Journal for Nature Conservation 34 (2016) 151–164

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.de/jnc

Effects of extreme land fragmentation on wildlife and livestock population abundance and distribution

Mohammed Y. Said[a,b,c], Joseph O. Ogutu[a,d,*], Shem C. Kifugo[a,e], Ogeli Makui[a,f], Robin S. Reid[a,g], Jan de Leeuw[a,h]

[a] International Livestock Research Institute, P.O. Box 30709, Nairobi 00100, Kenya
[b] Center for Sustainable Drylands Ecosystems and Societies, University of Nairobi, P.O. Box 30197, 00100, Nairobi, Kenya
[c] Kenya Market Trust, 14 Riverside, Cavendish Block 3rd Floor, Suite B, Riverside Drive, P.O. Box 44817, 00100, Nairobi, Kenya
[d] University of Hohenheim, Institute of Crop Science, Biostatistics Unit, 70599 Stuttgart, Germany
[e] Northern Rangelands Trust, Private Bag, Isiolo, 60300, Kenya
[f] Africa Wildlife Foundation, P.O. Box 48177, Nairobi 00100, Kenya
[g] Center for Collaborative Conservation, Colorado State University, Fort Collins, CO, 80523, USA
[h] Baku State University, Faculty of Ecology and Soil Science, AZ 1148 Baku, Azerbaijan

ARTICLE INFO

Article history:
Received 24 May 2015
Received in revised form 20 October 2016
Accepted 21 October 2016

Keywords:
Land fragmentation
Fences
Wildlife
Pastoralism
Livestock
Ungulates

ABSTRACT

Fragmentation, degradation and loss of natural habitats are now recognised as major threats to wildlife conservation and mobile pastoralism in East African savannas. These processes are driven primarily by land tenure and policy, increasing human population, expansion of settlements and agricultural farms, road networks, urban development and fencing. To understand and characterise the forces driving habitat fragmentation, we analyse how biophysical (soils, slope, rainfall, rivers) and human-created (roads, towns, parks, quarries) features influence where people choose to fence the land in the Athi-Kaputiei ecosystem of Kenya. We also explore the consequences of land fragmentation through fencing on the abundance and distribution of wildlife and livestock populations. We show that fences are most highly concentrated along the major roads and around the major urban centres. Movements of migratory wildebeest and zebra between the Nairobi National Park and the pastoral Kitengela Plains adjoining the park on the south are getting increasingly impeded by increasing concentration of fences. Populations of wildebeest and other herbivores have collapsed to a small fraction of their former abundance largely owing to destruction of their habitats and obstruction of their movements between the park and the pastoral lands by fences and other land use developments. Conserving the key seasonal wildlife dispersal areas in the Athi-Kaputiei Plains is critical to ensuring the future viability of several key wildlife species in Nairobi National Park. Several initiatives, including a conservation land lease program has been launched, but their spatial coverage and funding levels would need to be greatly expanded to secure sufficient open spaces for both wildlife and livestock.

1. Introduction

Global biodiversity is changing at an unprecedented speed and scale as a complex response to several human-induced changes in the global environment (Sala et al., 2000). In particular, human-induced fragmentation of landscapes is occurring on scales and at rates that are far greater than normally produced by natural events (Wiens, 1990). Fragmentation is a landscape level process in which a specific habitat is progressively subdivided into smaller and more isolated fragments (McGarigal & Cushman, 2002), with altered adjacency patterns and spatial characteristics (Garrison, 2005). At local scales, fragmentation and loss of natural habitats caused by human activities and changes in land use represent major threats to flora and fauna (Garrison, 2005; Leblois, Estoup, & Streiff, 2006; Ricketts & Imhoff, 2003).

Tropical grasslands and savannas are highly threatened ecosystems as a result of land use changes (Galvin & Reid, 2007; Sala et al., 2000). These global and local land use changes can adversely affect biodiversity through a variety of population and community

* Corresponding author at: University of Hohenheim, Institute of Crop Science, Biostatistics Unit, 70599 Stuttgart, Germany.
E-mail addresses: msaid362@gmail.com (M.Y. Said), jogutu2007@gmail.com, josephogutu@yahoo.com (J.O. Ogutu), ckifugo2014@gmail.com (S.C. Kifugo), omakui2009@yahoo.com (O. Makui), Robin.Reid@colostate.edu (R.S. Reid), jan45leeuw@gmail.com (J. de Leeuw).

http://dx.doi.org/10.1016/j.jnc.2016.10.005
1617-1381/

processes over a range of temporal and spatial scales (Cayuela, Golicher, Benayas, Gonzalez-Espinosa, & Ramirez-Marcial, 2006; Dunning et al., 1995). Yet, while fragmentation and its impacts on biodiversity has been the focus of many investigations (Debinski & Holt, 2000; Fahrig, 2003; McGarigal & Cushman, 2002), relatively few studies have thus far examined fragmentation and its impacts on habitat loss in grasslands or pastoral lands (McGarigal & Cushman, 2002; Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012; Reid, Thornton, & Kruska, 2004; Swift & Hannon, 2010). Thus, relative to other systems, the effects of fragmentation in pastoral savanna ecosystems are still poorly understood (Galvin & Reid, 2007), and little is currently known about the forces driving habitat loss and fragmentation and their ecological and economic consequences to pastoral communities.

