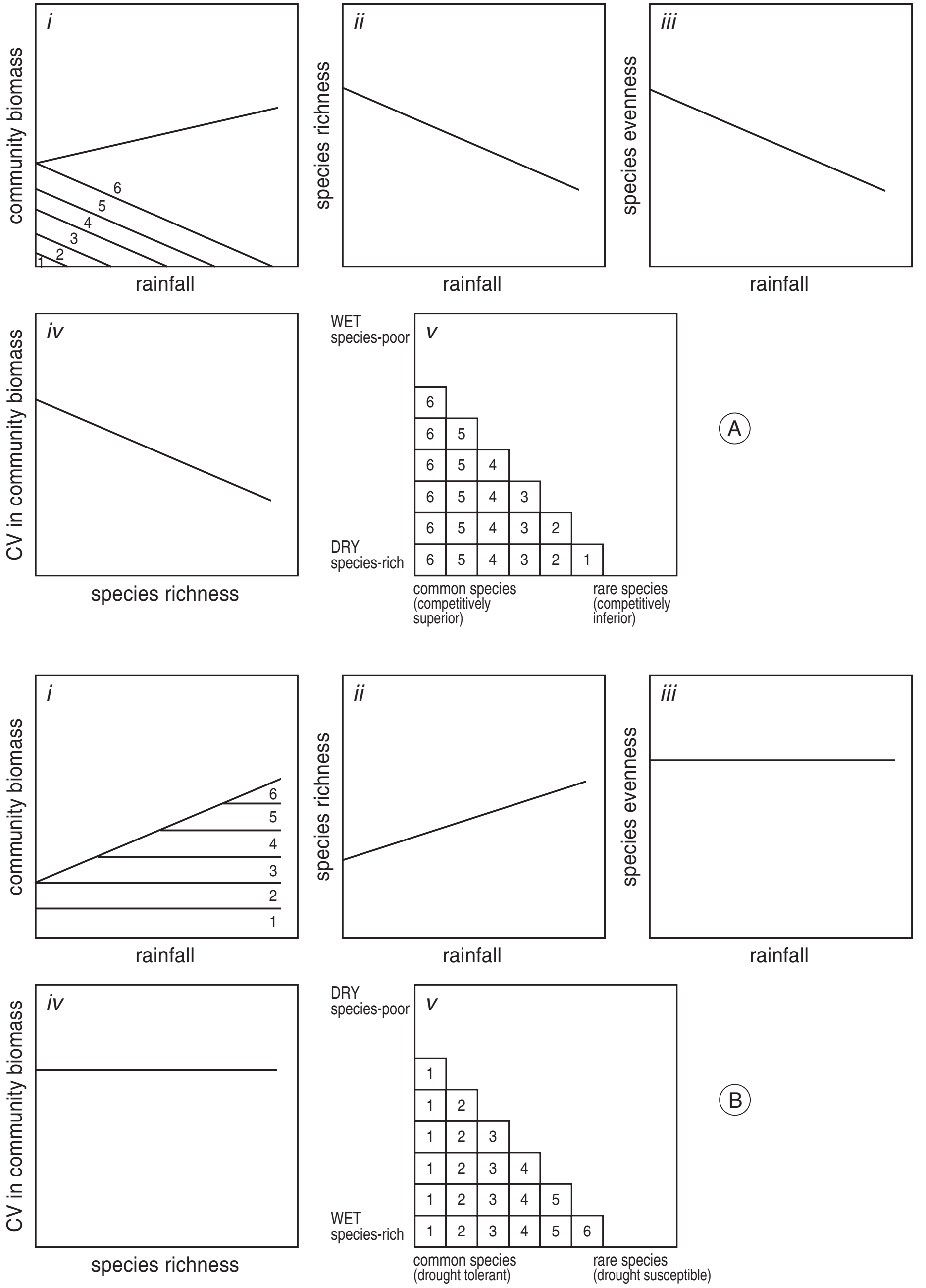
Contrary to this expectation, our results suggest that if disturbances by fire or by browsers are minimal then large sections of savanna woodlands would contain more stress-intolerant species that have higher chances of extinction in an event of a disturbance, thus reducing their overall diversity and stability.

Acknowledgements

The Masai Mara Ecological Monitoring Program (MEMP) was designed and supervised by Dr. Holly T. Dublin. The field work was conducted by Paul Chara, John Naiyoma and Paul Naiyoma (1989-1995), Alex Obara (1995-1999) and Charles Matankory (1993-2003). We would like to thank the Narok County Council (NCC) for providing security during data collection and, together with Base Camp Explorer, for providing accommodation and office space for the MMEMP field staff. We thank Charles Matankory and Joseph Kimiti for diligently checking all the electronic records against the field records. The monitoring program was funded by WWF-EARPPO and Friends of Conservation (FOC), the US Fish and Wildlife Service and the University of British Columbia. Data processing, analysis and writing were supported by the International Livestock Research Institute (ILRI), Alexander von Humboldt Research Fellowship to JO, a grant from the National Science Foundation of America (NSF, BCS 0709671) to ILRI and by the University of Groningen. NB was supported by the Ubbo Emmius scholarship through the University of Groningen.

SUPPLEMENTARY INFORMATION

Figure S1 Theoretical predictions of the relative importance of (A) competition, (B) habitat filtering and (C) stochastic processes in structuring woodland communities in savannas.



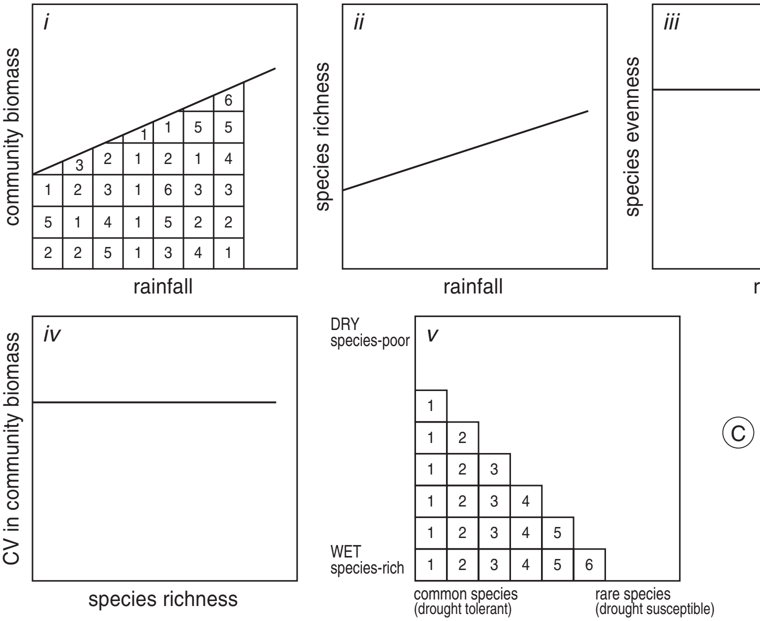

C
i
community biomass
rainfall
1 2 3 1 6 3 3
5 1 4 1 5 2 2
2 2 5 1 3 4 1
ii
species richness
rainfall
iii
species evenness
rainfall
iv
CV in community biomass
species richness
v
DRY
species-poor
WET
species-rich
common species
(drought tolerant)
rare species
(drought susceptible)
1 2 3 4 5 6

Table S1 The total number of all individuals of each tree species tallied in all the 8 plots (each measuring 20 m x 100 m each) in each sampled year in the Masai Mara National Reserve during 1989–2003.

Species	Species	Year							
	abbreviations	1990	1991	1992	1993	1995	1998	2002	2003
Acacia brevispica	ACBR	551	247	1288	309	759	164	104	501
Acacia drepanolobium	ACDR	0	0	0	0	0	0	0	1
Acacia gerrardii	ACGE	0	7	0	0	1	0	0	2
Acacia senegal	ACSE	0	2	0	4	1	0	0	0
Allophylus abyssinicus	ALAB	0	0	0	0	16	14	10	7
Albizia gummifera	ALGU	0	0	0	0	66	29	3	57
Albizia spp.	ALSP	0	23	0	0	0	0	0	0
Boscia angustifolia	BOAN	10	14	12	19	18	4	0	7
Boscia coreace	BOCO	1	6	80	5	0	0	0	0
Bocia salicifolia	BOSA	0	0	0	0	10	0	0	0
Boswelia spp.	BOSP	7	15	12	0	0	0	0	3
Cadaba farinosa	CAFA	0	0	0	0	2	0	0	2
Capparis tomentosa	CATO	0	0	0	0	11	0	22	27
Commiphora africana	COAF	1	0	3	0	15	7	2	7
Combretum molle	COMO	1	0	5	1	1	5	0	3
Cordia ovalis	COOV	7	10	7	3	19	11	16	10
Combretum spp.	COSP	1	0	0	0	0	0	0	0
Commiphora trothea	COTR	23	0	36	0	0	0	0	4
Croton dichogamus	CRDI	891	967	1437	738	1909	1375	330	1370
Diospyros abyssinica	DIAB	0	0	0	0	2	3	0	6
Dicrostachys cinerea	DICI	7	7	14	1	11	2	4	2
Elaeodendron buchananii	ELBU	0	0	0	0	4	13	0	10
Erythrococa bongensis	ERBO	0	0	0	0	441	237	63	301
Euphorbia candelabrum	EUCA	1	0	6	0	2	0	0	3
Euclea divinorum	EUDI	5	143	24	69	64	49	8	51
Flueggia virosa	FLVI	0	0	0	0	6	4	0	8
Gardenia volkensii	GAVO	0	0	0	0	8	1	13	5
Grewia bicolor	GRBI	46	62	63	26	86	61	26	49
Grewia similis	GRSI	50	204	192	93	230	122	105	100
Haplocoelum foliolosum	HAFO	0	0	0	0	155	58	57	59
Haplocoelum spp.	HASP	6	24	0	0	0	0	0	0
Lannea scweinfurthii	LASC	0	0	0	0	15	9	4	12
Maytenus senegalensis	MASE	1	33	7	34	42	6	23	16
Maerua triphylla	MATR	0	0	0	0	11	0	0	9
Maytenus undata	MAUN	0	0	0	0	4	0	0	0
Mystroxylon aethiopicum	MYAE	0	0	0	0	11	10	0	14
Ochna ovata	OCOV	0	0	0	0	16	12	0	19
Olea africana	OLAF	0	8	0	5	7	13	0	12
Oltangotua spp.	OLTA	0	0	1	0	0	0	0	0
Ormocarpum trichocarpum	ORKI	40	25	67	31	0	0	0	0
Elaeodendron buchananii	OSOK	0	12	0	1	0	0	0	0
Pappea capensis	PACA	0	0	0	0	1	0	0	0
Phyllanthus fischeri	PSSC	0	0	0	0	1	1	68	1
Pistacia aethiopica	PHFI	16	41	72	115	0	0	1	0
Psychotria kirkii	PISP	0	0	0	0	47	11	21	42
Psydrax schimperiana	PSKI	0	0	0	0	93	56	17	58
Rhus natalensis	RHUS	7	1	15	1	14	4	0	11
Scutra mytina	SCMY	0	0	0	0	4	3	0	2
Solanum spp.	SOSP	1	0	0	0	0	0	0	0
Strychnos henningsii	STHE	208	69	533	135	0	0	0	0
Tarenna graviolens	TAGR	80	102	154	92	243	138	32	117
Tarenna spp.	TASP	7	71	25	59	0	0	0	0
Teclea nobilis	TENO	17	45	46	26	83	38	0	39
Teclea simplifolia	TESI	79	127	171	100	0	0	0	0
Teclea trichocarpa	TETR	0	0	0	0	184	113	10	98
Turrea robusta	TURO	0	0	0	0	18	13	0	12
Vangueria madagascariensis	VAMA	0	0	0	0	2	2	0	3

Table S2 Selection of the best supported rainfall components for total community biomass, species richness and evenness of all trees over all plots in each year in the Masai Mara National Reserve based on AICc values. The selected rainfall component for biomass is highlighted in bold face.

Rainfall	Tree biomass		Tree species richness		Tree species evenness	
component	#Parameters	AIC	#Parameters	AIC	#Parameters	AIC
annual‡	3	84.809	3	41.923	3	-29.700
annual1‡	3	84.793	3	45.953	3	-31.850
annual2	3	83.689	3	41.742	3	-29.701
annual3	3	81.695	3	46.026	3	-31.319
annual4	3	81.310	3	45.650	3	-30.915
mavannual2	3	83.033	3	41.734	3	-30.487
mavannual3	3	84.863	3	41.454	3	-30.293
mavannual4	3	83.991	3	43.671	3	-30.999
dry	3	84.361	3	44.922	3	-30.079
dry1	3	79.893	3	45.435	3	-30.258
dry2	3	85.312	3	45.515	3	-33.501
dry3	3	80.083	3	44.700	3	-29.912
dry4	3	82.580	3	46.075	3	-30.404
mavdry2	**3**	**73.878**	**3**	**40.487**	**3**	**-28.380**
mavdry3	3	82.468	3	44.777	3	-32.572
mavdry4	3	80.575	3	43.398	3	-30.486
wet	3	83.025	3	46.046	3	-31.446
wet1	3	82.458	3	46.034	3	-31.441
wet2	3	85.414	3	43.930	3	-30.018
wet3	3	84.358	3	46.026	3	-31.808
wet4	3	81.851	3	45.736	3	-31.894
mavwet2	3	79.156	3	41.619	3	-30.710
mavwet3	3	80.270	3	41.300	3	-30.570
mavwet4	3	85.186	3	44.067	3	-31.575

‡ Numeric suffix after rainfall component names denote the time window over which the rainfall component was averaged or by which the component was lagged.
For example, mavannual3 means that the annual rainfall component was averaged over a three-year time window whereas annual3 means that the annual component was lagged by three years.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Chapter 4

The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya

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ABSTRACT

The overlap of large carnivores, livestock and people can engender conflicts that often threaten the future viability of carnivore populations in the pastoral systems of Africa. A playback survey of lions *Panthera leo*, spotted hyenas *Crocuta crocuta* and black-backed jackals *Canis mesomelas* and a transect count of wild herbivores was conducted in the Maasai Mara National Reserve and adjoining pastoral ranches to assess the effect of pastoralism and protection on the density and distribution of carnivores in June 2003. Reliability of the prey counts depended on an assumption of similar observability between the protected and pastoral areas, which we assessed using distance sampling in November 2003 and computer simulations and determined to be similar. Estimates of wild prey biomass density was 2.6 times higher in the ranches (14212 kg/km^2) than in the reserve (5472 kg/km^2) during this wet season count. Apparent hyena density estimates were 1.3 times higher in the ranches (0.561 hyenas/km^2)than in the reserve (0.404 hyenas/km^2), in correspondence with the regional pattern of prey density. This distribution of hyenas is biased towards the reserve, if it is dependent on prey density. Estimates of apparent jackal density were similar in both areas whereas lion density was anomalously 8.0 times lower in the ranches (0.046 lions/km^2) than in the reserve (0.369 lions/km^2). Lion and hyena densities and prey biomass did not differ between June 1991 (5172.273 kg/km^2) and June 2003 (5472 kg/km^2) in the reserve, but jackal density increased in the same period. Lions never responded to playbacks in the ranches, so the potential shift in lion behavioural response for different land use zones is another potential explanation for the patterns found here. We think a real shift in lion populations is a better explanation than a behavioural change in relation to playbacks based on additional data from independent systematic and intensive censuses and playback surveys conducted in the ranches. Lion populations in the pastoral ranches seemed headed for extinction, probably owing to conflicts with pastoralism, necessitating urgent conservation interventions that integrate pastoral economic welfare with large carnivore conservation goals to foster long-term viability of lion populations in the pastoral systems.

INTRODUCTION

Strong conflicts, threatening the future viability of carnivore populations, often characterize pastoral systems in which carnivores, livestock and people occur in close juxtaposition (Rudnai, 1979; Kruuk, 1980; Karani, 1994; Omondi, 1994; Mizutani, 1995; Mwangi, 1997; Ogada et al. 2003; Treves and Karanth, 2003). As land tenure, land use and human populations change in the pastoral systems of Narok District of Kenya, the land under cultivation and settlement expands, human predation on wildlife increases and habitat degradation, fragmentation and loss accelerates (Dublin, 1995; Homewood et al. 2001; Serneels, Said and Lambin, 2001). As a result, the natural prey base for carnivores has declined there rapidly (Otichillo et al. 2000), and this can amplify the threat of persecution and local extinction of carnivores (Woodroffe and Ginsberg, 1998; 2000). Recurrent epizootics of viral diseases exacerbate threats to the future viability of carnivores in some ecosystems, such as the Mara-Serengeti (Kock et al. 1998; Packer et al. 1999). However, behavioural plasticity of certain carnivore species facilitates their adaptive adjustment to an increasingly precarious lifestyle in proximity to humans (Woodroffe, 2000; Sunquist and Sunquist, 2001) and has done so with hyenas in the Mara ecosystem (Boydston et al. 2003).

Lion *Panthera leo* density in the Mara reserve ranks among the highest recorded in African savannas (Ogutu and Dublin, 2002) but is unusually low at the edge of the reserve adjoining pastoral ranches (Ogutu and Dublin, 2002; 2004), implicating possible negative impacts of pastoral-ism on lion density and distribution. Similarly, altered use of space, social behaviour, circadian activity rhythms and demographic structure in spotted hyenas *Crocuta crocuta* residing at the edge of the Mara reserve (Boydston et al. 2003) have also been linked to increased interference by livestock grazing within hyena clan territories. Although this forms a sharp contrast to the findings of Maddox (2003), who reported no difference in large carnivore densities for the adjacent and closely comparable areas of Serengeti National Park and the Loliondo and Ngorongoro regions inhabited by Maasai pastoralists, a clear change in habitat is evident from the Mara reserve to the adjacent pastoral lands in the Talek area studied by Boydston et al. (2003).

Human-carnivore conflicts in pastoral areas in neigh-bouring the Mara reserve are caused by increasingly close contact between people and carnivores as human populations rise and livestock depredation is perpetrated primarily by leopards, lions and hyenas (Karani, 1994). The depredation incidences peak in the wet season when wild prey availability is lowest (Karani, 1994; Patterson et al. 2004) and are highest closest to the reserve boundary (Mwangi, 1997), suggesting that the reserve acts as a reservoir for stock-raiding and dispersing predators that recolonize areas where resident predators have been extirpated in the ranches (Ogutu and Dublin, 2002). The pastoral Maasai community lose much more livestock to diseases yet surprisingly believe that their livestock losses to predators are more significant economically (Mwangi, 1997).

Progressive intensification of land use, sedenterization, diversification of livelihoods, land fragmentation through privatization of land tenure driven by dynamic socio-political, demographic and economic processes neces-sitates urgent strategic management interventions for integrating the social, cultural, and economic welfare of pastoralists with conservation goals for carnivores. Long-term management and conservation interventions for alleviating these conflicts and fostering long-term viability of carnivore populations in pastoral systems require a reliable knowledge of carnivore population levels, spatial distribution and the underpinning ecological correlates. This information is seldom available.

A survey of lions, spotted hyenas and black-backed jackals *Canis mesomelas* was conducted in the Mara reserve and adjoining pastoral ranches using broadcasts of tape-recorded vocalizations from 24 June to 5 July 2003 to test if pastoralism and protection influence carnivore density, distribution and behaviour. This hypothesis was tested by:(1) estimating the density and population size of lions, spotted hyenas and jackals; (2) characterizing their spatial distribution inside and outside the reserve; (3) establishing the extent to which land management influenced carnivore population levels and spatial distri-bution by controlling for the effects of grass height, elevation and prey biomass density. Evidence for changes in carnivore behaviour was inferred by comparing the patterns of carnivore responses to broadcasts inside and outside the reserve. The June 2003 estimates of carnivore and prey density for the reserve were compared with estimates made in June 1991 (Ogutu and Dublin, 1998) to infer evidence for population growth and to expand on the previous results by conducting a survey over a larger area.

MATERIALS AND METHODS

Study Area

The study area, which encompasses the Mara reserve and the adjacent Koyaki group ranch (and a small section of Siana group ranch), is located in south-western Kenya and bounded by the Serengeti National Park in Tanzania to the south, private group ranches to the north and east and the Siria escarpment to the west (Fig. 4.1). Animals and humans can easily climb the escarpment, so it is not an effective barrier either to anthropogenic activity or carnivore movements. Group ranches and agricultural farms are found west of the escarpment. The Mara, Talek and Sand rivers partition the reserve into the eastern (Sekenani), northern (Musiara) and western (Triangle) sections. Twelve habitat types dominated by grasslands, shrublands and mixtures of both characterize the study area (Epp and Agatsiva, 1980). Rainfall is seasonal, with the wet season spanning November–June and the dry season July–October and increases along a south-east to north-west cline and with increasing altitude (Pennycuick and Norton-Griffiths, 1976). The area supports a spectacularly high density and diversity of resident wild ungulates and is a critical dry season (July–October) dispersal range for the earth's largest remaining herds of migratory wildebeest *Connochaetus taurinus*, zebra *Equus burchelli* and Thomson's gazelle *Gazella thomsoni* from the neighbouring Loita Plains and Serengeti (Maddock, 1979; Stellfox et al. 1986).

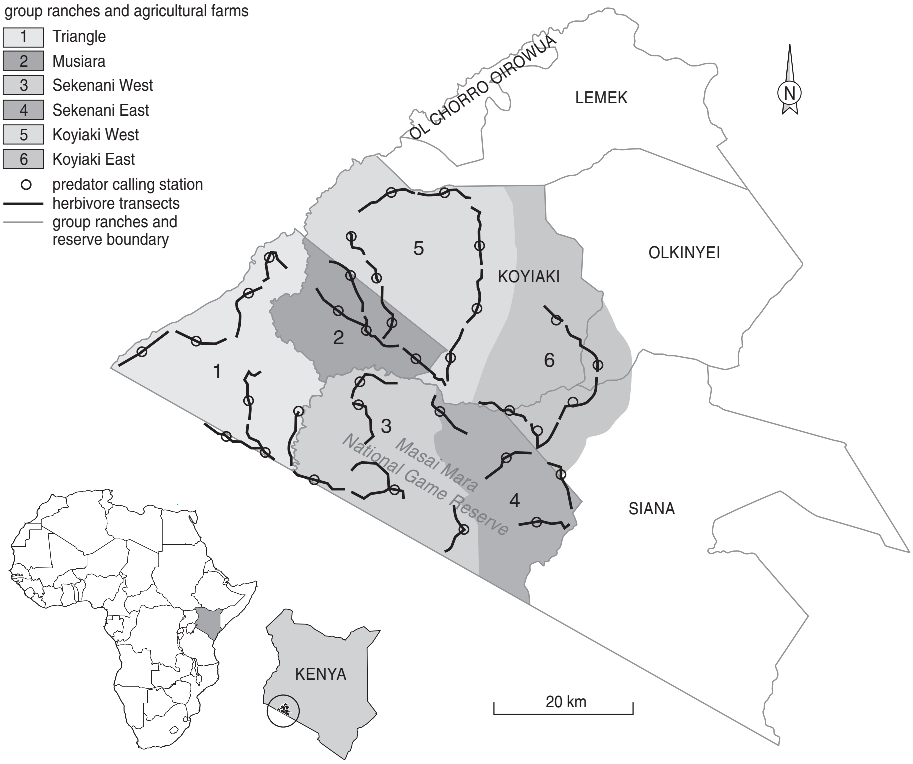

Figure 4.1 The Maasai Mara National Reserve and the neighbouring pastoral ranches, showing the sampled strata, herbivore transects and predator calling stations. The Reserve and Koyiaki group ranch are regions whereas areas within the Reserve (1-4) and Koyiaki (5 and 6) are the strata.

Distribution of call-in stations

A call-in survey is an effective and inexpensive technique for counting hyenas and lions in African savannas (Mills, 1985; Sillero-Zubiri and Gottelli, 1992; Creel and Creel, 1996; Mills and Gorman, 1997; Ogutu and Dublin, 1998; Mills, Juritz and Zucchini, 2001; Maddox, 2003) and jackals (Ogutu, 1994; Maddox, 2003). The reserve was stratified into the Triangle, Musiara, eastern and western sections of Sekenani and the Koyiaki group ranch into eastern and western sections to ensure a more representative distribution of carnivore calling stations and herbivore transects. The 6 strata were delineated using the predominant landmarks and topography and the 2 regions using land-use type (Fig. 4.1).

A map of the study area overlaid with 5 × 5 km^2 grid cells and numbered sequentially by rows or columns was used to distribute 35 calling stations over the strata in proportion to the area of each stratum using stratified systematic random sampling (Cochran, 1977) such that 22 stations fell within the reserve and 13 within the Koyiaki group ranch. We randomly selected a grid cell to locate the initial call-in station and placed subsequent stations in every second grid cell along either rows or columns. Systematic random sampling controlled the distribution of stations in each stratum by spreading them throughout the stratum at equal intervals, thus providing additional implicit stratification in each stratum. The resulting distribution of stations ensured no 2 stations were less than 7.5 km apart to minimize the likelihood of duplicate counting (Fig. 4.1).

Counting prey animals

We established 35 transects centred on, or traversing each calling station (Fig. 4.1), and counted potential prey animals for large carnivores within 100 m on either side of the transect centreline during daytime. We selected this narrow transect to clearly avoid any visibility or sightability problems. After the count, a test of different transect widths revealed that there was no difference in the number of animals sighted on the line, than at 100 m from the line, for the 5 most commonly sighted species in the Mara. Thus it was assumed that this lack of visibility bias also applied to the less common species that were counted, which is very probable given the open terrain along all of our transects (mean tree cover = 8.1%, mean shrub cover = 11.2%; Reid et al. 2003).

Transects often cut across several habitat types within each stratum and were randomly placed. However, where terrain features precluded accessibility by vehicle, would substantially slow travelling speed, pose the risk of an acci-dent, or potentially cause damage to the vehicle, transects followed the nearest roads or tracks. Although counting biases are often associated with roads, most tracks or roads used had limited or no vehicular traffic and thus were unlikely to have contributed substantial bias to the herbivore counts. The estimated prey density was used to calculate aggregate prey biomass in each 1 × 0.2 km block along each transect using unit weights as in Coe, Cumming and Phillipson (1976). The total number of the 1 × 0.2 km blocks was 335 because 3 of the 35 transects were only 5 km long owing to inaccessible terrain or boundary restrictions, while the rest were 10 km long.

Every 1 km along each transect the number of wild herbivores commonly eaten by large carnivores in the Mara-Serengeti were recorded (Scheel and Packer, 1995) including wildebeest, zebra, Thomson's gazelle, impala *Aepyceros melampus*, topi *Damaliscus korrigum*, hartebeest *Alcelaphus busephalus*, warthog *Phacocoerus aethiopicus*, and Grant's gazelle *Gazella grant*. The GPS coordinates, the elevation of the centre of each block, and visual estimates of grass height (0–30 cm, 30–60 cm, 60– 100 cm) in the block were also noted.

Presentation of call-ins

Playbacks were broadcast throughout the night at those calling stations where prey animals had been counted during the daytime and the GPS coordinates of the exact locations of all calling stations were recorded. The calling stations were located in open, short grass areas with good accessibility and at *c*. 2 km from the nearest Maasai settlements in Koyiaki. The broadcast vocalizations consisted of sounds of hyenas mobbing lions on a kill, involved in an inter-clan fight, squabbling on a kill and the bleats of a dying wildebeest calf (Mills, 1985). Although based primarily on hyena calls, these recordings have proved effective for eliciting lion and jackal responses (Ogutu, 1994; Ogutu and Dublin, 1998; Maddox, 2003). The vocalizations were broadcast from a MAX MX-550 R recorder with a 12-volt PA cassette amplifier and connected in series to two 22 cm long, 8-Ohm horn speakers facing opposite directions and powered by the vehicle's battery. The speakers were mounted onto the roof of the vehicle 2.2 m above ground.

The vocalizations were broadcast continuously for 5 min at full volume followed by a 5-min silent interval during which the speakers were rotated through 90°. The tape was then replayed for a further 5 min. Two observers counted responding (incoming) predators using powerful torches immediately after the last broadcast. Thirty minutes was spent at each call-in station and the maximum number of predators simultaneously in view before the responding predators began to disperse was recorded. When lion, jackal or hyena calls were heard but no animal arrived at the station within the standard 30 min, then we waited for another 15–30 min at the station.

Calibration experiments

We used calibration experiments to estimate the response range and probability.

For hyenas 6 independent trials for 16 individuals were conducted to estimate the distances within which hyenas heard and responded to the playbacks at the end of the call-in survey. Hyenas were first intensively searched for and located in areas where the tape had not been played during the survey to minimize the likelihood of habituation (Ogutu and Dublin, 1998; Mills et al. 2001; Maddox, 2003). One vehicle stayed with the hyenas to record their reactions while the other drove away and played the tape, exactly as done during the call-in surveys, at 5.0, 4.5, 4.2, 4.0 and 3.5 km, with the speakers facing the direction of the target hyenas. These tests, conducted between 17:30 and 19:00, showed that 58.3% of target hyenas heard and responded to the tape within a maximum radius of 4.0 km but were insufficient to calculate reliable confidence limits. For lions, the results of 27 calibration trials for 91 individuals conducted in the Mara reserve in 1991 were used (Ogutu and Dublin, 1998), which found that 26.4% of target lions heard and responded to the tape within a 2.5 km radius. It was assumed that these calibrations based on the reserve were applicable to carnivore populations on the group ranches despite reported suggestions of shifts in lion and hyena behaviour in the daytime (Maddox, 2003) because no lions were found for calibration experiments outside the reserve after 4 full days of intensive and systematic searches.

Estimation of predator population size and density and statistical analyses

The total population size of lions and hyenas in each stratum was estimated using the model of Mills et al. (2001) and the associated confidence intervals using the bias-corrected and accelerated non-parametric bootstrap (Efron and Tibshirani, 1993) in SAS JACKBOOT MACRO based on 10000 bootstrap replications. The expected number of predators within the response range ($\hat{u}$) was estimated by

$$\hat{u} = \tilde{y}/\hat{S}, \tag{1}$$

where $\tilde{y}$ is the mean number of predators of each species responding per station and $\hat{S}$ is the response probability from the calibration experiments (Mills et al. 2001).

Estimation of predator density, or the total population size requires use of the response radius to estimate sampled area. This was estimated as 4.0 km for hyenas and as 2.5 km for lions in the independent experiments. Thus, each calling station was assumed to cover an area of 50.27 km^2 for hyenas and 19.63 km^2 for lions and the response probabilities to be the same over all strata for hyenas and lions, respectively. The estimates of the number of hyenas (lions) per km^2 for the 6 strata and the 2 regions were computed as $\hat{u}/50.27$ for hyenas and $\hat{u}/19.63$ for lions (Table 4.2). The total number of hyenas (lions) in a stratum (region) was estimated using the relation

$$N_T = (A_H/A_S)\,\hat{u}, \tag{2}$$

where A_S = the area sampled around a call-in station and A_H = the area of the entire stratum or region (Mills et al. 2001). Estimates of jackal population size or density were not calculated because no independent experiment was conducted to estimate either their response range or response probability due to the limited time available.

We loge transformed prey biomass density for norma-lity, as indicated by the Box–Cox algorithm in SAS PROC TRANSREG (SAS, 2001), then regressed the transformed prey biomass density on region, grass height, elevation and interactions to establish if the mean aggregate prey biomass density differed between the reserve and Koyiaki, after statistically adjusting for variation in grass height and elevation. Model selection based on information theoretics, in particular the corrected Akaike information criterion (Burnham and Anderson, 2002), computed using restricted maximum likelihood in SAS PROC MIXED, showed the model assuming no autocorrelation to be better supported by the data than models incorporating either exponential, Gaussian, power, or spherical autocorrelation (Cressie, 1991) among residual errors.

Negative binomial regression was used for overd-ispersed count data (Gotway and Stroup, 1997) and regression parameters were estimated using penalized quasi-likelihood (Wolfinger and O'Connell, 1993) in SAS GLIMMIX MACRO to establish if the mean density of each predator species differed between the reserve and Koyiaki, after statistically controlling for variation in the mean aggregate biomass density of prey animals. We used the log link function and $\phi u(1+(u/k))$ for the variance function of the negative binomial model (Thurston, Wand and Wienecke, 2000), where u is the mean, ϕ is the overdispersion parameter and k is the 'aggregation parameter'. A common k was estimated for both regions by the method of moments for each predator species. Again, the model assuming independent and identically distributed residual errors had greater support in the data than models incorporating spatially autocorrelated error structures.

RESULTS

R egional and interspecific variation in response to call-ins

Lions, jackals and hyenas were seen at nine (25.7%), 23 (65.7%) and 34 (97.1%) of the 35 calling stations during the survey, respectively. The number of jackals, lions and hyenas attracted to calling stations ranged from 0–5, 0–11 and 0–27, respectively. A total of 475 hyenas responded to the playbacks. This was 8.6 and 11.3 times higher than the corresponding totals of either 55 jackals or 42 lions. Hyenas were present at eight of the nine stations (88.9%) where lions responded. The mean number of hyenas and jackals responding per station seemed to be higher for Koyiaki than for the reserve (Table 4.1). Within the reserve, the highest number of hyenas responding per station was recorded in Musiara and was comparable to the mean hyena response per station in Koyiaki. Hyena response to playbacks in the Triangle and Sekenani were similar but fewer than their responses in Musiara. Unlike hyenas and jackals, lions only responded to playbacks in the reserve and only at nine (40.9%) of 22 call-in stations.

Regional distinctions in estimated predator population sizes and densities and prey biomass

In the following section, we make estimates of predator population sizes in the reserve and pastoral lands, by assuming that there was no difference in behaviour between the two areas. It is known from Maddox's (2003) work that lions can change their activity levels during the day in Loliondo and Ngorongoro pastoral areas compared to Serengeti National Park, all areas just south of our study area. Here estimates are presented using the phrase 'apparent density' to indicate our uncertainty in making this assumption. The strength of the evidence for and against this assumption is given in the Discussion to make conclusions about the impacts of protection and pastoralism on carnivore populations.

'Apparent' lion density over the entire study area was estimated as 0.232 lions/km^2 for a total population size of 613 lions. There seem to be only *c.* 51 lions in Koyiaki group ranch based on the estimate of 613 lions for the entire study area and 562 lions for the reserve (Table 4.2). The strata level estimates show no lions outside the reserve because they use stratum-specific lion responses, but the whole system-level estimates show there are about 51 lions based on lion responses over the entire study area and over the reserve alone. Hence, calculated on a real basis, lion density was apparently 8.0 times higher in the reserve than in Koyiaki. The overall apparent hyena density was 0.463 hyenas/km^2 for a total of 1224 hyenas, which is twice the estimated total lion population size. Apparent hyena density was highest in Koyiaki and Musiara, lowest in Sekenani and the Triangle, and 1.3 times as high in Koyiaki as in the reserve (Table 4.2). Assuming a regionally uniform response range and probability, the estimated relative apparent density of jackals for the reserve was only 1.1 times that for Koyiaki, implying a uniform regional distribution (Table 4.2).

In the Mara reserve, prey biomass density in Sekenani and the Triangle, with tall grasslands, was only 71.2% and 85.4% of the reserve average (Table 4.3: 5472.4 kg/km^2),

Table 4.1 The total number of lions, hyenas and jackals responding (*n*), estimates of the expected number of individuals (μ) and the associated 95% bootstrap confidence limits (lower, upper) for each species within the response range of a calling station in each of 6 strata in the Mara Reserve and the adjoining Koyiaki group ranch during a call-in survey conducted from 24 June to 5 July 2003.

Region	Stratum	Calling stations	Area (km^2)	Lions				Hyenas				Jackals			
				n	μ	Lower	Upper	*n*	μ	Lower	Upper	*n*	μ*	Lower*	Upper*
Koyiaki	East	5	601.07	0	0.000	0.000	0.000	81	27.773	11.143	42.002	5	1.000	0.000	2.667
Koyiaki	West	8	519.05	0	0.000	0.000	0.000	133	28.51	19.144	36.516	17	2.125	0.750	3.400
Koyiaki	All	13	1120.12	0	0.000	0.000	0.000	214	28.219	20.572	35.21	22	1.692	0.786	2.667
Reserve	Musiara	4	259.52	11	10.417	0.000	41.667	67	28.716	18.429	42.86	2	0.500	0.000	1.000
Reserve	Sekenani East	5	334.11	9	6.818	0.000	12.625	54	18.515	0.000	24.98	9	1.800	0.000	4.000
Reserve	Sekenani West	5	451.15	9	6.818	0.000	34.091	50	17.144	5.878	36.431	5	1.000	0.000	2.000
Reserve	Triangle	8	480.46	13	6.174	1.894	14.61	90	19.287	13.715	29.487	17	2.125	1.000	3.375
Reserve	All	22	1525.24	42	7.235	3.389	13.939	261	20.333	15.627	25.579	33	1.500	1.000	2.150
Both	All	35	2645.36	42	4.545	2.056	9.199	475	23.264	19.053	27.64	55	1.571	1.114	2.086

* For jackals the response probability and range was not estimated, so μ and the confidence limits refer to the mean number responding per station.

Table 4.2 Estimated lion and hyena population density (number/km^2) and population size (number) for each of the six strata of the Mara Reserve and the adjoining Koyiaki group ranch and the associated 95% bootstrap confidence limits (lower, upper) based on 10000 bootstraps.

Region	Stratum	Lions			Hyenas			Lions			Hyenas		
		Density	Lower	Upper	Density	Lower	Upper	Number	Lower	Upper	Number	Lower	Upper
Koyiaki	East	0.000	0.000	0.000	0.552	0.222	0.836	0	0	0	332	133	502
Koyiaki	West	0.000	0.000	0.000	0.567	0.381	0.726	0	0	0	294	198	377
Koyiaki	All	0.000	0.000	0.000	0.561	0.409	0.7	0	0	0	629	458	785
Reserve	Musiara	0.531	0.000	2.123	0.571	0.367	0.853	138	0	551	148	95	221
Reserve	Sekenani, East	0.347	0.000	0.643	0.368	0.000	0.497	116	0	215	123	0	166
Reserve	Sekenani, West	0.347	0.000	1.737	0.341	0.117	0.725	157	0	784	154	53	327
Reserve	Triangle	0.315	0.096	0.744	0.384	0.273	0.587	151	46	358	184	131	282
Reserve	All	0.369	0.173	0.71	0.404	0.311	0.509	562	263	1083	617	474	776
Both	All	0.232	0.105	0.469	0.463	0.379	0.55	613	277	1240	1224	1003	1455

respectively, but was well above this average in Musiara. In Koyiaki, by contrast, mean prey biomass density was 2.6 times higher than the reserve average. The coefficient of variation in prey biomass density was 3, 2 and 1.5 times higher in the Triangle than in Koyiaki, Musiara and Sekenani, respectively (Table 4.3).

The influence of grass height and elevation on regional distinctions in prey biomass

Mean prey biomass density differed between the reserve and Koyiaki, and the size of the difference also varied with both grass height and elevation (Table 4.4), so elevation was fixed at its mean of 1642 m to examine how the size of the difference varied between regions at each level of grass height. These tests involved decomposing the region by grass-height interaction into simple effect slices (Winer, 1971). Mean prey

Table 4.3 The estimated mean aggregate biomass density (kg/km^2) of potential prey animals for lions, hyenas and jackals in the Mara Reserve and the adjacent Koyiaki group ranch during 24 June to 5 July 2003. Sample size equals the number of contiguous rectangular blocks (1 km × 0.2 km) constituting the 35 sampled (10 km × 0.2 km) strip- transects.

Region	Stratum	# Blocks	Mean biomass density (kg/km^2)	SE	Coeff.var
Koyiaki	Koyiaki East	90	14203.06	3384.95	2.261
Koyiaki	Koyiaki West	25	14243.1	5580.93	2.156
Koyiaki	All	115	14211.76	2902.77	2.255
Reserve	Musiara	40	10488.13	5525.47	3.332
Reserve	Sekenani East	60	7513.583	4318.54	4.144
Reserve	Sekenani West	50	282.3	183.259	4.59
Reserve	Triangle	80	4677.5	3436.11	6.571
Reserve	All	230	5472.413	1904.32	5.199
All	All	335	8385.529	1609.2	3.522

Table 4.4 Results of the linear regression of the mean aggregate prey biomass density on region, grass height, elevation and interactions. NDF is the numerator and DDF the denominator degrees of freedom for Wald type 3 F-tests.

Effect	NDF	DDF	*F*	*P* > *F*
Region	1	325	5.77	0.0168
Grass height	2	325	7.37	0.0007
Elevation	1	325	1.09	0.0007
Region x Grass height	2	325	3.89	0.0007
Region x Elevation	1	325	6.33	0.0007
Grass height x Elevation	2	325	6.79	0.0007

biomass was higher in Koyiaki than in the reserve within the short (0–30 cm: $F_{1,325}$ = 3.97, P = 0.0472) and medium (30–60 cm: $F_{1,325}$ = 9.2, P = 0.0026) grasslands but only marginally so within the tall grasslands (60–100 cm: $F_{1,325}$ = 3.09, P = 0.0795). Estimates of prey biomass density within the short and medium grasslands in Koyiaki, obtained by setting elevation at its mean value of 1642 m were 1.6 and 3.8 times higher than the corresponding estimates for the reserve (Fig. 4.2A). Prey biomass density was also always highest in the shortest grass in both locations. The prey biomass density predicted for the tall grasslands in the reserve, however, was higher than the value predicted for Koyiaki (Fig. 4.2A). This may suggest that tall grass is more dangerous to

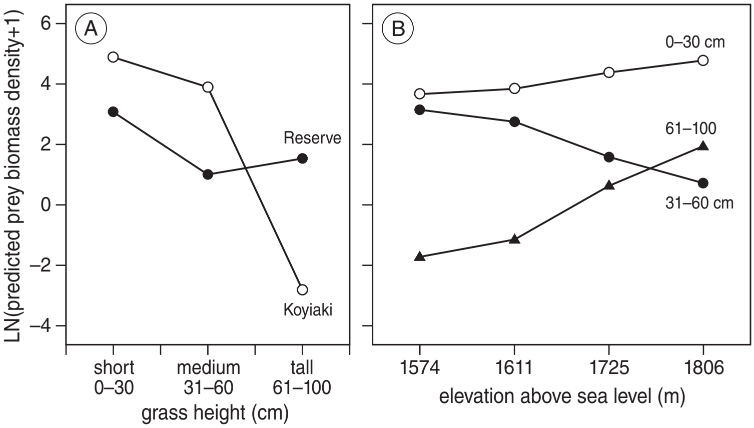

Figure 4.2 The variation in aggregate prey biomass density with grass height within each region, when elevation is fixed at its mean of 1642m (A) and with elevation within each grass height category (B).

