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

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Summary

1. 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.

2. We analyse 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 km² (n = 289 cells) in the Mara region of Kenya during 1977–2010. We compare the distributions across seasons, land use types (protection, pastoralism and agro-pastoralism) and 10 species with different body sizes and feeding styles.

3. 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 Masai 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.

4. 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. As 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.

5. 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.

6. 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.

Key-words: competition, facilitation, land use, Normalized Difference Vegetation Index, pastoralism, predation, protection

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 & Cumming 1999), recent empirical research suggests that moderate, more traditional forms of human land use may benefit wildlife in tropical ecosystems (Veblen & Young 2010; Augustine et al. 2011). In African savannas, native wildlife and humans have coexisted for centuries under moderate traditional human activities (Lamprey & Reid 2004; Galvin et al. 2008). However, because of intensifying anthropogenic activities, strong gradients often emerge between protected areas and their surrounding human-dominated pastoral ranches, creating spatial heterogeneity in
Mapping large herbivore hotspots

prey and environmental gradients within landscapes. Thus, variations in herbivore densities in protected areas may differ with life history traits of herbivores such as body size (Sensenig, Demment & Laca 2010; Hopcraft et al. 2012) because small herbivores are more susceptible to predators (Sinclair, Mduma & Brashares 2003) and require forage of higher quality than do large ones (Demment & Van Soest 1985). 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, 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 & Arce 1995b) and an exceptionally high abundance and diversity of resident wildlife species (Broten & 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 (Stelfox et al. 1986; Ogutu et al. 2008; Fynn & Bonyongo 2010). In particular, the resident herbivores disperse from the MMNR onto the adjoining ranches in the wet season (Stelfox 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 because of higher predator densities and taller and denser grass cover in the reserve (Hopcraft, Sinclair & Packer 2005; Ogutu, Bhola & Reid 2005). The resident herbivores return to the reserve in the dry season, likely because of 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, Demment & Laca 2010; Hopcraft et al. 2012). 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 (Georgiadis et al. 2007; Fynn & 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, Cumming & Phillipson 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 & Nicholson 1993; Camberlin et al. 2007). NDVI has thus successfully been used to predict the distribution and abundance of large mammalian herbivores (Bro-Jørgensen, Brown & Pettorelli 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, Tieszen & Imbamba 1988a,b; Georgiadis & McNaughton 1990) in most of the reserve and hence low in digestibility and heights predation risk for herbivores (Hopcraft, Sinclair & Packer 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 & McNaughton 2006) and hence promoting visibility against predators (Ogutu, Bhola & Reid 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, Tieszen & Imbamba 1988b; Georgiadis & McNaughton 1990). However, as grass height is generally taller inside than outside the reserve because of the absence of livestock grazing in the reserve, except during illegal incursions (Ogutu, Bhola © 2012 The Authors. Journal of Animal Ecology © 2012 British Ecological Society, Journal of Animal Ecology, 81, 1268–1287
& Reid 2005), we expected herbivore hotspots to increase with increasing NDVI in the reserve (H2a) but to show the opposite pattern in the ranches (H2b) because of 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. 2006) and that herbivores avoid wet and sticky soils found near drainage lines and on other low-lying areas (Telbot & Telbot 1963). Given these assumptions, we expected hotspots of small and medium herbivores to increase with (i) increasing distance away from rivers and (ii) decreasing soil moisture, but hotspots of large herbivores to follow the opposite patterns (H3a). In the ranches, as predator densities are lower (Ogutu, Bhol & Reid 2005), hotspots of small and medium herbivores should peak closer to rivers and in other areas of high soil moisture because of (i) facilitation by Masai livestock grazing near rivers in the dry season (Reid, Galvin & Russell 2008; Butt, Shortridge & WinklerPrins 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 because of shading from direct insolation by tree canopy (Treyde et al. 2008; Anderson et al. 2010) despite high predation risk. The presence of migratory herbivores inside the reserve lowers the predation pressure on the resident populations in the dry season (Saba 1979; Scheel & Pucker 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 & Reid 2004; Ogutu et al. 2009, 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 analysed influences of land use type (protection, pastoralism and 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; Hopcraft, Olff & Sinclair 2010) to human-dominated savanna landscapes.

Materials 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 km² of the protected 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 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. 1). The Mara can be subdivided into three main landscapes based on predominant land use (Seneels, Said & Lambin 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. 2009). 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 & Reid 2004). Human population density is lower here than in the ‘outer ranches’ but higher than in the ‘reserve’ (Ogutu et al. 2009). The Mara is characterized by the annual migration which brings over 1 million wildebeest (Connochaetes taurinus), zebra (Equus burchelli) and Thomson’s gazelle (Gazella thomsonii) 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, Shortridge & WinklerPrins 2009). We considered the 10 most common wild herbivore species (Table 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 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 (Pennycook & 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, creates 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 & 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 because of 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 km² grid cell over all replicate surveys conducted in each season in 1 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 km² 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 km² 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

Normalized Difference Vegetation Index 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 images at a pixel resolution of 8 × 8 km² for 1982–2010. A semi-parametric generalized linear mixed model 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 1 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 centre to the nearest drainage bed with clearly defined embankments was calculated for each land use type using 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, and proximity to water and riverine woodlands and grasses (Anderson et al. 2010; Hopcraft et al. 2012).