Understanding the principal underlying causes and consequences of fragmentation and habitat loss is fundamental to the effective management and conservation of human-dominated ecosystems, including the savannas of East Africa, for several reasons. First, studies of fragmentation can help enhance our understanding of the mechanisms underlying observed community and population level patterns (Debinski & Holt, 2000). Second, many studies have suggested that if fragmentation assessments involve more than two species with differing habitat relationships then they can provide a sound basis for effective conservation and management of multiple species of conservation concern (Debinski & Holt, 2000; Garrison, 2005; Johnson, Wiens, Milne, & Crist, 1992). Third, Wiens (1990) suggests that fragmentation will affect wildlife generally based on their ecological requirements. For example, disruptions of the migratory routes of wildebeest and zebra populations by livestock fences around Kruger National Park in South Africa, Etosha National Park in Namibia and the Kalahari in Botswana were associated with major contractions of their seasonal ranges and marked population declines (Berry, 1997; Spinage, 1992; Whyte & Joubert, 1988; Williamson & Williamson, 1985). Such large reductions in the population size of migrants can increase the rate of inbreeding, leading to loss of genetic variation, fixation of deleterious alleles, thus greatly reducing their adaptive potential and increasing the risk of local population extinctions (Leblois et al., 2006). Lastly, recent studies further suggest that landscape configuration becomes important at low levels of habitat suitability, with different species disappearing at different thresholds along habitat-loss gradients (Fahrig, 2003; Martensen et al., 2012; McAlpine et al., 2006; Swift & Hannon, 2010).

The arid and semi-arid savannas of East Africa are important areas for pastoralism and are also key areas holding large and diverse populations of wild ungulates (Norton-Griffiths & Said, 2010). However, most of the areas are now faced with increasing land-use changes, fragmentation and habitat loss due to increasing human population, land tenure changes, land subdivisions, (Kimani & Pickard, 1998; Norton-Griffiths et al., 2008; Reid et al., 2004; Rutten, 1992), agricultural expansion (Campbell, Gichohi, Mwangi, & Chege, 2000; Homewood et al., 2001; Norton-Griffiths et al., 2008), urbanization and inappropriate land use policies (Homewood et al., 2001; Reid et al., 2008; Rutten, 1992).

The Athi-Kaputiei Plains of Kenya (AKP) represent an extreme case where changes in land tenure, proximity to a major city, urbanization and immigration are causing rapid land use changes in a pastoral savanna and may well represent the future of other, currently less intensely used, pastoral ecosystems in East Africa (Ogutu et al., 2013; Reid et al., 2008).

Major land use developments, including fencing, are occurring in AKP, with important repercussions for wildlife and pastoralism. A major impact of fencing on animals is reduced food acquisition because of restriction on their movements (Western & Gichohi, 1993) and increased risk of predation of wild ungulates and depredation of livestock by large predators due to increasing scarcity of their supporting natural prey base (Fryxell & Sinclair, 1988; Tambling & Du Toit, 2005). In correspondence with the declining wild ungulate populations, livestock depredation has increased significantly in the AKP. As a result, a carnivore protection program operated by the Friends of Nairobi National Park (FoNNAP) paid livestock keepers in AKP a total of 6 million Kenya shillings between March 2001 and August 2008 for the loss of 1330 livestock to large carnivores to avert retaliatory killings of the carnivores (Ogutu et al., 2013).

Poaching has also contributed to the declining wildlife numbers in the AKP and is widespread in many areas bordering protected areas of East Africa (Newmark 2008; Ogutu, Piepho, Dublin, Bhola, & Reid, 2009; Western, Groom, & Worden, 2009). A recent increase in poaching incidences is linked to densification of fences in AKP and a large market for cheap bush meat. Poachers kill wildlife by running animals into fences and using spot lights to daze them at night. Poachers also set snares along fence lines and river banks (FoNNAP Newsletter May 2009). Recently, 3708 wire snares and traps targeting wild animals were detected and removed in AKP by FoNNAP and KWS staff. Anecdotal reports by long-term residents of AKP and major local newspapers in Kenya indicate that the number of snares in AKP increases during droughts when the price of meat increases. The combined impacts of fencing, habitat loss and poaching accelerate the rate of wildlife population declines and their range contraction in the AKP.

The adverse effects of fencing are not only limited to wildlife but also extend to livestock (Reid et al., 2004, 2008). Fencing reduces not only mobility, but also access to water and grazing range available to livestock and is also associated with declining livestock numbers in AKP, with negative consequences for the livelihoods of the local pastoral community. A high density of fences and settlements increases the sensitivity of both wildlife and livestock to recurrent severe droughts and occasional extreme floods (Hillman & Hillman, 1977; Ogutu et al., 2013) and the associated outbreaks of infectious diseases. Heavy losses of livestock during such droughts and floods hugely impacts on pastoral livelihoods (Nkedianye et al., 2011; Ogutu, Piepho, Said, & Kifugo, 2014). Notably, livestock keepers in AKP have lost substantial numbers of livestock during severe droughts or floods. For example, major epidemics of foot and mouth disease occurred in 1970-80, East coast fever in 1984 and blue tongue in sheep and goats in 2000 (Mwacharo, Otieno, & Okeyo, 2002; Mutune, Waruiru, & Kilelu, 2003; Moenga et al., 2013). In the neighbouring areas of Amboseli and Magadi, livestock keepers lost more than 90% of their livestock in the 2009 drought (Ogutu et al., 2014; Western, 2010). Huge herds of livestock migrated to AKP and worsened the effect of drought on wildlife and resident livestock (Ogutu et al., 2013).