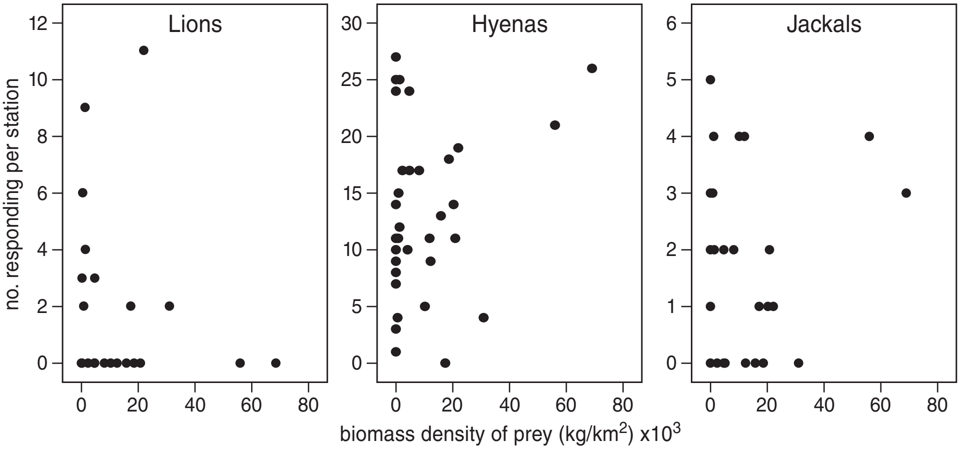

Figure 4.3 The variation in the number of predators of each species responding to playbacks per station with prey biomass density (kg/km2) in the Mara Area of Kenya.

herbivores in the pastoral area because the few predators there are all concentrated in the high grass or because people stalk wildlife in tall grass.

To establish how elevation modified the effect of grass height on prey biomass density, predicted values for prey biomass density were computed at the 25th (1574 m), 50th (1611 m), 75th (1725 m) and 90th (1806 m) quantiles of the frequency distribution of elevation and at each level of grass height (Fig. 4.2B). Prey biomass density increased as elevation increased in the short and the tall grass areas, but decreased with elevation in the medium grass areas (Fig. 4.2B).

The influence of prey biomass density on regional distinctions in predator response

The mean responses per station for hyenas ($F_{2,32} = 255.1$, $P < 0.0001$) and jackal ($F_{2,31} = 3.9$, $P < 0.032$) were higher in Koyiaki than in the reserve when the variation in prey biomass density was ignored. Prey biomass density was then fixed at a mean value over both regions to adjust for differences in prey biomass density when comparing carnivore response. It was found that hyena ($t = 1.390$, d.f. = 32, P = 0.1733) and jackal ($t = 0.690$, d.f. = 31, $P = 0.4960$) responses did not differ between the two regions when prey biomass density was fixed at its mean value over both regions of 10040 kg/km^2. Predator response apparently decreased as prey biomass density increased, but this relationship was weak and was distorted by the presence of unusually large herds of migratory prey from Loita plains along two transects in Koyiaki (Fig. 4.3). The weakness of this relationship suggests that high prey abundance in Koyiaki is probably not the reason that no lion responded to playbacks there.

DISCUSSION

Do playback responses reflect predator population densities or behaviour changes?

The chance that a lion or hyena would respond to a playback recording, when it is in their auditory range, is broadly similar in savanna ecosystems in eastern and southern Africa. The response probability and range for jackals to playbacks was not estimated. The response pro-bability (0.23) and range (2.5 km) for lions inside Serengeti National Park (Maddox, 2003) closely matched estimates for the lions inside the Mara reserve (0.26 probability, 2.5 km range), suggesting that response probability for lions does not differ throughout this region, at least within protected areas. Hyenas in the Mara responded as often in the Mara reserve (0.583; this study) as they do in Kruger National Park in South Africa (0.61; Mills et al. 2001), but about only two-thirds as often as they did just south of the Mara in the Serengeti (0.88; Maddox, 2003) and Selous Game Reserve in Tanzania (1.0; Creel and Creel, 1996). For hyenas, the response range of 4.0 km in the Mara was somewhat longer than either the 3.2 km obtained by Mills et al. (2001) for Kruger hyenas, 3.0 km for Serengeti hyenas (Maddox, 2003) but similar to the 3.7 km estimated by Creel and Creel (1996) for hyenas in Selous Game Reserve. Response probability might logically be expected to scale inversely as response range.

To our knowledge, there are no estimates of response probabilities for predators outside protected areas and no comparisons of responses in adjacent protected and unprotected populations. All research teams have as-sumed, as we did, that response probabilities are similar in areas reserved for exclusive wildlife use and in areas with human land uses. However, this assumption needs to be explicitly tested, based on the results of this study and recent evidence that predator behaviour can be affected by the presence of people, at least in the Mara (Boydston et al. 2003).

It was unexpected to find no response of lions to playback recordings in the pastoral areas, but these data are thought to be reliable because they are supported by other data collected previously using playbacks. Karani (1994) played call-in broadcasts at 20 calling stations in Koyiaki and Siana group ranches in July 1992 and again in February 1993 but attracted only 10 lions. She sighted a further four lions during intensive and systematic searches in the two group ranches. These results contrast with those of Maddox (2003) who found similar carnivore responses in Ngorongoro, Loliondo and Serengeti in Tanzania.

This lack of response by lions to our playback recordings in the pastoral areas can be explained in two different (but not mutually exclusive) ways. No response by lions suggests either that lions were absent, or occurred at extremely low densities in Koyiaki pastoral area during our counting period, or that residency in Koyiaki altered their behaviour such that lions avoided the broadcasts, or were too shy to approach the calling stations to within sighting range. There is evidence that supports both of these explanations for the Mara. In November 2002, our research team made a total daytime ground count of all wildlife and livestock species (including predators) in the same areas of the Mara and found 44 lions, 81 hyenas and 65 jackals in Koyiaki (793 km^2) and 123 lions, 167 hyenas and 89 jackals in an area of *c.* 1235 km^2 in the reserve (Reid et al. 2003). This shows that there are lions in Koyiaki and the numbers agree well with our estimate of 51 lions. These data clearly show that lions are present but are not responding to playbacks in Koyiaki. They also show either that true populations of lions are 50% smaller in Koyiaki (0.0555/km^2) than in the reserve (0.0996/km^2) or that counts were lower, per km^2, in the pastoral land because lions were avoiding vehicles there and not in the reserve. Since there is little history of hunting from vehicles in the Mara, it is unlikely that lions were avoiding vehicles, but they could have been hiding more generally and difficult to see during daylight hours. By contrast, Maddox (2003), in an area only 100 km south of the Mara, found no difference in populations of cheetah, lion and hyena inside Serengeti National Park, and in adjacent pastoral lands in Loliondo and Ngorongoro.

Although he did not demonstrate statistically significant differences in lion behaviour between the pastoral and protected areas, Maddox (2003) found evidence suggesting that lions were less active and rarely visible in the daytime and became more vigilant when they heard playbacks of Maasai cowbells in the pastoral lands of Loliondo and Ngorongoro than in the Serengeti. This, and the ground census above, suggests that lions change their behaviour and have inherently lower populations in the pastoral lands compared to the reserve in the Mara. Hyenas were similarly less active during daytime in the pastoral areas of Loliondo and Ngorongoro (Maddox, 2003). Boydston et al. (2003) found changes in the social behaviour and activity budgets of hyenas subject to increased interference by livestock, suggesting that hyenas and possibly jackals may respond differently to playbacks in the reserve than pastoral areas of the Mara.

Differences in visibility or prey biomass could also affect predator response to playbacks in the reserve and pastoral lands. However, the conditions in the two areas at the time of our study actually argue against these two explanations. Visibility at calling stations and prey biomass density in short and medium grasslands were generally higher in Koyiaki than in the reserve in June 2003, because of shorter grass height sustained by intense livestock grazing in Koyiaki, even though grass cover in the Mara ecosystem is typically highest in June, markedly lowering visibility. In November 2002, mean grass cover was 63.1% in Koyiaki and 73.3% in the reserve (Reid et al. 2003). Hence poor visibility almost certainly did not make it more difficult to see responding lions (or other predators) in Koyiaki than in the reserve, nor can prey density explain the estimated low lion density in Koyiaki at the time of our study. The higher prey biomass density in the pastoral areas compared to the reserve suggests seasonal movements of animals between the reserve and the pastoral ranches (Stellfox et al. 1986), because overall prey density has similarly declined in both the reserve and the pastoral lands (Ottichilo et al. 2000).

The available evidence thus suggests that lions occurred in Koyiaki, but at a much lower density than in the Mara reserve, and that these few lions did not respond to playbacks due to behavioural changes. The intensive and systematic searches for lions (Karani, 1994; Ogutu and Dublin, 2003, 2004; Reid et al. 2003) support inherently lower lion numbers in the pastoral areas, portending a severe threat to the long-term viability of the lion popu-lation in this pastoral system, as was previously forecast by Woodroffe and Ginsberg (1998, 2000). We expected lions to feel secure, at least under the cover of darkness, and to respond to the playbacks. That they did not respond at all reinforces the view that conflicts with pastoralism fundamentally adversely alter the behaviour of some large carnivore species (Woodroffe, 2000; Sunquist and Sunquist, 2001; Boydston et al. 2003). Although the frequent res-ponses of hyenas in both the reserve and group ranches would seem to contradict this view, Maddox (2003) also reported evidence for a shift in hyena behaviour between a protected area and pastoralist land use/hunting zones, based on a variety of data besides playback studies. The results for lions suggest the need to take the potential shift in behavioural response for different land-uses zones into account in playback surveys. Behavioural changes have also been documented for other species of exploited mammals outside protected areas (Caro, 1999).

Why might lion populations be lower in the presence of pastoral people and their domestic dogs than in the reserve? One explanation is that the canine distemper epidemic of 1993–94 killed more lions in the pastoral lands where there can be more frequent contact with domestic dogs. However, many lions in the Serengeti Park (Packer et al. 1999) died during this epidemic but no deaths were recorded in the Mara reserve (Kock et al. 1998). This is consistent with our historical data, which show that there was no difference in playback estimates of lion population size in the Mara reserve for June 1991 and 2003. Hence it is unlikely that diseases were responsible for the low lion density in the pastoral ranches.

A more likely explanation for low lion densities and behavioural changes is conflict with pastoral people and dogs in the pastoral ranches. An anomalously low lion density estimate in an area of high prey density, such as Koyiaki, is not too surprising if the Maasai often respond to livestock or human depredation by indiscriminately poisoning, snaring, shooting or chasing suspected predators (Rudnai, 1979; Karani, 1994; Omondi, 1994). However, lions, hyenas and jackals are sympatric in the group ranches, so it is unclear how hyenas and jackals would survive indiscriminate killing methods such as poisoning, given that all three species scavenge carcasses. The low estimate of lion density can result if the Maasai selectively harass or kill lions, as has happened in the buffer zones of Nairobi National Park where Maasai warriors have speared 87 lions since 1998 to avenge livestock deaths; 10 of these lions were killed in May and June 2003 alone (Kenya Wildlife Service, pers. comm.). Selective harassment or killing of lions may happen if the Maasai perceive lions as the most destructive, daring and aggressive large predators (Omondi, 1994) and thus respond to lion attacks with greater aggression. This may also happen if lions remain closer to bomas after attacks, are more reluctant to escape, or escape over shorter distances than hyenas if detected. The ability of hyenas to achieve a higher density in the ranches than in the reserve despite this is surprising and suggests that they are less of a target for pastoral harassment or killing or are behaviourally more flexible and adaptable to life in the ranches than are lions. Jackal density seemed to differ only marginally between the reserve and Koyiaki, suggesting that jackals too coexist well with pastoralism. However, our conclusions about hyenas and jackals are only tentative, because we (and others, but see Maddox, 2003 for hyenas) have not tested the assumption that these two species do not change their behavior in the presence of pastoralists

Unlike for lions, the regional differences in hyena response to playbacks corresponded positively with the regional distribution of prey biomass density. The higher density of hyenas in Koyiaki than in the reserve was perhaps due, in part, to reduced competition with lions and elevated prey density in Koyiaki. It could also be that pastoralism is compatible with robust hyena populations, but Boydston et al. (2003) found some substantial changes in hyena ranging and social behaviour, activity schedules and demography attributable to pastoralism at the edge of the reserve

Direct killing and kleptoparasitism are important forms of interference competition among large African carnivores (Frame, 1986; Laurenson, 1995; Creel and Creel, 1996; Mills and Gorman, 1997) and could, at least partially, also explain the high hyena density in the pastoral ranches, where lion density estimate was anomalously low. The abundance and species richness of small mammals has also been found to be greater outside than inside a national park in western Tanzania (Caro, 2001), perhaps supporting a hypothesis of competitor release. Keesing (2000) also reported a burst in small mammal populations but a decline in species diversity inside exclosures at the

Mpala ranch in Kenya owing to the removal of competition for food and/or habitat disturbance by ungulates.

Additional study is required to calibrate and evaluate the effectiveness of the playback technique in pastoral systems where predator behaviour is likely to change substantially (Kitchen, Gese and Schauster, 2000; Korb, 2000; Frank and Woodroffe, 2001; Boydston et al. 2003; Maddox 2003), in contrast to protected areas where the technique has been used with success, and to establish why hyenas, jackals and lions can coexist with the Maasai pastoralists without drastic reductions in their densities or major changes in their behaviour in some systems but not others. Such studies should help reconcile contrasting lion responses to playbacks, such as were found in the pastoral zones in the Mara region relative to Loliondo and Ngorongoro (Maddox, 2003) and reliably distinguish inherently low carnivore densities from low-density estimates that are potentially artefacts. Further studies should also establish if threshold densities exist below which different carnivore species can coexist harmoniously with pastoralists at specified densities of pastoralists, livestock and potential carnivore prey base and how decisions to hunt and spear lions are made given the effort and risks involved.

We agree with other assessments (Mills, 1985; Sillero-Zubiri and Gottelli, 1992; Creel and Creel, 1996; Mills and Gorman, 1997; Ogutu and Dublin, 1998; Mills et al. 2001; Maddox, 2003) that playback recordings have good potential to be a rapid, efficient and cost-effective method for estimating predator population sizes in Africa, characterizing their spatial distributions and hence could be ideal for the long-term monitoring of large carnivore numbers. It is critical, however, to collect more data on response probabilities when comparing areas with and without strong human interference to understand better when and if people affect predator behaviour and thus the reliability of playback estimates of population sizes. It is also essential to collect simultaneous data on lion densities in other ways (individual recognition, etc.) to establish how well response probabilities reflect true densities. In addition, we think it is important to collect linked data on prey populations to interpret predator data.

In particular, it is important to study why predators change their behaviour in response to pastoral people. For example, despite the high prey biomass density in Koyiaki, humans may hinder the hunting efforts of hyenas there, making the resident hyenas hungrier and hence more likely to appear at the broadcasts than hyenas inside the reserve. If true, such interference would lower hyena density in the long term. Obtaining separate estimates of response probabilities for inside and outside the reserve would test this hypothesis. Age and sex of carnivores, resident or nomadic status, state of hunger and feeding on a carcass are other factors that also influence carnivore response probabilities (Ogutu and Dublin, 1998; Maddox, 2003). We have also assumed minimal influence of diurnal and interdiurnal variation in atmospheric conditions on the response range (Garstang et al. 1995; Larom et al. 1997) but this assumption should also be tested. There is a need for more detailed behavioural studies in both areas to establish to what extent lions shift to more cryptic and guarded behaviour in pastoral land areas and how this affects response probabilities, but also in-depth interviews with pastoral people to understand how they behave towards predators and why they think lions are particularly susceptible to their presence.

In addition, conducting audio playback surveys in the Mara ecosystem in June when extra food for predators derived from migrant prey is lowest, dry tracks allow easy accessibility by vehicles and predator response is likely to be highest is recommended. The technique, however, needs careful calibration and cross-checking with respect to behaviour changes of target species in different land use zones. Since the migrant herbivores occupy the Mara from July to at least October each year, and since carnivore response is lowest at this time, conducting only one playback survey per year is recommended to minimize the potential for habituation (Ogutu and Dublin, 1998). Opportunistic observations showed that, in contrast to hyenas and jackals that arrived at call-in stations within 30 min, lions may arrive at call-in stations within 45–60 min after the first call-in broadcast and will therefore tend to be missed if shorter times are spent at a station, as was also found by Ogutu in 1991–92 (J. Ogutu, pers. obs.) and Maddox (2003). It should also be noted that hyenas are more than twice as responsive over broader areas than lions in both Mara and the Serengeti. Hyenas heard and responded to playbacks over a longer range than lions, hence hyena surveys require larger spacing between stations than lion surveys.

Are predator populations on decline in the Mara?

There is strong concern that populations of lions in Africa are on the decline and possibly severely endangered (Bauer and Van Der Merwe, 2004). Inside the reserve, however, there was no change in the number of lions or hyenas found by the first author of this paper in 1991 compared with 2003. The estimated expected number of hyenas (20.37) and the associated 95% confidence limits (15.44, 27.71) and lions (9.11, 95% CL (5.09, 15.26)) within the response range, based on the June 1991 playback survey for the Mara reserve (Ogutu and Dublin, 1998), were not different from the corresponding esti-mates for June 2003 (Table 4.1). If a constant response range and probability is assumed between the 2 years, then the estimated hyena density [0.405(0.307–0.551)] and population size (620 (470–843)) and lion density (0.464 (0.259–0.778)) and population size (710 (397–1190)) for the Mara reserve for June 1991, were no different than the corresponding estimates for the reserve for June 2003 (Table 4.2). Making these same assumptions, the estimated mean number of jackals responding per station suggests that there were many more jackals in 2003 (Table 4.1) than in 1991 (0.28125 (0.063–0.750)). Over this same period, there was no difference in the mean aggregate biomass density of lion and hyena prey between 1991 (5172.273 kg/km^2) and 2003 (Table 4.3; t =_0.120, DF = 21, P = 0.905). It is not known whether the increase in jackal density reflects an underlying increase in their prey density.

It is suspected that lion populations have declined over time outside the reserve, based on the work of our col-leagues, M. and J. Rainy. From 1982 to 1988, they identified individual lions in seven prides inside and six prides outside the Mara reserve. Over these 7 years, they found that the population remained stable inside but de-creased dramatically outside the reserve in pastoral lands where Maasai pastoralists had established permanent set-tlements by 1982–83 (M. Rainy and J. Rainy, per comm.). This probable loss of lion populations outside the reserve supports trends across the continent (Bauer and Van Der Merwe, 2004) and signals a serious threat to their long-term population viability. Further research is required to ascertain the reasons for the unusually low lion density estimates in the pastoral areas, as well as urgent conservation interventions to develop management strate-gies that integrate the economic welfare of pastoralists with the conservation of large carnivores to secure their populations from imminent extirpation in this and other similar pastoral systems.

Rapid human population growth and the associated intensification and diversification of land use, increasing sedenterization, settlement density, habitat deterioration, fragmentation and loss all exacerbate human-carnivore conflicts in the ranches. These processes continually erode grazing areas so that livestock compete more severely with wildlife with the result that the potential prey base for large carnivores shrinks. As a result, conservation interventions should consider improving livestock husbandry (Ogada et al. 2003), increasing wild ungulate populations and improving the attitudes of local communities and land-owners towards wildlife conservation in the ranches. Empowering pastoralists to earn more revenues from wildlife-based tourism or sport hunting, establishing effective wildlife damage control and conducting targeted environmental education can help improve attitudes towards wildlife. If an insurance fund is established to compensate pastoralists for livestock killed by predators, human injuries or fatalities, then the compensation scheme should be administered efficiently and incorporate careful assessments of claims to minimize abuse.

Successful interventions should take prevailing local circumstances into account because local management, culture, governmental policy, trade and law enforcement can all have overriding effects on large carnivore extinctions (Linnell, Swenson and Andersen, 2001). Hence it is important to enact and enforce policies and legis-lations that promote sustainable mixed livestock–wildlife enterprises. The national policy and legislation on wildlife conservation are hardly enforced in the pastoral ranches of the Mara so wildlife conservation there depends largely on the goodwill and support of the local communities and landowners. At present, a glaring contradiction exists in the national wildlife policy and devolution of rights, in that landowners and communities bear the burden of having wildlife on their land without compensation for wildlife damage to private property, human injuries or fatalities, rights of ownership or use of wildlife except through tourism revenues. The inconsistency of state ownership of wildlife, the prevailing inequitable distribution of tourism revenues and the ongoing privatization of land tenure in the ranches clearly undermine wildlife conservation goals. Landowners are already erecting fences, cultivating, renting or selling land for cultivation in key wildlife grazing and calving grounds, such as the Loita plains.

We urge the development of an effective and participatory planning system for land use that restricts migration of people into the area and encourages compatible land uses, alternative livelihood options to reduce the level of dependence on livestock as the only source of income and incorporates soft edges. Plans for land use should encourage the distribution of human settlements such that pastoralists live in designated areas to reduce the frequency of contact between people and carnivores and the development of agriculture and infrastructure away from the reserve boundary. Research should be conducted to assess the effectiveness of these measures in reducing human–wildlife conflicts.

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Chapter 5

Comparative changes in density and demography of large herbivores in the Masai Mara reserve and its surrounding human-dominated pastoral ranches in Kenya

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ABSTRACT

Wildlife habitats in pastoral lands adjoining protected areas in east African savannas are getting progressively degraded, fragmented and compressed by expanding human populations and intensification of land use. To understand the consequences of these influences on wildlife populations, we contrasted the density and demography of 13 wild and three domestic large herbivores between the Maasai Mara National Reserve and the adjoining pastoral ranches using aerial surveys conducted in the wet and dry seasons during 1977-2010. Species of different body sizes and feeding styles had different densities between landscapes and seasons. Small-sized herbivores, requiring short, nutritious grasses, and browsers were more abundant in the ranches than the reserve in both seasons. Medium-sized herbivores moved seasonally between landscapes. Larger-bodied herbivores, requiring bulk forage but less susceptible to predation, were more abundant in the reserve than the ranches. The proportions of newborn warthog (*Phacochoerus africanus*) and juvenile topi (*Damaliscus korrigum*) were higher in the ranches, with shorter grasses and lower predation risk than in the reserve. These results suggest that pastoral lands adjoining protected areas in African savannas are important as seasonal dispersal and breeding grounds for wild herbivores. However, human population growth and dramatic land use changes are progressively degrading wildlife habitats in pastoral areas, thus restricting the seasonal wildlife dispersal movements between the protected areas and adjoining pastoral lands. Conservation efforts should focus on (1) creating and maintaining functional heterogeneity in protected areas that mimic moderate pastoral grazing conditions to attract small and medium-bodied grazers and (2) securing dispersal areas, including corridors, to ensure continued seasonal large herbivore movements between protected and pastoral systems.

INTRODUCTION

Pastoralism is the economic mainstay of most inhabitants of grasslands of East Africa, who also often derive limited income from wildlife-based tourism. However, rapid human population growth, expansion of settlements (Lamprey and Reid 2004), cultivation (Serneels et al. 2001, Thompson and Homewood 2002) and transition from semi-nomadic pastoralism to a sedentary lifestyle (Western et al. 2009), are progressively altering the vegetation composition and structure of these savanna grasslands. Concurrent with these processes, a transition from communal land tenure to private land ownership in the pastoral ranches, habitat fragmentation through land privatization and subsequent subdivision (Buckland et al. 2001), rising temperatures and recurrent severe droughts (Ogutu et al. 2007) threaten the future survival of large mammalian populations in some savanna ecosystems, such as the Mara-Serengeti of Kenya and Tanzania (Ottichilo et al. 2001, Ogutu et al. 2009).

Settlements are expanding faster nearer than farther away from protected areas in Latin America and Africa due to enhanced economic activities and opportunities inside and around protected-area boundaries (Wittemyer et al. 2008). A spectacular example of this expansion is found on pastoral ranches surrounding the Masai Mara National Reserve (MMNR) in Kenya (Norton-Griffiths 2007). The progressive intensification of land use, sedentarization and diversification of livelihoods are associated with rapidly declining wildlife numbers in the last three decades in pastoral systems of east Africa, including the Mara (Broten and Said 1995, Ottichilo et al. 2001, Ogutu et al. 2009), Laikipia (Georgiadis et al. 2007a) and Athi-Kaputiei (Reid et al. 2008b) regions of Kenya and the Tanzanian Tarangire-Simanjiro Plains (Msoffe et al. 2011). The declines are related to increasing numbers of settlements, people, poaching and major land use changes on the pastoral ranches (Homewood et al. 2001, Georgiadis et al. 2007a, Reid et al. 2008b). The patterns of declining wildlife in protected areas of East Africa (Stoner et al. 2007; Western et al. 2009) are consistent with early forecasts of major reductions, and even extinctions of many wildlife populations expected in East African reserves as a consequence of increasing insularization (Newmark 1996, Woodroffe and Ginsberg 1998) and displacement of wildlife by increasing livestock incursions into protected areas (Butt et al. 2009).

These changes progressively impede traditional seasonal wildlife movements between protected areas and their adjoining pastoral systems. Several studies have demonstrated seasonal movements by ungulates between protected areas and adjoining pastoral ranches in Amboseli (Western 1975), Mara (Stellfox et al. 1986) and Athi-Kaputiei Plains (Reid et al. 2008), thus supporting the prediction that the processes associated with land use change will continue to erode grazing areas so that livestock will compete increasingly with wildlife for resources, resulting in wildlife and livestock population declines (Buckland et al. 2001).

By moving seasonally between protected and pastoral areas, ungulates maximize their resource requirements while minimizing predation risk (Hopcraft et al. 2010). However, these seasonal dispersal movements might be constrained by body size

(Hopcraft et al. 2011) through its influence on food quantity and quality requirements as well as vulnerability to predation.

More specifically, large herbivores can tolerate more fibrous and lower-quality diets than can small herbivores because of their larger gastrointestinal tracts and lower specific metabolic requirements (Owen-Smith 1988, Ritchie and Olff 1999, Hopcraft et al. 2010) Furthermore, a smaller fraction of large herbivores die from predation than do small herbivores because large herbivores are more difficult for predators to capture (Sinclair et al. 2003). Thus, body size can be expected to control responses of herbivore abundance to seasonal disparities in forage quantity and quality and predation risk between protected and pastoral landscapes.

The MMNR in Kenya supports a high abundance and diversity of resident wildlife and offers a dry season habitat for migratory ungulates from the Serengeti National Park in Tanzania to the south and the neighbouring Loita Plains to the northeast (Maddock 1979, Stellfox et al. 1986). Extensive grasslands in the pastoral areas adjacent to the MMNR also provide wet season dispersal ranges for resident wildlife (Stellfox et al. 1986). Yet, despite the significance of pastoral areas to wildlife, few studies have evaluated the relative impact of pastoralism versus protection on wildlife population density and demography in African savannas (Caro 1999a, Wallgren et al. 2008). Even fewer studies have investigated the impacts of pastoralism and protection on long-term comparative changes in density (Caro 1999b, Reid et al. 2008b).

Here, we analyze the influence of protection in the MMNR and pastoralism in the adjoining Koyiaki pastoral ranch (see below) on comparative changes in the density of 13 wild herbivores. We consider the following wild herbivores, in order of increasing body size, Thomson's gazelle (*Gazella thomsoni*), impala (*Aepyceros melampus*), warthog, Grant's gazelle (*Gazella granti*), topi, wildebeest (*Connochaetes taurinus*), Coke's hartebeest (*Alcelaphus buselaphus cokeii*), defassa waterbuck (*Kobus ellipsiprymnus*), zebra (*Equus burchelli*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), and elephant (*Loxodonta africana*) (Table 5.1). We also consider the densities of three domestic herbivore species, namely sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos indicus*). We used data collected from systematic reconnaissance aerial surveys conducted during wet and dry seasons by the Kenya Department of Resource Surveys and Remote Sensing (DRSRS) from 1977 to 2010. We supplemented these comparisons with parallel comparisons based on ground mapping censuses conducted in the MMNR and Koyiaki in November 1999 and 2002 (Reid et al. 2003). We also compared age and sex composition counts of a subset of six of the 13 wild herbivores, namely, impala, warthog, topi, hartebeest, zebra and giraffe, conducted in 2003 and 2004 to establish the influence of protection and pastoralism on the demography of these herbivore species. The six species were selected because reliable methods for ageing and sexing them had already been developed and tested as part of a 15-year monitoring program spanning 1989-2003 (Ogutu et al. 2008).

Our hypotheses were based on differences in grass heights and predator densities between the MMNR and the pastoral ranches quantified by Ogutu et al. (2005) and Reid et al. (2003). Grass height influences both forage quality and predation risk. In the wet season less heavily grazed grasses, such as occur in most parts of the Mara reserve, become tall and therefore allocate more energy to developing structural fibers with higher carbon to nitrogen ratios, thereby diluting the concentration of nitrogen and phosphorous available to herbivores (Anderson, et al. 2007). From an herbivore's perspective, the digestibility of grasses is therefore inversely related to rainfall amount (Hopcraft et al. 2011). Mature grasses of tall stature are thus particularly unfavourable for small and medium herbivores due to their low digestibility and nutritional quality (Fritz and Duncan, 1994; Olff, Ritchie and Prins, 2002). In contrast, short grasses maintained by heavy livestock grazing, such as those in the pastoral areas of the Mara in the wet season (Ogutu et al. 2005), have higher digestibility and nutritional quality. Heavy livestock grazing on the ranches, furthermore, tends to promote production of more net grass biomass, which in turn attracts more herbivores than in the reserve with no livestock. Consequently, sustained livestock grazing in the ranches, by keeping grass stem biomass low, renders grasses more digestible and enhances their nutritional quality (McNaughton, 1976). This enables herbivores to realize greater protein consumption on the ranches than they do in the reserve in the wet season. As well, nutrient-rich pastoral settlement (boma) sites in the ranches represent key sources of nutritionally sufficient forage, especially for lactating females in the wet season (Muchiru et al. 2008; Augustine et al. 2010).

Table 5.1 Functional groupings of species by body mass (Coe et al. 1976), feeding and foraging styles.

Common name	Scientific name	Mass (Kg)	Dietary guild	Residence guild
Thomson's gazelle	*Gazella thomsoni*	15	Grazer	migratory
Sheep + goats	*Ovis aries* + *Capra hircus*	16	Mixed feeder*	resident
Impala	*Aepyceros melampus*	40	Mixed feeder	resident
Warthog	*Phacocoerus africanus*	45	Grazer	resident
Grant's gazelle	*Gazella granti*	50	Mixed feeder	resident
Topi	*Damaliscus korrigum*	100	Grazer	resident
Wildebeest	*Connochaetes taurinus*	120	Grazer	migratory
Hartebeest	*Alcelaphus buselaphus cokeii*	125	Grazer	resident
Defassa waterbuck	*Kobus ellipsiprymnus*	160	Grazer	resident
Cattle	*Bos indicus*	180	Grazer	resident
Zebra	*Equus burchelli*	200	Grazer	migratory
Eland	*Taurotragus oryx*	350	Mixed feeder	migratory
Buffalo	*Syncerus caffer*	700	Grazer	resident
Giraffe	*Giraffa camelopardalis*	1250	Browser	resident
Elephant	*Loxodonta africana*	5500	Mixed feeder	dispersal†

†Wanders widely seasonally but do not engage in regular seasonal migrations. *Sheep are grazers, and goats are browsers

In addition, during the wet season, it is likely that lions are more abundant in the reserve (Reid et al. 2003), with taller grass cover, than in the ranches (Ogutu et al. 2005). Predator densities are also higher in the reserve than in the ranches in the dry season (Reid et al. 2003), reflecting not only their preference for high grass cover, but also avoidance of human and livestock activities on the ranches (Ogutu et al. 2005). Since predation risk increases with grass height in the Serengeti (Hopcraft et al. 2005) and Mara Region (Kanga et al, 2011) and since grass cover is shorter and predator density is lower on the ranches than in the reserve, small and medium herbivores likely experience lower predation risk on the ranches than in the reserve (Sinclair et al. 2003).

In the dry season, when surface water and forage availability are reduced, heavy livestock grazing in the pastoral ranches forces wildlife to disperse to the reserve, where the migratory wildebeest and zebra and fires have removed the taller grasses and improved visibility. Thus, heavy livestock grazing in the pastoral ranches facilitates small and medium-sized herbivores in the wet season, but competition with livestock in the dry season for food and water, pushes them into the reserve where they are facilitated by migratory herds, which also absorb most of the predation pressure (Ogutu et al. 2008).

Accordingly, we formulated the following four initial expectations based on herbivore body size. (1) The densities of the small-sized herbivores (15–50 Kg), would be higher in the Koyiaki pastoral ranch in both seasons due to the higher prevalence of short grass that is safer year round. (2) The densities of medium-sized grazers (100-200 Kg) would be higher in the Koyiaki ranch in the wet season when grass is short (and safe) and green (and nutritious), but would be higher in the reserve with higher quantities of grass in the dry season when grass dries out and becomes too short on the Koyiaki ranch. (3) The density of large wild herbivores (>350 Kg) would be higher year-round in the reserve than in Koyiaki ranch if they perceive lower predation risk (Sinclair et al. 2003) and satisfy their energy demands by ingesting large quantities of low-quality forage (Demment and Van Soest 1985). Finally, (4) the lower number of predators and presumably lower predation risk on Koyiaki ranch, due to the shorter grasses of higher nutritional quality, and better predator visibility, would lead to a higher proportion of the pregnant females bearing and raising their young on the ranches than in the reserve.

Since the changes in wildlife distribution between the reserve and the ranches constitute essentially an unreplicated natural experiment, we used the protected Mara reserve as an ecological baseline area or benchmark that is relatively free of human impact to understand the consequences of impacts of livestock and human use of the human-dominated pastoral lands on seasonal and long-term patterns of wildlife distributions in the Mara Region (Sinclair 1998; Sinclair et al. 2002). We conduct replicate comparisons of herbivore densities between the reserve and the ranches based on 50 independent aerial surveys spanning 41 years conducted using the same technique to increase our confidence in, and ability to, separate the impacts of livestock and human use of the pastoral ranches on wildlife distributions despite the lack of true replication, which is difficult to achieve experimentally at landscape scales.

Study Area

The Mara Reserve is located in southwestern Kenya and borders the Serengeti National Park in Tanzania to the south. It covers some 1530 km^2 and is bounded by the Siria escarpment on the west, Koyiaki (931 km^2) and Olkinyei (804 km^2) pastoral ranches on the north and Siana pastoral ranch (1315 km^2) on the east (Ogutu et al. 2005) (Fig. 5.1). The reserve and the surrounding pastoral areas support annual migrations of enormous herds of wildebeest and zebra and small herds of eland from the Tanzanian Serengeti and much smaller herds of wildebeest, zebra and Thomson's gazelles from the Kenyan Loita Plains, to the northeast of the reserve (Stellfox et al. 1986). Traditional pastoralism, cultivation, and wildlife tourism constitute the major forms of land use in the pastoral ranches (Homewood et al. 2001). The major livestock species kept in the ranches include cattle, sheep, goats and donkeys (Lamprey and Reid 2004). The reserve is a nationally protected area in which wildlife conservation and tourism are the only permitted land uses but illegal livestock grazing is common,

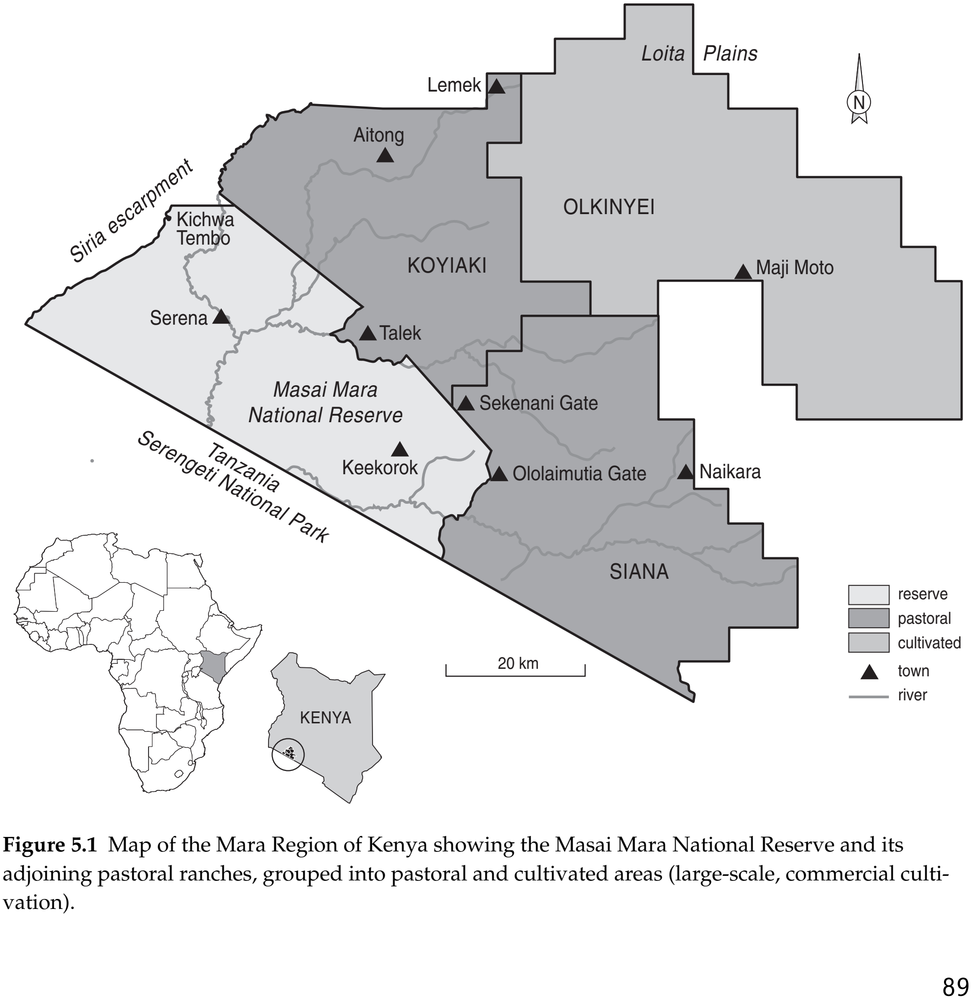


Figure 5.1 Map of the Mara Region of Kenya showing the Masai Mara National Reserve and its adjoining pastoral ranches, grouped into pastoral and cultivated areas (large-scale, commercial cultivation).

especially in dry years (Reid et al. 2003, Butt et al. 2009). There is no physical barrier to wildlife movements between the reserve and the surrounding pastoral areas. Hereafter, we refer to the reserve and all its surrounding pastoral ranches as the “Mara Region”.

The vegetation consists predominantly of open grass plains dominated by *Hyparrhenia filipendula* and *Themeda triandra*, interspersed with *Acacia gerrardii* and *Terminalia* trees, shrublands and riverine forests (Butt et al. 2009). Numerous seasonal streams drain the area, but only the Mara River and sections of the Sand and Talek Rivers typically contain water year-round. The Mara River originates in the Mau escarpment to the north of the Mara region(Krhoda 1988). Annual rainfall during 1989-2003 averaged 1010 mm and increased from 877 mm at Ololaimutia Gate in the south-east to 1341 mm at Kichwa Tembo in the northwest of the MMNR (Owen-Smith and Ogutu 2003). Rainfall is bimodal in the Mara Region, with the wet season spanning late November of the previous year to June of the current year and the dry season covering July-early November of the current year. The short rains fall during late November-December and the long rains during March-June. Rainfall increases spatially from 500 mm per year in the Serengeti Plains in the southeast to over 1200 mm in the northwest of the Mara Region (Pennycuick and Norton-Griffiths 1976).

METHODS

The Kenya Department of Resource Surveys and Remote Sensing (DRSRS) conducted 50 aerial surveys in the Mara Region from 1977 to 2010, covering the entire Mara Region (6400 km^2), including the reserve (1530 km^2), and the surrounding pastoral ranches (4870 km^2). Surveys were undertaken either in the wet (Jan–June or Nov–Dec) or dry (Jul–Oct) season month(s) of each year except 1981, 1988, 1995, 1998, 1999, 2001, 2003, 2004 and 2006 when surveys were not conducted due to financial constraints (Stellfox et al. 1986, Broten and Said 1995, Ottichilo et al. 2001). The surveys followed systematic strip transects located 5 km apart and segmented into sampling grid cells of 5×5 km^2 (Norton-Griffiths 1978). The transects were oriented in an east-west or north-south direction and were flown at a fixed height of about 90 m above the ground during 1977-1985 and about 120 m thereafter (Ottichilo et al. 2001). The number of animals observed within a calibrated survey strip defined by two parallel rods on the wing struts of the aircraft and running through the centre of the 5×5 km^2 grid cell was recorded. The survey strip spanned an average width of 263 m on the ground, corresponding to an average sampling intensity or fraction of 4.8 % of the 5×5 km^2 grid cell area (Owen-Smith and Ogutu 2003). The expected number of animals per 25 km^2 grid cell area was thus estimated as the actual number counted in each 25 km^2 grid cell times 100 divided by the sampling fraction. The mean count for each species per survey in the reserve was expressed as the average of the estimated population size over all the 25 km^2 grid cells in the reserve ($n = 61$ cells, covering a total area of 1525 km^2). The same applies to the Koyiaki pastoral ranch ($n = 37$, for a total area of 925 km^2). Ottichilo et al. (1999) and Ottichilo and Khaemba (2001) have demonstrated the reliability of the estimates of wildlife and livestock population sizes from the DRSRS count method. From the 50 surveys, we selected counts of 13 wild herbivore species, comprising four small-sized herbivores: Thomson's gazelle, Grant's gazelle, impala and warthog, five medium-sized herbivores: topi, hartebeest, wildebeest and zebra, four large herbivores: eland, buffalo, giraffe and elephant; and three species of livestock, namely sheep and goats (which are lumped together during surveys as 'sheep and goats' because they occur in mixed herds that are hard to distinguish reliably from the air) and cattle to represent a range of functional groups based on body size, feeding and foraging styles (Table 5.1). Of the 50 surveys 33 were conducted in the wet season and 17 in the dry season. Averaging population density estimates for each species in each grid cell over all surveys conducted in each season in one year produced 20 surveys for the wet season (late November-June) and 12 for the dry season (July-early November), which we used for analysis.