**TOPOGRAPHIC WETNESS INDEX**

We calculated TWI from the 90 m² 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 \( \ln(A_s/\tan \beta) \), where \( A_s \) is the watershed catchment area (i.e. the drainage area per unit width orthogonal to a stream line) and \( \beta \) 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, Sinclair & Packer 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 1979–2010 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 km² 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. 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 grey, and the intensity of this shade increased with increasing quantiles. The same greyscale was assigned to the same quantile for all species in each landscape to facilitate direct visual comparisons.

**STATISTICAL MODELLING AND DATA ANALYSES**

We used multivariate semi-parametric quantile regression analysis (Koenker & 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 km² 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. Modelling 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 modelled the rate of change in density at the 75th conditional quantile of the distribution as a function of the above covariates to establish how variation in these covariates influenced hotspots of herbivore abundance in the Mara (Cade & Noon 2003). The choice of the 75th quantile was reasonable for modelling 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 package quantreg. We used dummy coding of landscapes to enable herbivore density to have possibly different non-linear 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 & 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 2). We related density separately to the best selected NDVI component and each of the other covariates using semi-parametric models and AICc to tune the smoothing parameter (\( k \)) 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. If the AICc for the new model reduced compared to that for the initial model, then the new covariate was retained in the model. On the contrary, if the AICc for the new model increased relative to that of the initial model, then we removed the new covariate from the model and added the covariate with the second smallest AICc. We
Fig. 2. Distribution of decadal density averages over the $5 \times 5$ 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 greyscale 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.
continued this way until we had considered all the covariates (Table S1, Supporting information), 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 ($\lambda$), which determines the degree of smoothness of the fitted function for each covariate, for functions with a single $\lambda$, and the simulated annealing option of `optimize` for functions with multiple $\lambda$s (Koenker 2005). We then plotted and visually inspected shapes of the functions fitted to each covariate for ecological plausibility.

Fig. 2b. (Continued).
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. 2). Livestock were abundant and their distribution expanded over time in the ranches in both seasons (Fig. 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 (Fig. 2b,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. 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. 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. 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

Fig. 2c. (Continued).
the Loita migrants (Fig. 2g,h). The declines in wildebeest and zebra hotspots in the reserve and ranches during the 1990s and 2000s coincided with a reduction in the numbers of both the Serengeti migrants reaching the Mara and the resident herds (Fig. 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. 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. 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. 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, Fig. 3a, Figs S1a and S3b, Supporting information) or low (wildebeest, Fig. S1d, Supporting information) levels of livestock density, or were unresponsive to livestock (zebra, Fig. 3c). Hotspots of Grant’s gazelle and hartebeest (Fig. S1b,c, Supporting information) showed the same patterns but were unrelated to both NDVI and livestock density (Table S1, Supporting information).

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, Supporting information) to intermediate (Thomson’s gazelle and impala, Fig. 3a and Fig. S1a, Supporting information) livestock densities. Only hotspots of Grant’s gazelle and hartebeest were unrelated to NDVI (Table S1, Supporting information), and together with those of zebra, to livestock density as well (Table S1, Supporting information). In addition, impala hotspots were little affected by variation in NDVI (Fig. S1a, Supporting information), whereas topi hotspots were unrelated to all the predictor variables in the outer ranches (Fig. 3b).

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: (i) areas of high NDVI values (buffalo, Fig. S1e, Supporting information), (ii) close to rivers and in areas of low human population density (giraffe, Fig. S1f, Supporting information) and (iii) 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, Supporting information)

### Table 2. Selection of the best supported NDVI component for each species in the dry and wet seasons based on AICc values

<table>
<thead>
<tr>
<th>Season</th>
<th>NDVI component</th>
<th>Thomson’s gazelle</th>
<th>Impala</th>
<th>Grant’s gazelle</th>
<th>Topi</th>
<th>Hartebeest</th>
<th>Wildebeest</th>
<th>Zebra</th>
<th>Buffalo</th>
<th>Giraffe</th>
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<td>29521.0</td>
<td>37782.4</td>
<td>41674.7</td>
<td>3782.4</td>
<td>24235.3</td>
<td>25560.2</td>
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<tr>
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<td>31221.1</td>
<td>36365.9</td>
<td>29371.9</td>
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<td>23960.2</td>
<td>25391.2</td>
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<tr>
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<td>30871.3</td>
<td>36528.7</td>
<td>29542.0</td>
<td>38353.7</td>
<td>41652.3</td>
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<tr>
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AICc, Akaike Information Criterion; NDVI, normalized difference vegetation index. 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.
tion). In the ranches, other than giraffe hotspots that concentrated close to rivers and in areas of low human population density (Fig. S1f, Supporting information), similarly to the reserve, hotspots of the large herbivores were unresponsive to all the predictors (Table S1, Supporting information), 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. (i) 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 (Fig. 4a and Fig. S2a, Supporting information). (ii) Grant’s gazelle occurred in areas of high NDVI in the dry season (Fig. S2b, Supporting information) 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, Supporting information) and wetter areas, closer to rivers (topi and hartebeest) and at intermediate distances from rivers (zebra) in the dry (Fig. 4b,c and Fig. S2c, Supporting information) 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, Supporting information) than in the wet season.