The AKP epitomises the type and extent of land use changes occurring across most pastoral lands of East Africa and may, unfortunately, well represent the future state of many pastoral savanna ecosystems in the absence of urgent and effective remedial interventions. Changing land tenure arrangements, *lasses-faire* land use policies, increasing human population and the associated fences and settlements, urbanization and sedentarization of the formerly semi-nomadic Maasai are adversely impacting wildlife and livestock populations and pastoral wellbeing in AKP, as in other pastoral rangelands of East Africa. Fragmentation through densification of fences and settlements raises the risk of transmission of infectious diseases between wildlife and livestock (Bedelian, Nkedianye, & Herrero, 2006), predation risk and illegal human harvests of wildlife (poaching).

Many initiatives are being undertaken since 2000 to slow down or stop the rate of fencing in the AKP including a conservation land lease program that pays land owners about $4 per acre ($10 per hectare) per year not to fence or cultivate but keep their land open for use by wildlife and livestock. This program has helped

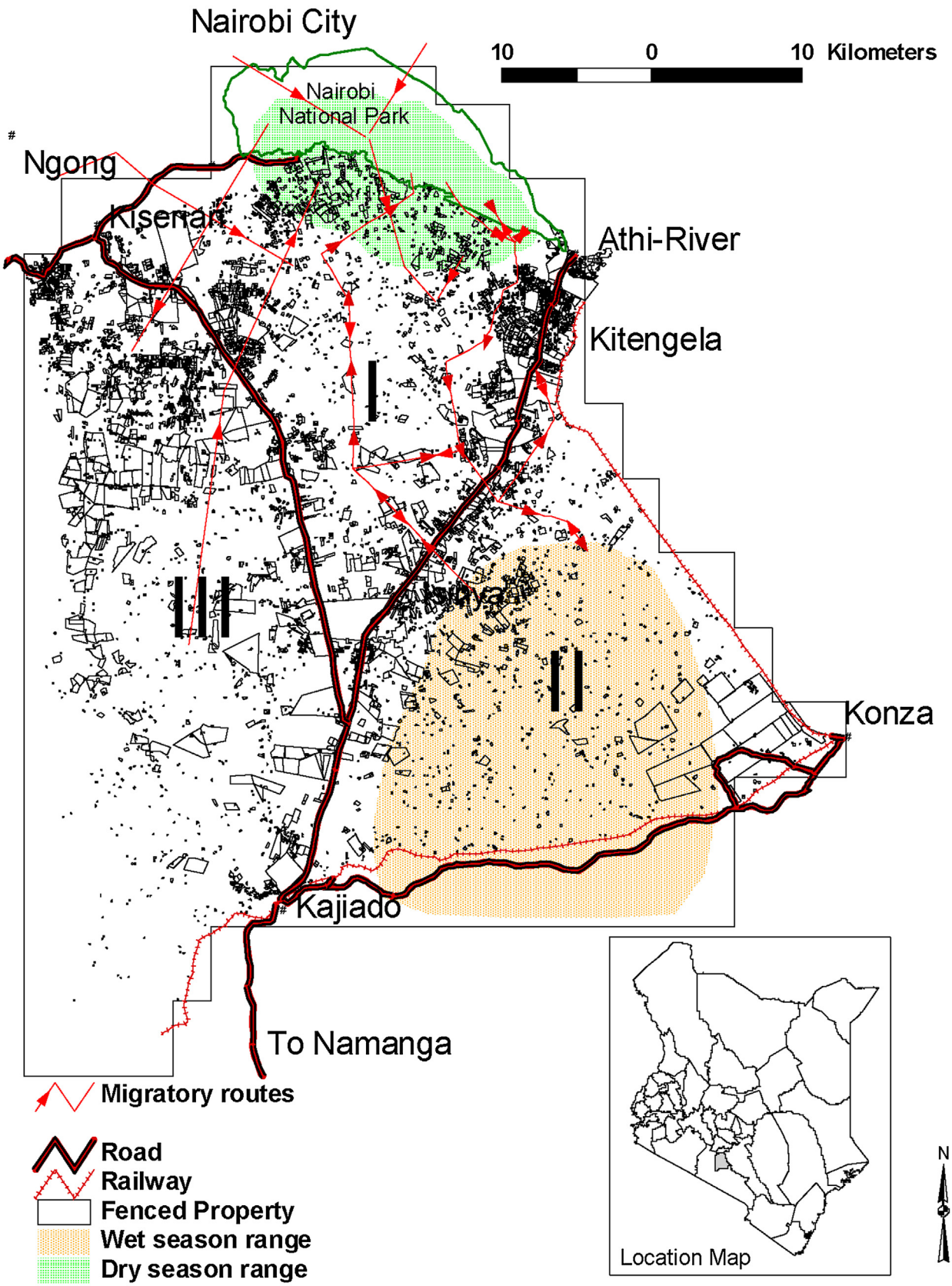

Fig. 1. (a) Map of the Athi-Kaputiei ecosystem showing the distribution of fenced plots, towns, roads, Nairobi National Park, and the wet and dry season ranges of the migratory wildebeest. The wildebeest move from Triangle I and the Nairobi National Park to Triangles II and III during the wet season (November-June) and return in the dry season (August–October) each year. The historical migratory paths are also provided. (b) The current status and level of threats facing the routes used by wildlife for seasonal migration or dispersal in the Athi-Kaputiei Ecosystem of Kajiado County, Kenya. Narratives on the routes, their current status and the threats facing each route (numbers 1–7) are provided in Table S2.