Ground mapping census of wildlife and livestock

Two ground mapping censuses of wildlife and livestock in the MMNR and the adjacent pastoral ranches were conducted in early November 1999 and 2002 when dry conditions prevailed and the grass was still short, due to heavy grazing by migratory wildlife (Reid et al. 2003). The first census covered an area of 1544.2 km^2, including sections of Koyiaki and Lemek pastoral ranches, and the MMNR. This census was carried out by 12 teams totaling 40 people using 12 vehicles in both the reserve and the ranches. The second census covered 2212 km^2 and included Koyiaki, Lemek, Siana and a small part of southwestern Olkinyei ranches. This census was carried out by 22 teams totaling 84 people. The census area was partitioned into contiguous 0.33×0.33 km^2 sub-blocks to obtain fine resolution counts. The teams counted 7606 sub-blocks in the reserve and 6295 sub-blocks in the ranches in 1999 and 11117 sub-blocks in the reserve and 8794 sub-blocks in the ranches in 2002 (Reid et al. 2003, Ogutu et al. 2010). The sampling teams navigated vehicles down the centers of each 1×1 km^2 block and allocated all animals observed into one of the nine nearest 0.33×0.33 km^2 sub-blocks using a global positioning system (GPS). The counts per 0.33×0.33 km^2 sub-blocks were converted to densities per km^2 by multiplying them by nine. The mean density and corresponding standard errors were calculated as the average density over all sub-blocks in the reserve and ranches. The mean count for each species in the reserve was expressed as the average of the estimated population size over all the per 0.33×0.33 km^2 sub-blocks in the reserve. The same applies to Koyiaki pastoral ranch. We used these censuses to validate distribution patterns derived from the aerial surveys during the dry season, including one aerial survey that was conducted at the same time as the ground mapping census in 2002.

Age and sex composition counts of wildlife

Ogutu et al. (2006a), in collaboration with the World Wide Fund for Nature (WWF), carried out two further vehicle ground sample counts of impala, warthog, topi, hartebeest, zebra, and giraffe including their age and sex. These counts were conducted in the MMNR, Koyiaki and a small section of Siana ranch in November 2003 and April 2004. The November 2003 survey was also conducted during the dry season. In contrast, the April 2004 survey was conducted in the late-wet season. They used a strip-transect sampling technique assuming complete census of all animals within a fixed strip width of 100 m either side of the transect centerline (Ogutu et al. 2006). The transects were distributed over the MMNR and pastoral ranches in proportion to their areas, with 22 transects established in the reserve and 13 in Koyiaki. Each transect was 10 km long. After every 1 km along each transect, the vehicle was stopped and the numbers, age class relative to adult size, sex and GPS locations of wildlife were recorded within 200 m on either side of the transect centerline. These species were classified, whenever possible, into three age classes: newborns (< 1 month), juveniles (1–18 months), adults (> 18 months). A combination of horn shape and length and body size were used to assign the herbivores to sex and age categories, however, ages were not assigned to adults (Sinclair 1995). Only the number of individuals sighted per age class in each transect, summed over all transects in the reserve and the ranches, from this dataset were used in analyses.

Comparing wildlife and livestock densities between landscapes

To account for clustering, non-normality and non-homogenous variances of animal counts, and varying frequency of counts we used negative binomial regression model for overdispersed count data to compare the mean density for each herbivore species in each 5×5 km^2 grid cell between the MMNR and Koyiaki pastoral ranch using the aod package in R (Lesnoff and Lancelot 2010, R Development Core Team 2010). More specifically, we used the log link function and specified the variance function for the negative binomial model as $\phi u(1+(u/k))$, where u is the mean, ϕ is the overdispersion parameter and k is the 'aggregation parameter'. Differences in the expected herbivore counts between landscapes were tested for significance using the Wald chi-squared test (Draper and Smith 1998)). A similar analysis was performed to compare the mean densities from the ground mapping censuses per 1×1 km^2 grid cells between the MMNR and Koyiaki pastoral ranch (Reid et al. 2003).

Comparing age ratios and female proportions between landscapes

Due to low sample sizes for certain cross-classification cells, we used a chi-square test for independence in a 2×2 frequency table, corrected for continuity using the Yates' correction for small sample sizes, to compare the ratio of newborns to adult females to that of juveniles to adult females for impala, topi and giraffe and the ratios of newborns to adults of both sexes to that of juveniles to adults of both sexes for warthog and zebra between the two areas based on counts pooled over the 2003 and 2004 surveys. We similarly compared the female proportion (F/(F+M), where F = female counts and M = male counts) for impala, topi and giraffe computed by pooling all individuals of the same sex over all age classes and the 2003 and 2004 surveys, separately for each area.

RESULTS

Comparative changes in herbivore density

The details of differences in wildlife densities between the reserve and the ranches were complex and varied with species and season, but some consistent overall patterns were nevertheless evident.

Small sized herbivores

Most small herbivores were consistently more abundant in the ranches than in the reserve in both seasons (Figs 5.2A-E). Interestingly, warthog did not conform to this pattern and showed a preference for the reserve in the dry season but for the ranches in the wet season (Fig. 5.2D). Sheep and goats were more abundant in the ranches than in the reserve, and their numbers increased noticeably during 2000–2010 relative to earlier years (Fig. 5.2B, Tables S1 and S2).

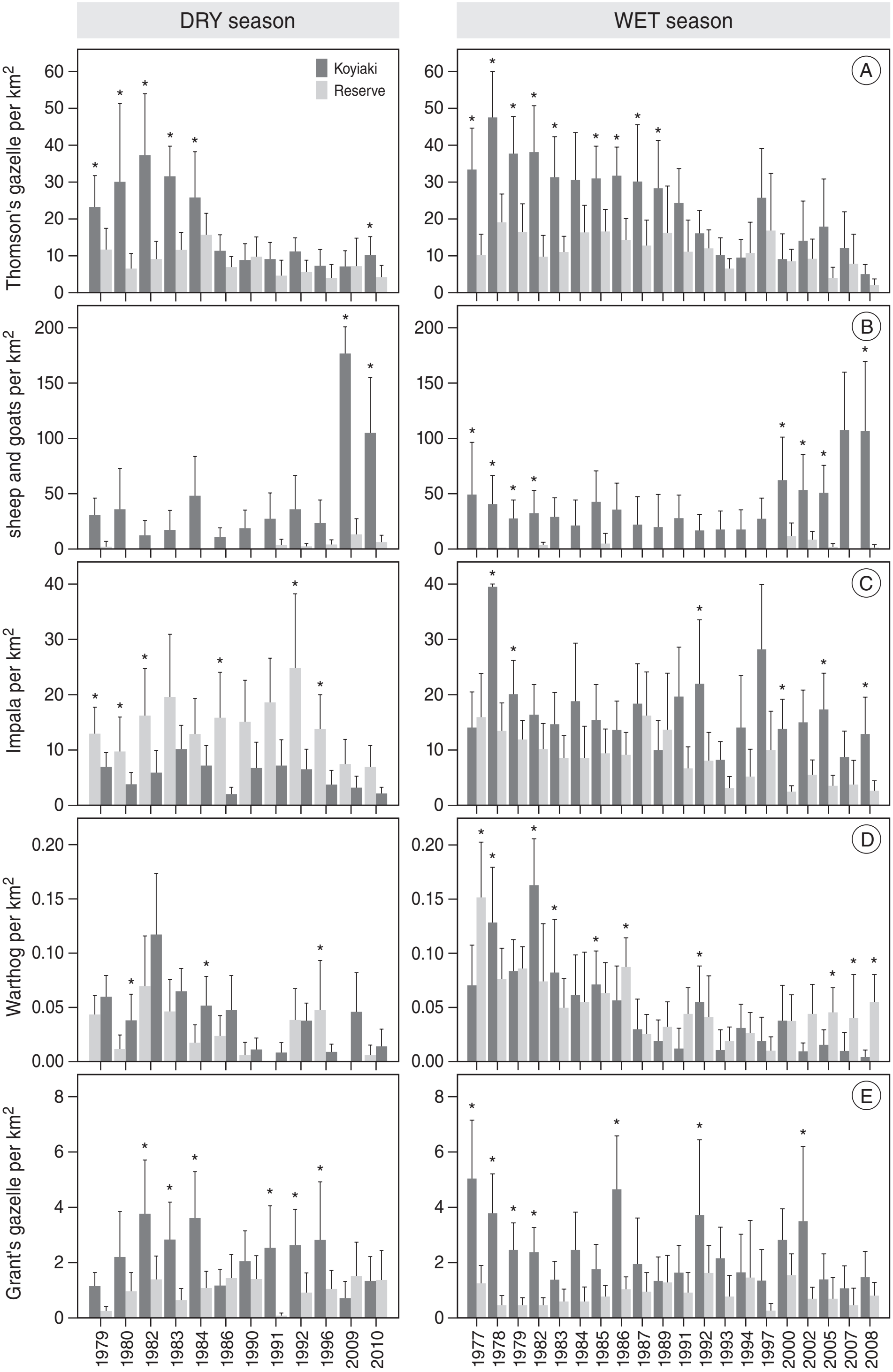
Medium sized herbivores

Most medium-sized herbivores moved seasonally between the reserve and the ranches (Fig. 5.3A-F). However, hartebeest and waterbuck had slightly higher densities in the reserve during both seasons, but more especially in the wet season (Figs. 5.3C and 5.3D, Tables S1 and S2). Topi, wildebeest and zebra had slightly higher densities in the reserve in the dry season when the migrants are present but somewhat higher densities in the ranches in the wet season (Figs 5.3A, 5.3B and 5.3F, Tables S1 and S2). More specifically, the resident wildebeest had lower densities in the ranches than in the reserve in the dry season but higher densities in the ranches than in the reserve in the wet season (Fig. 5.3B). Cattle were more abundant in the ranches than in the reserve in the dry season but more occurred in the reserve in the dry than in the wet season, and more recently (2000–2010) than in earlier years 1970–1999 (Fig. 5.3E, Tables S1 and S2).

Large sized herbivores

Buffalo and elephant were consistently more abundant in the reserve than in the ranches in both seasons (Figs 5.4B and 5.4D, Tables S1 and S2). Eland had higher densities in the ranches than in the reserve in the wet season but lower densities in the ranches than in the reserve in the dry season (Fig. 5.4A). Giraffe did not show significant differences between the reserve and the ranches during the dry season, but were somewhat more abundant in the reserve. However, they were consistently more abundant in the ranches than the reserve in the wet season (Fig. 5.4C, Tables S1 and S2).

The ground counts conducted in 1999 and 2002 confirmed that both gazelles, impala and giraffe were indeed more abundant in the ranches and that topi, hartebeest, wildebeest, zebra, eland, buffalo and elephant were more abundant in the reserve than in the ranches in the dry season, as revealed by the aerial survey data. High variance in herd sizes rendered the apparently large differences in wildebeest densities between landscapes statistically insignificant. The ground counts also confirmed the greater abundance of livestock in the ranches than in the reserve shown by the aerial survey data (Table 5.2).


DRY season
WET season
Koyiaki
Reserve
A
B
C
D
E
Thomson's gazelle per km²
sheep and goats per km²
Impala per km²
Warthog per km²
Grant's gazelle per km²
0
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20
30
40
50
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50
100
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200
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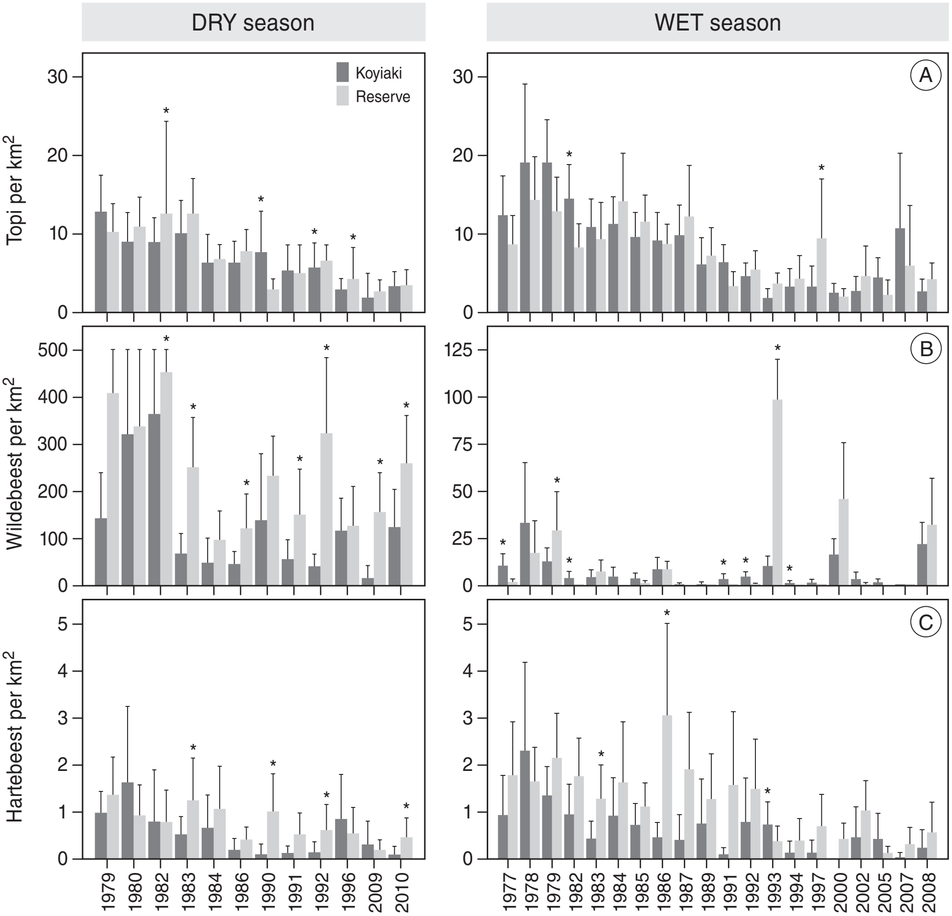

Figure 5.3 Comparative changes in densities (number/km^2) of medium pure grazers, A) topi, B) wildebeest, C) hartebeest, D) waterbuck E) cattle and F) zebra between the Mara Reserve (light grey bars) and the adjoining Koyiaki pastoral ranch (dark grey bars) during the dry and wet seasons based on the DRSRS aerial surveys from 1977 to 2010. Vertical lines show the 95% pointwise confidence limits whereas stars indicate that the mean densities differed significantly between the reserve and Koyiaki.

Figure 5.2 (left) Comparative changes in densities (number/km^2) of small pure grazers and mixed gazer/ browsers, A) Thomson's gazelle, B) sheep and goats, C) impala, D) warthog and E) Grant's gazelle between the Mara Reserve (light grey bars) and the adjoining Koyiaki pastoral ranch (dark grey bars) during the dry and wet seasons based on the DRSRS aerial surveys from 1977 to 2010. Vertical lines show the 95% pointwise confidence limits whereas stars indicate that the mean densities differed significantly between the reserve and Koyiaki.

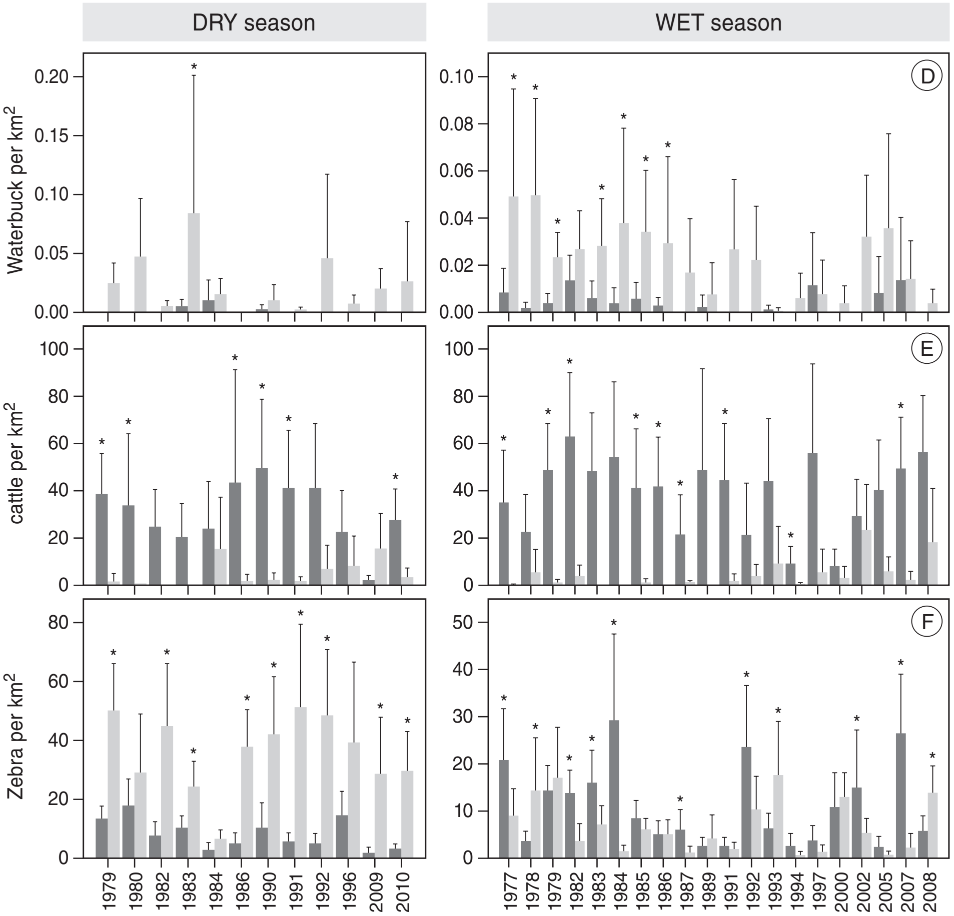

Figure 5.3 Continued

Comparisons of age ratios and female proportions between the reserve and the ranches

The population age composition of species differed between areas for warthog, topi and zebra. There were greater proportions of newborn warthog and juvenile topi in the ranches than in the reserve, but greater proportions of newborn topi and zebra in the reserve than in the ranches (Table 5.3). For hartebeest and waterbuck, numbers were too small for similar statistical tests. Only impala, topi, hartebeest and giraffe had sufficient sample sizes to statistically test differences in female proportions between the two areas. Among these species, female proportion was similar between landscapes for hartebeest and giraffe but was higher in the reserve than in the ranches among impala and topi (Table 5.4).

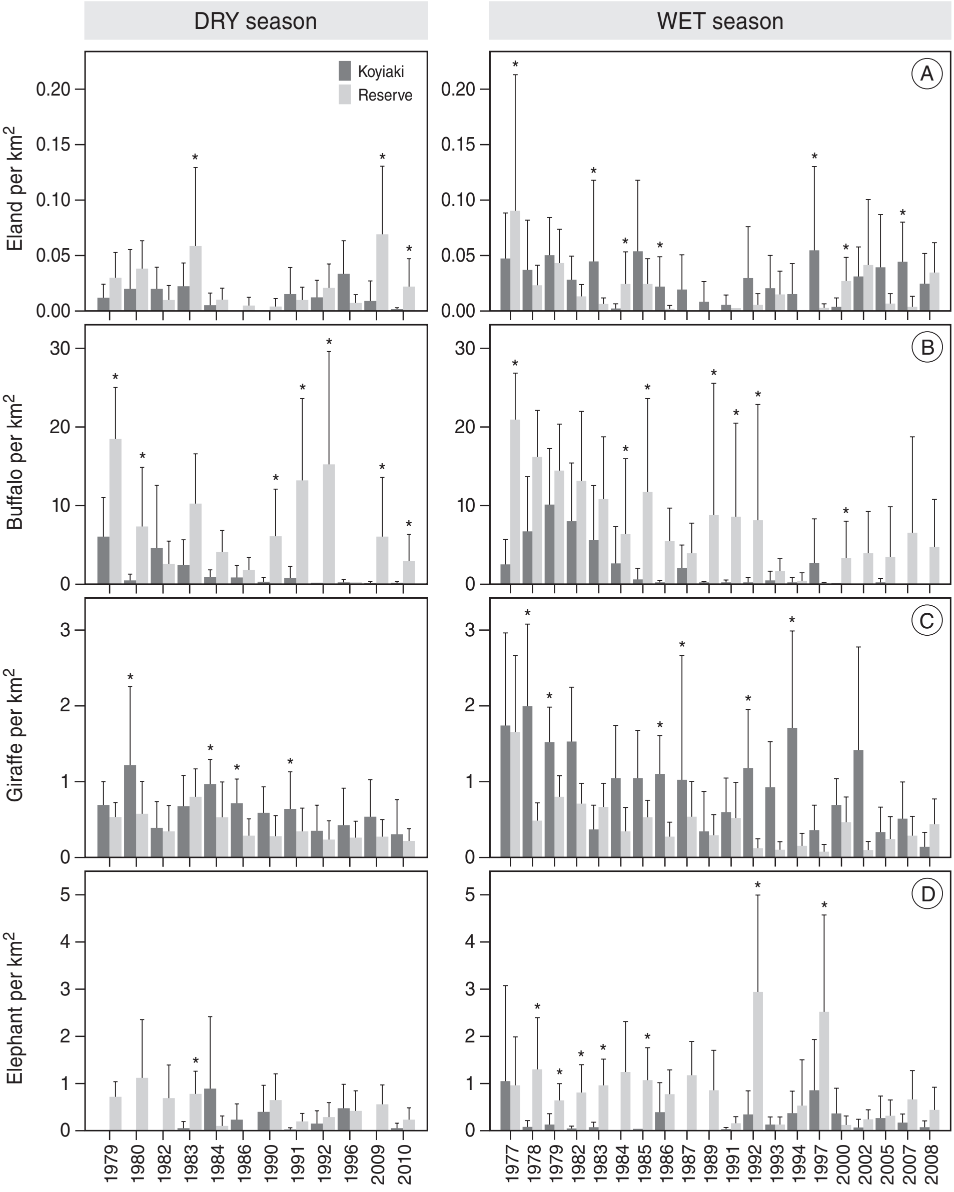

Figure 5.4 Comparative changes in densities (number/km^2) of large pure grazers and mixed grazer/browsers, A) eland, B) buffalo, C) giraffe and D) elephant between the Mara Reserve (light grey bars) and the adjoining Koyiaki pastoral ranch (dark grey bars) during the dry and wet seasons based on the DRSRS aerial surveys from 1977 to 2010. Vertical lines show the 95% pointwise confidence limits whereas stars indicate that the mean densities differed significantly between the reserve and Koyiaki.

DISCUSSION

Comparative changes in herbivore density

Although the differences in herbivore densities between the pastoral ranches and the reserve in any one year may also be influenced by inherent differences between the landscapes which are unrelated to livestock or human use, such as geomorphology, which can cause underlying differences in wildlife use, our results suggest that livestock and human use of the pastoral ranches are the two most important causes of the differences between the patterns we observed in the two landscapes.

There were strong seasonal differences in wild herbivore densities between the reserve and the ranches during 1977-2010. Individual species responded differentially to pastoralism and protection. Three distinct patterns were apparent, all of which could be explained in terms of distinctions in body size and feeding guild and their consequences for nutritional quality and quantity of forage, predation risk and competition with livestock.

Small sized herbivores

Small species that are constrained by food quality and predation tend to prefer short grass areas (Fryxell 1991, Illius and Gordon 1992) and were thus more abundant in the

Table 5.2 Comparisons of mean herbivore densities between the Mara Reserve (808 km^2) and Koyiaki pastoral ranch (649 km^2) based on ground mapping censuses conducted in November 1999 and 2002. Densities that differ significantly (P <0.05) between the two landscapes in each year are highlighted in bold face font.

Species	November 1999		November 2002	
	Ranches	Reserve	Ranches	Reserve
Thomson's gazelle	15.97	16.7	**28.13**	**21.3**
Sheep + goats	**31.28**	**2.02**	**61.96**	**9.19**
Impala	**9.24**	**4.49**	**12.22**	**6.08**
Warthog	**0.5**	**0.83**	**0.74**	**1.38**
Grant's gazelle	1.68	1.52	**1.96**	**2.72**
Topi	**2.68**	**4.38**	3.79	4.21
Wildebeest	12.75	79.21	25.58	108.35
Hartebeest	**0.14**	**0.38**	**0.16**	**0.42**
Waterbuck	0.25	0.34	0.35	0.27
Cattle	**16.84**	**4.08**	**34.3**	**15.98**
Zebra	7.9	11.95	15.8	21.01
Eland	**0.2**	**1**	**0.15**	**1.37**
Buffalo	0.5	1.27	**0.08**	**1.31**
Giraffe	**0.59**	**0.24**	**0.65**	**0.25**
Elephant	**0.07**	**0.56**	**0.09**	**0.55**

ranches than the reserve regardless of season or feeding guild as revealed by the significant differences between their densities in the reserve and the ranches during 1977-2010. Repeated livestock grazing in the same areas of the ranches probably increased the crude protein production of grasses (Anderson et al. 2010, Augustine et al. 2010), enabling the small grazers to derive sufficient energy by selecting high-quality forage from the low-biomass areas (Fryxell et al. 2005). Reduced predation risk as a result of

Table 5.3 Tests for differences in age ratios (newborn/adult females, juveniles/adult females; for warthog and zebra adults of both sexes were used in place of adult females and subadults+adults/total) of each species between the Masai Mara Reserve and Koyiaki pastoral ranch based on pooled data for November 2003 and April 2004. The total number aged in both landscapes and years was 2410, 201, 2284, 175, 7957, and 183 for impala, warthog, topi, hartebeest, zebra and giraffe, respectively. LCL and UCL are the 95% lower and upper binomial confidence limits for each age ratio, respectively.

Species	Age	Ranch	Reserve	LCL	UCL	χ^2	*P*
Warthog	Newborn	**0.41**	0.17	0.04	0.42	7.58	**<0.01**
Topi		0.02	**0.06**	-0.06	-0.01	10.44	**<0.01**
Zebra		0.004	**0.02**	-0.02	-0.01	10.38	**<0.01**
Impala	Juveniles	0.12	0.12	-0.03	0.02	0.1	0.74
Warthog		0.13	0.3	-0.32	-0.01	3.35	0.06
Topi		**0.19**	0.11	0.03	0.11	18.1	<**0.01**
Zebra		0.07	0.08	-0.03	0.003	2.23	0.13
Giraffe		0.13	0.16	-0.15	0.09	0.06	0.79
Impala	Subadults+Adults	0.85	0.85	-0.03	0.03	0.003	0.95
Warthog		0.45	0.52	-0.28	0.13	0.24	0.62
Topi		0.78	0.82	-0.08	0.01	2.98	0.08
Zebra		**0.92**	0.59	0.01	0.05	7.28	**<0.01**
Hartebeest		0.81	0.78	-0.16	0.22	0.003	0.95
Giraffe		0.79	0.74	-0.1	0.2	0.24	0.62

Table 5.4 Tests for differences in female proportions (F/(F+M)) of each species between the Masai Mara Reserve and Koyiaki pastoral ranch based on pooled data for November 2003 and April 2004. The total number sexed in both years and landscapes was 2219, 1381, 296, and 133 for impala, topi, hartebeest, and giraffe, respectively. LCL and UCL are the 95% lower and upper confidence limits for each proportion. Bold values indicate the significance at alpha = 0.05.

Species	Ranch	Reserve	LCL	UCL	χ^2	*P*
Impala	0.72	0.8	0.05	0.13	23.26	**<0.01**
Topi	0.46	0.56	-0.15	-0.03	10.4	**<0.01**
Hartebeest	0.54	0.62	-0.34	0.18	0.17	0.68
Giraffe	0.57	0.59	-0.22	0.17	0	0.93

lower vegetation cover on the ranches (Ogutu et al. 2005) is yet another advantage of concentrating in the short grass plains, since tall grasses conceal ambush predators and significantly increase their efficiency at catching prey animals (Hopcraft et al. 2005). The distribution patterns we observed for small herbivores are therefore concordant with the initial expectation that small herbivores (except warthog) should concentrate in areas of relatively fewer predators (safer) and shorter grasses maintained by heavy livestock grazing in the ranches. This outcome also concurs with findings of studies encompassing a variety of spatial scales and species (Olff and Ritchie 2002; Cromsigt and Olff 2006) besides reinforcing the notion that both predation and resource limitation act simultaneously in limiting herbivore populations (Sinclair et al. 2003).

Medium sized herbivores

The second pattern was expressed by species that moved between the ranches and the reserve seasonally, suggesting that they preferred either the reserve or the ranches depending on season. Specifically, the medium-sized topi, wildebeest and zebra moved seasonally between the reserve and the ranches, thus supporting our second prediction. As a result, medium herbivores had higher densities in the ranches in the wet season but higher densities in the reserve in the dry season. This pattern suggests that medium herbivores tend to utilize the ranches when water and short, nutritious grasses, created and maintained by heavy livestock grazing (Rannestad et al. 2006), are widely available, enabling them to enhance their total protein consumption (McNaughton 1976). In addition, the short grasses also enhance visibility of predators, thus potentially lowering predation risk in the ranches than the reserve (Hopcraft et al. 2005, Ogutu et al. 2005). In contrast, since heavy and sustained livestock grazing depletes both forage and surface water faster in the ranches than in the reserve (Reid et al. 2003), the medium-sized grazers are likely forced to disperse from the ranches to the reserve in the dry season to access more forage and water. Consequently, the medium-sized species were more abundant in the reserve during the dry season, implicating elevated competition with livestock on the ranches for food and water. These patterns accord with the finding of Odadi et al. (2011), who recently reported greater competitive effects of livestock on wildlife in the dry season when food is scarcest.

Interestingly, hartebeest and waterbuck, both medium-sized grazers that select long grasses (Murray and Brown 1993), did not conform to this pattern; instead, they showed a slight preference for the reserve where long grasses are more abundant year-round (Reid et al. 2003, Ogutu et al. 2005). Because zebra can process large quantities of low quality diet due to their non-ruminant digestive physiology than can, say, the ruminant wildebeest (Ben-Shahar and Coe 1992) it could be argued that zebra should be more abundant in the reserve where tall grasses are more abundant in both seasons (Reid et al. 2003, Ogutu et al. 2005). The occurrence of zebra at high densities in the ranches may thus suggest attraction to the short, high-quality grasses there and/or lower predation risk, since zebra suffer heavy lion (Panthera leo) predation in the Mara-Serengeti ecosystem (Grange et al. 2004). The short grass plains in the ranches also may provide seasonal predator refugia for lekking topi (Bro-Jørgensen and Durant 2003).

Large sized herbivores

The third pattern involved species that prefer long grasses all year, or for part of the year and, thus are most likely to compete strongly with livestock. These species were more abundant in the reserve than in the ranches. Since species such as buffalo and elephant are exposed to less predation risk because of their very large body sizes (Sinclair et al. 2003), they do not have to avoid areas with high risk of predation (Hopcraft et al. 2011) and can therefore, relatively safely, use areas of high food abundance. Furthermore, by often occurring in large herds these herbivores, reduce predation risk even further. Also, their digestive physiology allows them to utilize the low-quality tall grasses predominantly found inside the reserve to maximize their specific metabolic requirements (Illius and Gordon 1992, Wilmshurst et al. 2000). The distribution patterns of the large herbivores thus conform to the expectation that large herbivores should select areas with taller grasses than small herbivores (Sinclair et al. 2003, Hopcraft et al. 2011). The patterns shown by the large-bodied eland did not conform fully to this expectation. Instead, eland moved seasonally between the reserve and the ranches. It is plausible that short, nutritious forbs which eland selects in the wet season (Watson and Owen-Smith 2000) occurred at higher densities in the livestock-dominated areas in the ranches in the wet season. By contrast, giraffe are almost exclusively browsers favouring trees and shrubs and feeding almost entirely on forage at least 1 m off the ground (Owen-Smith and Cooper 1987). The ranches support 11–12% woody cover and the reserve 4% as measured by Reid et al. (2003). This higher abundance of trees and shrubs on the ranches may be partially the result of rocky topography in parts of the ranches, but may also be because combined livestock and wildlife grazing removes more grass fuel on the ranches than in the reserve, thus discouraging extensive fires that suppress tree and shrub establishment (Scholes and Archer 1997). As a result, giraffe were more abundant in the ranches with more trees and shrubs in the wet season.

Comparisons of age ratios and female proportions between landscapes

We predicted that the lower number of predators, lower predation risk, and shorter grass (Ogutu et al. 2005), and better predator visibility (Kanga et al. 2011), will lead to a higher proportion of the pregnant females bearing and raising their young on the ranches than in the reserve. As expected, newborn warthog and juvenile topi were significantly more abundant in the ranches, suggesting a preference for shorter grass areas where predation risk is lower. Contrary to our expectation, however, the proportions of newborn topi and zebra were higher in the reserve, suggesting a push from pastoralists or a pull by something in the reserve, such as tall and dense grass cover for young to hide. The ratio of females to males varied significantly from parity for impala and topi, for which a female biased sex ratio is common (Sinclair et al. 2000). Our results suggest that female impala and topi were more abundant in the reserve, consistent with our speculation that competition with livestock and disturbance by humans and dogs in the ranches forces more females accompanied by their young into the reserve. Female giraffe and hartebeest were evenly distributed between the reserve and ranches, suggesting little influence of land use on the distribution of females relative to males.

Implications for pastoralism, wildlife management and conservation

Dispersal areas for wildlife in pastoral systems and their adjoining protected areas in African savannas represent wet season refuges for many wild herbivores that range seasonally beyond the protected area boundaries (Woodroffe and Ginsberg 1998, Ogutu et al. 2008). Our study shows that these areas can, and indeed do, support a high diversity of wildlife, especially in the wet season when resources are widely available due to maintenance of grasslands by livestock in short, nutritious growth stage. However, several other studies have shown that increasing human population growth, settlement, cultivation and sedentarization of formerly semi-nomadic pastoralists in these areas are increasingly restricting seasonal wildlife movements (Coughenour 2008) and potentially negating their otherwise positive effects on wildlife. These movements give both wildlife and livestock the flexibility and mobility necessary to optimally exploit heterogeneity in resources in space and time, including that caused by the directional impacts of a warming and drying climate (Ogutu et al. 2007). Our results reinforce and extend the conclusions of these studies by also revealing that, even though wildlife evidently move seasonally between the reserve and the ranches, their densities have declined strikingly in both the reserve and the ranches, most likely due to ongoing land use changes (Ogutu et al. 2009; 2011). Land use changes in the pastoral lands thus portend a precarious future for wild herbivores that depend on the pastoral areas. Furthermore, the land use changes exacerbate the adverse effects of recurrent climatic extremes on the availability of forage and water, forcing ever more pastoralists to graze their livestock illegally in protected areas (Ogutu et al. 2009). The land use changes also likely intensify competition between wildlife and livestock and thus adversely affect demographic processes such as reproduction and juvenile recruitment besides the seasonal dispersal movements of wild herbivores between protected areas and their adjoining pastoral lands. If the ongoing losses of key dispersal areas and calving grounds of wildlife in key ecosystems of East Africa, such as the Mara Region, continue unabated, they will accelerate wildlife population declines (Ogutu et al. 2011) and even cause local population extirpations (Newmark 1996, Brashares et al. 2001).

We therefore suggest that effective management of pastoral lands as well as their adjoining protected areas in East Africa and possibly elsewhere is urgently necessary and should aim to prevent further losses of wildlife. Furthermore, management should aim to secure dispersal areas, including corridors for seasonal wildlife and livestock movements, and effectively couple traditional knowledge of seasonal herders, management and scientific knowledge (Reid et al. 2009) into an integrated approach incorporating both protected areas and their adjoining pastoral lands.

Acknowledgements

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SUPPLEMENTARY MATERIAL

Table S.1 Results of Wald Chi-squared tests of differences in expected herbivore densities between the Masai Mara National Reserve and the adjoining Koyiaki pastoral ranch during the dry season based on aerial surveys conducted by the Kenya Department of Resource Surveys and Remote Sensing from 1977 to 2010. All models were fitted using the negative binomial regression model except for elephant for which the Poisson model was used due to failure of the negative binomial model to converge to optimal parameter estimates.

	Thomson's gazelle			Sheep			Impala			Warthog			Grant's gazelle		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1979	3.283	1	**0.07**	0	1	0.898	3.111	1	**0.078**	1.351	1	0.245	6.392	1	**0.011**
1980	4.992	1	**0.025**	0	1	0.798	3.456	1	**0.228**	3.281	1	**0.07**	0.739	1	0.39
1982	6.658	1	**0.01**	0	1	0.956	3.761	1	**0.184**	1.261	1	0.262	3.623	1	**0.02**
1983	6.997	1	**0.008**	0	1	0.938	3.419	1	0.023	0.865	1	0.352	4.785	1	**0.029**
1984	3.438	1	**0.023**	0	1	0.975	0.964	1	0.326	3.298	1	**0.069**	3.639	1	**0.01**
1986	0.714	1	0.398	0	1	0.998	7.912	1	**0.005**	1.042	1	0.307	0.048	1	0.826
1990	0.027	1	0.87	0.002	1	0.964	1.872	1	0.171	1.088	1	0.297	0.204	1	0.652
1991	1.088	1	0.297	1.207	1	0.272	1.984	1	0.159	0.001	1	1	10.717	1	**0.001**
1992	1.287	1	0.257	2.383	1	0.123	3.559	1	**0.059**	0.001	1	0.971	1.365	1	**0.024**
1996	0.377	1	0.539	1.163	1	0.281	2.873	1	**0.09**	3.337	1	**0.068**	0.94	1	**0.033**
2009	0.001	1	0.974	7.699	1	**0.006**	1.03	1	0.31	0.001	1	0.972	0.545	1	0.46
2010	3.456	1	**0.023**	6.723	1	**0.01**	2.271	1	0.132	0.421	1	0.516	0	1	0.9

	Topi			Wildebeest			Hartebeest			Waterbuck			Cattle		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1979	0.593	1	0.441	9.132	1	**0.003**	0.314	1	0.575	0	1	0.991	8.904	1	**0.003**
1980	0.165	1	0.685	0.006	1	0.94	0.195	1	0.658	0	1	0.989	8.753	1	**0.003**
1982	3.481	1	**0.488**	0.502	1	0.479	0	1	0.993	0.005	1	0.945	0.001	1	0.996
1983	0.152	1	0.697	6.587	1	**0.01**	3.103	1	**0.294**	5.802	1	**0.016**	0.001	1	0.997
1984	0.972	1	0.324	0.83	1	0.362	0.092	1	0.762	0.092	1	0.761	0.074	1	0.785
1986	0.138	1	0.71	3.096	1	**0.078**	0.404	1	0.525	0	1	1	4.458	1	**0.035**
1990	3.038	1	**0.081**	0.767	1	0.381	2.145	1	**0.143**	1.231	1	0.267	5.82	1	**0.016**
1991	0.017	1	0.898	4.544	1	**0.031**	1.116	1	0.291	0	1	1	5.141	1	**0.023**
1992	3.422	1	**0.052**	10.291	1	**0.001**	2.966	1	**0.033**	0	1	0.97	2.017	1	0.156
1996	0.351	1	**0.062**	0.012	1	0.914	0.066	1	0.798	0	1	0.992	0.347	1	0.556
2009	0.118	1	0.731	6.983	1	**0.008**	0.046	1	0.831	0	1	0.983	1.252	1	0.263
2010	0.001	1	0.976	3.968	1	**0.016**	3.783	1	**0.376**	0	1	0.985	3.802	1	**0.051**

Table S.1 Continued

	Zebra			Eland			Buffalo			Giraffe			Elephant		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1979	28.468	1	**0**	2.264	1	0.132	3.44	1	**0.064**	0.354	1	0.552	1.057	1	0.304
1980	0.539	1	0.463	0.401	1	0.526	3.826	1	**0.05**	3.481	1	**0.049**	0.1	1	0.752
1982	6.822	1	**0.009**	0.694	1	0.405	0.276	1	0.599	0.009	1	0.924	0.007	1	0.933
1983	4.841	1	**0.028**	3.976	1	**0.032**	3.702	1	0.01	0.074	1	0.786	3.73	1	**0.053**
1984	1.205	1	0.272	0.156	1	0.693	2.545	1	0.111	3.002	1	**0.097**	0.712	1	0.399
1986	18.607	1	**0**	0	1	0.994	0.292	1	0.589	4.06	1	**0.081**	0.592	1	0.442
1990	7.106	1	**0.008**	0	1	0.991	3.405	1	**0.065**	0.004	1	0.948	0.095	1	0.758
1991	10.628	1	**0.001**	0.105	1	0.745	4.091	1	**0.043**	3.24	1	0.062	1.057	1	0.304
1992	13.392	1	**0**	0.175	1	0.675	10.302	1	**0.001**	0.087	1	0.768	0.1	1	0.752
1996	2.251	1	0.134	2.286	1	0.131	0.299	1	0.584	0.112	1	0.738	0.007	1	0.933
2009	14.186	1	**0**	3.19	1	**0.074**	3.491	1	**0.062**	0.296	1	0.586	0	1	0.989
2010	15.446	1	**0**	3.984	1	**0.046**	3.507	1	**0.061**	0.048	1	0.827	0.592	1	0.442

Table S.2 Results of Wald chi-squared tests of differences in expected herbivore densities between the Masai Mara National Reserve and the adjoining Koyiaki pastoral ranch during the wet season based on aerial surveys conducted by the Kenya Department of Resource Surveys and Remote Sensing from 1977 to 2010. All models were fitted using the negative binomial regression model except for elephant for which the Poisson model was used due to failure of the negative binomial model to converge optimal parameter estimates.