Apart 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 (Fig. 4a, Fig. S2a,b, Supporting information). 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) (Fig. 4b,c and Fig. S2c,d, Supporting information).

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 (i) giraffe became more evenly distributed relative to human presence (Fig. S2f, Supporting information) and (ii) elephant moved to wetter areas and closer to rivers (Fig. S2g, Supporting information). An even greater similarity between seasons was evident in the distributions of the large herbivores in the ranches (Fig. S2e,g, Supporting information). 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 dry season in the ranches (Fig. S1f, Supporting information).

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. (i) 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. (ii) Small herbivores (Thomson’s gazelle, impala) show a pronounced tendency to concentrate in the ranches outside the protected reserve during both seasons. (iii) 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. (iv) Large herbivores (buffalo and elephant) concentrate in the reserve throughout the year, except for giraffe. (v) 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. (vi) 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, and minimizing exposure to risks (Jarman 1974; Sinclair & Arcese 1995a; Olif, Ritchie & Prins 2002; Hopcraft, Olif & Sinclair 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, Sinclair & Packer 2005; Riginos & Grace 2008). Consequently, small herbivores seek areas that are relatively free from predators in the ranches as they are more susceptible to predation because of their small sizes (Sinclair, Mduma & Brashares 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
Fig. 3. Partial predictions of the expected conditional 75th quantile of density and its 95% confidence limits based on the multivariate semi-parametric 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.
but also satisfy their high-quality forage requirements by feeding on short, nutritious grasses maintained by livestock, whereas large herbivores similarly fulfill their high biomass needs by feeding on tall grasses in the reserve (Jarman 1974; Senesig, Demment & Laca 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 & 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. 1988a; Georgiadis & McNaughton 1990), river banks and wet and sticky soils (Talbot & Talbot 1963) and have elevated risks of predation because of dense vegetation cover (Hopcraft, Sinclair & Packer 2005; Riginos & Grace 2008). 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 as the areas are either highly productive or support high-quality forage but have low NDVI signals as a result of intensive grazing, or have lower predation risk because of 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 because of their low numbers. These areas likely have forage of high nutritional quality and digestibility and lower predation risk as a result of 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, Bhola & Reid 2005). Furthermore, these patterns suggest exclusion from the short grass
Fig. 4. Partial predictions of the expected conditional 75th quantile of density and its 95% confidence limits based on the multivariate semi-parametric 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.
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, Sinclair & Packer 2005; Hopcraft, Olff & Sinclair 2010) jointly determine the location of hotspots of the small and medium herbivores.

Both buffalo and elephant are less susceptible to predation (Sinclair, Mduma & Brashares 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 as a result of strong exclusion by livestock, people and settlements. Giraffe are almost exclusively browsers and favour trees (Owen-Smith 1988), suffer relatively little from predation (Sinclair, Mduma & Brashares 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 Reid et al. (2003), 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. Therefore, 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 & 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 portray 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). Therefore, although it is likely true that migratory herbivores and livestock jointly facilitate the resident small and medium grazers 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 because of competition for food in the dry season with the migrants. From this perspective, livestock not only 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 are reduced throughout the region, but are higher inside the reserve compared to that in the ranches (Reid et al. 2003; Ogutu, Bhola & Reid 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. 2007); 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 suggest 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 as their mouth morphology and digestive physiology are specialized for selecting high-quality components of vegetation in-between the low-quality dry vegetation (Wilmshurst, Fryxell & Colucci 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 & 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, provide evidence for displacement by the migratory herds from their preferred open grassland habitats (Sinclair 1979). However, as migrants absorb most predation pressure on resident ungulates when they are present in the reserve (Saha 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 as a result of 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, Galvin & Russell 2008; Butt, Shortridge & WinklerPrins 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, Bhola & Reid 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 forces 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. 2007). 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 & 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; Ogotu et al. 2009) 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, Russell & Cuthill 2009) and Tanzania’s Tarangire-Simaniro (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.

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References


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Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** The factors influencing the distribution of (a) Impala, (b) Grant’s gazelle, (c) hartebeest, (d) wildebeest, (e) buffalo, (f) giraffe and (g) elephant hotspots in the Mara region of Kenya in the wet season during 1977–2010.

**Fig. S2.** The factors influencing the distribution of (a) Impala, (b) Grant’s gazelle, (c) hartebeest, (d) wildebeest, (e) buffalo, (f) giraffe and (g) elephant hotspots in the Mara region of Kenya in the dry season during 1977–2010.

**Table S1.** 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.

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