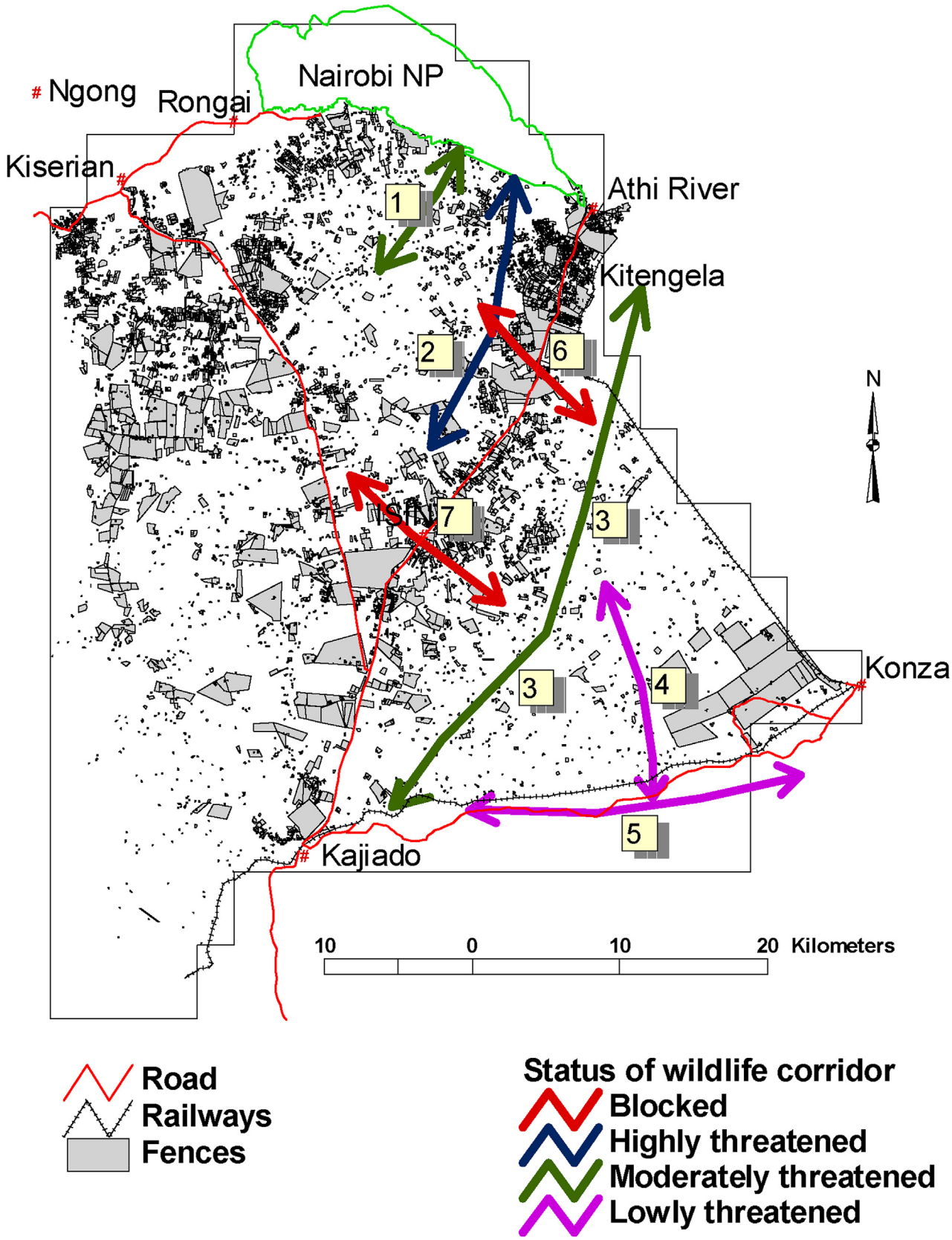

Fig. 1. (*Continued*)

keep parts of Triangle I (Fig. 1a) open and the program is also being expanded to cover other parts of the AKP, especially areas deemed critical for wildlife including the wet season dispersal ranges and migratory wildlife corridors. The land lease program covered about 216 km^2 by 2012 (Ogutu et al., 2013) and is anticipated to expand to cover an area of about 600 km^2. These programs

have almost certainly helped to slow down the loss of wildlife and livestock and their habitats in AKP. However, rapid expansions of urban centres in Isinya, Kitengela (Fig. S1), Ngong and elsewhere in AKP and expansion of existing and development of new major roads through AKP, excision of the northern border of Nairobi National Park to build the Southern bypass road and current plans to build a standard gauge railway line above ground but right across the park, will progressively accelerate fragmentation of the landscape. These developments reduce the few remaining open spaces for wildlife and pastoral livestock and hence also the connectivity among the different parts of AKP, portending a highly insecure future for wildlife populations and pastoral livestock production in AKP. However, although worthwhile and timely, initiatives such as the land lease program are likely to prove unsustainable in the long-term given the spiraling land prices in AKP. A stronger and more vibrant societal involvement possibly through establishment of community conservancies, negotiated land purchases, permanent conservation easements (restriction), stronger control of illegal harvests by intensifying anti-poaching efforts and regulation of livestock stocking levels, land subdivision and construction of fences and settlements, would be necessary to protect the remaining critical areas for wildlife and pastoral livestock in AKP.

Here, we analyze how natural (soils, slope, rainfall, rivers) and human-created (roads, towns, park, quarries) features influence where people choose to fence the land in the Athi-Kaputiei ecosystem. We also explore the consequences of this land fragmentation through fencing on the abundance and distribution of wildlife and livestock populations. We analyse the temporal and spatial trends of two migratory wildlife species; the wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga burchelli*) which utilise both the Nairobi National Park and the adjoining AKP under a mixture of private and communal tenure and two resident small herbivore species; Thomson's gazelle (*Gazella thomsoni*) and impala (*Aepyceros melampus*) that are relatively abundant on the AKP, and livestock. The livestock species comprise cattle (*Bos indicus*), sheep (*Ovies aries*) and goats (*Capra hircus*). We compare the trends of the four wildlife species outside the park and examine shifts in their spatial distribution in the AKP.