	Thomson's gazelle			Sheep			Impala			Warthog			Grant's gazelle		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1977	4.827	1	0.028	3.896	1	0.048	0.041	1	0.84	9.82	1	0.002	5.113	1	0.024
1978	6.153	1	0.013	10.924	1	0.001	5.242	1	0.022	6.469	1	0.011	11.679	1	0.001
1979	5.023	1	0.025	19.727	1	0	3.465	1	0.063	0.02	1	0.887	15.125	1	0
1982	9.427	1	0.002	4.672	1	0.031	1.41	1	0.235	14.867	1	0	8.829	1	0.003
1983	7.248	1	0.007	0.001	1	0.996	1.296	1	0.255	4.699	1	0.03	1.415	1	0.234
1984	1.278	1	0.258	1.278	1	0.258	1.24	1	0.265	1.027	1	0.311	1.896	1	0.169
1985	3.226	1	0.072	1.953	1	0.162	1.284	1	0.257	4.955	1	0.026	1.721	1	0.19
1986	5.678	1	0.017	0	1	0.986	0.875	1	0.35	3.565	1	0.059	10.223	1	0.001
1987	4.013	1	0.016	2.195	1	0.138	0.073	1	0.787	0.129	1	0.72	0.552	1	0.458
1989	3.558	1	0.046	0	1	1	0.17	1	0.68	0.715	1	0.398	0.003	1	0.958
1991	1.293	1	0.255	0	1	0.997	2.918	1	0.098	7.108	1	0.008	0.402	1	0.526
1992	0.39	1	0.532	3.453	1	0.063	3.064	1	0.151	0.263	1	0.608	3.06	1	0.03
1993	0.617	1	0.432	0	1	0.996	2.853	1	0.091	0.55	1	0.458	1.997	1	0.158
1994	0.014	1	0.904	5.813	1	0.016	1.328	1	0.249	0.529	1	0.467	0.009	1	0.925
1997	0.185	1	0.668	0	1	0.99	1.82	1	0.177	0.765	1	0.382	1.976	1	0.16
2000	0.04	1	0.841	3.498	1	0.221	8.683	1	0.003	0	1	0.998	0.826	1	0.363
2002	0.028	1	0.867	3.317	1	0.251	8.777	1	0.003	0	1	0.999	4.458	1	0.05
2005	3.09	1	0.079	6.902	1	0.009	7.117	1	0.008	6.127	1	0.013	0.376	1	0.54
2007	0.269	1	0.604	0	1	0.989	0.897	1	0.344	4.051	1	0.044	0.329	1	0.566
2008	1.333	1	0.248	15.11	1	0	4.528	1	0.033	25.323	1	0	0.368	1	0.544

Table S.2 Continued

	Topi			Wildebeest			Hartebeest			Waterbuck			Cattle		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1977	0.631	1	0.427	4.934	1	**0.026**	0.429	1	0.512	4.471	1	**0.034**	9.294	1	**0.002**
1978	0.535	1	0.465	0.622	1	0.43	0.229	1	0.632	9.526	1	**0.002**	0.737	1	0.391
1979	2.453	1	0.117	3.05	1	**0.081**	0.953	1	0.329	8.447	1	**0.004**	18.117	1	**0.000**
1982	2.966	1	**0.085**	9.444	1	**0.002**	0.993	1	0.319	1.564	1	0.211	7.97	1	**0.005**
1983	0.171	1	0.68	0.226	1	0.635	4.949	1	**0.016**	3.93	1	**0.047**	0	1	0.986
1984	0.175	1	0.676	14.136	1	**0**	0.231	1	0.631	2.707	1	**0.1**	0	1	0.993
1985	0.263	1	0.608	1.863	1	0.172	0.447	1	0.504	5.51	1	**0.019**	10.465	1	**0.001**
1986	0.026	1	0.871	0.017	1	0.897	6.226	1	**0.013**	5.161	1	**0.023**	74.311	1	**0.000**
1987	0.219	1	0.64	1.393	1	0.238	1.914	1	0.166	0.005	1	0.941	5.78	1	**0.016**
1989	0.062	1	0.803	0.322	1	0.57	0.17	1	0.68	0.408	1	0.523	0.002	1	0.968
1991	1.172	1	0.279	6.864	1	**0.009**	3.693	1	**0.055**	0	1	0.98	7.364	1	**0.007**
1992	0.083	1	0.773	3.842	1	**0.05**	0.431	1	0.511	0	1	0.981	1.176	1	0.278
1993	1.047	1	0.306	10.577	1	**0.001**	3.313	1	**0.058**	0.092	1	0.761	1.884	1	0.17
1994	0.113	1	0.736	3.873	1	**0.049**	0.286	1	0.593	0	1	0.991	3.168	1	**0.075**
1997	3.097	1	**0.029**	1.091	1	0.296	0.599	1	0.439	0.021	1	0.885	2.243	1	0.134
2000	0.211	1	0.646	2.736	1	**0.098**	0.002	1	0.968	0	1	0.991	0.406	1	0.524
2002	0.165	1	0.685	0.693	1	0.405	1.322	1	0.888	0.002	1	0.962	0.83	1	0.362
2005	0.864	1	0.353	2.694	1	0.999	0.517	1	0.472	0.779	1	0.378	2.655	1	0.103
2007	0.428	1	0.513	0.023	1	0.879	0.83	1	0.362	0	1	0.993	6.153	1	**0.013**
2008	0.52	1	0.471	0.162	1	0.687	0.185	1	0.667	0	1	0.992	1.243	1	0.265

Table S.2 Continued

	Zebra			Eland			Buffalo			Giraffe			Elephant		
Year	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
1977	3.203	1	**0.074**	0.504	1	0.478	5.476	1	**0.019**	0.006	1	0.938	0.002	1	0.963
1978	5.364	1	**0.021**	3.43	1	**0.051**	1.194	1	0.274	4.495	1	**0.034**	3.178	1	**0.075**
1979	0.356	1	0.551	0.178	1	0.673	0.52	1	0.471	3.882	1	**0.049**	3.727	1	**0.054**
1982	11.834	1	**0.001**	1.588	1	0.208	0.363	1	0.547	2.307	1	0.129	8.762	1	**0.003**
1983	5.119	1	**0.024**	3.662	1	**0.056**	0.693	1	0.405	0.706	1	0.401	5.347	1	**0.021**
1984	22.693	1	**0.000**	2.883	1	**0.09**	0.41	1	0.522	0.994	1	0.319	0.001	1	0.980
1985	0.882	1	0.348	0.585	1	0.444	6.578	1	**0.01**	1.092	1	0.296	13.217	1	**0.000**
1986	0.004	1	0.952	4.499	1	**0.034**	13.142	1	**0.000**	4.105	1	**0.043**	0.327	1	0.567
1987	3.183	1	**0.074**	0.249	1	0.618	0.185	1	0.667	3.242	1	**0.062**	0.371	1	0.543
1989	0.251	1	0.616	1.682	1	0.195	4.639	1	**0.031**	0.015	1	0.903	0.15	1	0.699
1991	0.193	1	0.661	1.814	1	0.178	4.141	1	**0.042**	0.019	1	0.891	0.609	1	0.435
1992	2.725	1	**0.099**	0.656	1	0.418	3.306	1	**0.069**	4.604	1	**0.032**	3.255	1	**0.071**
1993	9.466	1	**0.002**	0.036	1	0.849	0.414	1	0.52	3.756	1	**0.053**	0.001	1	0.980
1994	2.007	1	0.157	0.414	1	0.52	0.062	1	0.803	4.146	1	**0.042**	-0.405	1	1.000
1997	1.451	1	0.228	3.42	1	**0.064**	1.433	1	0.231	0.962	1	0.327	4.864	1	**0.035**
2000	0.249	1	0.618	3.665	1	**0.056**	3.153	1	**0.076**	0.166	1	0.684	0.191	1	0.662
2002	0.054	1	0.816	2.077	1	0.149	0.001	1	0.977	0.099	1	0.752	0.371	1	0.543
2005	1.948	1	0.163	1.682	1	0.195	1.025	1	0.311	0.035	1	0.851	0.015	1	0.902
2007	9.562	1	**0.002**	4.021	1	**0.045**	0.019	1	0.89	0.15	1	0.699	0.661	1	0.416
2008	3.078	1	**0.079**	0.144	1	0.705	0.026	1	0.871	0.558	1	0.455	1.126	1	0.289

Chapter 6

The distribution of large herbivore hotspots in relation to environmental and anthropogenic correlates in the Mara region of Kenya

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ABSTRACT

The distributions of large herbivores in protected areas and their surroundings are becoming increasingly restricted by changing land use, with adverse consequences for wildlife populations. We analyze changes in distributions of herbivore hotspots to understand their environmental and anthropogenic correlates using 50 aerial surveys conducted at a spatial resolution of 5×5 km^2 ($n = 289$ cells) in the Mara region of Kenya during 1977-2010. We compare the distributions across seasons, land use types (protection, pastoralism, agro-pastoralism) and 10 species with different body sizes and feeding styles. Small herbivores that are the most susceptible to predation and dependent on high-quality forage, concentrate in the greenest and wet areas and close to rivers in Maasai pastoral ranches in both seasons. Livestock grazing creates conditions favouring small herbivores in these ranches, including high-quality short grasses and better visibility, implying facilitation. But in the reserve, they concentrate in browner, drier and flatter areas and farther from rivers, suggesting facilitation by large grazers in the wet season, or little competition with migratory herbivores occupying the reserve in the dry season. In the wet season, medium herbivores concentrate in similar areas to small herbivores in the ranches and reserve. However, in the dry season, they stay in the reserve and also concentrate in green and wet areas close to rivers, when migrants occur in the reserve. Since such areas typically have higher predation risk this suggests facilitation by the migrants by absorbing most predation pressure or, alternatively, competitive displacement by the migrants from preferred habitats. Large herbivores, which suffer the least predation, depend on bulk forage and are the most likely to engender conflicts with people, concentrate in the reserve all year. This suggests attraction to the taller and denser grass and perceived greater safety in the reserve in both seasons. These results reveal how, predation risk, forage quantity and quality, water, competition with and facilitation by livestock interact with individual life-history traits, seasons and land use in shaping the dynamics of herbivore hotspots in protected and human-dominated savannas.

INTRODUCTION

The dominant traditional conservation paradigm emphasizes the importance of national parks and reserves in protecting terrestrial biodiversity against human activities (Terborgh et al. 2002). This paradigm implicitly assumes that human activities, such as agricultural and livestock production, predominantly harm wildlife. Although there is abundant evidence that high levels of human activity indeed limit wildlife abundance and species diversity (Prins 1992, Du Toit and Cumming 1999), recent empirical research suggests that moderate, more traditional forms of human land use may benefit wildlife in tropical ecosystems (Veblen and Young 2010, Augustine et al. 2011). In African savannas native wildlife and humans have coexisted for centuries under moderate traditional human activities (Lamprey and Reid 2004, Galvin et al. 2008). However, due to intensifying anthropogenic activities, strong gradients often emerge between protected areas and their surrounding human-dominated pastoral ranches, creating spatial heterogeneity in predation risk, resource availability and quality. Consequently, locations with conditions that maximize the net effects of forage availability and quality and minimize predation risk will support above-average herbivore abundances (McNaughton 1988, McNaughton 1990, Anderson et al. 2010). We call locations where high densities of wild herbivores persist for extended periods of time, "hotspots". Long-term persistence of hotspots depends upon the stability, predictability and sufficiency of forage despite variability mediated through rainfall seasonality (Fryxell et al. 2005). Furthermore, hotspots are relatively predator-free refugia (Valeix et al. 2009) that reduce predation risk. Additionally, what qualifies as a hotspot may differ with life history traits of herbivores such as body size (Sensenig et al. 2010, Hopcraft et al. 2011) because small herbivores are more susceptible to predators (Sinclair et al. 2003) and require forage of higher quality than do large ones (Kerr and Packer 1997). Moreover, large herbivores are more constrained by forage quantity than by predation (Owen-Smith 1988).

In African savannas the distribution and persistence of hotspots have been relatively well studied within protected areas, such as the Mara-Serengeti ecosystem of Kenya and Tanzania (McNaughton 1988, McNaughton 1990, Anderson et al. 2010), but are much less well understood in human–dominated pastoral systems, such as the pastoral ranches of the Mara region in Kenya. The Mara region is well-known for its annual concentration of migratory ungulate populations, constituting one of the largest remaining migrations of large herbivores on earth (Sinclair and Arcese 1995b) and an exceptionally high abundance and diversity of resident wildlife species (Broten and Said 1995). The resident wildlife often persist in spatially restricted locations (McNaughton 1990) but move seasonally between the protected Masai Mara National Reserve (MMNR) and its adjoining pastoral ranches in response to seasonal variation in forage quantity, quality and predation (Stellfox et al. 1986, Ogutu et al. 2008, Fynn and Bonyongo 2010). In particular, the resident herbivores disperse from the MMNR onto the adjoining ranches in the wet season (Stellfox et al. 1986) for at least two reasons. Firstly, grass is widely available and is maintained in a shorter and more active growth stage by livestock grazing on the ranches than in the reserve. Secondly, predation risk is presumably higher in the reserve than on the ranches due to higher predator densities, taller and denser grass cover in the reserve (Hopcraft et al. 2005, Ogutu et al. 2005). The resident herbivores return to the reserve in the dry season, likely due to heightened competition with livestock for food and water on the ranches (Prins 1992, Ogutu et al. 2008).

Although food availability and quality and predation risk have all been identified as key determinants of herbivore hotspots in savannas (Anderson et al. 2010), their influences on hotspots vary considerably with herbivore body size and environmental gradients within landscapes (Valeix et al. 2009, Sensenig et al. 2010, Hopcraft et al. 2011). This raises fundamental questions about the extent to which ecological factors and mechanisms identified as shaping distributions of hotspots in protected areas can be extrapolated to human-dominated systems such as pastoral lands. Wildlife share these pastoral landscapes with people, their settlements and livestock. However, human population growth, expansion of settlements and livestock stocking levels and intensification of land use on the pastoral lands are increasingly denying wildlife access to their traditional wet season resources, similar to other areas of Africa (Fynn and Bonyongo 2010), thus contributing to severe declines in their numbers (Ogutu et al. 2011).

Rainfall seasonality exerts fundamental controls on vegetation growth, quantity and quality in savannas (Deshmukh 1984), and need to be accounted for before the effects of other factors can be reliably revealed. Vegetation productivity also varies considerably spatially, reflecting spatial patchiness in rainfall, soil moisture and nutrients in African savannas (Coe et al. 1976, East 1984). As vegetation quantity increases linearly with rainfall (Deshmukh 1984) a similar relationship exists between the Normalized Difference Vegetation Index (NDVI) and vegetation productivity (Pettorelli et al. 2005) given the tight positive association between NDVI and rainfall in African savannas (Davenport and Nicholson 1993, Camberlin et al. 2007). NDVI has thus successfully been used to predict the distribution and abundance of large mammalian herbivores (Bro-Jørgensen et al. 2008, Pettorelli et al. 2011).

Consequently, we tested predictions of several hypotheses to establish factors influencing herbivore hotspots in the protected Mara reserve and its adjoining ranches.

The hypotheses on vegetation quantity and quality assume that in the late wet season grass is tall and dense, low in crude protein and high in lignin (Boutton et al. 1988a, Boutton et al. 1988b, Georgiadis and McNaughton 1990) in most of the reserve and hence low in digestibility and heightens predation risk for herbivores (Hopcraft et al. 2005). As a result, high NDVI values can be associated with taller, more mature and less nutritious grasses (Kawamura et al. 2005, Mueller et al. 2008) leading to the prediction of a negative association between NDVI and hotspots of small and medium herbivores but a positive association with hotspots of large herbivores in the reserve (H1a). However, in the ranches the grass is kept in a short, active growth stage by livestock grazing, thereby increasing its quality but decreasing its biomass (Augustine and McNaughton 2006) and hence promoting visibility against predators (Ogutu et al.

2005). Thus, high NDVI values associated with higher vegetation quality would lead to a positive association between NDVI and hotspots of small and medium herbivores but a negative association with hotspots of large herbivores in the ranches in the wet season (H1b). During the dry season, in contrast, vegetation quality and quantity are lower in the region (Boutton et al. 1988b, Georgiadis and McNaughton 1990). However, because grass height is generally taller inside than outside the reserve due to the absence of livestock grazing in the reserve, except during illegal incursions (Ogutu et al. 2005), we expected herbivore hotspots to increase with increasing NDVI in the reserve (H2a) but to show the opposite pattern in the ranches (H2b) due to competition with livestock for forage and water.

Besides vegetation, we tested hypotheses related to other landscape features associated with predation risk, in particular distance to rivers and soil moisture (Anderson et al. 2010). We assumed that in the wet season in the reserve predation risk is higher closer to rivers because many large predators rest inside riverine vegetation in the daytime (Ogutu et al. 2006b) and that herbivores avoid wet and sticky soils found near drainage lines and on other low-lying areas (Talbot and Talbot 1963). Given these assumptions we expected hotspots of small and medium herbivores to increase with (1) increasing distance away from rivers and (2) decreasing soil moisture but hotspots of large herbivores to follow the opposite patterns (H3a). In the ranches, since predator densities are lower (Ogutu et al. 2005) hotspots of small and medium herbivores should peak closer to rivers and in other areas of high soil moisture due to (*i*) facilitation by Maasai livestock grazing near rivers in the dry season (Reid et al. 2008a, Butt et al. 2009) or (*ii*) displacement from open short grass plains on uplands by Masai livestock that are densely distributed over these plains in the wet season (H3b). In the reserve in the dry season when forage availability and surface water are highly reduced, herbivores of all sizes should be attracted to rivers, springs and green grasses inside riverine woodlands. Grasses in such areas retain green leaves for extended periods due to shielding from direct insolation by tree canopy (Treydte et al. 2008, Anderson et al. 2010) despite high predation risk. The presence of the migratory herbivores inside the reserve lowers the predation pressure on the resident populations in the dry season (Saba 1979, Scheel and Packer 1995) (H4a). In the ranches, in sharp contrast, competition for resources with livestock increases steeply. The Masai pastoralists change the grazing orbits of their livestock herds to concentrate along rivers and in areas of high soil moisture in the dry season. Thus, we expected hotspots of wild herbivores to increase farther from rivers or other wet areas (H4b). Finally, high human population and livestock densities and the associated settlements, farms and harassment of wildlife by human presence and dogs (Lamprey and Reid 2004, Ogutu et al. 2011) would predict a decrease in herbivore hotspots with increasing human and livestock densities in both seasons on the ranches (H5).

To test these hypotheses, we analyzed influences of land use type (protection, pastoralism, agro-pastoralism), annual and seasonal NDVI components, soil moisture indexed by topographic wetness index (TWI), distance to the nearest river, livestock and human population densities on the distribution of hotspots of wild herbivores in the Mara region of Kenya. We used 50 aerial surveys of wildlife and livestock conducted in the Mara region from 1977 to 2010 to locate and characterize the hotspots. This analysis complements and extends recent research on distribution of herbivore hotspots in protected areas (Anderson et al. 2010) to human-dominated savanna landscapes.

MATERIAL AND METHODS

Study Area

The Mara Region is located in southwestern Kenya and borders the Serengeti National Park in Tanzania to the south. It encompasses 1530 km^2 of the protected Masai Mara National Reserve (MMNR) in which only wildlife conservation and tourism is permitted, as well as about 4000 km^2 of the adjoining pastoral ranches in which traditional pastoralism by the Masai people and pastoral settlements, some cultivation and wildlife tourism constitute the major forms of land use. We refer to the Mara Region as the Mara and the pastoral ranches as ranches (Fig. 6.1). The Mara can be subdivided into three main landscapes based on predominant land use (Homewood et al. 2001). The first landscape, the outer ranches, covers the eastern and productive northern reaches of the Mara. Parts of this area have been converted to cultivation and settlements as human population has increased in recent decades (Ogutu et al. 2011). We classified these areas as the "outer ranches". The southwestern part of the Mara consists mainly of grasslands and comprises the MMNR, which we therefore classified as the "reserve". The third area lies within the central and eastern part of the Mara. This area comprises extensive pastoral areas, classified here as the "inner ranches", which support vast herds of cattle, sheep and goats and a rapidly expanding human population (Lamprey and Reid 2004). Human population density is lower here than in the "outer ranches" but higher than in the "reserve"(Ogutu et al. 2011). The Mara is characterized by the annual migration which brings over one million wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and Thomson's gazelle (*Gazella thomsoni*) from the Serengeti Plains to the south and Loita Plains to the northeast of the MMNR from July to October, or later. It is also home to vast herds of cattle, sheep and goats in the ranches that are kept in bomas (temporary livestock corrals) during the night and herded elsewhere during the day in search of forage and drinking water. Although prohibited, illegal livestock grazing is common inside the reserve (Butt et al. 2009). We considered the 10 most common wild herbivore species (Table 6.1) each of which occupied at least 50% of all grid cells surveyed during 1977-2010 and also calculated combined livestock density, including sheep, goats and cattle. The 10 species can be classified by feeding style as pure browsers, grazers and mixed feeders and by body size as small (15-50 kg), medium (100-200 kg) and large (700-1725 kg) herbivores. The mixed feeders seasonally switch between grazing and browsing.

Rainfall is bimodal in the Mara, with the wet season spanning November-June and the dry season covering July-October. The short rains fall during November-December

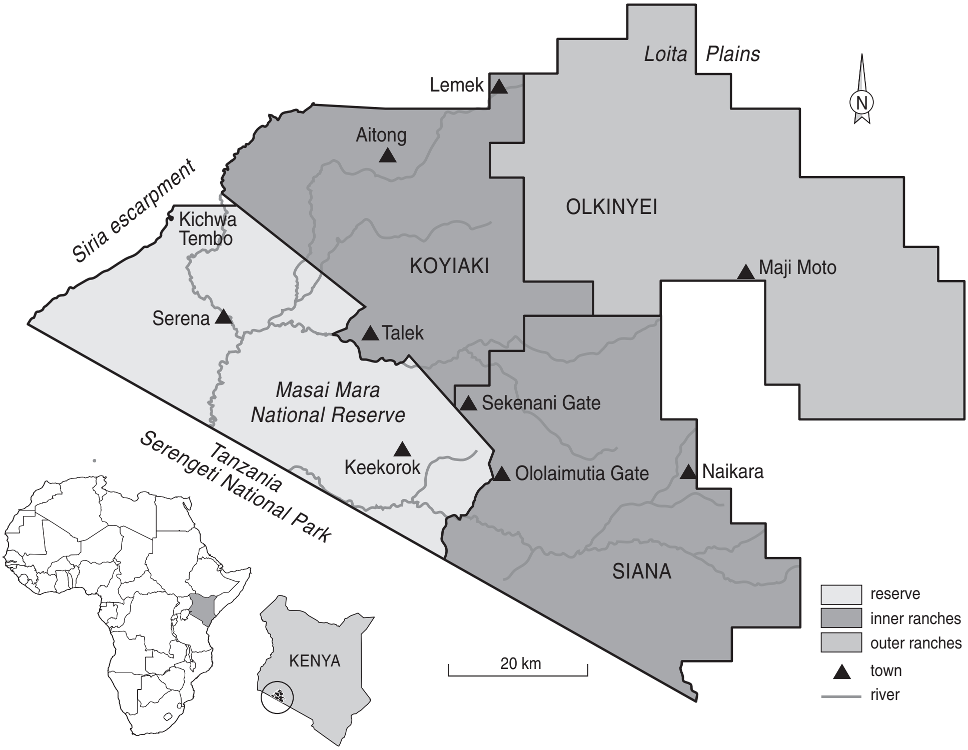


Figure 6.1 Map of the Mara Region of Kenya showing the Masai Mara National Reserve and its adjoining pastoral ranches, grouped into the inner and outer ranches.

Table 6.1 The 10 most common species in the Mara region and their functional groupings by body mass, feeding style and foraging guild. The mixed feeders seasonally switch between grazing and browsing.

Common name	Scientific name	Mass (Kg)[‡]	Dietary guild	Foraging guild
Thomson's gazelle	*Gazella thomsoni*	15	Grazer	migratory
Impala	*Aepyceros melampus*	40	Mixed feeder	resident
Grant's gazelle	*Gazella granti*	50	Mixed feeder	resident
Topi	*Damaliscus korrigum*	100	Grazer	resident
Hartebeest	*Alcelaphus buselaphus cokeii*	120	Grazer	resident
Wildebeest	*Connochaetes taurinus*	125	Grazer	migratory
Zebra	*Equus burcheli*	200	Grazer	migratory
Buffalo	*Syncerus caffer*	700	Grazer	resident
Giraffe	*Giraffa camelopardalis*	1250	Browser	resident
Elephant[†]	*Loxodonta africana*	1725	Mixed feeder	wide ranging

[†] Wanders widely seasonally but do not engage in regular seasonal migrations. [‡] The body weights are based on (Coe et al. 1976)

and the long rains during March-June. Rainfall increases from 500 mm per year in the southeast to 1200 mm in the northwest of the Mara-Serengeti ecosystem (Pennycuick and Norton-Griffiths 1976) but increases from 877 mm in the south-east to 1341 mm in the north-west of the MMNR (Ogutu et al. 2011). This variability, coupled with topographic heterogeneity and fires, create considerable spatial and temporal heterogeneity that underlies the clustered and patchy spatio-temporal distributions of herbivores in the Mara-Serengeti, similar to many other African savannas (Scholes and Archer 1997, Owen-Smith 2004).

Aerial surveys

The Department of Resource Surveys and Remote Sensing of Kenya (DRSRS) conducted 50 aerial surveys in the Mara from 1977 to 2010, with at least one survey conducted each year except in 1981, 1988, 1995, 1998, 1999, 2001, 2003, 2004 and 2006 due to financial and logistical constraints. Overall, 33 surveys were conducted in the wet season and 17 in the dry season. Averaging population density estimates for each species in each 5×5 km^2 grid cell over all replicate surveys conducted in each season in one year produced 21 surveys for the wet season and 17 for the dry season, which we used for analysis. The surveys follow strip transects located 5 km apart and segmented into sampling grid cells of 5×5 km^2 for a total of 289 such cells in the Mara. The number of animals observed within a calibrated survey strip defined by two parallel rods on the wings of the aircraft running through the centre of the 5×5 km^2 grid cell is recorded. Norton-Griffiths (1978) and Ogutu et al. (2011) provide further details of the counting and population estimation procedures used by DRSRS.

Normalized Difference Vegetation Index (NDVI)

NDVI measures the biomass and quality of vegetation at the land surface. It is used as a proxy for vegetation productivity and biomass (Pettorelli et al. 2005). The NDVI indices were obtained from the National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) images at a pixel resolution of 8×8 km^2 for 1982-2010. A semiparametric generalized linear mixed model (SGLMM) described comprehensively by Ogutu et al.(2011) was used to impute missing NDVI values between 1977 and 1982. To index temporal variation in biomass, we calculated seasonal and annual averages of NDVI for each pixel, which we call integrated NDVI. The seasonal NDVI components consisted of the dry (July-October) and wet (November-June) seasons whereas the annual component covered November-October. The three NDVI components were calculated separately for each land use type and lagged by one year to capture vegetation conditions in the year preceding surveys, indexing delayed or carryover effects of prior habitat conditions.

Distance to the nearest river

The distance from each grid cell center to the nearest drainage bed with clearly defined embankments was calculated for each land use type in ArcGIS 9.3.2. Most drainage beds in the Mara remain dry for most of the year, and are characteristically associated with erosion embankments and riverine thickets interspersed with tall grasses. We thus use distance to rivers to index predation risk, proximity to water and riverine woodlands and grasses (Anderson et al. 2010, Hopcraft et al. 2011).

Topographic Wetness Index (TWI)

We calculated TWI from the 90 m^2 digital elevation model (DEM) derived from the Shuttle Radar Topography Mission, as a relative measure of the long-term soil moisture availability of a given site in the landscape (Iverson et al. 1997). TWI is a function of watershed catchment area (the area draining into a pixel) and slope, and is calculated as $\ln(As/\tan \beta)$, where As is the watershed catchment area (i.e., the drainage area per unit width orthogonal to a stream line) and β is the slope gradient (Iverson et al. 1997). We use TWI to index the soil water retention capacity of a grid cell. Grid cells having high TWI values are more likely to have taller vegetation, so that TWI also serves as a proxy for predation risk (Hopcraft et al. 2005, Anderson et al. 2010), proximity to water and comparatively greener riparian zone woodlands and grasses.

Human population density

We used human population density to index human activities such as land use and harassment of wildlife. We obtained human population density estimates for the Mara for 1979 to 2010 from decadal national census records available from the Central Bureau of Statistics of Kenya. We used linear interpolation to impute missing human population densities for each landscape.

Identifying and mapping hotspots of herbivore density

To establish how herbivore density changed over time and space in the Mara, we calculated the mean density of each species in each 5 × 5 km^2 grid cell over all surveys (1977-2010) separately for each of the three landscapes. To account for differences in absolute densities of different species in occupied cells we computed the 0–25th, 26–50th, 51–75th and >75th quantiles of the frequency distribution of the mean density of each species over all surveys and grid cells occupied by the species. We next calculated the mean density of each species in each grid cell, separately for each landscape and decade combination (1970s, 1980s, 1990s and 2000s) and assigned the resulting decadal cell means to each of the four quantiles. We used the decadal cell means to reduce the influence of temporal variability in the individual estimated densities. The combined livestock density was similarly treated. If the mean cell density for a given landscape and decade combination fell within the fourth quantile, then we classified the cell as a hotspot in that decade, and as a non-hotspot otherwise. Moreover, grid cells that were not occupied by individuals of a species throughout the survey period were assigned a zero density and classified as non-hotspots. We developed a sequence of maps to display the temporal evolution of hotspots in each grid cell over the four decades spanned by the surveys in ARC GIS 9.3.2. The same scale was used for density in each landscape in each decade (1970s, 1980s, 1990s and 2000s) to enable direct temporal comparisons between landscapes for each species. We created separate maps for each season for the 10 herbivore species (Fig. 6.2) and livestock to account for seasonal differences in distribution. The scales for density were selected to represent quantiles of density for each species over the entire survey period. For each species all cells with estimated densities falling within the first quantile were assigned the lightest shade of gray and the intensity of this shade increased with increasing quantiles. The same grayscale was assigned to the same quantile for all species in each landscape to facilitate direct visual comparisons.

STATISTICAL MODELING AND DATA ANALYSES

We used multivariate semiparametric quantile regression analysis (Koenker and Hallock 2001, Koenker 2005) to relate herbivore density to NDVI (considering seasonal, annual and lagged components), livestock density/mean density (to make its scale comparable to those for the other covariates), distance to the nearest river, TWI and human population density measured within each 5 × 5 km^2 grid cell in each of the three landscapes covering the entire Mara, separately for each species and season. The model enabled exploration of how density responds to variation in the covariates near its upper limit, a region more relevant to understanding variation in hotspots of abundance than the median. Modeling such a limiting relationship using standard regression procedures would otherwise pose considerable statistical difficulties, in particular when densities are widely scattered beneath a specified upper limit. More precisely, we modeled the rate of change in density at the 75th conditional quantile of the distribution of density as a function of the above covariates to establish how variation in these covariates influenced hotspots of herbivore abundance in the Mara (Cade and Noon 2003). The choice of the 75th quantile was reasonable for modeling hotspots of most of the common species but for rare species higher quantiles may be necessary to yield conditional quantiles greater than zero. Confidence bands around the quantile regression functions were estimated using the bootstrap method with 500 replications (Koenker 2005). All analyses were conducted in the R *quantreg* package. We used dummy coding of landscapes to enable herbivore density to have possibly different nonlinear functional relationships with the same covariate in different landscapes in the same model.

We used a stepwise elimination procedure to select covariates with the greatest strength of support in the data based on the corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2002) and choose between the NDVI components. Specifically, we selected the best supported NDVI component from the current (annual, wet, dry, wet + dry) and lagged (annual1, wet1, dry1 and wet1+dry1) components, separately for each species (Table 6.2). We related density separately to the best selected NDVI component and each of the other covariates using semiparametric models and AICc to tune the smoothing parameter (λ) for each covariate. The variable with the smallest AICc was taken as the initial best model in the model selection process and added to the covariate with the next smallest AICc. On the contrary, if the

Table 6.2 Selection of the best supported NDVI component for each species in the dry and wet seasons based on AICc values. The selected NDVI component for each species in each season is highlighted in bold face. A numeric suffix after NDVI component name indicates the number of years by which the component was lagged.

Season	NDVI component	Thomson's gazelle	Impala	Grant's gazelle	Topi	Hartebeest	Wildebeest	Zebra	Buffalo	Giraffe	Elephant
Wet	Annual	44555.7	**41651.1**	31203.2	36313.8	29512.0	37782.4	41674.7	**37782.4**	24235.3	25560.2
	Wet	44578.2	41764.6	31221.1	36365.9	29371.9	**38162.7**	**41632.6**	38162.7	23960.2	**25391.2**
	Dry	44631.0	41731.3	30871.3	36528.7	29542.0	38353.7	41652.3	38353.7	24282.3	25542.2
	Wet + Dry	44539.5	41721.7	**30794.2**	36257.8	29319.2	38670.9	41667.4	37831.4	23960.2	25466.8
	Annual1	44586.1	41720.2	31201.0	36329.5	29466.1	38956.6	41682.9	37812.6	**23441.0**	25676.1
	Wet1	**44568.8**	41702.5	31213.5	**36311.2**	**29315.8**	39242.3	41680.8	37814.5	24098.5	25635.2
	Dry1	44522.4	41753.1	31179.9	36353.8	29554.7	39527.9	41647.4	37890	24170.5	25731.2
	Wet1 + Dry1	44574.1	41681.8	31124.0	36267.1	29362.1	39813.6	41644.9	37819.9	24098.5	25552.3
Dry	Annual	24283.7	**23827.9**	18461.6	20600.6	15167.6	39242.3	26354.8	22217.8	13649	**11701.7**
	Wet	24318.7	23875.2	18340.8	20591.1	15178.5	39527.9	26864.2	22198.7	13431.3	11828.9
	Dry	**24298.0**	23864.3	18236.1	20284.0	15274.5	39813.6	26701.0	**22091.9**	14001.2	11728.3
	Wet + Dry	24306.9	23866.6	18212.8	20507.3	15108.8	40099.3	26348.3	22198.7	13566.4	11728.3
	Annual1	24296.2	23850.8	18215.2	20565.4	15132.6	40384.9	26345.4	22216.0	13438.1	11726.0
	Wet1	24288.2	23949.3	18164.4	20446.9	15098.8	40670.6	26281.4	22251.0	13470.0	11748.6
	Dry1	24266.2	23850.9	**18229.1**	**20392.8**	15126.1	**40956.3**	**26264.5**	22207.8	13119.6	11711.9
	Wet1 + Dry1	24296.4	23852.0	18167.2	20484.6	**15083.6**	37808.7	26291.5	22160.9	**13077.0**	11748.6

AICc for the new model reduced compared to that for the initial model then the new covariate was retained in the model. Otherwise, if the AICc for the new model increased relative to the initial model then we removed the new covariate from the model and added the covariate with the second smallest AICc. We continued this way until we had considered all the covariates (Table S1), ending with a multivariate semi-parametric regression model for each species. We used the *optimize* R function in the *quantreg* package to fine-tune the smoothing parameter (λ), which determines the degree of smoothness of the fitted function for each covariate, for functions with a single λ, and the simulated annealing option of *optimize* for functions with multiple λs (Koenker, 2005). We then plotted and visually inspected shapes of the functions fitted to each covariate for ecological plausibility.

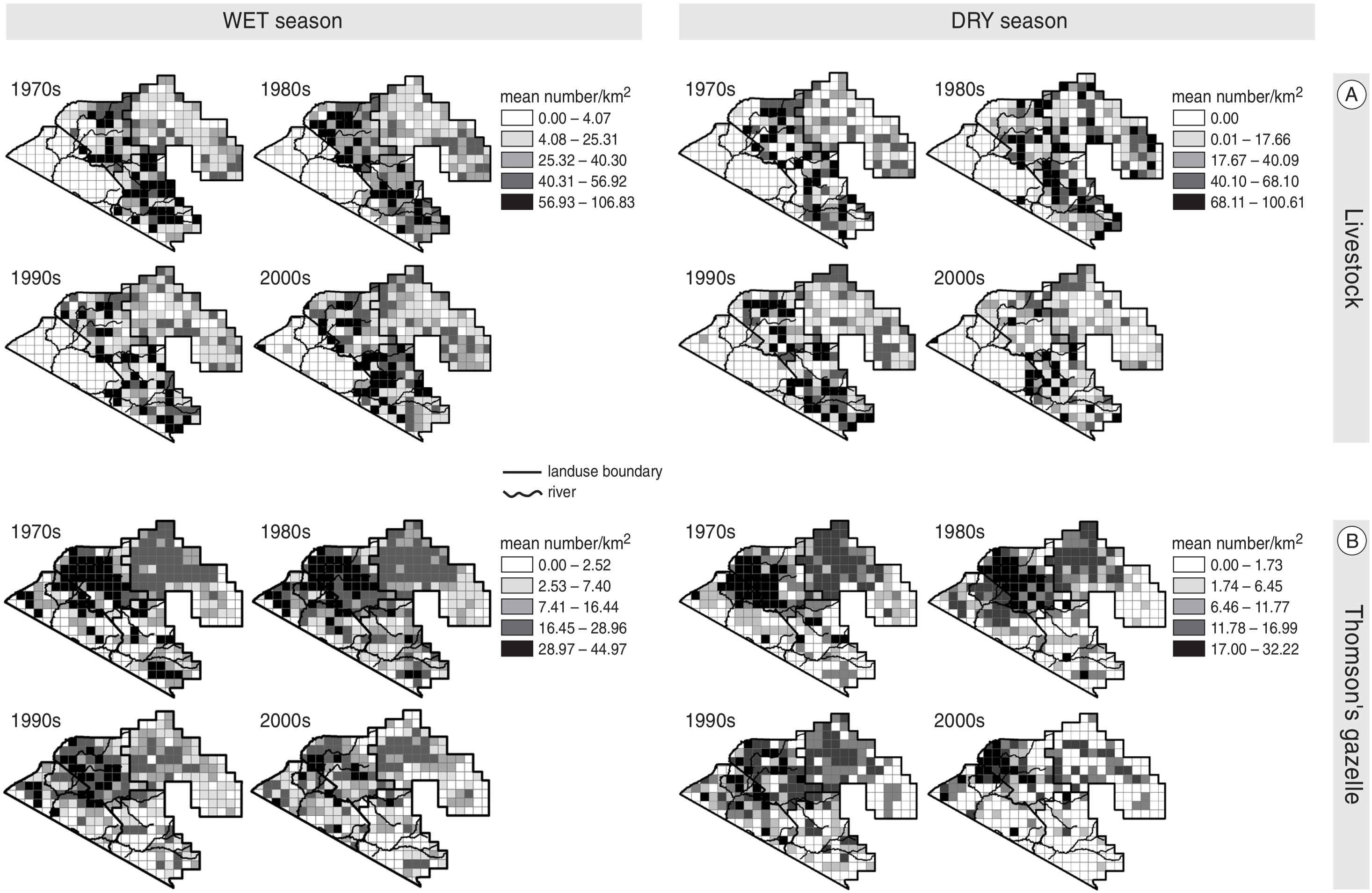
RESULTS

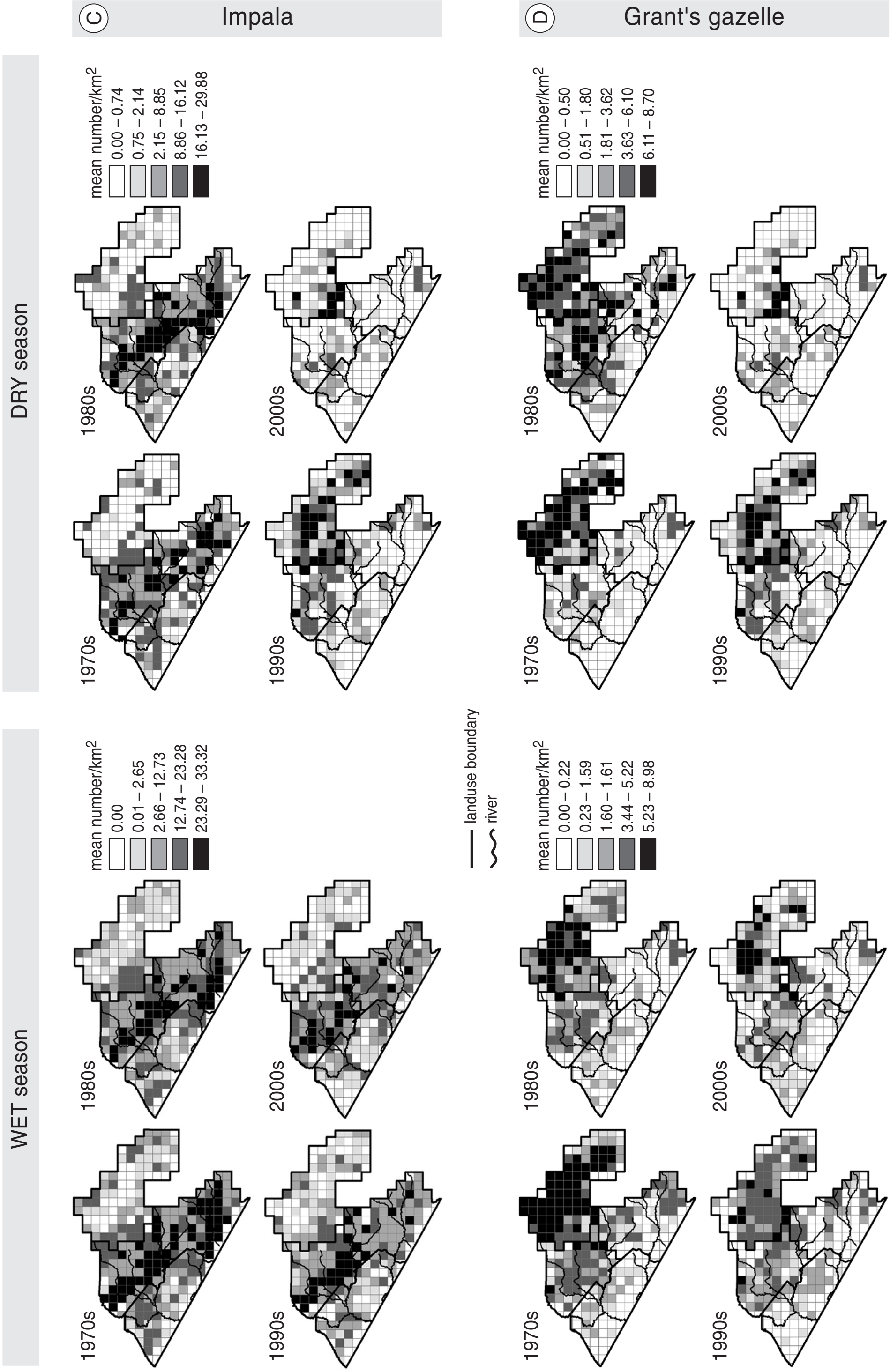
Distribution of herbivore hotspots during 1977–2010

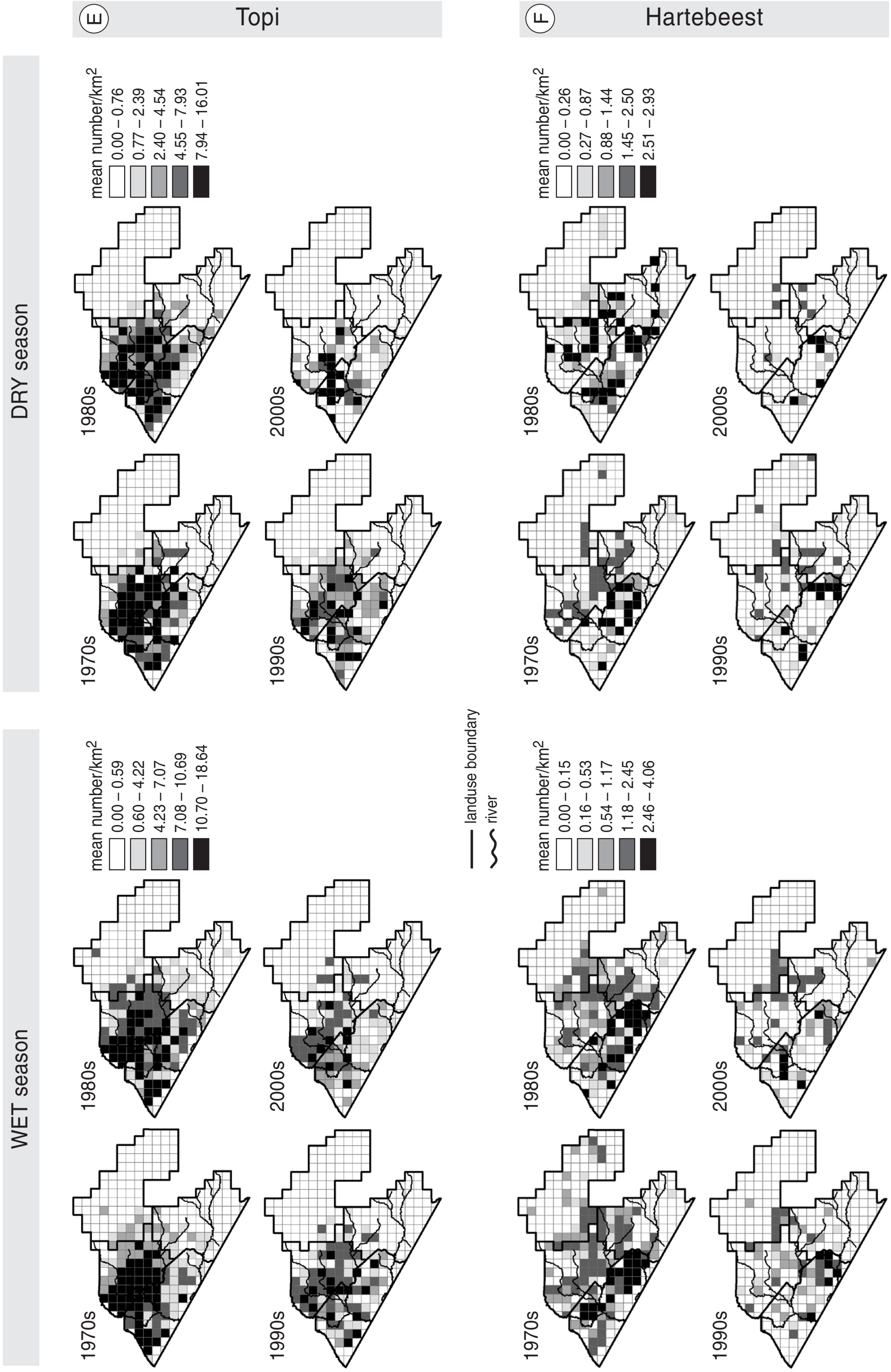
There were marked temporal variations in the locations and extents of herbivore hotspots in the reserve, the inner and outer ranches over the survey period (Fig. 6.2). Livestock were abundant and their distribution expanded over time in the ranches in both seasons (Fig 6.2A). Livestock incursions into the reserve also increased over time, with distinctively more livestock using the reserve in the 2000s than in the 1970s. Among small herbivores Thomson's and Grant's gazelles concentrated in the outer ranches and in the central plains of the inner ranches (mainly Koyiaki and Olkinyei ranches) and the reserve (Figs 6.2B and D). The distribution of hotspots of both gazelles contracted markedly during 1977-2010 especially in the ranches. Impala, hotspots concentrated in a band oriented southeast-northwest in the inner ranches but a sizable number also occurred in the reserve (Fig. 6.2C).