2. Materials and methods

2.1. Study area

The study was conducted in the AKP located south of the city of Nairobi and Nairobi National Park (Fig. 1). The plains are the traditional home to the Kaputiei Maasai who depend principally on pastoral livestock production but are also increasingly diversifying their livelihood options (Kristjanson et al., 2002; Nkedianye, Radeny, Kristjanson, & Herrero, 2009; Rutten, 1992). A large number of urban residents, industries and civil society organisations are purchasing land in the plains and local towns are growing rapidly. The plains host sizable livestock and wildlife populations and constitute a critical wet season dispersal range for wildlife inhabiting the Nairobi National Park (Foster & Coe, 1968; Foster & Kearney, 1967; Gichohi, 1996; Ogutu et al., 2013; Petersen & Casebeer, 1972). The plains extend to the large commercial ranches in the vast Machakos County to the east and are linked to the Amboseli National Park to the south by the gently descending Emarti Valley.

Major land use and tenure changes have occurred in the AKP in the last century. These changes include privatization of the formerly communal land tenure arrangement (Rutten 1992) and fencing of the individual land parcels from the mid 1960s (Kimani & Pickard, 1998; Reid et al., 2008). Changes in land tenure, land use, relocation of old and development of new industries and urban development in the AKP have constrained the use of water from local rivers and dams and forage resources and thus the seasonal dispersal of both livestock and wildlife (ACC, 2005; Ogutu et al., 2013). In some cases, important habitats for wildlife have been lost to other land uses, such as development of settlements, towns, factories or flower farms (Ogutu et al., 2013; Fig. S1).

2.2. Data

All fences in the Kitengela section of the AKP were mapped to document the distribution of fences in relation to rainfall, terrain slope and altitude, locations of Nairobi National Park, rivers, towns, quarries, and tarmacked roads. The mapping exercise was conducted by members of Kitengela community, Kitengela Ilparakuo Land Association (KILA), The Wildlife Foundation (TWF) and Friends of Nairobi National Park (FoNNAP), with financial, scientific, technical and logistical support provided by the International Livestock Research Institute (ILRI). The field researchers consisted of 24 local community members mostly secondary and college graduates trained in the use of Geographic Positioning System (GPS). Each of the 10 teams was located in an area near their homesteads and were equipped with GPS and topographic maps. Mapping of the first two sections of the study area, locally known as Triangles I (575 km^2) and II (836 km^2, Fig. 1a) was conducted during June–October 2004. The third section, called Triangle III (943 km^2, Fig. 1a), was mapped in 2009 when fence maps for Triangles I and II were also updated. The field teams mapped 15540 fences, 4433 settlements, 1138 quarries, 487 dams, 1081 water points, towns, 15 flower farms and 712 tree plantations in 2009.

We derived spatial datasets on distances to the nearest roads, rivers, towns, quarries and from the southern boundary of the Nairobi National Park, soils, slope, elevation and rainfall. The GIS layers for roads, rivers, and park boundary were acquired from the Survey of Kenya based on topographic maps of 1: 50,000 and recent satellite images. Similar recent information for Nairobi National Park boundaries was obtained from satellite images and maps provided by the Kenya Wildlife Service (KWS). Data on soils were obtained from Kenya Soils Surveys. Data on slopes were derived from a Digital Elevation Model with a 90 m resolution obtained from the Shuttle Radar Topographic Mission. Data on rainfall were extracted from the Almanac Characterization Tool database (Mudsprings Inc, 1999). All the GIS layers for soils, slope, and rainfall were overlaid in a raster GIS and resampled to a common spatial resolution of 100 m × 100 m, determined by the spatial resolution of the areas enclosed within the fences.

The Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS) has been conducting aerial surveys in the rangelands of Kenya since 1977. DRSRS conducted a total of 26 surveys in AKP from 1977 to 2014. The 2197.9 km^2 AKP is partitioned into 5 km × 5 km UTM grids except in 1977 when 5 km × 10 km grids were used. The grids forming a counting strip constitute a transect. Each 5-km transect segment is treated as an observation unit. Systematic transect lines are flown through the centre of each grid on a north-south axis at a nominal height of 91–122 m above ground. Widths of counting strips averaged 293.7 ± 52.0 m (range 224–490 m) during 1977–2014. Two rear-seat observers count all wild and domestic animals the size of Thomson's gazelle (15 kg) and larger within each strip and record all counts on tape recorders. Animals in large herds of more than 10 are photographed and later counted under a binocular microscope (in early years) or on a large digital screen. The sample fraction averaged 6.0 ± 1.6% of the total counting area. Reliability of the DRSRS counts has been established using multiple calibrations (Ottichilo & Khaemba, 2001). Population estimates (PE) and their standard errors (SE) for each species are calculated from the sample fraction by treating each transect as a sample unit using Jolly's Method 2 (Jolly, 1969; Norton-Griffiths,

Table 1
Tests of significance of the effects of rainfall, terrain slope, altitude and distance of fences to the nearest rivers, roads, towns, Nairobi National Park boundary, quarries and their interactions on the expected probability of occurrence of fences in the Athi-Kaputiei Plains of Kenya. The estimated effect size (Estimate) and its standard error (SE), the numerator degrees of freedom (NDF), the denominator degrees of freedom (DDF) and *t*-test of the hypothesis that the estimate is significantly different from zero and the associated probability (P > |T|) are also provided.