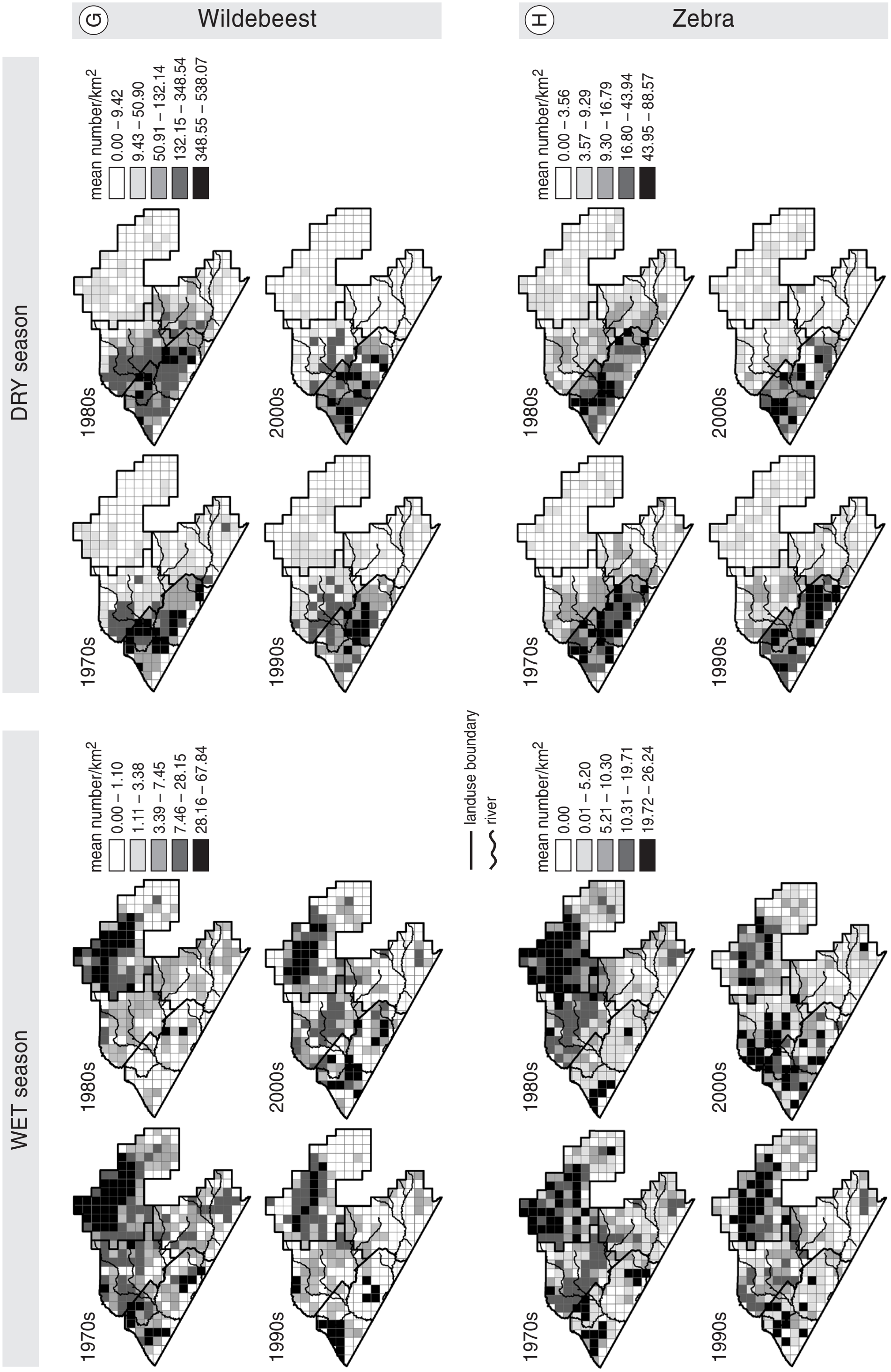
Topi concentrated in the high rainfall western and northwestern parts of the inner ranches and in the reserve but avoided the outer ranches. Topi hotspots decreased strongly during the 1990s and 2000s in both the reserve and the inner ranches (Fig. 6.2E). Hartebeest hotspots occurred in similar locations and decreased sharply as did those of topi but their distribution in the reserve and the inner ranches also evidently fragmented during the 1990s and 2000s (Fig. 6.2F). Wildebeest and zebra hotspots concentrated in the reserve and inner ranches in the dry season, reflecting the combined presence of migrants from the Serengeti and Loita Plains but in the outer ranches in the wet season, following the return of the Loita migrants (Figs 6.2G &H). The declines in wildebeest and zebra hotspots in the reserve and ranches during the

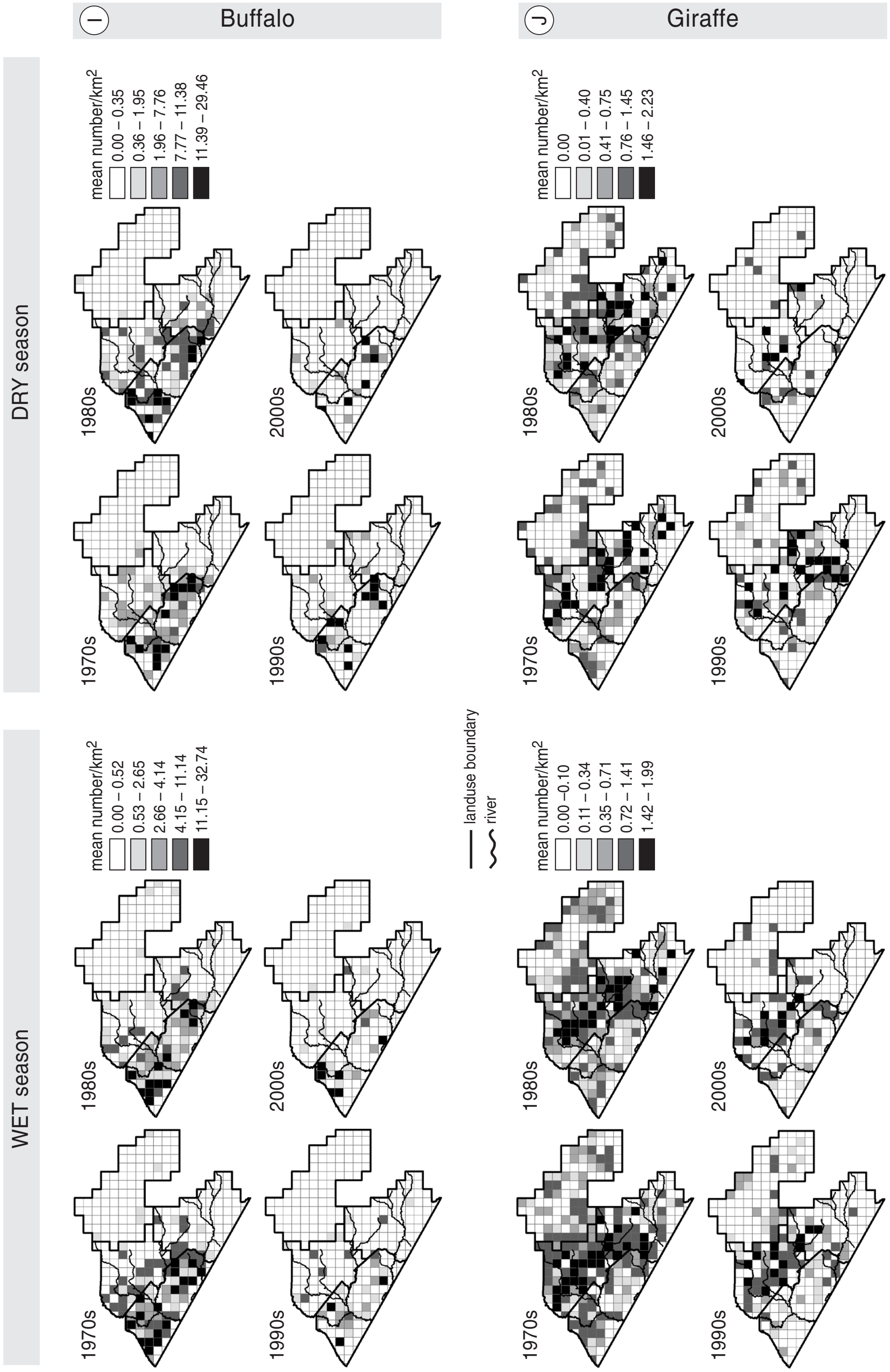
Figure 6.2 (next pages) Distribution of decadal density averages over the 5 × 5 km^2 grid cells in the Mara region during the 1970s, 1980s, 1990s and 2000s for A) Livestock, B) Thomson's gazelle C) impala, D) Grant's gazelle, E) topi, F) hartebeest, G) wildebeest, H) zebra, I) buffalo, J) giraffe and K) elephant. The grayscale shows densities falling within the 0–25th (lightest cells), 26–50th, 51–75th and >75th (darkest cells) quantiles of the frequency distribution of mean grid cell densities computed over all surveys (1977–2010) and all grid cells occupied by each species in each land use type.

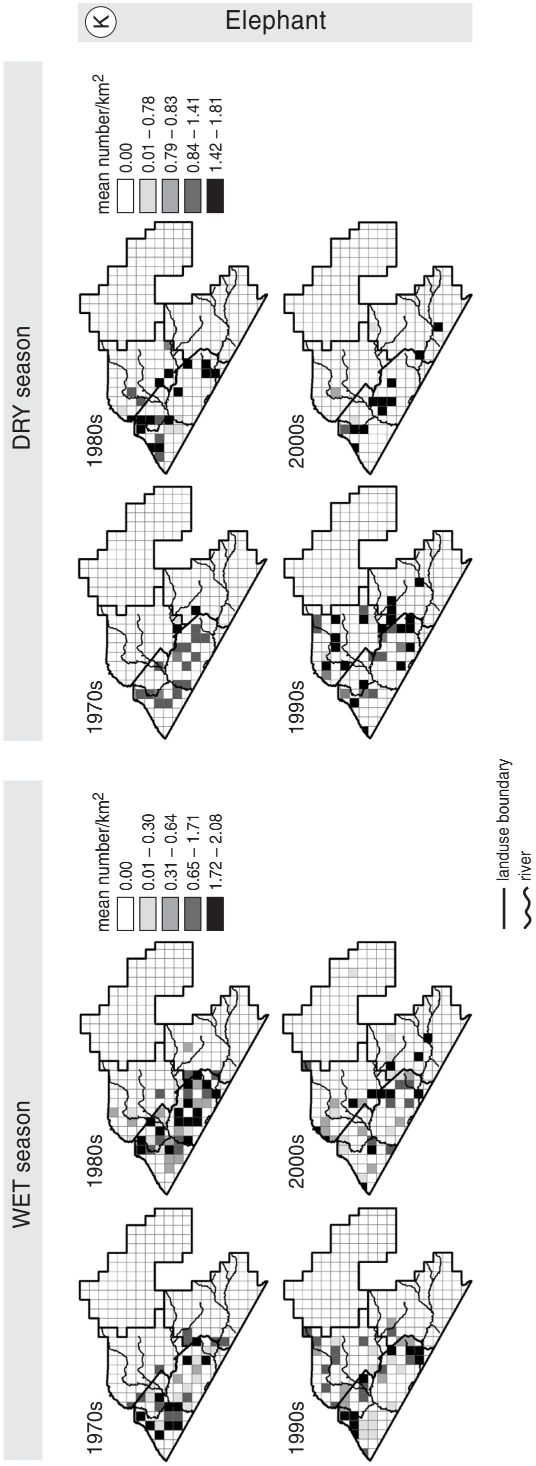

WET season
DRY season
A
Livestock
B
Thomson's gazelle
1970s
1980s
1990s
2000s
mean number/km²
0.00 – 4.07
4.08 – 25.31
25.32 – 40.30
40.31 – 56.92
56.93 – 106.83
0.00
0.01 – 17.66
17.67 – 40.09
40.10 – 68.10
68.11 – 100.61
landuse boundary
river
0.00 – 2.52
2.53 – 7.40
7.41 – 16.44
16.45 – 28.96
28.97 – 44.97
0.00 – 1.73
1.74 – 6.45
6.46 – 11.77
11.78 – 16.99
17.00 – 32.22


C
Impala
D
Grant's gazelle
DRY season
WET season
1970s
1980s
1990s
2000s
mean number/km^2
0.00 – 0.74
0.75 – 2.14
2.15 – 8.85
8.86 – 16.12
16.13 – 29.88
mean number/km^2
0.00
0.01 – 2.65
2.66 – 12.73
12.74 – 23.28
23.29 – 33.32
mean number/km^2
0.00 – 0.50
0.51 – 1.80
1.81 – 3.62
3.63 – 6.10
6.11 – 8.70
mean number/km^2
0.00 – 0.22
0.23 – 1.59
1.60 – 1.61
3.44 – 5.22
5.23 – 8.98
landuse boundary
river


E
Topi
F
Hartebeest
DRY season
WET season
1970s
1980s
1990s
2000s
mean number/km²
0.00 – 0.76
0.77 – 2.39
2.40 – 4.54
4.55 – 7.93
7.94 – 16.01
0.00 – 0.59
0.60 – 4.22
4.23 – 7.07
7.08 – 10.69
10.70 – 18.64
0.00 – 0.26
0.27 – 0.87
0.88 – 1.44
1.45 – 2.50
2.51 – 2.93
0.00 – 0.15
0.16 – 0.53
0.54 – 1.17
1.18 – 2.45
2.46 – 4.06
landuse boundary
river


G
Wildebeest
H
Zebra
DRY season
WET season
1970s
1980s
1990s
2000s
mean number/km^2
0.00 – 9.42
9.43 – 50.90
50.91 – 132.14
132.15 – 348.54
348.55 – 538.07
mean number/km^2
0.00 – 1.10
1.11 – 3.38
3.39 – 7.45
7.46 – 28.15
28.16 – 67.84
mean number/km^2
0.00 – 3.56
3.57 – 9.29
9.30 – 16.79
16.80 – 43.94
43.95 – 88.57
mean number/km^2
0.00
0.01 – 5.20
5.21 – 10.30
10.31 – 19.71
19.72 – 26.24
landuse boundary
river


I
Buffalo
J
Giraffe
DRY season
WET season
1970s
1980s
1990s
2000s
mean number/km²
0.00 – 0.35
0.36 – 1.95
1.96 – 7.76
7.77 – 11.38
11.39 – 29.46
0.00 – 0.52
0.53 – 2.65
2.66 – 4.14
4.15 – 11.14
11.15 – 32.74
0.00
0.01 – 0.40
0.41 – 0.75
0.76 – 1.45
1.46 – 2.23
0.00 –0.10
0.11 – 0.34
0.35 – 0.71
0.72 – 1.41
1.42 – 1.99
landuse boundary
river


K
Elephant
DRY season
WET season
1970s
1980s
1990s
2000s
mean number/km²
0.00
0.01 – 0.78
0.79 – 0.83
0.84 – 1.41
1.42 – 1.81
mean number/km²
0.00
0.01 – 0.30
0.31 – 0.64
0.65 – 1.71
1.72 – 2.08
landuse boundary
river

1990s and 2000s coincided with a reduction in the numbers of both the Serengeti migrants reaching the Mara and the resident herds (Figs 6.2G-H). Wildebeest and zebra hotspots increased in the reserve and the inner ranches in the wet season over time, reflecting progressive exclusion from the outer ranches by changing land use (Ogutu et al. 2011).

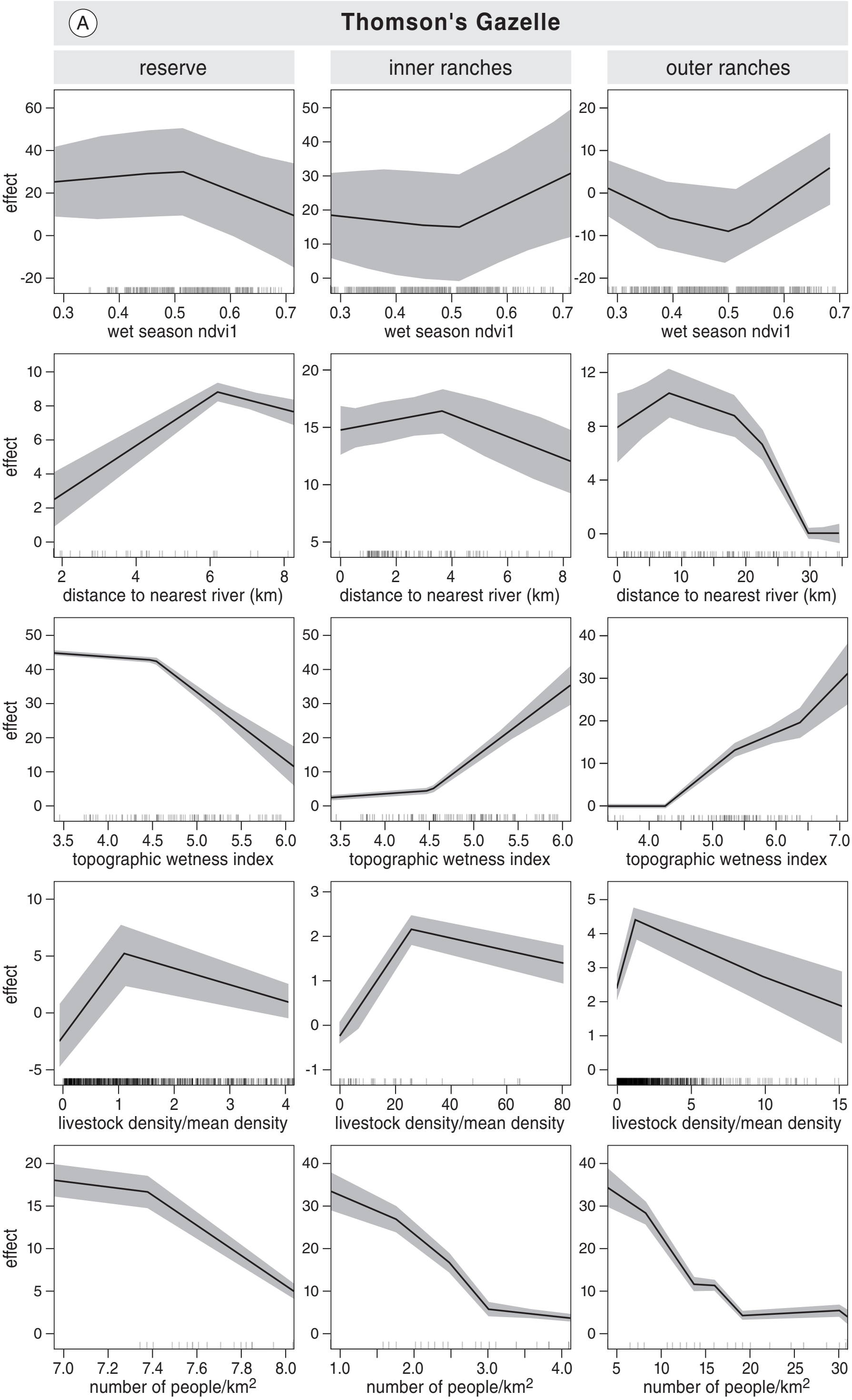
Buffalo hotspots were concentrated in the high rainfall western and northwestern parts of the reserve and inner ranches during the 1970s and 1980s but decreased sharply in the 1990s and 2000s, during which time they occurred almost exclusively in the reserve, suggesting exclusion from the ranches by livestock (Fig. 6.2I). Giraffe hotspots concentrated in the reserve and the inner ranches in the 1970s and 1980s but declined during the 1990s and 2000s, when most hotspots occurred in the inner ranches, a few in the reserve and very few in the outer ranches (Fig. 6.2J). Finally, elephant hotspots occurred almost exclusively inside the reserve throughout the monitoring period but, starting in the 1980s, elephants expanded their range into the inner ranches (Fig. 6.2K).

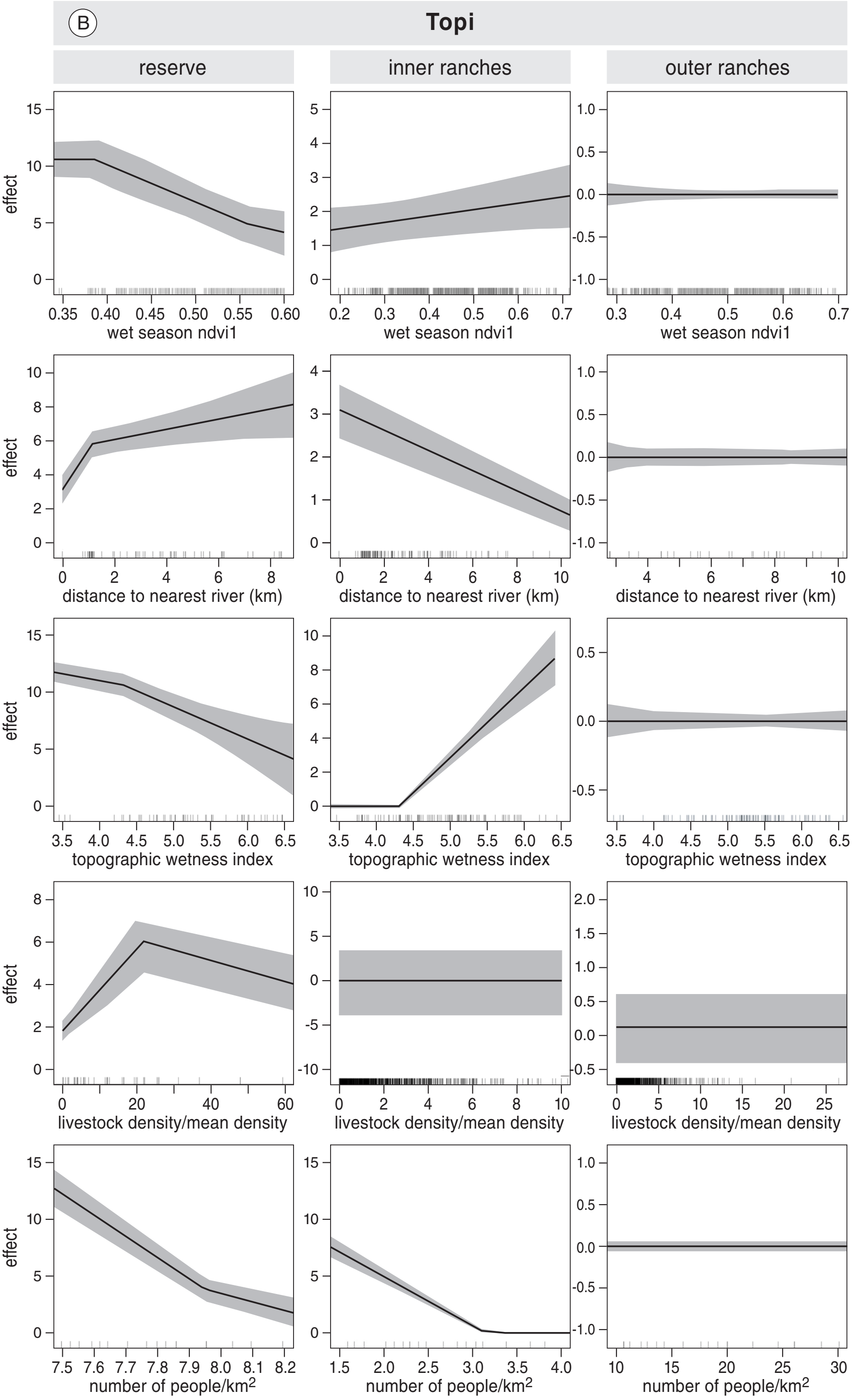
Factors influencing herbivore hotspots during the wet season

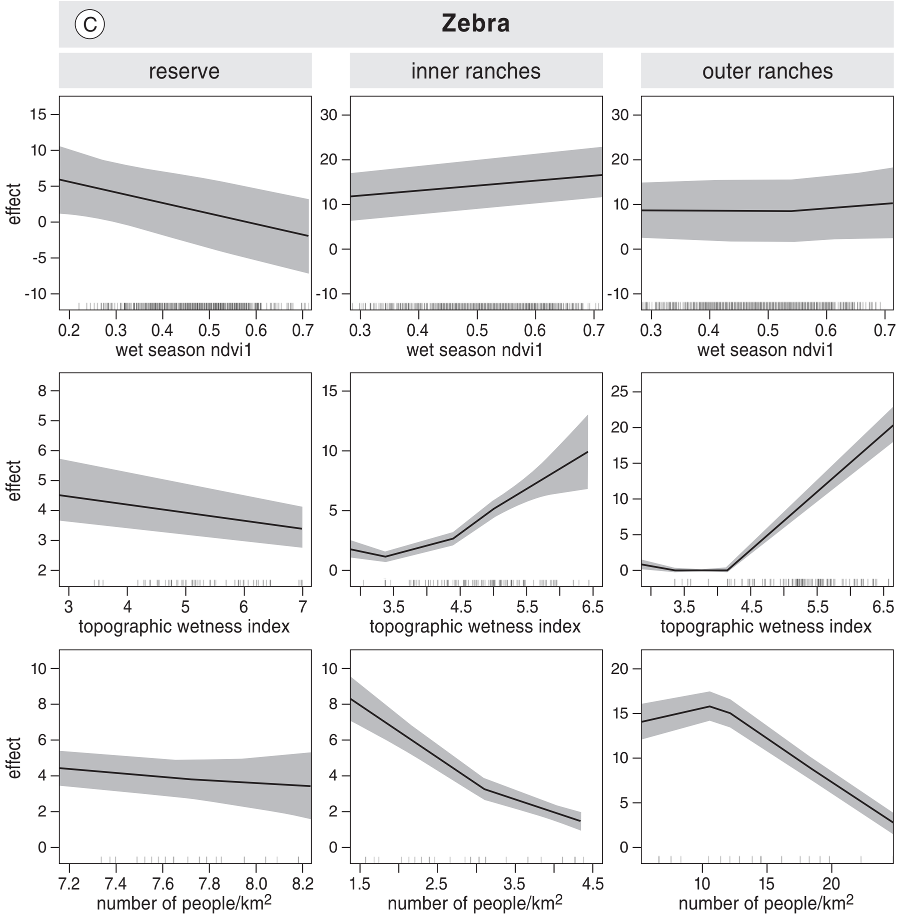
During the wet season in the reserve, hotspots of the small and medium herbivores were influenced similarly by variation in almost all the environmental and anthropogenic variables considered, with only two species showing minor deviations from this general pattern. Specifically, hotspots of two species of the small (Thomson's gazelle, impala) and three of the medium (topi, wildebeest and zebra) herbivores occurred in areas of low NDVI, topographic wetness (except for wildebeest) and human population density, but farther from rivers (except for zebra) and at intermediate (Thomson's gazelle, impala and topi, Figs 6.3A, S1a and 3b) or low (wildebeest, Fig S1d) levels of livestock density, or were unresponsive to livestock (zebra, Fig. 6.3C). Hotspots of Grant's gazelle and hartebeest (Figs S1b and c) showed the same patterns but were unrelated to both NDVI and livestock density (Table S1).

In sharp contrast to the patterns observed in the reserve, hotspots of the small and medium herbivores peaked in greener and wetter (except for wildebeest) localities situated closer to rivers (except for zebra) in the ranches. The hotspots were also concentrated distant from areas of high human population density and having low (wildebeest, Fig. S1d) to intermediate (Thomson's gazelle and impala, Figs 6.3A and S1a) livestock densities. Only hotspots of Grant's gazelle and hartebeest were unrelated to NDVI (Table S1), and together with those of zebra, to livestock density as well (Table S1). Additionally, impala hotspots were little affected by variation in NDVI (Fig. S1a) whereas topi hotspots were unrelated to all the predictor variables in the outer ranches (Fig. 6.3B).

Figure 6.3 (next pages) Partial predictions of the expected conditional 75th quantile of density and its 95% confidence limits based on the multivariate semiparameteric quantile regression models for A) Thomson's gazelle, B) topi and C) zebra hotspots in the Mara region of Kenya in the wet season during 1977–2010. Tick marks on the x-axis represent locations of observations along the predictor space.


A
Thomson's Gazelle
reserve
inner ranches
outer ranches
effect
wet season ndvi1
distance to nearest river (km)
topographic wetness index
livestock density/mean density
number of people/km2
0.3
0.4
0.5
0.6
0.7
60
40
20
0
-20
50
30
10
-10
2
4
6
8
12
15
5
3.5
4.0
4.5
5.0
5.5
6.0
7.0
1
3
-1
-5
80
1.0
2.0
3.0
7.2
7.4
7.6
7.8
8.0
25


B
Topi
reserve
inner ranches
outer ranches
effect
wet season ndvi1
distance to nearest river (km)
topographic wetness index
livestock density/mean density
number of people/km2



Unlike those of the small and medium herbivores, hotspots of the large herbivores were responsive to variation in fewer environmental and anthropogenic variables and the responses were more differentiated among species. Inside the reserve, the distributions of hotspots of the large herbivores peaked in the following three types of areas. (1) Areas of high NDVI values (buffalo, Fig. S1e). (2) Close to rivers and in areas of low human population density (giraffe, Fig. S1f). (3) Areas of low topographic wetness (hill tops and ridge tops), located at intermediate distances from rivers and areas of low human population density (elephant, Fig. S1g). In the ranches, other than giraffe hotspots that concentrated close to rivers and in areas of low human population density (Fig. S1f), similarly to the reserve, hotspots of the large herbivores were unresponsive to all the predictors (Table S1), partly reflecting the very low numbers of buffalo and elephant in the ranches.

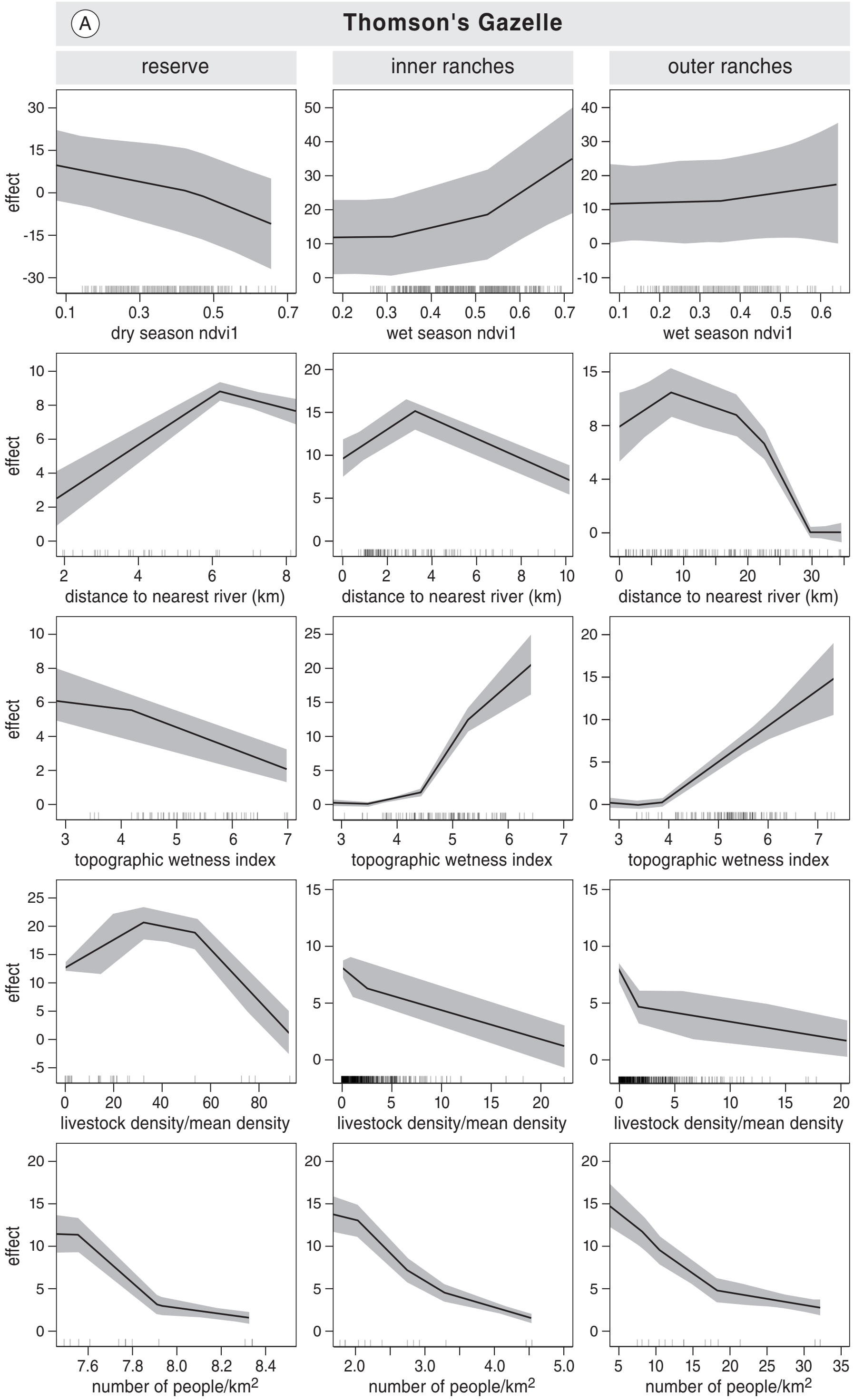
Factors influencing herbivore hotspots during the dry season

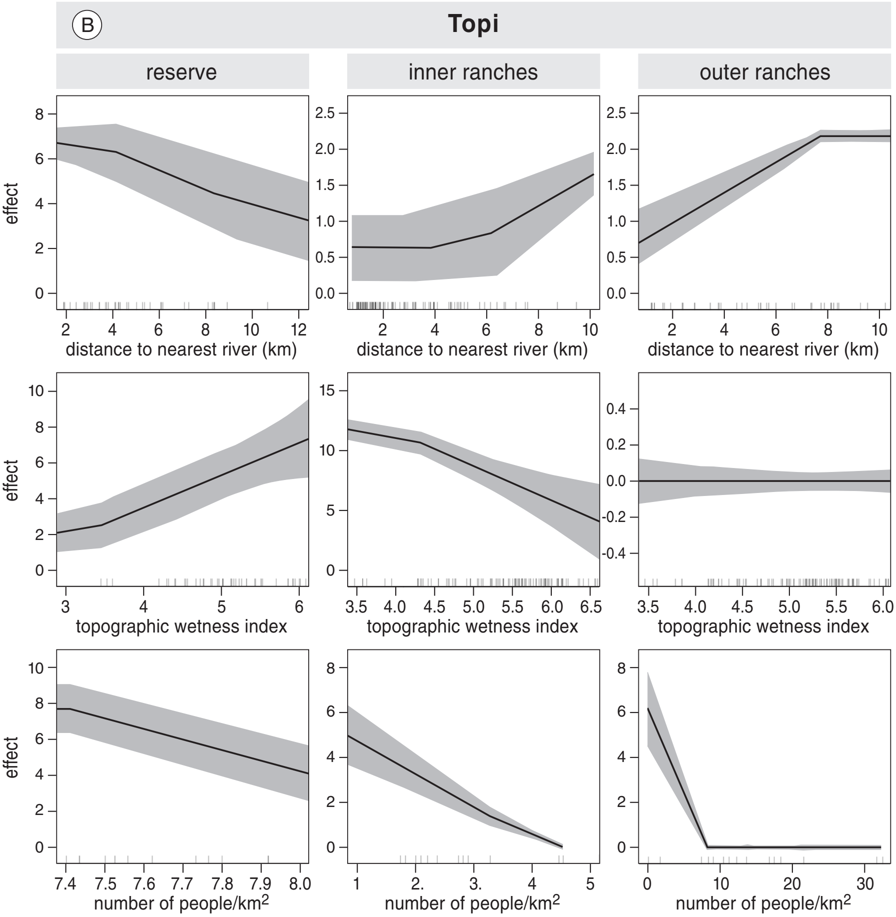
The pattern of distribution of hotspots of small herbivores in the reserve in the dry season was remarkably similar to that for the wet season except for two minor differences. (1) Thomson's gazelle and impala concentrated in areas of medium livestock density in the wet season but avoided livestock in the dry season in all landscapes (Figs 6.4A and S2a). (2) Grant's gazelle occurred in areas of high NDVI in the dry season (Fig. S2b) but was insensitive to NDVI in the wet season. In contrast to the wet season, the medium herbivores concentrated in greener (except topi and hartebeest that were insensitive to NDVI, Table S1) and wetter areas, closer to rivers (topi and hartebeest) and at intermediate distances from rivers (zebra) in the dry (Figs 6.4B and C and S2c) than in the wet season. Otherwise, small and medium herbivores avoided areas of dense human concentrations and were little affected by livestock density, similarly to the wet season. Wildebeest deviated from this general pattern as their hotspots were more evenly spread with respect to distance to rivers, topographic wetness and human presence in the dry (Fig. S2d) than in the wet season.

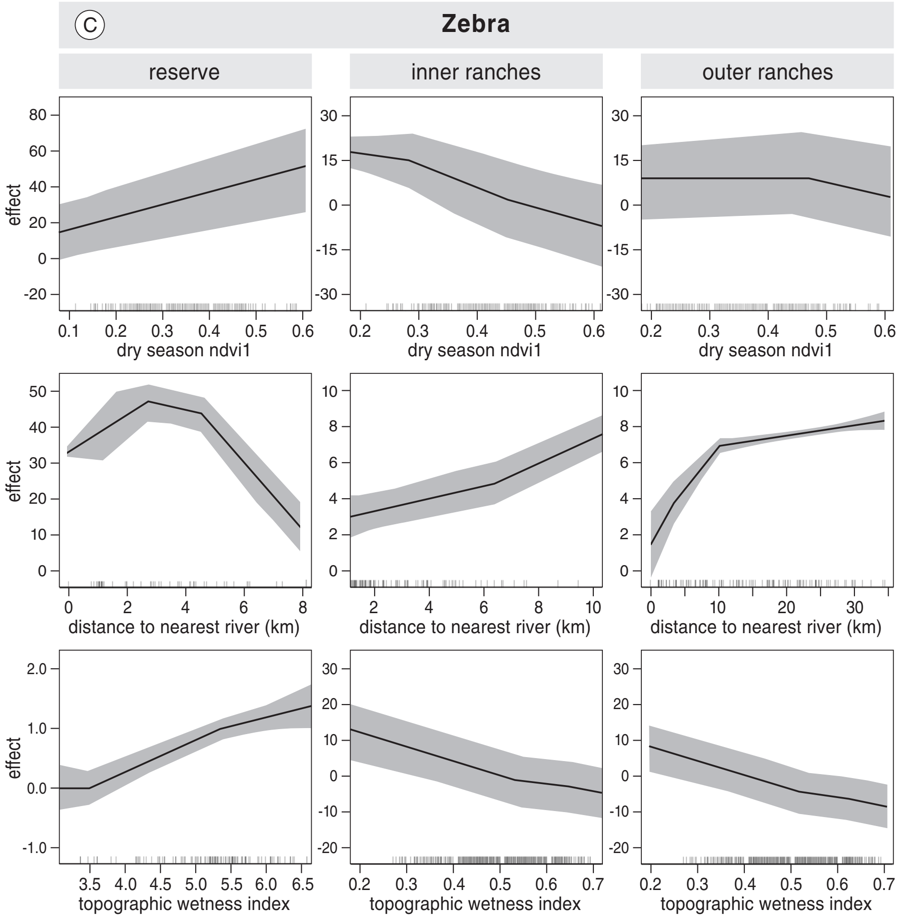
A part from concentrating in areas with lower livestock densities in the dry season or being insensitive to livestock (Grant's gazelle), the distributions of hotspots of all the three small herbivores in the ranches were similar to those for the wet season (Figs 6.4A, S2a and b). The medium herbivores also displayed contrasting distribution patterns between seasons in the ranches, with notable differences between the two seasons being the concentration of their hotspots in drier areas located farther from rivers and characterized by lower NDVI (especially for zebra and wildebeest) (Figs 6.4B, C and S2c and d).

The distribution of hotspots of large herbivores in the dry season in the reserve was also largely similar to that for the wet season except that (1) giraffe became more evenly distributed relative to human presence (Fig. S2f) and (2) elephant moved to wetter areas and closer to rivers (Fig. S2g). An even greater similarity between seasons was evident in the distributions of the large herbivores in the ranches (Figs S2e and g). The only minor difference between patterns for the two seasons was shown by giraffe that avoided locations of dense human presence in the wet season but were evenly distributed relative to human population density in the in dry season in the ranches (Fig. S1f).

Figure 6.4 (next pages) Partial predictions of the expected conditional 75th quantile of density and its 95% confidence limits based on the multivariate semiparameteric quantile regression models for A) Thomson's gazelle, B) topi and C) zebra hotspots in the Mara region of Kenya in the dry season during 1977-2010. Tick marks on the x-axis represent locations of observations in the predictor space.


A
Thomson's Gazelle
reserve
inner ranches
outer ranches
effect
30
15
0
-15
-30
0.1
0.3
0.5
0.7
dry season ndvi1
50
40
30
20
10
0
0.2
0.3
0.4
0.5
0.6
0.7
wet season ndvi1
40
30
20
10
0
-10
0.1
0.2
0.3
0.4
0.5
0.6
wet season ndvi1
10
8
6
4
2
0
2
4
6
8
distance to nearest river (km)
20
15
10
5
0
0
2
4
6
8
10
distance to nearest river (km)
15
8
4
0
0
10
20
30
distance to nearest river (km)
10
8
6
4
2
0
3
4
5
6
7
topographic wetness index
25
20
15
10
5
0
3
4
5
6
7
topographic wetness index
20
15
10
5
0
3
4
5
6
7
topographic wetness index
25
20
15
10
5
0
-5
0
20
40
60
80
livestock density/mean density
15
10
5
0
0
5
10
15
20
livestock density/mean density
15
10
5
0
0
5
10
15
20
livestock density/mean density
20
15
10
5
0
7.6
7.8
8.0
8.2
8.4
number of people/km2
20
15
10
5
0
2.0
3.0
4.0
5.0
number of people/km2
20
15
10
5
0
5
10
15
20
25
30
35
number of people/km2


B
Topi
reserve
inner ranches
outer ranches
effect
distance to nearest river (km)
topographic wetness index
number of people/km2
0
2
4
6
8
10
12
0.0
0.5
1.0
1.5
2.0
2.5
15
-0.4
-0.2
0.0
0.2
0.4
3
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.4
7.5
7.6
7.7
7.8
7.9
8.0
1
2.
3.
5
20
30



DISCUSSION

Distribution of herbivore hotspots

Our results show that clusters of herbivores of different body sizes were persistent in spatially distinct localities in the Mara during 1977-2010. Six general patterns were evident. 1) The distribution of livestock within the ranches greatly expanded whereas illegal livestock incursions into the reserve increased markedly during 1977-2010, in particular in the 2000s. Both patterns accord with and reinforce similar findings by Ogutu et al. (2011) and their observation that the proportional contribution of livestock to the total domestic plus wild herbivore biomass within the reserve increased by an order of magnitude from an average of 2% in the 1970s to 23% in the 2000s and now (2009) vastly surpasses that of any resident wildlife species, except buffalo. 2) Small herbivores (Thomson's gazelle, impala) show a pronounced tendency to concentrate in the ranches outside the protected reserve during both seasons. 3) The medium herbivores (topi, zebra and wildebeest) move seasonally between the reserve and the ranches and tend to concentrate in the reserve in the dry season but in the ranches in the wet season. 4) Large herbivores (buffalo, elephant) concentrate in the reserve throughout the year, except for giraffe. 5) Hotspots of medium and large herbivores decreased sharply, in particular during the 1990s and 2000s, implicating intensifying land use change and progressive exclusion by changing land use from the ranches. 6) Finally, hotspots of species belonging to different size classes occur at the boundary between the protected reserve and the adjoining pastoral ranches, a place where wildlife presumably benefit from greater safety because predators avoid humans just outside the reserve, experience less competition from livestock, or are facilitated by livestock grazing, consistent with the observations of Ogutu et al. (2011). These patterns are concordant with ecological theory predicting that herbivores should occupy and persist in the best locations in the landscape to optimize their fitness by maximizing their access to resources, while minimizing exposure to risks (Jarman 1974, Sinclair and Arcese 1995a, Olff et al. 2002, Hopcraft 2010).

The influences of seasonal variations in the environmental and anthropogenic correlates of herbivore hotspots reflected differences in herbivore body sizes and feeding styles. In general, predation risk is tightly linked to body size and vegetation height and cover in savannas (Hopcraft et al. 2005, Riginos and Grace 2008). Consequently, small herbivores seek areas that are relatively free from predators in the ranches because they are more susceptible to predation due to their small sizes (Sinclair et al. 2003). Large herbivores that are less vulnerable to predation and so are able to "risk" being in areas of relatively high predation risk (Owen-Smith 1988), and are the most likely to engender conflicts with humans, cluster in the reserve instead. Furthermore, by concentrating in the ranches, small and medium herbivores presumably not only incur less predation but also satisfy their high-quality forage requirements by feeding on short, nutritious grasses maintained by livestock, while large herbivores similarly fulfill their high biomass needs by feeding on tall grasses in the reserve (Jarman 1974, Sensenig et al. 2010). The observed seasonal distributions of hotspots in the Mara therefore support the argument that most African parks, including the MMNR, are not sufficiently large to satisfy the year-round requirements of their full complement of wild herbivore populations as they encompass mostly the dry season concentration areas (Fynn and Bonyongo 2010). By moving to the protected area (less accessible for livestock), when food availability becomes limiting, they limit strong competition with livestock in the dry season. In the wet season, in absolute contrast, wild herbivores disperse from the protected areas to their adjoining landscapes, often consisting of short-grass plains maintained by livestock grazing, and thereby benefit from facilitation by livestock.

Factors influencing herbivore hotspots in the wet season

In the wet season small and medium herbivores avoided areas of high NDVI, close to rivers and wetter areas in the reserve. These areas are likely associated with poor-quality, tall grasses (Boutton et al. 1988; Georgiadis and McNaughton 1990), river banks and wet and sticky soils (Talbot and Talbot 1963) and have elevated risks of predation due to dense vegetation cover (Hopcraft et al. 2005). Instead, they concentrated in areas of low NDVI values inside the reserve, away from rivers and in drier localities. This suggests that they select these areas because the areas are either highly productive or support high-quality forage but have low NDVI signals due to intensive grazing, or have lower predation risk due to short grasses, or both. These patterns are consistent with H1a and H3a.

In the ranches, in sharp contrast to the reserve, small and medium herbivores concentrated in areas of high NDVI, except topi that remained unresponsive in the outer ranches, likely due to their low numbers. These areas likely have forage of high nutritional quality and digestibility and lower predation risk due to high visibility associated with grasses maintained by livestock grazing (Fryxell 1995). The concentration of herbivores closer to rivers in the ranches than in the reserve likely reflects the lower predator densities than in the reserve (Ogutu et al. 2005). Furthermore, these patterns suggest exclusion from the short grass plains distant from rivers, or attraction to short grasses and better visibility conditions created by heavy livestock grazing near rivers in the ranches. The concentration of herbivores in areas of high soil moisture content in the ranches is surprising as these areas are expected to have high predation risk and low food quality (Anderson et al. 2010). This distribution likely reflects both displacement from the drier, open short grass plains and facilitation by livestock grazing along rivers in the dry season, which keeps grasses short and nutritious and enhances visibility in the wet season as predicted by H3b. These observations provide indirect evidence that vegetation quality and height as well as predation risk associated with vegetation structure (Hopcraft et al. 2005, Anderson et al. 2010) jointly determine the location of hotspots of the small and medium herbivores.

Both buffalo and elephant are less susceptible to predation (Sinclair et al. 2003) and are more strongly dependent on bulk grass intake because of their large body sizes. This likely explains why both species concentrated in the reserve in the wet season where vegetation was most abundant. However, both species were unresponsive to all the predictors in the ranches. This partly reflects the low numbers of buffalo and elephant in the ranches due to strong exclusion by livestock, people and settlements. Giraffe are almost exclusively browsers and favour trees (Owen-Smith, 1988), suffer relatively little from predation (Sinclair et al. 2003) and therefore, concentrated close to rivers in both landscapes. However, giraffe were more common close to rivers in the pastoral ranches. The ranches support 11–12% woody cover and the reserve 4% as measured by (Ogutu et al. 2005) indicating greater forage availability for giraffe. As a result, the future population viabilities of buffalo and elephant are the most strongly dependent on protection of the 10 species given the ongoing dramatic land-use changes and human population growth in the Mara ranches (H5).

Our results show that small and medium herbivores concentrate in the human-dominated ranches in the wet season but in the protected area in the dry season. So, why do the small and medium herbivores move seasonally between the protected reserve and the adjoining ranches? The results suggest that large herbivores, including livestock, play an important facilitative role in the dispersal of small and medium herbivores from protected areas to neighbouring pastoral lands in the wet season. In particular, large herbivore grazing creates short, high-quality grass favoured by the small and medium herbivores (Cromsigt and Olff 2006). The facilitative function of livestock in the ranches is apparently not being accomplished by the large, resident herbivores inside the reserve in the wet season as would be expected from ecological theory. One likely explanation for this failure relates to the migration of vast herds of wildebeest and zebra in the Mara-Serengeti ecosystem. These migrants indirectly contribute to the seasonal dispersal movements of the small and medium grazers from the reserve to the pastoral lands by competing with and hence keeping populations of the large resident grazers too low to maintain the grass sufficiently short for the small and medium herbivores in the reserve in the late wet and dry seasons. It follows that seasonal dispersal movements of the small and medium herbivores to the pastoral lands partly portrays an inability of the resident ungulate assemblage to create and maintain short grass lawns favoured by the small and medium herbivores inside the protected areas. Accentuating the competition between the large resident grazers and the enormous herds of migratory herbivores are the large and growing herds of livestock grazing in the Mara reserve in the dry season. This is corroborated by the observation that savanna ecosystems without large-scale migrations, such as the Hluhluwe-iMfolozi Park in South Africa, are dominated by high densities of large, resident herbivores such as buffalo and white rhino (*Ceratotherium simum*) (Fynn & Bonyongo, 2010). So, while it is likely true that migratory herbivores and livestock jointly facilitate the resident small and medium ungulates by removing most of the dry, rank vegetation in the dry season, they probably also force them to spend more time in the ranches in the wet season than they would otherwise. They do this not only indirectly by keeping numbers of the large resident grazers low, but also directly by keeping numbers of the small and medium grazers far below the level at which they themselves would be able to keep the grass low enough to satisfy their needs all year-round due to competition for food in the dry season with the migrants. From this perspective livestock facilitate the small and medium herbivores in the ranches in the wet season but also contribute to creating and maintaining the conditions that make such movements possible in the first place.

Factors influencing herbivore hotspots in the dry season

Protected reserves still provide relatively intact dry-season refuges for seasonal movements of both migratory and resident wildlife populations (Fynn & Bonyongo, 2010). During the dry season, forage quality and surface water as well as quality is reduced throughout the region, but is higher inside the reserve compared to the ranches (Reid et al. 2003; Ogutu et al. 2005). Therefore, it can be expected that resident herbivores should occur in areas where forage and water availability are higher than average (H2a and H4a). In contrast to these expectations the small herbivores (Thomson's gazelle and impala) concentrated in areas of low NDVI values, farther from rivers and in drier areas inside the reserve. However, Grant's gazelle occurred in areas of high NDVI in the reserve but concentrated farther from rivers and in drier areas. This is in contrast to observations made in the Serengeti, where Grant's gazelle usually concentrate in the short grass plains (Sinclair 1979). A likely explanation for this is that Grant's gazelle feed on forbs and shrub foliage besides grasses in the dry season (Georgiadis et al. 2007b); hence they select areas of high NDVI but are sensitive to potentially risky areas inside the reserve because of their small size. Over all, these patterns suggests that the small herbivores are facilitated by or compete less with the migratory herds for resources, presumably because they can forage in low biomass patches due to their mouth morphology and digestive physiology specialized for selecting high-quality components of vegetation in-between the low-quality dry vegetation (Wilmshurst et al. 1999).

Unlike those for small herbivores, hotspots of medium herbivores were more differentiated among species. The lack of correlation between hotspots of both topi and hartebeest with NDVI, suggests feeding on short and dry grasses that are not reflected by NDVI, or displacement from open habitats by migrants. However, wildebeest and zebra select areas of high NDVI in the dry season, suggesting that the out-migration of wildebeest and zebra from the Loita plains to the reserve (Serneels and Lambin 2001) enables them to access abundant forage, thus supporting (H2a).The utilization of areas close to rivers by these herbivores and attraction to wetter areas, except for wildebeest, provides evidence for displacement by the migratory herds from their preferred open grassland habitats (Sinclair, 1979). However, since migrants absorb most predation pressure on resident ungulates when they are present in the reserve (Saba 1979) topi, hartebeest and zebra can concentrate in areas often associated with high predation risk (H4a). Wildebeest hotspots were widely distributed but were uncorrelated with distance to rivers or TWI, reflecting the ubiquitous distribution of wildebeest across the reserve.

In the ranches, the concentration of small herbivores, in areas of both high NDVI, and soil moisture content that typically neighbour streams, rivers and water points is surprising. Such areas often support high-quality forage in the dry season due to retention of green leaves by grasses for longer periods because of higher soil moisture (shallow ground water tables) and protection of grass leaves from direct sunlight by riverine woodlands fringing streams and rivers (Treydte et al. 2008, Anderson et al. 2010). As a result, Masai herders graze their livestock in riverine woodlands in the pastoral ranches of the Mara (Reid et al. 2008; Butt et al. 2009). These areas may thus contain short grasses and have enhanced visibility through livestock grazing and trampling. Furthermore, large predators are far fewer in the ranches than in the reserve (Ogutu et al. 2005). As a result of the better visibility and lower predation risk near riverine woodlands in the ranches than in the reserve, small herbivores, requiring high-quality forage because of their small body size used areas of high soil moisture content. Hence small grazers forage in areas where intense livestock grazing in the dry season keeps grasses short and visibility high in the wet season. Their specialized feeding strategies enable small herbivores to select high-quality components of short grass (Wilmshurst, Fryxell & Colucci, 1999), thereby reducing competition with livestock, contrary to H2b and H4b.

However, the medium herbivores (topi, hartebeest and zebra) concentrated far from rivers and in drier areas in the ranches, indicating avoidance of livestock, or heavy grazing near rivers in the ranches, consistent with H4b. The absence of any relationship between hotspots of hartebeest and topi and NDVI also likely indicates their displacement from preferred greener areas in the ranches. Similarly, competition with livestock in productive areas (Odadi et al. 2011) probably force both wildebeest and zebra to occupy less productive areas, farther from rivers in the ranches, as predicted by H2b. The weak correlation between wildebeest hotspots and distance to rivers or wetter areas in the dry season similarly indicates displacement by livestock from suitable areas (H2b).

Among the large herbivores, buffalo concentrate in areas of high vegetation biomass in the reserve, as expected by their bulk feeding style, but not in the ranches where they compete with livestock (Georgiadis et al. 2007b). Giraffe and elephant, both of which browse on woody plants, showed no relationship with NDVI but concentrated in riparian woodlands in the reserve, especially in the dry season, similar to patterns observed elsewhere in African savannas (Owen-Smith, 1988). The concentration of giraffe close to rivers in the ranches despite the Masai pastoralists also herding their livestock there in the dry season reflects the lack of competition between giraffe and livestock. Even though most giraffe hotspots occurred closest to rivers, they showed no relationship to soil moisture in the dry season. The lack of any relationship between buffalo and elephant and any of the predictors partly reflects their low densities in the ranches. This supports the hypothesis that the presence of livestock and humans should more strongly displace large herbivores from the pastoral ranches (H5).

Influence of livestock density

Livestock apparently facilitated some wildlife species as indicated by the peaking in hotspots of Thomson's gazelle, impala and topi in areas moderately grazed by livestock in the reserve in the wet season. The concentration of hotspots of Thomson's gazelle and impala at intermediate levels of livestock density in the ranches indicates facilitative effects of livestock grazing, which stimulates forage growth, enhances forage quality, keeps grass short, increases visibility and reduces predation risk, especially in the wet season (Augustine et al. 2011). Similar facilitative effects operate on the reserve edges frequented by livestock, creating conditions similar to those found in the ranches. The decline in Thomson's gazelle, impala and wildebeest densities with increasing livestock density in all landscapes in the dry season indicates negative interactions with livestock, as predicted by H5. Besides the direct negative effects captured by livestock such as displacement of large herbivores, livestock also had indirect negative influences on the location of wildlife hotspots through their intense grazing and trampling on vegetation, leading to competitive exclusion of species requiring tall grasses such as buffalo, topi hartebeest and elephant. The observation that livestock can both facilitate and compete with wildlife depending on season has also recently been reported by Odadi et al.(2011).

Influence of human population density

The concentration of all wild herbivores declined sharply and consistently in areas with high human population density, irrespective of land use type, body size or feeding style of herbivores, consistent with H5. This is particularly noteworthy because rapid human population growth in the Mara and the associated expansion of settlements (Lamprey and Reid 2004), sedentarization of Masai pastoralists from a formerly nomadic pastoral lifestyle, intensification of land use and diversification of livelihood options in recent decades (Homewood et al. 2001, Ogutu et al. 2011) are progressively impairing the ability of this ecosystem to support its full complement of wildlife populations. This pattern is widespread and similar developments have been documented for other East African ecosystems such as Kenya's Amboseli (Western et al. 2009) and Tanzania's Tarangire-Simanjiro (Msoffe et al. 2010).

In response to the changes occurring in the Kenya pastoral ranches, wildlife conservancies have recently been formed, for example in the Mara ranches, as part of new initiatives aimed at enhancing wildlife conservation and improving livelihoods of pastoralists through partnerships in which private investors in tourism pay land rents to landowners for voluntarily vacating their land for wildlife conservation (Norton-Griffiths et al. 2008). Our analytical approach may be used to assess the extent to which these conservancies are beneficial for wildlife by comparing changes in wildlife densities in grid cells located within the conservancies before and after their formation against contemporaneous changes in similar grid cells located deep within neighbouring protected reserves as benchmarks. This approach can also be more broadly applied to study spatio-temporal changes in herbivore hotspots in other systems. Finally, these results reveal how competition with and facilitation by livestock, predation risk, forage quantity and quality and water interact with life history traits, seasons and land use in shaping dynamics of herbivore hotspots in savannas.

Acknowledgements

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SUPPLEMENTARY INFORMATION

Table S.1 Selection of covariates for quantile regression models for predicting hotspots of herbivore species in each season and land use type in the Mara region of Kenya based on a stepwise elimination procedure in which only covariates that reduce the corrected Akaike Information Criterion (AICc) are retained in models. Selected best models are highlighted in bold face. Dummy coding is used to accommodate possibly different nonlinear functional relationships between herbivore density and different covariates in the same model for each land use type and season.

Season	Species	Models	Effect	AICc
Wet	Thomson's gazelle	Model 1	Landuse + Topographic wetness index	43763
		Model 2	Landuse + Number of people per km^2	43672
		Model 3	Landuse + Distance to nearest river (km)	44119
		Model 4	Landuse + Wetndvi1	44522
		Model 5	Landuse + Livestock density/Mean density	44581
		Model 6	Landuse + Topographic wetness index + Number of people per km^2	43660
		Model 7	Landuse + Topographic wetness index + Number of people per km^2 + Distance to nearest river (km)	42673
		Model 8	Landuse + Topographic wetness index + Number of people per km^2 + Distance to nearest river (km) + Wetndvi1	42044
		Model 9	**Landuse + Topographic wetness index + Number of people per km^2 + Distance to nearest river (km)+ Wetndvi1 + Livestock density/Mean density**	**42000**
	Impala	Model 1	Landuse + Topographic wetness index	41542
		Model 2	Landuse + Number of people per km^2	41572
		Model 3	Landuse + Annualndvi	41647
		Model 4	Landuse + Distance to nearest river (km)	41701
		Model 5	Landuse + Livestock density/Mean density	41796
		Model 6	Landuse + Topographic wetness index + Number of people per km^2	41299
		Model 7	Landuse + Topographic wetness index + Number of people per km^2 + Annualndvi	41111
		Model 8	Landuse + Topographic wetness index + Number of people per km^2 + Annualndvi + Distance to nearest river (km)	40750
		Model 9	**Landuse + Topographic wetness index + Number of people per km^2 + Annualndvi + Distance to nearest river (km) + Livestock density/Mean density**	**40650**
	Grant's gazelle	Model 1	Landuse + Distance to nearest river (km)	30500
		Model 2	Landuse + Wetndvi + Dryndvi	30794
		Model 3	Landuse + Topographic wetness index	30895
		Model 4	Landuse + Number of people per km^2	31097
		Model 5	Landuse + Livestock density/Mean density	31197
		Model 6	Landuse + Distance to nearest river (km)+ Wetndvi + Dryndvi	30573
		Model 7	Landuse + Distance to nearest river (km) + Topographic wetenss index	29132
		Model 8	**Landuse + Distance to nearest river (km) + Topographic wetness index + Number of people per km^2**	**28396**
		Model 9	Landuse + Distance to nearest river (km) + Topographic wetness index + Number of people per km^2 + Livestock density/Mean density	29396

Table S.1 Continued

Season	Species	Models	Effect	AICc
Wet	Topi	Model 1	Landuse + Livestock density/Mean density	35588
		Model 2	Landuse + Distance to nearest river (km)	36045
		Model 3	Landuse + Wetndvi1	36311
		Model 4	Landuse + Topographic wetness index	36685
		Model 5	Landuse + Number of people per km^2	37120
		Model 6	Landuse + Livestock density/Mean density + Distance to nearest river (km)	35486
		Model 7	Landuse + Livestock density/Mean density + Distance to nearest river (km) + Wetndvi1	35271
		Model 8	Landuse + Livestock density/Mean density + Distance to nearest river (km) + Wetndvi1 + Topographic wetness index	35220
		Model 9	**Landuse + Livestock density/Mean density + Distance to nearest river (km) + Wetndvi1 + Topographic wetness index + Number of people per km^2**	**34263**
	Hartebeest	Model 1	Landuse + Topographic wetness index	29145
		Model 2	Landuse + Distance to nearest river (km)	29445
		Model 3	Landuse + Livestock density/Mean density	29503
		Model 4	Landuse + Wetndvi1	29613
		Model 5	Landuse + Number of people per km^2	29906
		Model 6	Landuse + Topographic wetness index + Distance to nearest river (km)	28680
		Model 7	Landuse + Topographic wetness index + Distance to nearest river (km) + Livestock density/Mean density	28680
		Model 8	Landuse + Topographic wetness index + Distance to nearest river (km) + Wetndvi1	28795
		Model 9	**Landuse + Topographic wetness index + Distance to nearest river (km) + Number of people per km^2**	**28395**
	Wildebeest	Model 1	Landuse + Livestock density/Mean density	47087
		Model 2	Landuse + Distance to nearest river (km)	47427
		Model 3	Landuse + Topographic wetness index	47446
		Model 4	Landuse + Wetndvi	47705
		Model 5	Landuse + Number of people per km^2	48091
		Model 6	Landuse + Livestock density/Mean density + Distance to nearest river (km)	46622
		Model 7	Landuse + Livestock density/Mean density + Distance to nearest river (km) + Topographic wetness index	46622
		Model 8	Landuse + Livestock density/Mean density + Distance to nearest river (km) + Wetndvi	46323
		Model 9	**Landuse + Livestock density/Mean density + Distance to nearest river (km) + Wetndvi + Number of people per km^2**	**45890**
	Zebra	Model 1	Landuse + Topographic wetness index	41358
		Model 2	Landuse + Distance to nearest river (km)	41389
		Model 3	Landuse + Number of people per km^2	41479
		Model 4	Landuse + Wetndvi	41625
		Model 5	Landuse + Livestock density/Mean density	41777

Table S.1 Continued

Season	Species	Models	Effect	AICc
Wet	Zebra	Model 6	Landuse + Topographic wetness index + Distance to nearest river (km)	41369
		Model 7	Landuse + Topographic wetness index + Number of people per km^2	41278
		Model 8	**Landuse + Topographic wetness index + Number of people per km^2 + Wetndvi**	**41108**
		Model 9	Landuse + Topographic wetness index + Number of people per km^2 + Wetndvi + Livestock density/Mean density	41108
	Buffalo	Model 1	**Landuse + Annualndvi**	**38104**
		Model 2	Landuse + Distance to nearest river (km)	38154
		Model 3	Landuse + Number of people per km^2	38277
		Model 4	Landuse + Topographic wetness index	38232
		Model 5	Landuse + Livestock density/Mean density	39007
		Model 6	Landuse + Annualndvi + Distance to nearest river (km)	38144
		Model 7	Landuse + Annualndvi + Number of people per km^2	38277
		Model 8	Landuse + Annualndvi + Topographic wetness index	38168
		Model 9	Landuse + Annualndvi + Livestock density/Mean density	39007
	Giraffe	Model 1	Landuse + Number of people per km^2	21841
		Model 2	Landuse + Livestock density/Mean density	22135
		Model 3	Landuse + Topographic wetness index	22192
		Model 4	Landuse + Distance to nearest river (km)	22278
		Model 5	Landuse + Annualndvi1	23441
		Model 6	Landuse + Number of people per km^2 + Livestock density/Mean density	21943
		Model 7	Landuse + Number of people per km^2 + Topographic wetness index	22142
		Model 8	**Landuse + Number of people per km^2 + Distance to nearest river (km)**	**19612**
		Model 9	Landuse + Number of people per km^2 + Distance to nearest river (km) + Annualndvi1	29126
	Elephant	Model 1	Landuse +Distance to nearest river (km)	25147
		Model 2	Landuse + Topographic wetness index	25274
		Model 3	Landuse + Wetndvi	25391
		Model 4	Landuse + Number of people per km^2	25382
		Model 5	Landuse + Livestock density/Mean density	26828
		Model 6	Landuse + Distance to nearest river (km) + Topographic wetness index	24947
		Model 7	Landuse + Distance to nearest river (km) + Topographic wetness index + Wetndvi	24951
		Model 8	**Landuse + Distance to nearest river (km) + Topographic wetness index + Number of people per km^2**	**24674**
		Model 9	Landuse +Distance to nearest river (km) + Topographic wetness index + Wetndvi + Number of people per km^2 + Livestock density/Mean density	24694

Table S.1 Continued

Season	Species	Models	Effect	AICc
Dry	Thomson's gazelle	Model 1	Landuse + Topographic wetness index	24161
		Model 2	Landuse + Number of people per km^2	24168
		Model 3	Landuse + Dryndvi	24282
		Model 4	Landuse + Distance to nearest river (km)	24289
		Model 5	Landuse + Livestock density/Mean density	24307
		Model 6	Landuse + Topographic wetness index + Number of people per km^2	24157
		Model 7	Landuse + Topographic wetness index + Number of people per km^2 + Dryndvi	23801
		Model 8	Landuse + Topographic wetness index + Number of people per km^2 + Dryndvi + Distance to nearest river (km)	23665
		Model 9	**Landuse + Topographic wetness index + Number of people per km^2 + Dryndvi + Distance to nearest river (km) + Livestock density/Mean density**	**23586**
	Impala	Model 1	Lanudse + Topographic wetness index	23825
		Model 2	Landuse + Annualndvi	23933
		Model 3	Landuse + Livestock density/Mean density	24158
		Model 4	Landuse + Number of people per km^2	24426
		Model 5	Landuse + Distance to nearest river (km)	24571
		Model 6	Landuse + Topographic wetness index + Annualndvi	23720
		Model 7	Landuse + Topographic wetness index + Annualndvi + Livestock density/ Mean density	23686
		Model 8	Landuse + Topographic wetness index + Annualndvi + Livestock density/ Mean density + Number of people per km^2	23596
		Model 9	**Landuse + Topographic wetness index + Annualndvi + Livestock density/Mean density + Number of people per km^2 + Distance to nearest river (km)**	**23479**
	Grant's gazelle	Model 1	Landuse + Number of people per km^2	17502
		Model 2	Landuse + Livestock density/Mean density	17650
		Model 3	Landuse + Distance to nearest river (km)	17789
		Model 4	Landuse + Topographic wetness index	18142
		Model 5	Landuse + Dryndvi1	18158
		Model 6	Landuse + Number of people per km^2 + Livestock density/Mean density	17603
		Model 7	Landuse + Number of people per km^2 + Distance to nearest river (km)	17515
		Model 8	Landuse + Number of people per km^2 + Distance to nearest river (km) + Topographic wetness index	17484
		Model 9	**Landuse+Number of people per km^2 + Distance to nearest river (km) + Topographic wetness index + Dryndvi1**	**16938**
	Topi	Model 1	Landuse + Distance to nearest river (km)	20294
		Model 2	Landuse + Dryndvi1	20320
		Model 3	Landuse + Livestock density/Mean density	20620
		Model 4	Lanudse + Topographic wetness index	20809
		Model 5	Landuse + Number of people per km^2	20831
		Model 6	Landuse + Distance to nearest river (km) + Dryndvi1	20720

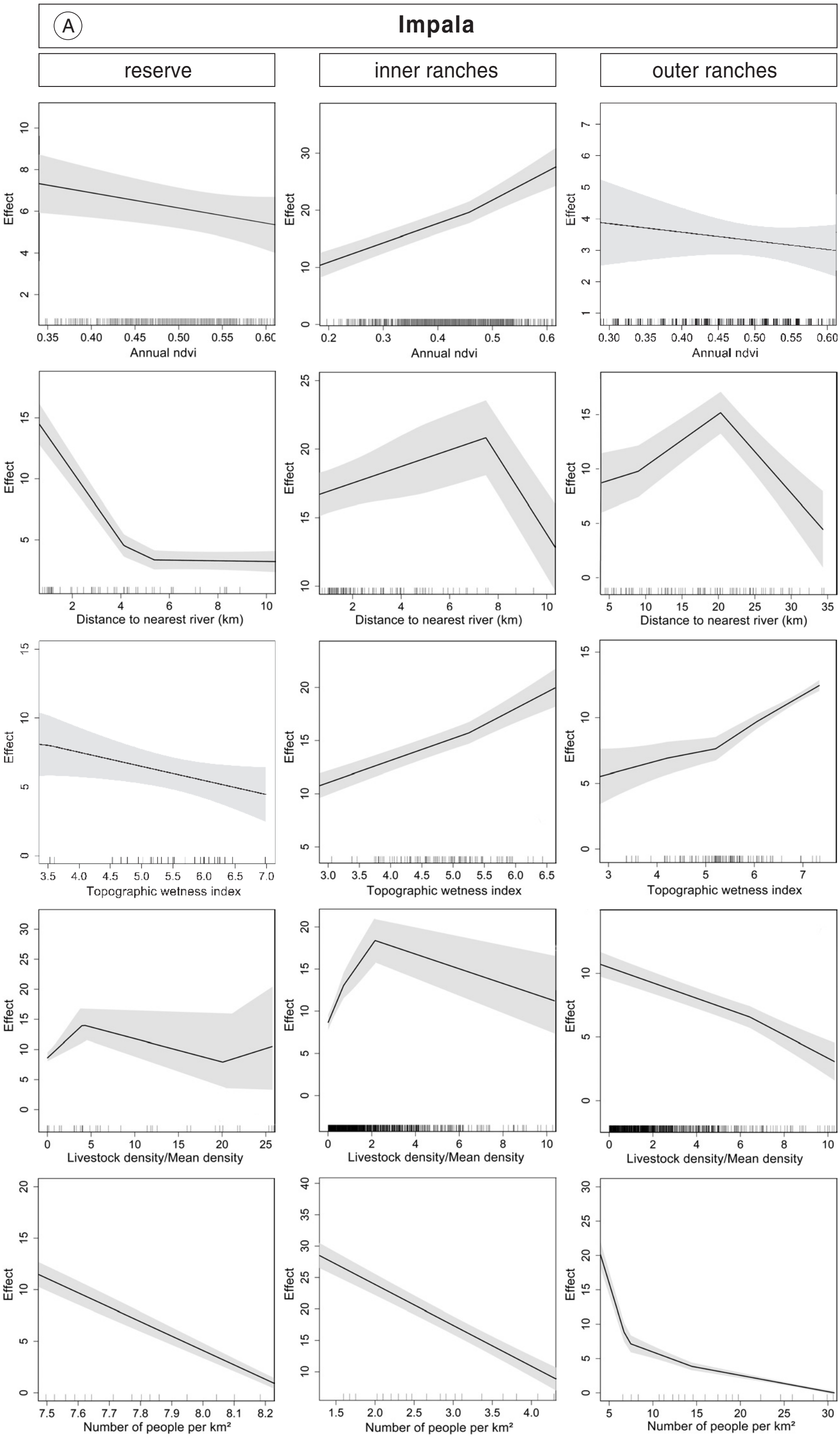
Table S.1 Continued

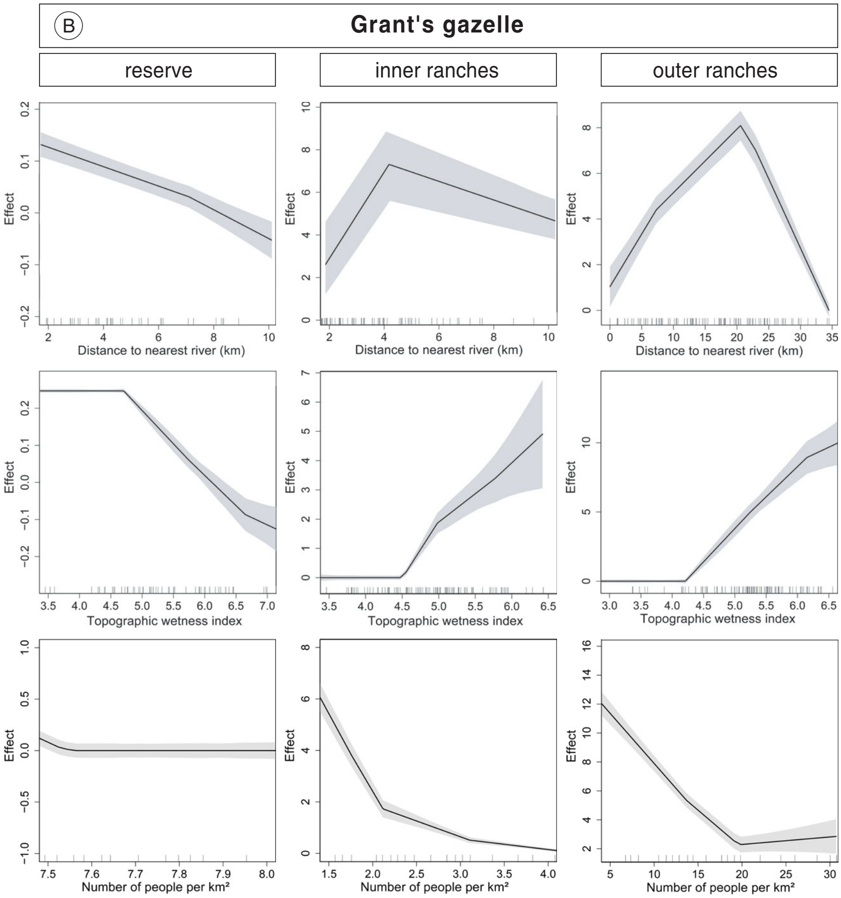
Season	Species	Models	Effect	AICc
Dry	Topi	Model 7	Landuse + Distance to nearest river (km) + Livestock density/Mean density	20602
		Model 8	Landuse + Distance to nearest river (km) + Topographic wetness index	19527
		Model 9	**Landuse + Distance to nearest river (km) + Topographic wetness index + Number of people per km^2**	**19434**
	Hartebeest	Model 1	Landuse + Distance to nearest river (km)	15641
		Model 2	Landuse + Topographic wetness index	15855
		Model 3	Landuse + Wetndvi1 + Dryndvi1	15884
		Model 4	Landuse + Livestock density/Mean density	16179
		Model 5	Landuse + Number of people per km^2	17260
		Model 6	Landuse + Distance to nearest river (km) + Topographic wetness index	15283
		Model 7	Landuse + Distance to nearest river (km) + Topographic wetness index + Wetndvi1+ Dryndvi1	15803
		Model 8	Landuse + Distance to nearest river (km) + Topographic wetness index + Livestock density/Mean density	15924
		Model 9	**Landuse + Distance to nearest river (km) + Topographic wetness index + Number of people per km^2**	**14524**
	Wildebeest	Model 1	Landuse + Dryndvi1	37808
		Model 2	Landuse + Topographic wetness index	38349
		Model 3	Landuse + Distance to nearest river (km)	38396
		Model 4	Landuse + Number of people per km^2	38731
		Model 5	Landuse + Livestock density/Mean density	38995
		Model 6	Landuse + Dryndvi1 + Topographic wetness index	38123
		Model 7	Landuse + Dryndvi1 + Distance to nearest river (km)	38223
		Model 8	Landuse + Dryndvi1 + Number of people per km^2	38594
		Model 9	**Landuse + Dryndvi1 + Livestock density/Mean density**	**37608**
	Zebra	Model 1	Landuse + Dryndvi1	26262
		Model 2	Landuse + Topographic wetness index	26350
		Model 3	Landuse + Distance to nearest river (km)	26478
		Model 4	Landuse + Number of people per km^2	27036
		Model 5	Landuse + Livestock density/Mean density	27175
		Model 6	Landuse + Dryndvi1 + Topographic wetness index	26232
		Model 7	**Landuse + Dryndvi1 + Topographic wetness index + Distance to nearest river (km)**	**26196**
		Model 8	Landuse + Dryndvi1 + Topographic wetness index + Distance to nearest river (km) + Number of people per km^2	26811
		Model 9	Landuse + Dryndvi1 + Topographic wetness index + Distance to nearest river (km) + Livestock density/Mean density	26210