[a]Effect	Estimate	SE	NDF	DDF	T	P > |T|
Intercept	−8.90589	0.528023	1	193564	−16.87	<0.0001
annpre	0.017898	0.001584	1	193564	11.30	<0.0001
annpre × annpre	-2.1×10^{-5}	1.31×10^{-6}	1	193564	−16.21	<0.0001
slp × slp	−0.00049	5.44×10^{-5}	1	193564	−8.99	<0.0001
dstrd	−1.83124	0.036497	1	193564	−50.17	<0.0001
dstrd × dstrd	0.02014	0.000286	1	193564	70.51	<0.0001
dstrv	0.51813	0.018015	1	193564	28.76	<0.0001
dstrv × dstrv	−0.04269	0.004078	1	193564	−10.47	<0.0001
alt	0.003801	0.000188	1	193564	20.23	<0.0001
dstrd × alt	0.000952	2.19×10^{-5}	1	193564	43.36	<0.0001
dstq	0.060775	0.006159	1	193564	9.87	<0.0001
dstq × dstq	−0.01403	0.000536	1	193564	−26.19	<0.0001
dstrd × dstq	−0.02676	0.000492	1	193564	−54.42	<0.0001
dstq × dstpk	0.006907	0.000265	1	193564	26.05	<0.0001
dsttwn	−0.13867	0.008058	1	193564	−17.21	<0.0001
dsttwn × dsttwn	0.024352	0.000738	1	193564	33.00	<0.0001
dstrd × dsttwn	−0.01892	0.000572	1	193564	−33.07	<0.0001
dstrv × dsttwn	−0.03171	0.001729	1	193564	−18.34	<0.0001
dstpk	−0.06138	0.002131	1	193564	−28.80	<0.0001
dstrv × dstpk	−0.00863	0.000474	1	193564	−18.22	<0.0001
dstrd × dstpk	0.002841	0.000217	1	193564	13.06	<0.0001
dstpk × dsttwn	−0.00099	0.000227	1	193564	−4.37	<0.0001

[a] alt = altitude, annpre = annual precipitation, slp = slope, dstrd = distance to road, dstrv = distance to river, dstpk = distance to park, dsttwn = distance to town, dstq = distance to quarry.

1978) as $PE = N\bar{y}$ and $SE = \sqrt{N(N-n)s^2}/n$, where N is the number of observations required to fully cover the study area, $\bar{y}$ is the sample mean, n is the sample size and s^2 is the sample variance. The transect lines are systematically distributed in space, hence the surveys also give spatial distributions of wildlife and livestock. More detailed accounts of the survey methodology can be found elsewhere (Norton-Griffiths, 1978; Ogutu, Owen-Smith, Piepho, & Said, 2011; Ogutu et al., 2013; Ogutu et al., 2016; Western et al., 2009).

Therefore, we computed the density (animals/km^2) of each species found in each 5 km × 5 km grid cell within the three Triangles during each survey. The variation in the density and the proportion of each triangle occupied by each species were averaged over three periods spanning 1977–1987, 1988–1998 and 1999–2014 to minimise the influence of stochastic variation in the count totals (Ogutu et al., 2011, 2013). These periods were chosen to represent increasing intensities of land transformation in the AKP through time (Ogutu et al., 2013; Reid et al., 2008). Lastly, we produced spatial distribution maps of the average densities of wildlife and livestock species calculated over the 1977–87, 1988–1998 and 1999–2014 periods to portray temporal changes in their spatial distributions. The start and end dates and technical details of each of the aerial surveys are provided in S1Data. The survey details, the UTM coordinates for each sampling unit, the area of each sampling unit and the total number of animals of each species counted in each sampling unit are provided in S2Data. The estimated total population sizes of the common wildlife and livestock species in AKP and their associated standard errors derived from DRSRS surveys conducted in January 1977 and January 2014 are provided in S3Data.

2.3. Statistical analysis

We used a Multiple Logistic Regression (MLR) model to evaluate the significance of factors influencing the probability of occurrence of fences in the pastoral areas of the Athi-Kaputiei ecosystem. The MLR model was used to estimate coefficients of the explanatory variables with the presence or absence of a fence in a grid cell as the dependent variable. The MLR model was fitted using restricted log pseudo-likelihood in the SAS GLIMMIX module (SAS Institute, 2016). The predictive abilities of logistic regression models containing various subsets of the explanatory variables were evaluated using the corrected Akaike information criterion AICc (Akaike 1974; Burnham & Anderson, 2002).

We first fitted univariate regression models including linear, standard quadratic or quadratic without a linear term in each of the eight predictor variables and computed AICc values for each model ($n = 3$) and predictor variable ($n = 7$) combinations. The eight predictor variables were distances to the nearest town, river, park, quarry, road and point on the Nairobi National Park boundary, annual precipitation and terrain slope. We then used AICc to rank the three candidate models for each of the eight variables. Model selection was based on the difference between the AICc value for each of the three models for each predictor variable and the smallest AICc, ΔAICc (Burnham & Anderson, 2002). The model with the smallest value of ΔAICc was chosen as providing the best approximate fit to the data (Burnham & Anderson, 2002). Starting with a model containing only the predictor variable with the best overall support among all the eight predictor variables we sequentially added predictor variables and their interaction terms and retained extra variables or interaction terms in the model only if their addition reduced the value of the AICc (Burnham & Anderson, 2002). This procedure was repeated until all the explanatory variables had been considered. To minimize collinearity, we included only one member of a pair of variables with a Spearman rank correlation coefficient of at most 0.75 (Sokal & Rohlf, 1995). The goodness-of-fit of the final model was evaluated using the maximum rescaled Nagelkerkes' r^2 and concordance between the predicted and observed occurrence of fences.

The selected model was then used to predict the probability of occurrence of fences in the entire study area. Based on the frequency distribution of the predicted probabilities of fences and the probability map we categorized areas as having high (above the median) and low (below the median) probability of fences. We further analysed spatial variation in the distribution of the four wildlife species and livestock in the two landscapes with high and low prob-

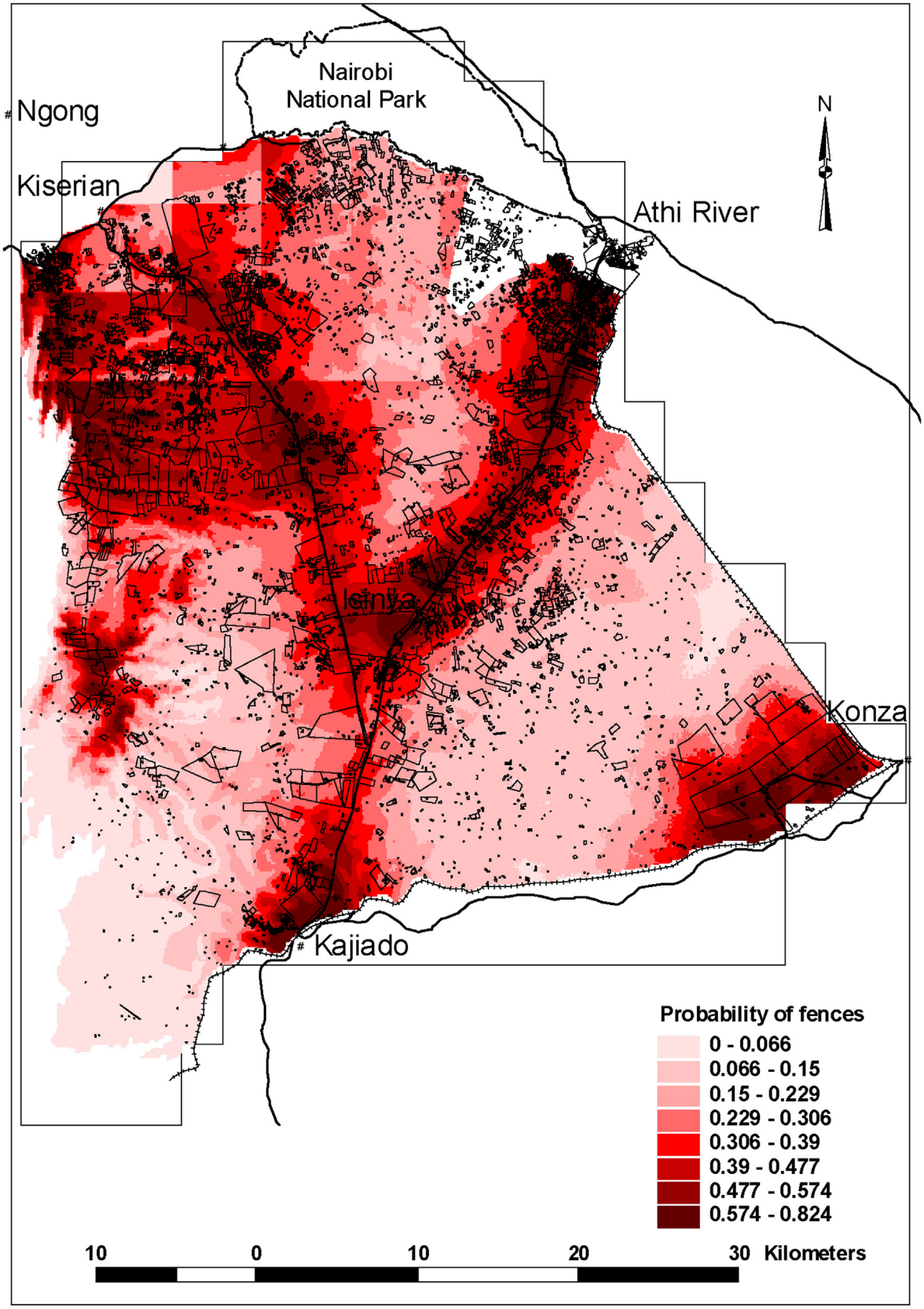

Fig. 2. The expected probability of occurrence of fences based on the selected best model.

ability of fences. The objective was to establish the impacts of fences on changes in wildlife and livestock abundances and distributions. We hypothesised that the impact of fences will vary across the three triangles because the intensity of driving factors also varied across the three triangles.

3. Results

Model selection based on AICc showed that for all the variables considered the quadratic models were better supported than the linear models (Table S1). The predictor variables and interactions with significant influences on the expected probability of occurrence of fences are summarized in Table 1. Thus, variation in the expected probability of occurrence of fences was associated with variation in rainfall, terrain slope, altitude, distances to the nearest town, road, quarry and river and proximity to Nairobi National Park and complex patterns of interactions among these variables. Reliable prediction of the probability of occurrence of fences thus needs to consider the effects of these multiple array of factors and interactions. Goodness-of-fit tests showed that the selected global model had a good explanatory power, expressed in terms of a high level of concordance between the predicted and observed occurrence of fences (75.3%) and a maximum rescaled Nagelkerke's r^2 of 0.22.