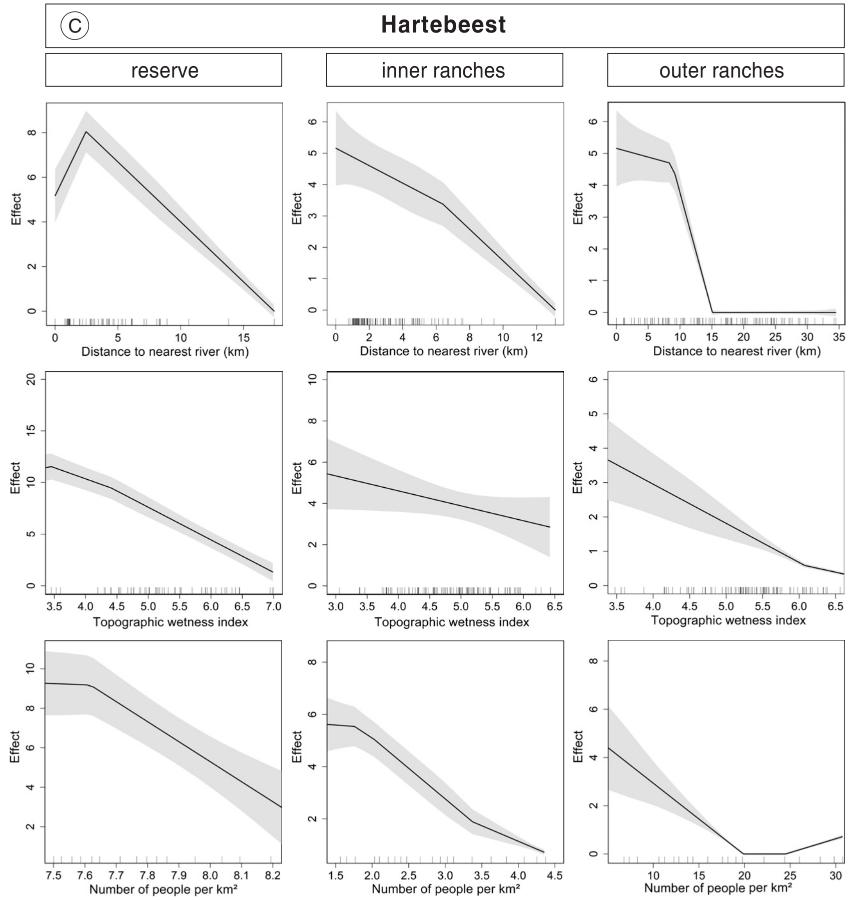
Table S.1 Continued

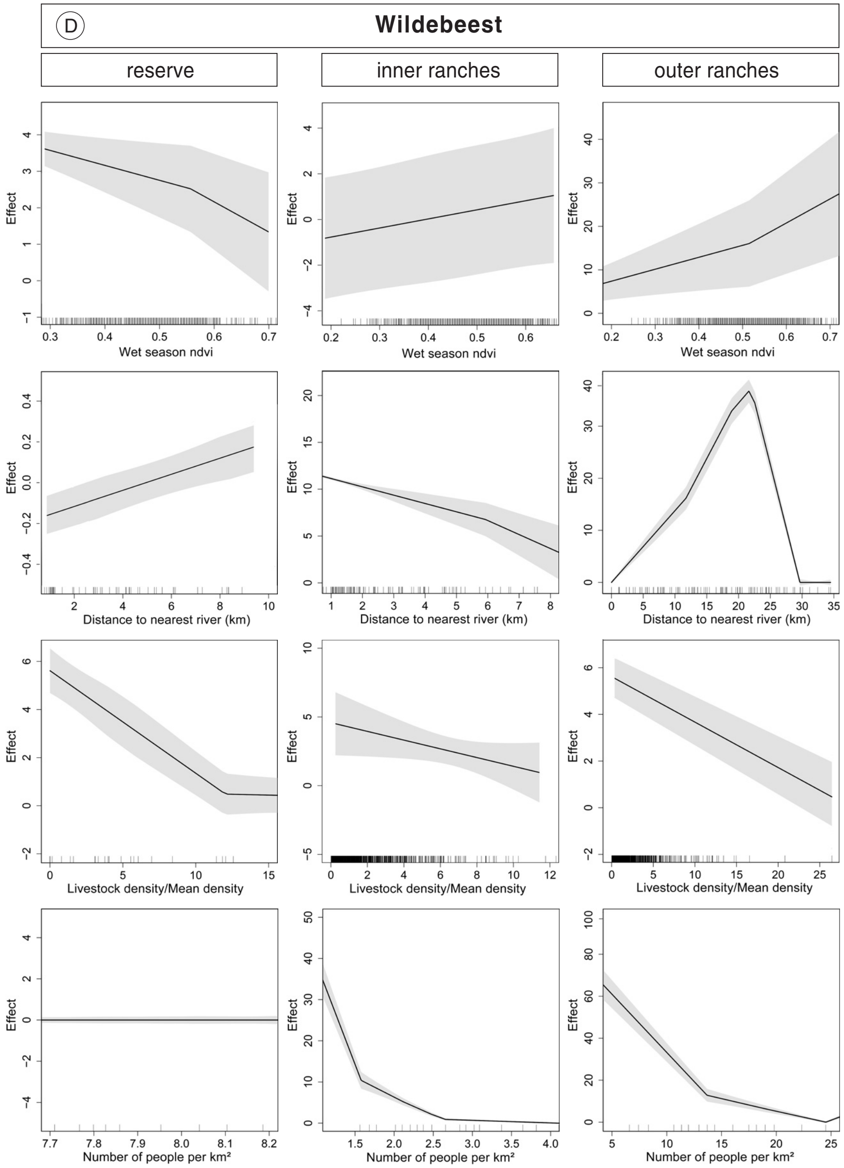
Season	Species	Models	Effect	AICc
Dry	Buffalo	Model 1	**Landuse + Dryndvi**	**22092**
		Model 2	Landuse + Distance to nearest river (km)	22210
		Model 3	Landuse + Topographic wetness index	22255
		Model 4	Landuse +Number of people per km^2	22332
		Model 5	Landuse + Livestock density/Mean density	22865
		Model 6	Landuse + Dryndvi + Distance to nearest river (km)	22210
		Model 7	Landuse + Dryndvi + Topographic wetness index	22255
		Model 8	Landuse + Dryndvi + Number of people per km^2	22332
		Model 9	Landuse + Dryndvi + Livestock density/Mean density	22432
	Giraffe	Model 1	**Landuse + Distance to nearest river (km)**	**11384**
		Model 2	Landuse + Wetndvi1 + Dryndvi1	13072
		Model 3	Landuse + Livestock density/Mean density	13313
		Model 4	Landuse + Topographic wetness index	14271
		Model 5	Landuse+ Number of people per km^2	14793
		Model 6	Landuse + Distance to nearest river (km) + Wetndvi1 + Dryndvi1	12420
		Model 7	Landuse + Distance to nearest river (km) + Wetndvi1 + Dryndvi1 + Livestock density/Mean density	12152
		Model 8	Landuse + Distance to nearest river (km) + Wetndvi1 + Dryndvi1 + Livestock density/Mean density + Topographic wetness index	12101
		Model 9	Landuse + Distance to nearest river (km) + Wetndvi1 + Dryndvi1 + Livestock density/Mean density + Topographic wetness index + Number of people per km^2	11913
	Elephant	Model 1	Landuse + Number of people per km^2	11385
		Model 2	Landuse + Distance to nearest river (km)	11397
		Model 3	Landuse + Livestock density/Mean density	11500
		Model 4	Landuse + Topographic wetness index	11690
		Model 5	Landuse + Annualndvi	11702
		Model 6	Landuse + Number of people per km^2 + Distance to nearest river (km)	11178
		Model 7	Landuse + Number of people per km^2 + Distance to nearest river (km) + Livestock density/Mean density	11836
		Model 8	**Landuse + Number of people per km^2 + Distance to nearest river (km) + Topographic wetness index**	**11136**
		Model 9	Landuse + Number of people per km^2 + Distance to nearest river (km) + Topographic wetness index + Annualndvi	11786

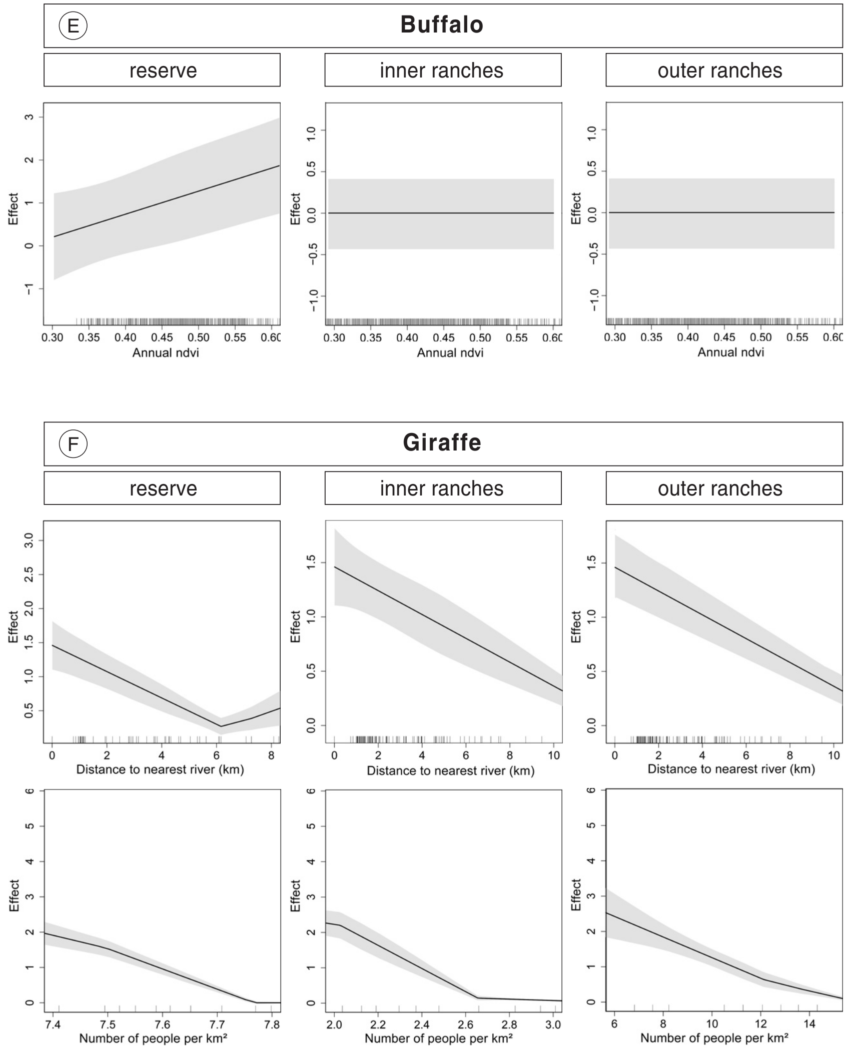
Figure S.1 (Next pages) The Factors influencing hotspots of A) Impala, B) Grant's gazelle, C) hartebeest, D) Wildebeest, E) buffalo, F) giraffe and G) elephant in the Mara region of Kenya in the wet season during 1977-2010.


A
Impala
reserve
inner ranches
outer ranches
Effect
Annual ndvi
0.35 0.40 0.45 0.50 0.55 0.60
0.2 0.3 0.4 0.5 0.6
0.30 0.35 0.40 0.45 0.50 0.55 0.60
Distance to nearest river (km)
2 4 6 8 10
5 10 15 20 25 30 35
Topographic wetness index
3.5 4.0 4.5 5.0 5.5 6.0 6.5 7.0
3.0 3.5 4.0 4.5 5.0 5.5 6.0 6.5
3 4 5 6 7
Livestock density/Mean density
0 5 10 15 20 25
0 2 4 6 8 10
Number of people per km²
7.5 7.6 7.7 7.8 7.9 8.0 8.1 8.2
1.5 2.0 2.5 3.0 3.5 4.0
5 10 15 20 25 30


B
Grant's gazelle
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
Topographic wetness index
Number of people per km²


C
Hartebeest
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
Topographic wetness index
Number of people per km²


D
Wildebeest
reserve
inner ranches
outer ranches
Effect
Wet season ndvi
0.3 0.4 0.5 0.6 0.7
0.2 0.3 0.4 0.5 0.6
0.2 0.3 0.4 0.5 0.6 0.7
−1 0 1 2 3 4
−4 −2 0 2 4
0 10 20 30 40
Distance to nearest river (km)
2 4 6 8 10
1 2 3 4 5 6 7 8
0 5 10 15 20 25 30 35
−0.4 −0.2 0.0 0.2 0.4
0 5 10 15 20
0 10 20 30 40
Livestock density/Mean density
0 5 10 15
0 2 4 6 8 10 12
0 5 10 15 20 25
−2 0 2 4 6
−5 0 5 10
−2 0 2 4 6
Number of people per km²
7.7 7.8 7.9 8.0 8.1 8.2
1.5 2.0 2.5 3.0 3.5 4.0
5 10 15 20 25
−4 −2 0 2 4
0 10 20 30 40 50
0 20 40 60 80 100


E
Buffalo
reserve
inner ranches
outer ranches
Effect
Annual ndvi
0.30 0.35 0.40 0.45 0.50 0.55 0.60
F
Giraffe
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
Number of people per km²

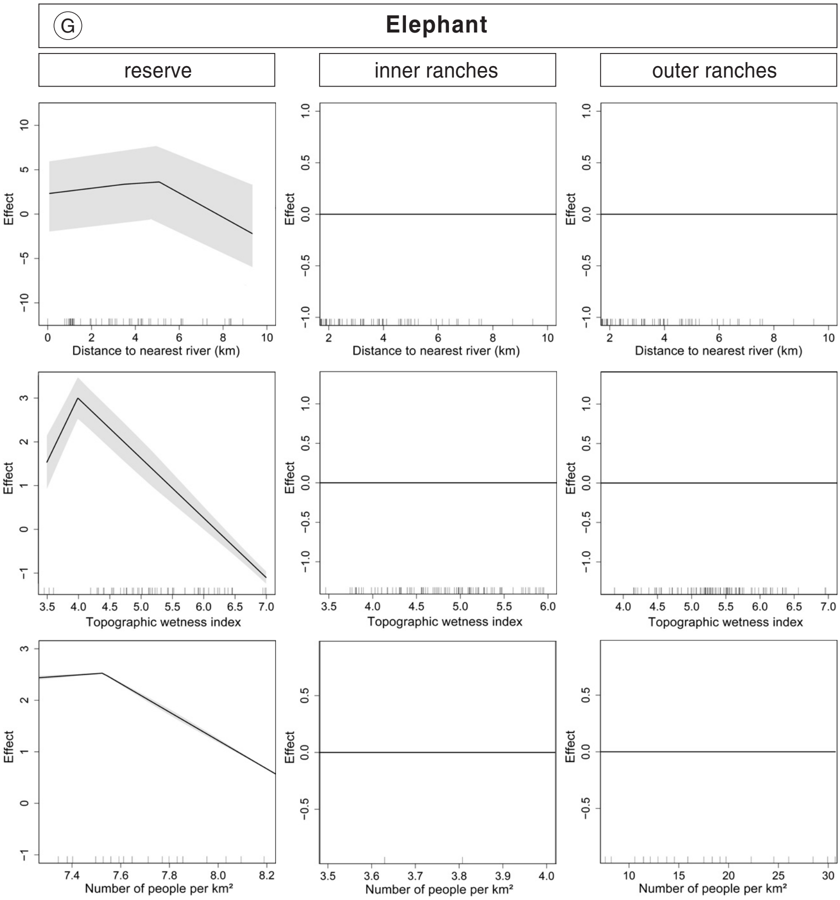
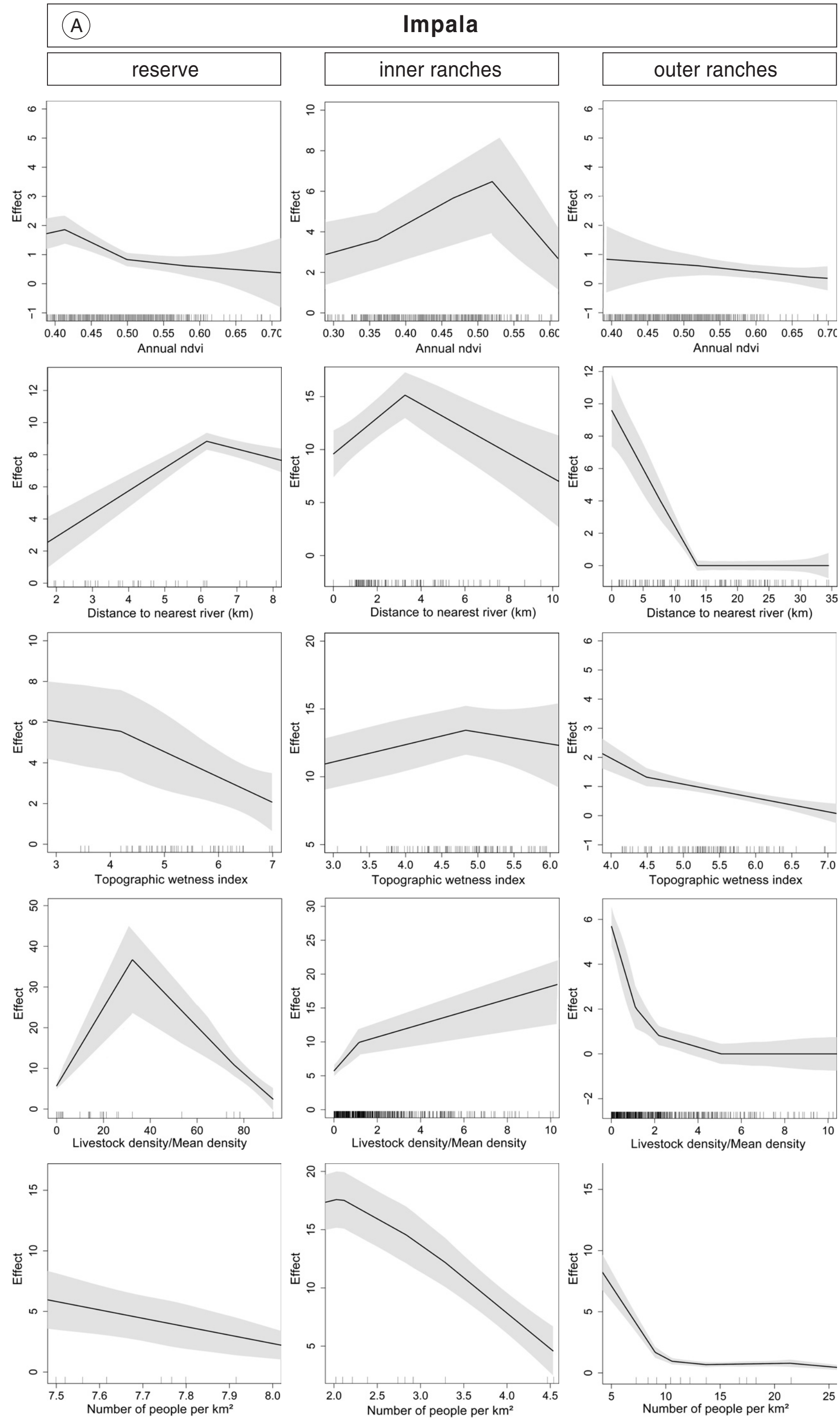
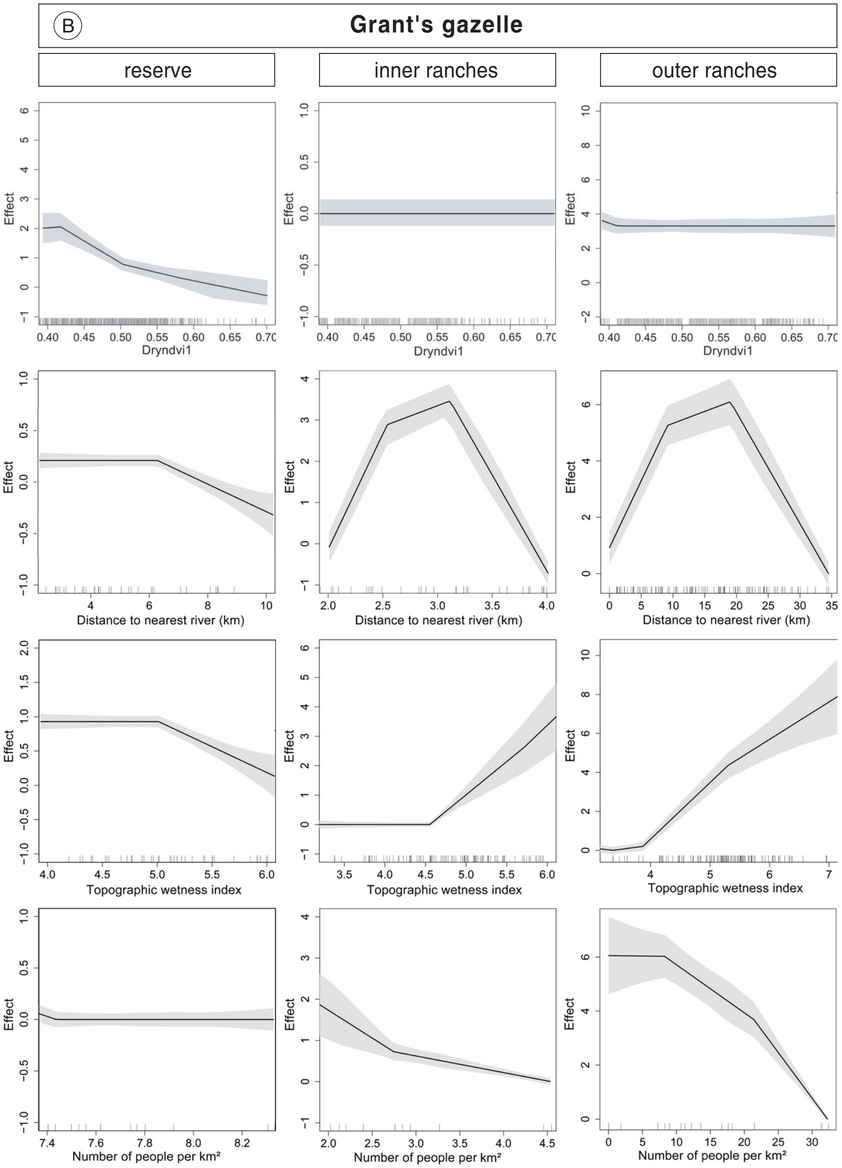
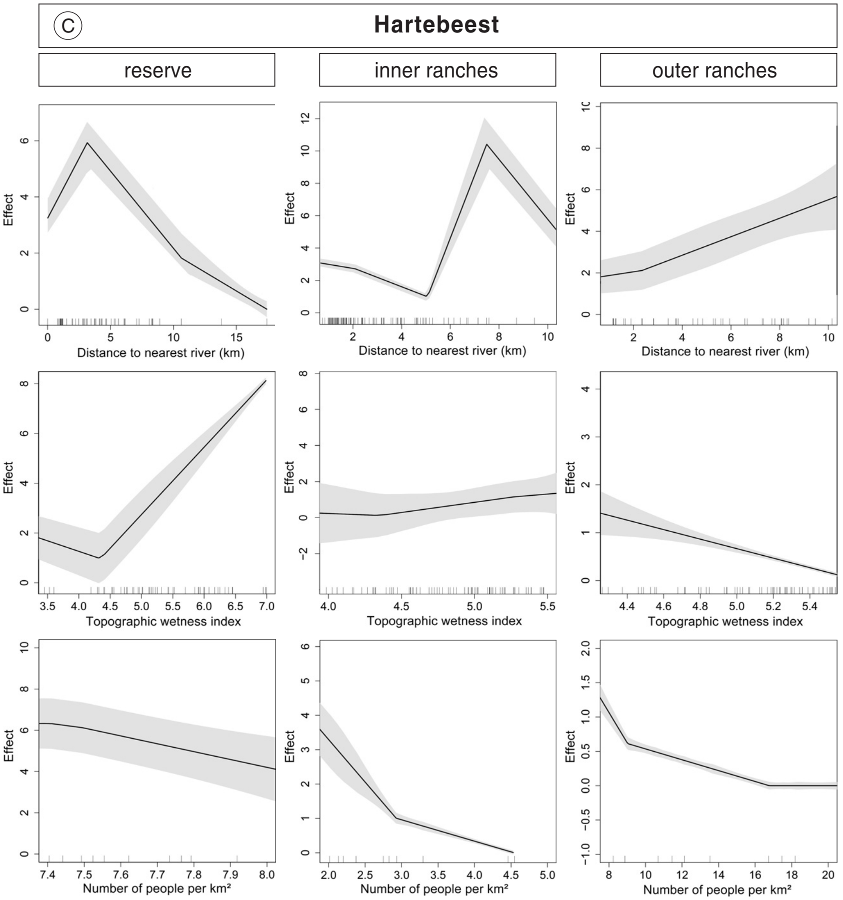
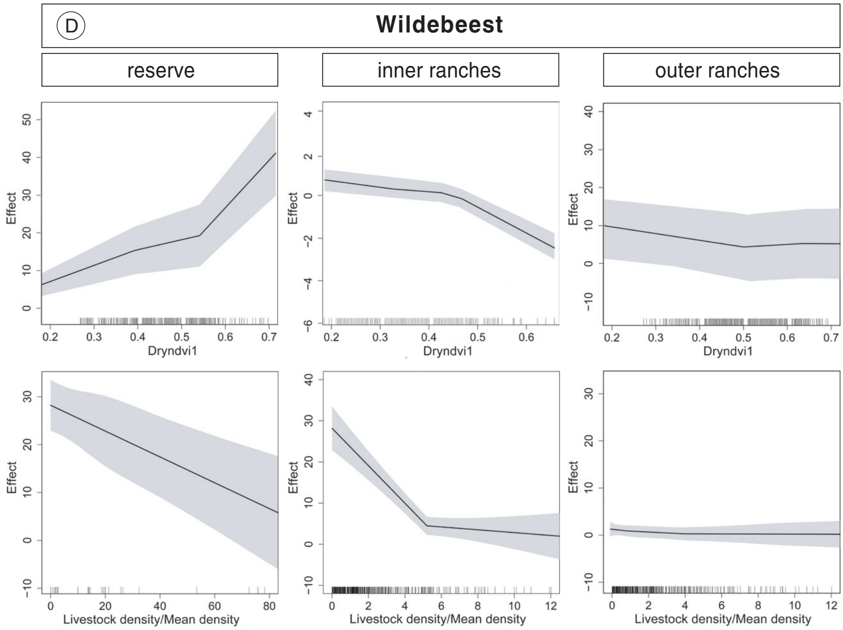


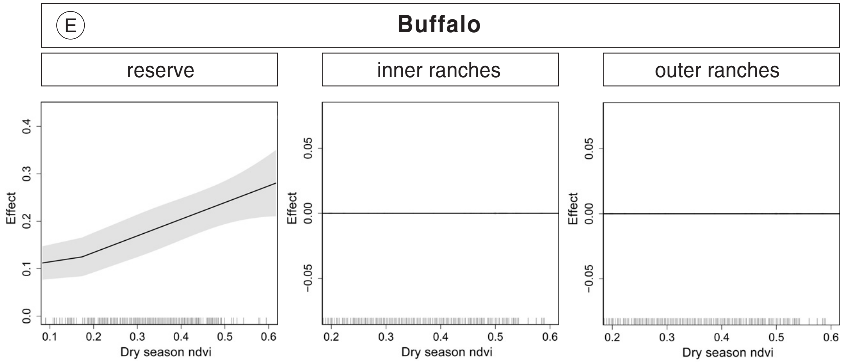
Figure S.2 (Next pages) The factors influencing hotspots of A) impala, B) Grant's gazelle, C) hartebeest, D) wildebeest, E) buffalo, F) giraffe and G) elephant in the Mara region of Kenya in the dry season during 1977-2010.

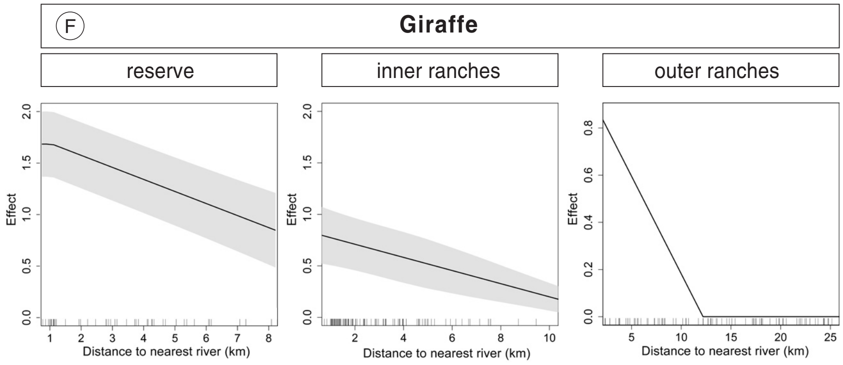

A
Impala
reserve
inner ranches
outer ranches
Effect
Annual ndvi
0.40 0.45 0.50 0.55 0.60 0.65 0.70
0.30 0.35 0.40 0.45 0.50 0.55 0.60
Distance to nearest river (km)
2 3 4 5 6 7 8
0 2 4 6 8 10
0 5 10 15 20 25 30 35
Topographic wetness index
3 4 5 6 7
3.0 3.5 4.0 4.5 5.0 5.5 6.0
4.0 4.5 5.0 5.5 6.0 6.5 7.0
Livestock density/Mean density
0 20 40 60 80
0 2 4 6 8 10
Number of people per km²
7.5 7.6 7.7 7.8 7.9 8.0
2.0 2.5 3.0 3.5 4.0 4.5
5 10 15 20 25

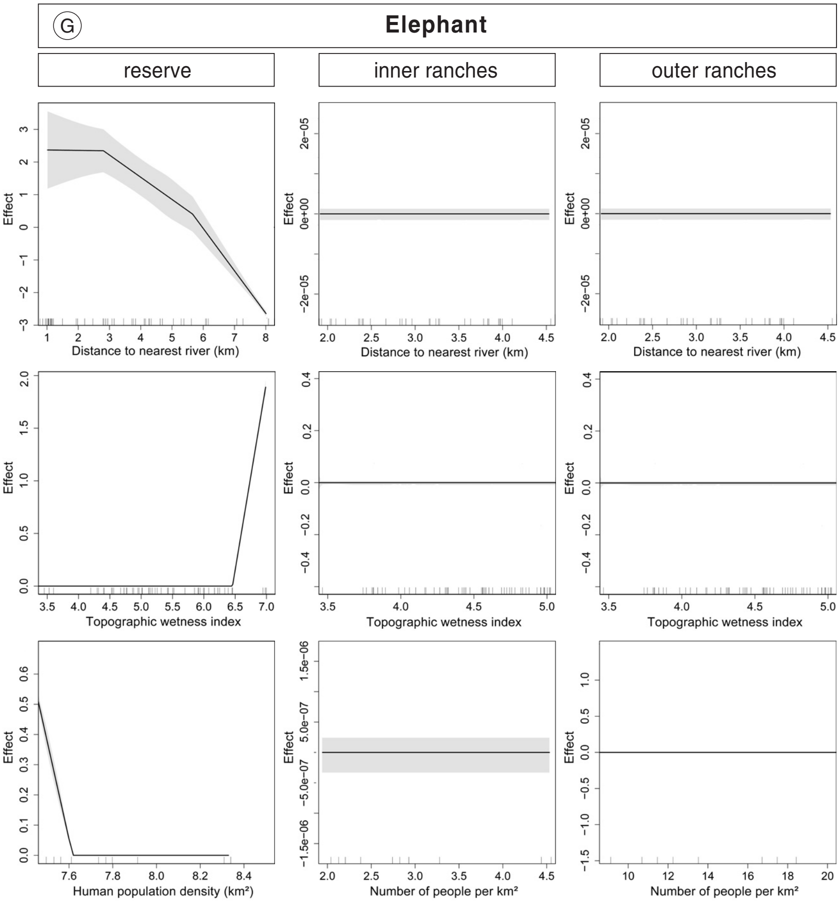

B
Grant's gazelle
reserve
inner ranches
outer ranches
Effect
Dryndvi1
0.40 0.45 0.50 0.55 0.60 0.65 0.70
−1 0 1 2 3 4 5 6
−1.0 −0.5 0.0 0.5 1.0
−2 0 2 4 6 8 10
Distance to nearest river (km)
4 6 8 10
2.0 2.5 3.0 3.5 4.0
0 5 10 15 20 25 30 35
−1.0 −0.5 0.0 0.5 1.0
−1 0 1 2 3 4
0 2 4 6
Topographic wetness index
4.0 4.5 5.0 5.5 6.0
3.5 4.0 4.5 5.0 5.5 6.0
4 5 6 7
−1.0 −0.5 0.0 0.5 1.0 1.5 2.0
−1 0 1 2 3 4 5 6
0 2 4 6 8 10
Number of people per km²
7.4 7.6 7.8 8.0 8.2
2.0 2.5 3.0 3.5 4.0 4.5
0 5 10 15 20 25 30
−1.0 −0.5 0.0 0.5 1.0
−1 0 1 2 3 4
0 2 4 6


C
Hartebeest
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
0 5 10 15
2 4 6 8 10
Topographic wetness index
3.5 4.0 4.5 5.0 5.5 6.0 6.5 7.0
4.0 4.5 5.0 5.5
4.4 4.6 4.8 5.0 5.2 5.4
Number of people per km²
7.4 7.5 7.6 7.7 7.8 7.9 8.0
2.0 2.5 3.0 3.5 4.0 4.5 5.0
8 10 12 14 16 18 20


D
Wildebeest
reserve
inner ranches
outer ranches
Effect
Dryndvi1
Livestock density/Mean density
0.2
0.3
0.4
0.5
0.6
0.7
0
10
20
30
40
50
−2
−4
−6
2
4
−10
20
40
60
80
2
4
6
8
10
12


E
Buffalo
reserve
inner ranches
outer ranches
Effect
Dry season ndvi
0.1
0.2
0.3
0.4
0.5
0.6
0.0
0.05
0.00
−0.05


F
Giraffe
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
0.0
0.5
1.0
1.5
2.0
0.2
0.4
0.6
0.8
1
2
3
4
5
6
7
8
10
15
20
25


G
Elephant
reserve
inner ranches
outer ranches
Effect
Distance to nearest river (km)
1 2 3 4 5 6 7 8
−3 −2 −1 0 1 2 3
2.0 2.5 3.0 3.5 4.0 4.5
−2e−05 0e+00 2e−05
Topographic wetness index
3.5 4.0 4.5 5.0 5.5 6.0 6.5 7.0
0.0 0.5 1.0 1.5 2.0
3.5 4.0 4.5 5.0
−0.4 −0.2 0.0 0.2 0.4
Human population density (km²)
7.6 7.8 8.0 8.2 8.4
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Number of people per km²
2.0 2.5 3.0 3.5 4.0 4.5
−1.5e−06 −5.0e−07 5.0e−07 1.5e−06
10 12 14 16 18 20
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Chapter 7

Synthesis: the influence on wildlife populations of changing human-dominated landscapes and protected areas of Africa

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INTRODUCTION

With limited resources for conservation, it is necessary to identify the conditions required for maintaining diverse assemblages of plants and wildlife. The disruption of the wide-ranging movements of wildlife resulting in rapid population declines by cultivation of large tracts of grazing land adjacent to core protected areas, rapid human population growth, expanding human settlements, fencing and other land use transformations makes this particularly urgent (Ottichilo et al. 2001, Owen-Smith and Mills 2006, Ogutu et al. 2009, Western et al. 2009). This research suggests three important characteristics that influence the vulnerability of a protected area to land use intensification. First, the size, heterogeneity and productivity of a protected area. Second, the proximity of a protected area to human population, specifically in areas of intense land use in critical portions of ecosystems. Third, the lack of incentives or resources to conserve wildlife outside of protected areas. Understanding how these factors affect wildlife species richness, abundance, demography and persistence is essential to identifying protected areas most at risk due to land use changes and developing appropriate conservation and management for them.

The size of an area is widely recognized as a primary determinant of species richness (Preston 1960, Simberloff 1976, Rosenzweig 1995). The main mechanism thought to drive species richness in an area is the balance between colonization and extinction processes, such that the greater the size of an area, the greater is the likelihood that individual species will persist in them and support large populations which tend to have smaller risks of extinction (Berger 1990, Pimm 1991). Furthermore larger areas are more likely to support more diverse habitat types or contain more energy in terms of vegetation productivity (Currie and Paquin 1987, Kerr and Packer 1997, Ricklefs and Lovette 1999). This makes it difficult to distinguish between the direct and indirect effects of area on species richness (Hart and Horwitz 1991). Thus, the key to assessing the vulnerability of a protected area is to evaluate not just its absolute size, but its size relative to its heterogeneity and productivity (Hansen and DeFries 2007).

In addition to considering how variation in heterogeneity and productivity within a protected area influences its vulnerability to conservation threats (**Chapter 2**), the intensity and type of land use and conservation incentives in surrounding landscapes must be considered when developing conservation strategies (**Chapters 4-6**). It is likely that protected areas surrounded by intense land use activities, such as intensive livestock grazing, cultivation, expanding settlements and development, are more vulnerable than those situated in topographically complex areas with little human influence. Intensively managed landscapes become increasingly homogenized and fragmented, resulting in a rapid decrease in their effective sizes, making wild populations increasingly vulnerable to extinction, whereas areas consisting of high habitat heterogeneity are more buffered from human influence and climate change. Protected areas located where communities rely on bushmeat, forest products or poaching are also likely to be more vulnerable (Hansen and DeFries 2007). Animals that require specific ‘key resources’, such as specific dry-or wet-season habitats, often lie outside the boundaries of protected areas (Illius and O'Connor 2000, DeFries et al. 2007, Hansen and DeFries 2007, Coughenour 2008), making animal communities within protected areas more vulnerable to land use change. Where communities surrounding protected areas receive no benefits from the protected areas they will tend to value these areas less are more likely to degrade them. However, communities that benefit from wildlife conservation through enterprises such as wildlife conservancies or ecotourism are more likely to protect wildlife and their habitats. Therefore, there is a pressing need to evaluate the intensity of land use changes outside protected areas as a basis for designing effective strategies to mitigate the effects of anthropogenic activities on wildlife populations.

BRIEF RE-CAP OF THIS THESIS

In this thesis I evaluated the relative importance of area per se, habitat heterogeneity and productivity on mammalian richness within 300 protected areas across Africa (Chapter 2). This chapter attempts to elucidate how the species-area relationship is generated by exploring its underlying processes. Using data from a well-studied savanna ecosystem in East Africa, I investigated the processes structuring community assembly of woodland vegetation (**Chapter 3**) and the influence of cultivation, pastoralism and protection on the abundance of carnivores (**Chapter 4**) and the density, demography and persistence of herbivores (**Chapter 5 & 6**) in the Maasai Mara National Reserve of Kenya and its surrounding rangelands. It is important to recognize that protected areas are often parts of larger ecosystems. Thus, in addition to understanding the conditions necessary to maintain species assemblages inside protected areas, we need to understand both the proximal ecological factors, such as variation in resources, competition, facilitation and predation, and the effects of land use change on plant and animal communities. It is only after this that we can begin to develop appropriate conservation strategies.

In this chapter, I first discuss a) species-area relationships at the continental scale (**Chapter 2**). This sets the framework to discuss b) the ecological importance of critical habitats outside protected areas in shaping wildlife density, demography and distribution at ecosystem scales (**Chapter 4, 5 & 6**). Next, I discuss c) the influence of land use and climate change, on wildlife populations when their movements get increasingly obstructed, and finally I discuss d) the implications of this study for wildlife conservation and management and highlight some conservation and management steps that are being undertaken to counter these effects, including expanding parks, establishing conservancies and promoting land leases.

In C**hapter 2**, I first show the distribution of primate, ungulate (Artiodactyla), and carnivore (Carnivora) richness within protected areas across Africa, with primates concentrated in the more productive areas of Central Africa whereas ungulates and carnivores concentrated in the more heterogeneous areas around the Great Rift Valley in Eastern Africa. More importantly, I show that, although area does correlate significantly with species richness for all the three taxa, namely primates, ungulates and carnivores (correlation coefficients of 0.18, 0.26, 0.14, respectively, with $P < 0.05$ for each coefficient), the size of an area becomes insignificant after factoring out the effect of landscape heterogeneity and productivity. This demonstrates a fundamental link between habitat heterogeneity and productivity rather than area *per se* in structuring mixed assemblages of wildlife in African protected areas, consistent with those of (Báldi) 2008 who similarly showed a general lack of fit for the species-area relationship. In the next section I critically evaluate several possible explanations of why I found no significant area effect after accounting for heterogeneity/productivity.

Why was there no significant area effect after accounting for heterogeneity/productivity?

The insignificant effect of area on the functioning of protected areas at the continental scale in Africa after accounting for heterogeneity/productivity is surprising and could be due to several reasons. According to the island biogeographic theory (MacArthur and Wilson 1967) large reserves or parks are better able to maintain large populations and high diversity of wildlife species. The findings in Chapter 2 imply that the effects of habitat heterogeneity and productivity (Wright 1983) override that of area if habitat heterogeneity/productivity are uncorrelated with reserve area. However, the fact that heterogeneity/productivity explain only part of the variation in species richness patterns across Africa, suggests the involvement of other factors not considered in our study. Such factors would be necessary to explain why some large parks, including the Kruger National Park (19,485 km^2, wildlife biomass = 3185 kg/km^2), have experienced significant losses of wildlife (Simberloff 1976) whereas relatively much smaller but heterogeneous parks, such as the Hluhluwe-Imfolozi Park (HiP) (900 km^2, wildlife biomass= 8949 kg/km^2) also in South Africa like Kruger, have maintained diverse and abundant wildlife species (Fynn and Bonyongo 2010). Hence differences in species loses between parks, such as that between Kruger and Hluhluwe-Imfolozi, likely reflect differences in management regimes and not merely reserve size alone (Chapter 2). Under similar management regimes as assumed by the theory of island biogeography, we would expect to find a significant species-area relationship. The absence of such a relationship in our data therefore partly reflects differences in management regimes between reserves.

Besides differences in management regimes, the scale at which organisms perceive resources in their environment may also partly account for the weak species-area relationship we found. Large-bodied organisms perceive their habitats at larger spatial scales and are primarily influenced by such macro-scale factors as geology, topography and regional climate ((Anderson et al. 2008{Holling, 1992 #944{Olff, 1998 #898)}}). In contrast, small-bodied organisms perceive their habitats at small spatial scales and are more influenced by micro-scale grass/tree mosaics, soil catenas and microclimate (Anderson et al. 2008). Hence, considering all species regardless of functional differences, would mask the interaction expected between heterogeneity/productivity and area due to differences in life-history traits such as body size (**Chapter 2**).

Furthermore, by using a 'snapshot' of data, this analysis ignored population dynamics which may influence the rates of extinction and migration between protected areas and result in a weak species-area relationship. Notably, many of the protected areas are intensively managed and translocations from large "source" to smaller "sink" parks could result in the rescue of populations on the verge of local extinction further obscuring the relationship between area and richness.

Nevertheless, the insignificance of the species-area relationship after accounting for heterogeneity and productivity does not necessarily imply that area per se is not important. Large parks are essential not only for hosting (large) source populations for small areas but also for ensuring long-term viability of wide-ranging species. The findings in **Chapter 2** suggest that protected areas of all sizes should contain sufficiently high heterogeneity and/or productivity. While there is little doubt that richness and diversity in an area is a consequence of immigration and extinction processes, heterogeneity and productivity over-ride the influence of area on species richness at the continental-scale. However, proximal ecological factors such as trophic interactions and processes such as facilitation (Arsenault and Owen-Smith 2002), competition (Sinclair 1985), predation pressure (Sinclair et al. 2003) or resource perception (Ritchie and Olff 1999), as well as human interference, (Sinclair et al. 2008a) also influence the density, demography and persistence of carnivores and ungulates at ecosystem scales.

Why are dispersal areas necessary to complement the functioning of protected areas?

In this section, I discuss b) the importance of areas surrounding protected areas and the proximal ecological factors that influence distribution of mammalian communities. It is clear from the evidence provided in **Chapters 4 and 5**, that protected areas often exclude a portion of the area that is needed to maintain populations of wildlife. Protected area boundaries were not established with animal movement / dispersal in mind. Accordingly, it is vital to retroactively protect these areas to prevent populations declines.

Protected areas are not only often located in relatively more topographically complex areas, but also in less fertile portions of the ecosystems (Scott et al. 2001), while, the fertile areas are often used for livestock grazing and agriculture (Serneels et al. 2001, Thompson and Homewood 2002). Nevertheless, these fertile plains are also often utilized by large mammals with home ranges extending beyond the boundaries of national parks and reserves (Newmark 1995). For example, the high-rainfall (800 mm) Nairobi National Park in Kenya forms the dry season range and the low-rainfall (500) mm) grasslands of the unprotected Athi-Kaputiei Plains the wet season range for ungulate migrations (Norton-Griffiths 1977). Tarangire National Park (TNP), lying in the Maasai steppe in northern Tanzania, forms the dry season concentration area for wild ungulates which disperse into the surrounding Maasai steppe during the wet season (Kahurananga and Silkiluwasha 1997, Morrison and Bolger 2012). Similar seasonal movements have been observed in the Kgalagadi ecosystem in Botswana, Etosha National Park and several other African conservation areas (Fynn and

Bonyongo 2010). Thus, it is clear, that protected areas often exclude a portion of the area that is needed to maintain populations of wildlife.

Often the unprotected portions of ecosystems contain one of these two crucial habitats for wild herbivores that reside within the protected areas for part of the year. As discussed in **Chapter 4**, the wet season range often occurs at the lower end of the rainfall gradient, typically serve as a breeding ground and consists of short, nutritious grasses with high concentrations of protein and minerals in the late wet season (McNaughton and Banyikwa 1995, Murray 1995). By contrast, the dry season range for wildlife often occurs at the high end of the rainfall gradient with dependable green grass in the late dry season and more often than not do not contain breeding grounds for wildlife (Fynn & Bonyongo, 2010). The dry-season range provides buffer resources for wildlife, particularly during droughts. Often the protected areas contain the dry season concentration areas, and exclude the wet season habitats for wild herbivores residing in the protected areas (Bolger et al. 2008, Fynn and Bonyongo 2010).

In **Chapter 6** I show that the influences of seasonal variation in forage availability, quality and anthropogenic factors directly determine the distribution and density of wildlife and are reflected through differences in body sizes and feeding guild. In **Chapter 4 and 5**, I show that during the wet season in the Maasai Mara National Reserve, grass height is tall and therefore inherently risky because the tall grass provides cover for predators (Hopcraft et al. 2005). **Chapters 5 and 6** show that both small and medium-sized herbivores (Thomson's gazelle, impala) were more abundant in the ranches than in the reserve. These results suggest that small and medium herbivores tend to prefer short grass areas (Fryxell 1991, Illius and Gordon 1992) found in the ranches due to repeated livestock grazing. This is supported by evidence from several studies showing that repeated grazing increases the crude protein production of grasses, enabling the small grazers to derive sufficient energy by selecting high-quality forage from the low-biomass areas (Fryxell et al. 2005). Reduced predation risk as a result of lower vegetation cover on the ranches as shown in **Chapter 5** is yet another advantage of concentrating in the short grass plains, since tall grasses conceal ambush predators and significantly increase their efficiency at catching prey animals (Hopcraft et al. 2005). As a result the combined effect of high predation and low-quality grazing associated with tall grass lead to a higher wild prey biomass density in the ranches than in the reserve. These results accord with the findings of Hopcraft et al. (2012). In contrast, larger-bodied herbivores (buffalo, elephant), requiring bulk forage but less susceptible to predation, are more abundant in the reserve than the ranches. Although, these patterns of wildlife distribution during the wet season are remarkably similar to those in the dry season for the small and large sized herbivores (**Chapter 6**), the presence of the migrants consisting of 1.3 million wildebeest, 0.2 million zebra, and 0.45 million gazelle, modifies the distribution of medium-sized resident herbivores (Sinclair et al. 2008b).

What is the influence of the migration on the distribution of resident herbivores?

As mentioned in the **Chapter 1**, the wildebeest and zebra concentrate on the southern grasslands of the Serengeti National Park during the wet season (December–May). In May or June they move northwest and concentrate in the northern woodlands of the Serengeti and MMNR during the dry season (August–November). During this season forage quantity, quality and surface water are reduced throughout the Mara region, but are higher inside the reserve than in the ranches (**Chapter 4**).

From the distribution maps presented in **Chapter 6**, I show that medium-sized herbivores concentrate inside the protected area during the dry season. However, the concentration of zebra and wildebeest are located in greener areas whereas topi and hartebeest concentrate closer to rivers. Since such areas typically have higher predation risk this aggregation pattern suggests that by absorbing most of the predation pressure, migrant herbivores facilitate the resident herbivores. This conclusion is supported by evidence from (Arsenault and Owen-Smith 2002, Ogutu et al. 2008)who showed that predation on resident ungulates is highly reduced in the dry season when enormous herds of migratory ungulates are present in the Mara, meaning that an increase in numbers of migrants in the reserve would reduce predation on resident herbivores. Alternatively, I argue in **Chapter 6** that the migrants may displace resident herbivores from preferred habitats forcing them to concentrate in areas potentially "risky" areas. The large herbivores (buffalo and elephant) remain inside the reserve, except for the browsing giraffe that concentrate in the ranches. Contrary to expectation, smaller-sized herbivores (both gazelles and impala), concentrate in the greener and wetter areas situated closer to rivers in the pastoral ranches suggesting that livestock grazing creates conditions that favour small herbivores, including high-quality short grasses and better visibility.

Unfortunately, most conservation areas no longer allow ungulates access to all the critical seasonal foraging regions that they once utilized. Illegal livestock incursions, recurrent severe droughts (linked to stronger and more frequent El Niño events) and habitat desiccation (due to rising temperatures) accentuates the need for these movements. Yet intensification of land use, spreading settlements and sedentarization are inhibiting free movements resulting in extensive population declines in several protected areas (Newmark 2008, Ogutu et al. 2009).

What are the influences of land use and climate change on herbivore populations when their movements get increasingly restricted?

In this section, I use evidence provided in this thesis together with the well-documented historical changes in the Mara-Serengeti dating as far back as the 1800s (Sinclair and Norton-Griffiths 1979, Dublin 1991, Sinclair et al. 2008a) to interpret historical changes that have shaped the distribution patterns of herbivores today (Fig. 7.1). This may provide us with insights into the importance of the seasonal dispersal areas now compared to the past.

About 300 years ago, pastoralism was dependent on grazing areas with strong seasonal livestock movements, suggesting that the ecosystem was primarily domi-

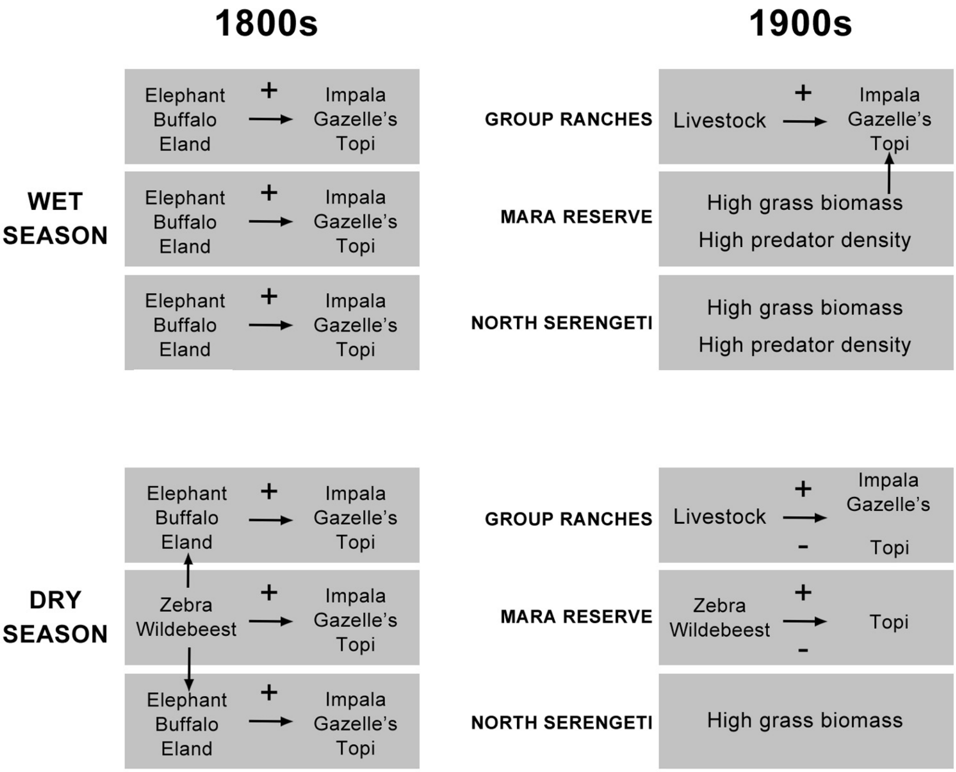

Figure 7.1 Before the rinderpest outbreak (1800s) large resident herbivores (mainly buffalo) occurred in the entire landscape. During the wet season large herbivores facilitated small (gazelles and impala) and medium-sized herbivores (topi) by keeping the vegetation in a nutritious state and increasing visibility of predators. In the dry season migratory herds of wildebeest and zebra displaced large herbivores into the wet season range that consisted of low human population densities. Here, large herbivores facilitated small herbivores. However, after the rinderpest eradication (1960s) large herbivore populations were decimated due to poaching and subsequent droughts. At the same time the Mare reserve was established. As a result people and livestock increased in the adjacent areas. The large wild-herbivore population could no longer facilitate small herbivores forcing them to move into the human-dominated landscapes, where livestock maintained the grass in a short state. During the dry season, the extensive herds of migrants likely kept the resident populations low via interspecific competition (Sinclair 1985). The residents could not escape competition from the migrants by moving into the adjacent areas, because, livestock compete with resident wildlife.

nated by extensive grasslands (described in more detail in **Chapter 1**). The grasslands may have been partly developed through an increase in the frequency of burning (Olff and Hopcraft 2008). Fire suppresses the establishment of dense woody vegetation, consequently maintaining the system in a grassland state. Due to limited human activities, wildlife populations were widespread over entire landscapes. This implies that the smallest grazers, which are the most nutritionally constrained and prone to most predators, could occur in areas of short grass and high visibility. Since livestock densities were likely lower than at present, it is likely that before the onset of the rinderpest (1890s), large herbivores such as buffalo, which are less susceptible to predation, as discussed in **Chapters 5 & 6**, were widely distributed and able to maintain the grass in a short and nutritious state, enabling both small and medium-sized herbivores to also persist on the landscapes. During the dry season, migratory herds from the Serengeti plains would concentrate in the core dry-season range (Stellfox et al. 1986). These vast herds likely competed with resident herbivores forcing them to disperse into the surrounding areas. Nevertheless, resident herbivores could still access abundant forage supply as a result of low livestock densities in the surrounding landscape.

During the outbreak of the rinderpest pandemic, catastrophic losses of livestock, wildebeest and buffalo were evident. Rinderpest remained in the Serengeti region until the early 1960s (Talbot and Talbot 1963), when it disappeared from wildlife populations as a result of a cattle vaccination campaign (Sinclair 1977). After the eradication of the epidemic there was a marked increase in human and settlement numbers along the western boundaries of both the Serengeti National Park and Mara Reserve (Dublin 1991). The human population growth around the protected area forced large herbivores into the reserve, altering the state of the vegetation (Dublin and Douglas-Hamilton 1987). During the 1970s after the Kenya-Tanzania border was closed, severe poaching activities decimated the population of elephant and buffalo in Northern Serengeti. The Serengeti lost about 80% of their large-herbivore population, however, the Mara was little affected by poaching and the population remained stable. In 1993, a severe drought decimated the population of buffalo by almost 70%. Until today (2012), these numbers have not recovered (Ogutu et al. 2009, 2011). The inability of the buffalo population to recover suggests competitive displacement by livestock, possibly exacerbated by drought conditions when remaining forage became inadequate to support both bulk grazers with similar forage needs (Ogutu et al. 2011). Furthermore, heightened competition between resident grazers and the enormous herds of migratory herbivores in the Mara reserve in the dry season likely kept the numbers of other resident herbivores low (Sinclair 1985, 1995, Arsenault and Owen-Smith 2002). As human population growth and increasing settlement densities increasingly obstruct the seasonal movements of herbivores between inside and outside the protected areas, wildlife are increasing getting excluded from their wet season ranges.

The dispersal movements of both small and medium herbivores (Thomson's and Grant's gazelles and topi) to the pastoral lands portray an inability of the fewer remaining large wild grazers (buffalo) to create and maintain short grass lawns favored by the small and medium herbivores inside the protected areas. Other ongoing processes such as illegal livestock incursions into the reserve and recurrent severe droughts and habitat desiccation due to rising temperature may accentuate the need for small and medium-sized herbivores to move into the human-dominated landscapes, yet intensification of land use, spreading settlements and sedentarization are restricting or excluding the resident herbivores from using their traditional dispersal ranges. Furthermore, herbivores that move into the human-dominated areas often experience high levels of poaching and human interference (Newmark 2008, Ogutu et al. 2009). So, although competition between resident grazers and migrants might limit recovery of resident populations to their former abundance levels, the fundamental cause of wildlife population declines seems to be the expanding human population in the ranches along with livestock influences spreading into the protected area (Ogutu et al. 2011).

Implications of this study for wildlife conservation and management

This study provides some new insights into the factors that influence the vulnerability of protected areas. Disentangling the relative contributions of reserve size, heterogeneity and productivity to the functioning of protected areas is an important milestone towards identifying suitable areas for their establishment. Furthermore, the proximity of protected areas to human populations and development makes them increasingly vulnerable to population declines. As protected areas become increasingly isolated from their surroundings, human population growth and development threaten the future survival of wildlife that depend on seasonal movements (Bolger et al. 2008, Newmark 2008). In environments with high seasonal variability in rainfall, such as savannas, protected areas are susceptible to unpredictable climatic extremes such as droughts and floods. Obstructions of wildlife movements by land use changes constrain their exploitation of their seasonal ranges located outside protected areas. Reduced flexibility and mobility due to progressive habitat loss in the Mara ranches thus amplifies the vulnerability of wildlife to recurrent climatic extremes, exacerbating population declines.

As human activities increasingly insularize protected areas, conflicts between humans and wildlife, including carnivores, appear to be increasing in frequency and intensity in many areas (Woodroffe et al. 2005, Valeix et al. 2009). This is primarily because human population growth presents a significant threat to many wildlife species, including already threatened ones. Human–wildlife conflicts such as crop-raiding (Sitati 2003, Valeix et al. 2009) or livestock depredation (Kolowski and Holekamp 2006), affect the responses of people leading to killing or harming both herbivores and carnivores. Research that advances our understanding of wildlife–livestock interactions is important to mitigate conflicts and conserve wildlife, yet most ecological research on herbivores has been conducted in areas without livestock (Graham et al. 2005). As a result, this research contributes towards enhancing our understanding of factors necessary to maintain rich assemblages of species inside protected areas as well as providing insights into why some herbivores engage in seasonal movements and the consequences of land use change on these movements.

Future outlook and suggestions for further work

Although, the Mara-Serengeti ecosystem is an ideal case-study for assessing how changes in human and livestock-dominated systems influence wildlife in pastoral systems over time, very few studies have examined the direct and indirect effects of pastoralism on wildlife. For example, in **Chapter 6** I suggest that resident herbivores may either be facilitated by or compete with the migrants during the dry season, whereas during the wet season livestock facilitates wildlife in the surrounding rangelands. It would be interesting to test the role of competition and facilitation via experiments, by comparing, for example, the body condition of these herbivores inside and outside the reserve during both the dry season and wet seasons

In response to the changes occurring in the pastoral ranches, wildlife conservancies have recently been formed, for example in the Mara ranches, as part of new initiatives aimed at enhancing wildlife conservation and improving livelihoods of pastoralists through partnerships in which private investors rent large tracts of land for wildlife conservation (Norton-Griffiths et al. 2008). Furthermore, management should focus on maintaining effective ecosystem size, critical seasonal habitats and on reducing negative edge effects. Several larger-scale initiatives are underway such as in Namibia where 31 registered conservancies managing some 78,000 km^2 of communal land through eco-tourism and managed hunting have been established. Local communities are beginning to earn an income and see regular employment opportunities. Currently, there are another 40 areas emerging as conservancies, which will involve another additional 100,000 people across another 80,000 km^2. It is estimated that in the future, one out of every nine Namibians will be a participant in the conservancy movement (WWF-LIFE, 1993). It will be a challenge to monitor the success of these conservancies. It would be interesting to apply the “hotspot” approach in **Chapter 6** in the field to assess the extent to which these conservancies are benefitting wildlife by comparing changes in wildlife densities in areas located within the conservancies before and after their formation against contemporaneous changes in similar areas located within neighbouring protected reserves as benchmarks.

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Summary

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Summary

African protected areas are becoming increasingly surrounded by rapidly growing human populations and expanding settlements. As a result, the protected reserves and areas surrounding reserves are getting progressively degraded, fragmented and compressed. Moreover, changes in rainfall patterns and rising temperatures, as predicted by global climate change, makes vegetation growth and hence food production for large mammals less predictable, especially during dry periods. These changes, limit the potential for large mammals to move between climatically suitable resource areas. Some of these resource areas lie outside the protected area boundaries, making movements of large mammals increasingly crucial in coping with the adverse consequences of both land use and climate changes. Restricting these movements would thus likely threaten the future viability of many wildlife populations. Understanding the consequences of climate change and human activities in and around protected areas on vegetation communities and the distribution of large herbivore and carnivore populations is important for conservation to prevent further losses of wildlife and their habitats.

The aims of this study are to a) assess the relative importance of area, landscape heterogeneity and vegetation productivity in shaping large mammalian communities in protected areas across continental Africa where the influence of humans is minimal (Chapter 2), b) investigate the processes structuring vegetation communities that represent important and reliable habitats for large mammals, especially during dry periods (Chapter 3), c) evaluate the influence of protection and pastoralism on the distributional patterns of carnivores (Chapter 4) and herbivores (Chapter 5 & 6) using the Mara-Serengeti ecosystem in east Africa as a case study. Finally, in (Chapter 7), I synthesize the findings on the consequences of such processes as expanding livestock densities, cultivation and human population growth in regions neighbouring reserves on herbivore and carnivore diversity and distributions.

CAN THE LOSS OF AREA BE SUBSTITUTED BY AN INCREASE IN HETEROGENEITY/PRODUCTIVITY?

In Chapter 2, I first set the broad stage of how the size of a protected area, heterogeneity and vegetation productivity affect species richness of large mammals in protected areas. In this chapter I highlight one of the oldest generalizations of ecology, i.e. the number of species in an area is related to the size of the area. The idea behind this is that species diversity is maintained by a balance between immigration and extinction, such that, in larger areas there is a higher number of species while smaller areas have less species diversity simply because the chances of becoming extinct are greater in small areas. The size of a protected area might also influence its species richness indirectly via other factors. Large areas are more likely to contain a higher diversity of habitats than smaller ones, hence support more species. Complementary, an increase in vegetation productivity, and thus food supply supports more individuals, reducing extinction chances. I test the relative importance of area, heterogeneity and productivity on species richness of large mammals. I Compile and analyse a database containing 300 protected areas from the World Database on Protected Areas, a total of 75 carnivores, 95 ungulates and 57 primates species from the African Mammal Databank and remotely sensed vegetation indices, habitat types and elevation. The results show that the role of area is mediated through variation in habitat heterogeneity for all taxa. Complementary to this, productivity determines species richness of primates. The relevance for conservation is that the protected areas should be located in either heterogeneous or productive locations that can potentially buffer them from increasing human pressure in unprotected parts of the ecosystem.

WHICH COMMUNITY ASSEMBLY PROCESSES STRUCTURE SAVANNA WOODLANDS?

Most protected areas in Africa lie within the savanna biome. They are home to an exceptionally high diversity and abundance of large mammalian herbivores. Rainfall is the primary climatic variable which influences the high spatial heterogeneity and productivity of savanna ecosystems, offering a diverse range of habitat types that support multiple assemblages of large mammal species. Of these habitat types, the closed thickets often consist of diverse and dense patches of woody species. These diverse woodlands represent important and reliable habitats for many large mammals, especially during dry periods. Thus, understanding the processes structuring these diverse vegetation communities in savanna systems is crucial to the conservation and management of savanna ecosystems. In Chapter 3, I use a long term dataset collected by the Masai Mara Ecological Monitoring Program over a 15–year period in Kenya's Masai Mara National Reserve to calculate measures of vegetation productivity, diversity, composition and stability to get an indication of whether the resulting patterns are most likely caused by (1) interspecific competitive interactions, (2) habitat filtering due to disturbances or stresses or (3) stochastic processes. The results from this study reveal that the savanna tree communities are not structured predominantly by competition, but rather by tolerance to stress and disturbances at in the drier areas and more complex interactions between species, including facilitation, that are more likely to operate at higher rainfall. A rising temperature trend, recurrent severe droughts and other environmental stresses increasingly threaten the survival prospects of these diverse woodland communities that support a highly diverse herbivore community.

HOW DOES PROTECTION AND PASTORALISM INFLUENCE CARNIVORE AND HERBIVORE DENSITY, DISTRIBUTION AND PERSISTENCE?

Rapid human population growth and the associated intensification and diversification of land use, increasing sedenterization, settlement density and habitat fragmentation in human-dominated pastoral lands of Africa threaten the long-term population viability of the natural prey base for carnivores. As a result, human-carnivore conflicts appear to be increasing and is now an urgent conservation issue. Human–carnivore conflicts typically occur when wild carnivores prey on livestock, and the people affected respond by killing or harming carnivores. Lion density in the Mara reserve is among the highest in African savannas, but is unusually low at the edge of the reserve adjoining the pastoral ranches. Therefore, in Chapter 4, our aim is to test if pastoralism and protection influence carnivore density, distribution and behavior given the human-predator conflicts. To test this we designed and implemented a playback survey to estimate the response probabilities of lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) and black-backed jackals (*Canis mesomelas*) inside and outside the protected Masai Mara National Reserve.

Our results reveal that lions did not respond to playback recordings in the pastoral areas. This can be explained in two different ways. Either lions were absent or occurred at extremely low densities in the pastoral area during our counting period, or pastoral activities altered their behavior such that lions avoided the broadcasts, or were too shy to approach the calling stations to within sighting range.

From previous ground counts in 2002, lions were found in the pastoral ranches, but at a much lower density than in the reserve. This shows that lions are not absent in the pastoral ranches. Therefore, the second explanation is likely to be true. Conflicts with pastoralists adversely alter the behavior of lions resulting in inherently low densities. Human persecution of large carnivores, through poisoning, snaring shooting or chasing suspected predators has been reported to be the main cause of the inherently low densities of lions in the pastoral ranches compared to the reserve.

From the playback surveys, the surprisingly high densities of hyena and jackals in the pastoral ranches can be explained, at least in part, by reduced competition with the few lions or higher prey density in the pastoral ranches. In general both hyena and jackals (*Canis mesomelas*) seem to face less harassment by pastoralists and to be better adapted to life in the ranches.

In chapters 5 & 6, I compare and contrast the density, demography and persistence of 13 wild and three domestic herbivore species of varying body sizes (15–1725 kg) between the Maasai Mara National Reserve and its adjoining pastoral ranches using 50 aerial surveys conducted in the wet and dry seasons during 1977–2010. I show that large grazers and browsers concentrate and persist at relatively higher densities in distinct localities (hotspots) in both the protected and pastoral landscapes of the Mara. The locations of high densities of herbivores vary with the body size of the herbivores. Herbivores weighing more than 700 kg concentrate inside the protected reserve to avoid competition with livestock, whereas smaller species concentrate in adjoining Masai pastoral ranches, at the reserve-ranch interfaces and move seasonally between both areas. The number, size and spread of hotspots for almost all species reduced strikingly during 1977-2010 due to land use changes and human population growth in the ranches.

In the wet season when food and water are plentiful, small and medium herbivores are attracted to the pastoral ranches by short, nutritious grasses and better visibility of ambush predators due to livestock grazing. In contrast, in the dry season when food and water supplies are low, medium herbivores (100–200 kg), avoid competition with livestock in the ranches by moving into the Mara reserve. Moreover, when vast herds of migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus burcheli*) from the Serengeti occupy the Mara reserve in the dry season, they supply enough food for large predators to enable resident herbivores use areas with green grass but located near rivers where the risk of being killed by predators is otherwise very high. The migrants also displace some resident grazers to the ranches. These results support the conclusion that pastoral lands are critical habitats for wildlife inhabiting protected areas and often include the wet season breeding grounds for some species. But land use changes in pastoral areas neighbouring parks are increasingly excluding large herbivores and obstructing seasonal wildlife dispersal movements between parks and their surroundings. Continued coexistence of wildlife and livestock on pastoral lands will only be possible if land use practices and livestock stocking levels are regulated and monitored on such lands.

Finally, in Chapter 7, I synthesize the key results and evaluate the influences of area, landscape heterogeneity, productivity, landuse and climate change on herbivore populations and their distribution. The results suggest three important characteristics that influence the vulnerability of a protected area to land use intensification. First, the size, heterogeneity and productivity of a protected area. Second, the proximity of a protected area to human population, specifically in areas of intense land use in critical portions of ecosystems (e.g. breeding grounds). Third, the lack of incentives or resources to conserve wildlife outside of protected areas. This study increases our understanding of how these factors affect wildlife species richness, abundance, demography and persistence. This information is essential to identify protected areas most likely to be at risk due to land use changes and develop appropriate conservation and management strategies. There is an urgent need to launch conservation and management initiatives that promote the continued availability of pastoral lands to wildlife in adjacent parks, including setting up conservancies, and monitoring the effectiveness of these initiatives. I present an approach that can form the basis for this monitoring in chapter 6.

Samenvatting

Door bevolkingsgroei en een sterke uitbreiding van permanente nederzettingen worden beschermde natuurreservaten in Afrika steeds vaker omgeven door menselijke activiteit. Hierdoor worden natuurreservaten en de gebieden rond de reservaten geleidelijk aan verkleind en gefragmenteerd. Daarnaast zijn er veranderingen in neerslag en een toename van de temperatuur door klimaatverandering. Dit beïnvloedt de groei van de vegetatie en dus wordt voedselproductie voor herbivoren minder voorspelbaar, vooral tijdens droge periodes. Deze veranderingen reduceren de mogelijkheden voor grote zoogdieren om te migreren naar gebieden met geschikte klimaten. Sommige geschikte gebieden liggen buiten de grezen van beschremde gebieden, wat de migratie van grote zoogdieren zelfs nog crucialer maakt voor het omgaan met de negatieve consequenties van klimaatsverandering en veranderingen in landgebruik. Het limiteren van migratie patronen zou dus waarschijnlijk de toekomstige overlevingskans van veel zoogdierpopulaties bedreigen. Om grote herbivoren, carnivoren en hun habitat te behouden, moet begrepen worden wat de consequenties zijn van menselijke activiteit en klimaatverandering in natuurreservaten en op de omliggende weidegronden, voor zowel de dichtheid als de verspreiding van deze soorten.

Het doel van deze studie is om (a) inzicht te krijgen in het belang van de grootte, de heterogeniteit en de productiviteit van natuurreservaten op de samenstelling van levensgemeenschappen van grote herbivoren, carnivoren en primaten in Afrikaanse reservaten waar de invloed van mensen minimaal is (hoofdstuk 2). (b) Een ander doel is inzicht te krijgen in de processen die de vegetatiegemeenschappen beïnvloeden die belangrijk zijn voor grote herbivoren, vooral tijdens het droge seizoen (Hoofdstuk 3). (c) Verder wordt een evaluatie gedaan van de invloed van weidegronden rond reservaten op de dichtheid en verspreiding van grote carnivoren (Hoofdstuk 4) en herbivoren (Hoofdstuk 5 en 6) in het geval van de Mara-Serengeti in Oost-Afrika. In het laatste hoofdstuk (Hoofdstuk 7) worden de bevindingen van de studies samengevoegd en worden de mogelijke consequenties van de toename van menselijke activiteit in de natuurreservaten en op de weidegronden bediscussieerd.

KAN HET VERLIES VAN OPPERVLAKTE WORDEN GECOMPENSEERD DOOR HETEROGENITEIT/PRODUCTIVITEIT?

In Hoofdstuk 2 wordt gekeken naar de invloed van oppervlakte, de heterogeniteit van het landschap en de productiviteit van vegetatie op soortenrijkdom van grote zoogdieren. In deze studie benadrukken we één van de oudste ecologische principes, namelijk dat soortenrijkdom toeneemt met oppervlakte. Het achterliggende idee is dat soortenrijkdom wordt behouden door een balans van immigratie en extinctie. Omdat de extinctie negatief wordt beïnvloed door oppervlakte kunnen er meer soorten zijn in gebieden met een relatief groot oppervlak. Het oppervlakte van natuurreservaten kan soortenrijkdom ook indirect beïnvloeden. Grotere gebieden zijn vaak heterogener en hebben daarom meer niches, waardoor meer soorten samen kunnen voorkomen. Aanvullend kan productiviteit, en dus voedselproductie, meer individuen onderhouden. Dit verkleint tevens de extinctiekans en dus wordt soortenrijkdom vergroot. Om het belang van oppervlakte, heterogeniteit en productiviteit te testen voor soortenrijkdom van grote herbivoren heb ik een dataset samengesteld. Deze dataset bestaat uit 300 beschermde gebieden (data van de *World Database on Protected Areas*), 75 soorten carnivoren, 95 soorten herbivoren en 57 soorten primaten (data van de *African Mammal Databank*) en indicatoren voor habitattype en hoogte (gemeten door middel van remote sensing). De resultaten van de analyse laten zien dat het effect van oppervlakte verklaard kan worden door heterogeniteit voor alle taxa. Daarnaast wordt soortenrijkdom van primaten ook door productiviteit beïnvloed. Deze bevindingen laten zien dat natuurreservaten met hogere heterogeniteit en productiviteit sterker gebufferd zijn tegen de negatieve consequenties van de bevolkingsgroei in Afrika.

WELKE PROCESSEN VORMEN DE LEEFGEMEENSCHAPPEN VAN HOUTIGE GEWASSEN IN DE SAVANNE?

De meeste natuurreservaten in Afrika liggen in de savanne. De savanne staat bekend om zijn uitzonderlijke hoge diversiteit aan grote zoogdieren. Ruimtelijke variatie in regenval creëert heterogeniteit in de productiviteit van savannes. Hierdoor ontstaan een groot aantal verschillende habitattypen, die verschillende gemeenschappen van herbivoren kunnen onderhouden. Een van deze habitattypen is het gesloten struweel dat wordt gedomineerd door houtige gewassen van veel verschillende soorten. Dit diverse landschap is een belangrijk habitat voor grote herbivoren tijdens het droge seizoen. Het begrijpen van de processen die dit habitat vormen is dus van belang voor het beheer van savanne ecosystemen. In hoofdstuk 3 gebruik ik een dataset (afkomstig van *Masai Mara Ecological Monitoring Program*, Kenia, uit her *Masai Mara National Reserve*, gemeten durende 15 jaar) om de productiviteit, diversiteit, compositie en stabiliteit van de vegetatie te bepalen. Met deze gegevens is bepaald of de gemeenschap wordt gevormd door (1) competitie tussen soorten, (2) habitat filtering door verstoring of stress of (3) door stochastische processen. De resultaten laten zien dat levensgemeenschappen van houtige gewassen in de savanne niet gevormd zijn door competitie tussen soorten. Tolerantie voor stress en verstoring in de drogere gebieden en meer complexe interacties, o.a. facilitatie in gebieden met meer regenval, spelen een belangrijkere rol. Temperatuurstijging, terugkomende lange periodes van droogte en ander factoren die de mate van stress in een systeem beïnvloeden bedreigen deze diverse gemeenschappen, die erg belangrijk zijn voor het in stand houden van een soortenrijke herbivorengemeenschap.

HOE BEÏNVLOEDEN NATUURRESERVATEN EN DE OMLIGGENDE WEIDEGRONDEN CARNIVOREN EN HERBIVOREN DICHTHEID, VERSPREIDING EN OVERLEVING?

De snelle bevolkingsgroei in Afrika gaat gepaard met intensivering en diversificatie van het landgebruik, een toename van het aantal permanente nederzettingen en fragmentatie van weidegronden. Als gevolg hiervan stijgt het aantal conflicten tussen mensen en carnivoren. Mens-carnivoor conflicten ontstaan wanneer predatie op vee plaatsvindt, waarop de veehouders reageren door carnivoren te doden of verwonden. In het natuurreservaat de Mara is de leeuwendichtheid één van de hoogste van alle Afrikaanse savannes. Bij de grens van het reservaat, waar de weidegronden liggen, is de dichtheid echter erg laag. In hoofdstuk 4 testen we daarom of menselijk handelen op de weidegronden carnivorendichtheid, verspreiding en gedrag beïnvloed hebben. Om dit te testen hebben we een playback survey ontworpen om reactiekans van leeuwen (*Panthera leo*), gevlekte hyena (*Crocuta crocuta*) en jakhals (*Canis mesomelas*) te schatten in het natuurreservaat de Masai Mara en de omliggende weidegronden.

Onze resultaten laten zien dat leeuwen niet reageerden op de *playbacks* op de weidegronden. Er zijn twee mogelijke verklaringen hiervoor: ofwel leeuwen waren aanwezig in extreem lage dichtheden (of zelf compleet afwezig), of menselijke activiteit op de weidegronden veranderde hun gedrag zodanig dat leeuwen de uitzendingen vermeden, mogelijk omdat ze te schuw waren.

Tijdens eerdere grondtellingen in 2002 werden leeuwen aangetroffen in de weidegronden, maar wel in een veel lagere dichtheid dan in het reservaat. Dit laat zien dat er wel leeuwen op de weidegronden aanwezig zijn. De tweede verklaring voor het uitblijven van een reactie van de leeuwen op onze *playbacks* is daarom waarschijnlijker: conflicten met mensen op de weidegronden hebben geleid tot het bejagen en verjagen van leeuwen. Dit vormt waarschijnlijk de voornaamste reden voor hun gedragsverandering en hun lage dichtheden op de weidegronden in vergelijking met het natuurreservaat.

De resultaten van onze playback survey laten verassende hoge dichtheden op de weidegronden zien van zowel hyena als jakhals. Dit kan, althans gedeeltelijk, verklaard worden door de verminderde concurrentie met leeuwen of een hogere prooidichtheid op de weidegronden. Het lijkt erop dat hyena's en jakhalzen beter zijn aangepast aan een leven op de weidegronden.

In hoofdstuk 5 en 6 vergelijken ik het Masai Mara National Reserve met de omringende weidegronden met betrekking tot dichtheden, demografie en overleving van 13 wilde en drie gedomesticeerde soorten herbivoren. Deze herbivoren hebben variërende lichaamsgrootten (15–1725 kg). Voor deze studie hebben we gebruik gemaakt van 50 tellingen, die tijdens het droge en natte seizoen vanuit een vliegtuig gedaan zijn. Deze tellingen zijn uitgevoerd tussen 1977–2010. De resultaten laten zien dat herbivoren zich op duidelijk te onderscheiden locaties bevinden (*hotspots*) in zowel het reservaat als de omliggende weidegronden. De locaties variëren met lichaamsgrootte. Herbivoren met een gewicht van meer dan 700 kg concentreren zich in het reservaat en omzeilen zo competitie met vee op de weidegronden. Middelgrote herbivoren (100 - 200 kg) concentreren zich ook in het reservaat, maar alleen tijdens het droge seizoen. Tijdens het regenseizoen concentreren deze herbivoren zich op de weidegronden. De kleinere herbivoren concentreren zich altijd op de weidegronden. Het aantal hotspots, maar ook de grootte en de verspreiding ervan zijn allemaal drastisch gereduceerd sinds 2010 door verandering in landgebruik en een groeiende bevolking.

Tijdens het regenseizoen, wanneer voedsel en water volop aanwezig is, zijn de weidegronden erg aantrekkelijk voor kleine en middelgrote herbivoren omdat de vegetatie hier kort gehouden wordt door het vee. Deze korte vegetatie bevat een hoge concentratie voedingsstoffen. Verder is het gemakkelijker om een roofdier op te merken in korte vegetatie. Tijdens het droge seizoen, wanneer er weinig voedsel en water is, vermijden de middelgrote herbivoren competitie met vee op de weidegronden door naar het reservaat te migreren. Daarnaast is de kans op predatie binnen het reservaat sterk verminderd, doordat tijdens het droge seizoen gnoes en zebra's vanuit de Serengeti in hoge aantallen naar het reservaat komen. Deze resultaten laten het belang van omliggende weidegronden voor natuurreservaten zien. Helaas worden weidegronden steeds minder toegankelijk voor wilde herbivoren, door veranderingen in landgebruik. Vee en wilde herbivoren (vooral kleine en middelgrote) kunnen alleen naast elkaar blijven leven, wanneer de dichtheid van het vee en de veranderingen in landgebruik gereguleerd en gemonitord worden.

Tenslotte worden in hoofdstuk 7 de belangrijkste bevindingen uit de vorige hoofdstukken samengevoegd. Dit hoofdstuk suggereert 3 belangrijke groepen van factoren die mogelijk de kwetsbaarheid van een beschermd natuurgebied voor land gebruik intensivering bepalen. Ten eerste, de grootte, heterogeniteit en productiviteit van een beschermd natuurgebied. Ten tweede, de nabijheid van het natuurgebied aan een menselijke nederzetting, vooral in gebieden met intensief landgebruik in kritieke delen van het ecosysteem (belangrijke broedgebieden). Ten derde, het gebrek aan motieven of middelen om natuur buiten beschermde gebieden te behouden. Deze studie vergroot ons begrip van hoe dit type factoren soortenrijkdom, dichtheid, populatiedynamica en kwetsbaarheid van planten en dieren bepalen. Dit begrip is essentieel om te detecteren welke beschermde natuurgebieden het grootste risico lopen als gevolg van veranderingen in landgebruik en voor het ontwikkelen van geschikt behoud en beleid van die natuurgebieden. Er is een urgente noodzaak voor het lanceren van behoudd en beleid initiatieven die heterogeniteit en connectiviteit tussen weidegronden en aanliggende natuurgebieden vergroten. Mogelijk bevat dit het opzetten van beheersorganisaties in de weidegronden en het monitoren van de effectiviteit van deze initiatieven. Ik presenteer een methode die hier de basis voor kan vormen in hoofdstuk 6.

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June 2003	World Bank-Monitoring and evaluation workshop, Kampala, Uganda WWF- EARPO Conservation of East African mountain ecosystems workshop, Kenya

SUPERVISING

January 2009	Master thesis co-advisor, University of Groningen.
April 2010	Bachelor course supervisor, University of Groningen
November 2010	Top Master mini- project co-advisor, University of Groningen

SCHOLARSHIPS AND AWARDS

2007 – 2011	Ubbo Emmius Scholarship-Ph.D. Award, University of Groningen.
2005 – 2007	Top Master Scholarship, University of Groningen, The Netherlands.
2005	WWF-EARPO East African Best Performer Award, Annual General Meeting, Tanzania.

LIST OF PUBLICATIONS

Bhola, N., Ogutu, J.O., Piepho, Said, M., H.P., Olff, H (In Prep). Dissecting the interplay between area, landscape heterogeneity and productivity in shaping species richness: A meta-analysis of African game reserves.

Bhola, N., Ogutu, J.O., Piepho, H.P., Olff, H. (In Prep). Community assembly processes in savanna woodlands in relation to rainfall.

Bhola, N., Ogutu, J.O., Piepho, H.P., Olff, H (2012). The distribution of large herbivore hotspots in relation to environmental and anthropogenic correlates in the Mara region of Kenya. *Journal of Animal Ecology*. doi: 10.1111/j.1365-2656.2012.02000.x.

Bhola, N., Ogutu, J.O., Piepho, H.P., Reid, R.S., Hobbs, T., Olff, H. (2012) Comparative changes in density and demography of large herbivores in the Maasai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. *Biodiversity and Conservation* **2**:1509–1530.

Ogutu, J.O., Piepho, H.P., Dublin, H.T., **Bhola, N.** & Reid, R.S. (2010). Dynamics of births and juvenile recruitment in Mara–Serengeti ungulates in relation to climatic and land use changes. *Population Ecology* (2011) **53**:195–213

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Ogutu, J.O., Piepho, H.P., Dublin, H.T., **Bhola, N.** & Reid, R.S. (2007) El Niño-Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-Serengeti ecosystem. *African Journal of Ecology* **46**:132–143.

Ogutu, J.O., Piepho, H.P., **Bhola, N.** & Reid, R.S. (2006) Efficiency of strip- and line-transect surveys of African savanna mammals. *Journal of Zoology* **269**:149–160.

Ogutu, J.O., **Bhola, N.** & Reid, R. (2005) The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology* **265**:281–293.