3.1. Correlates of probability of occurrence of fences

Fig. S2 shows the distribution of fences and predictor variables whereas Fig. S3 shows the relationship between the expected probability of fences and the different predictor variables. The expected probability of fences showed a humped distribution with respect to the terrain slope, rainfall and distance from the nearest river, park and quarry, with peak probabilities occurring at intermediate distances (Fig. S3). However, fences were more likely to be found closer to rivers than to the park or quarries and in areas with gentle slopes, generally below 20° (Fig. S3). The distribution of the expected probability of fences from the nearest road was U-shaped, indicating a higher likelihood of getting fences nearer to and farther from roads. A similar pattern was evident for altitude, with fences more likely to be located at both low and high than at intermediate altitudes. In contrast, the expected probability of fences declined exponentially with increasing distance from urban centres, indicating a greater concentration of fenced properties in urban and peri-urban areas (Fig. S3).

The predicted probability of fences based on the selected global model (Fig. 2) showed that fences were highly concentrated along the major roads, most notably along the Nairobi-Namanga and Kiserian-Kajiado roads, near the southern boundary of the Nairobi National Park, around Ngong Town, with high rainfall, and Konza Town. Movements of migratory wildebeest and zebra between Nairobi National Park and Triangle I, among and within the three triangles on the AKP, were getting increasingly impeded by the high concentration of fences (Fig. 2). Open areas located in the central sections of Triangle II and southern sections of Triangle III were also becoming increasingly fragmented by the spreading fences. In 2004 the total area fenced in Triangle I was 99.8 km^2 whereas in Triangle II it was 122.2 km^2. However, about 20% of the landscape in Triangles I (156.9 km^2), II (137.2 km^2) and III (157.2 km^2) combined was fenced by the end of 2009 with nearly 45% of all the fenced areas located within 3 km of the main Nairobi-Namanga trunk road, 34% along the Kiserian-Isinya trunk road and 22% along the Isinya-Kajiado road. Thus, the total area fenced in Triangles I and II increased by 24.9% from 221 km^2 in 2004 to 294.1 km^2 by 2009. Of the historical migratory paths (Fig. 1a), there are currently only a few natural passages along Isinya-Kajiado and Kiserian-Isinya and other parts of the AKP (Fig. 1b) where wildlife can still pass in the ecosystem but even the few remaining passages are severely threatened by land use developments. Overall, there were more than 15000 fenced land parcels of which about 10700 were located along the major roads. These roads traverse the migratory routes of wildebeest and zebra between their wet and dry season ranges.

3.2. Impacts of fences on wildlife and livestock population trends and distribution

The temporal trends for wildlife and livestock varied among species and between sparsely and densely fenced sections of the AKP (Fig. 3). The total wildebeest population exceeded 30,000 animals in the 1970s but had dropped to about 509 animals by 2014. The migratory wildebeest population was virtually exterminated from Triangles I and III where their density dropped by 99–100% in both the sparsely and densely fenced areas between 1977 and 1987 and 1999–2014. Wildebeest populations collapsed to a small fraction of their former abundance due to obstruction of their movements by the fences between Triangles I and II, poaching, habitat degradation and loss to roads, settlements and other developments (Ogutu et al., 2013); exemplified by the rapid expansion of Kitengela town (Fig. S1).

Wildebeest density also declined precipitously between 1977 and 1987 and 1999–2014 in the sparsely fenced areas in Triangles I (100%), II (93.4%) and III (99.8%) as well as in the densely fenced areas in Triangles I (99.4%), II (71.4%) and III (100%) (Fig. 3). As a result, most of the few surviving wildebeest were confined to the more sparsely fenced parts of Triangle II during 1999–2014 (Fig. 3). The spatial distribution of wildebeest thus changed markedly from initial dense concentrations in Triangles I and II and sparse concentrations in Triangle III during 1977–1987 to very sparse concentrations in Triangle II and virtually complete extirpation from Triangles I and III during 1999–2014 (Fig. 4a). These changes resulted in wildebeest being confined almost exclusively to a section of Triangle II by 1999–2014, with very few wildebeest herds observed in Triangles I and III (Fig. 4a). Unlike wildebeest, zebra density increased in both the sparsely and densely fenced parts of all the three triangles during 1988–1998 before declining thereafter. However, compared to 1977–1987, zebra density decreased substantially in both the sparsely (88.4%) and densely (47.3%) fenced parts of Triangle I, marginally decreased in the sparsely (34.0%) but increased in the densely (342.9%) fenced sections of Triangle II during 1999–2014. A similar pattern of decrease in density, albeit less pronounced, was apparent in the sparsely (33.1%) and densely (54.6%) fenced parts of Triangle III (Fig. 3). The spatial distribution of zebra widened during 1988–1998 compared to 1977–1987 due to the increase in their population during this period but had contracted noticeably during 1999–2014, when there was a general decline in zebra densities across the landscape and progressive local extirpations in the western sections of Triangle III, especially in the settled areas (Fig. 4b).

Thomson's gazelle density declined between 1977 and 1987 and 1999–2014 in both the sparsely (56.0–95.8%) and densely (41.1–83.1%) fenced areas in the three triangles (Fig. 3). Thomson's gazelle exhibited a general reduction in densities across the landscape due to their declining populations with range contraction most evident in the western section of Triangle III (Fig. 4c). Similarly to wildebeest, impala density decreased dramatically between 1977 and 1987 and 1999–2014 and the magnitude of the population declines was little affected by the density of fences. Thus, impala density declined by 90.1% in the sparsely and by 97.2% in the densely fenced areas in Triangle I but by 73.7% in the sparsely and 86.4% in the densely fenced parts of Triangle III. In Triangle II, in contrast to Triangles I and III, impala were nearly extirpated from the densely fenced areas (a decline of 96.1%) but decreased

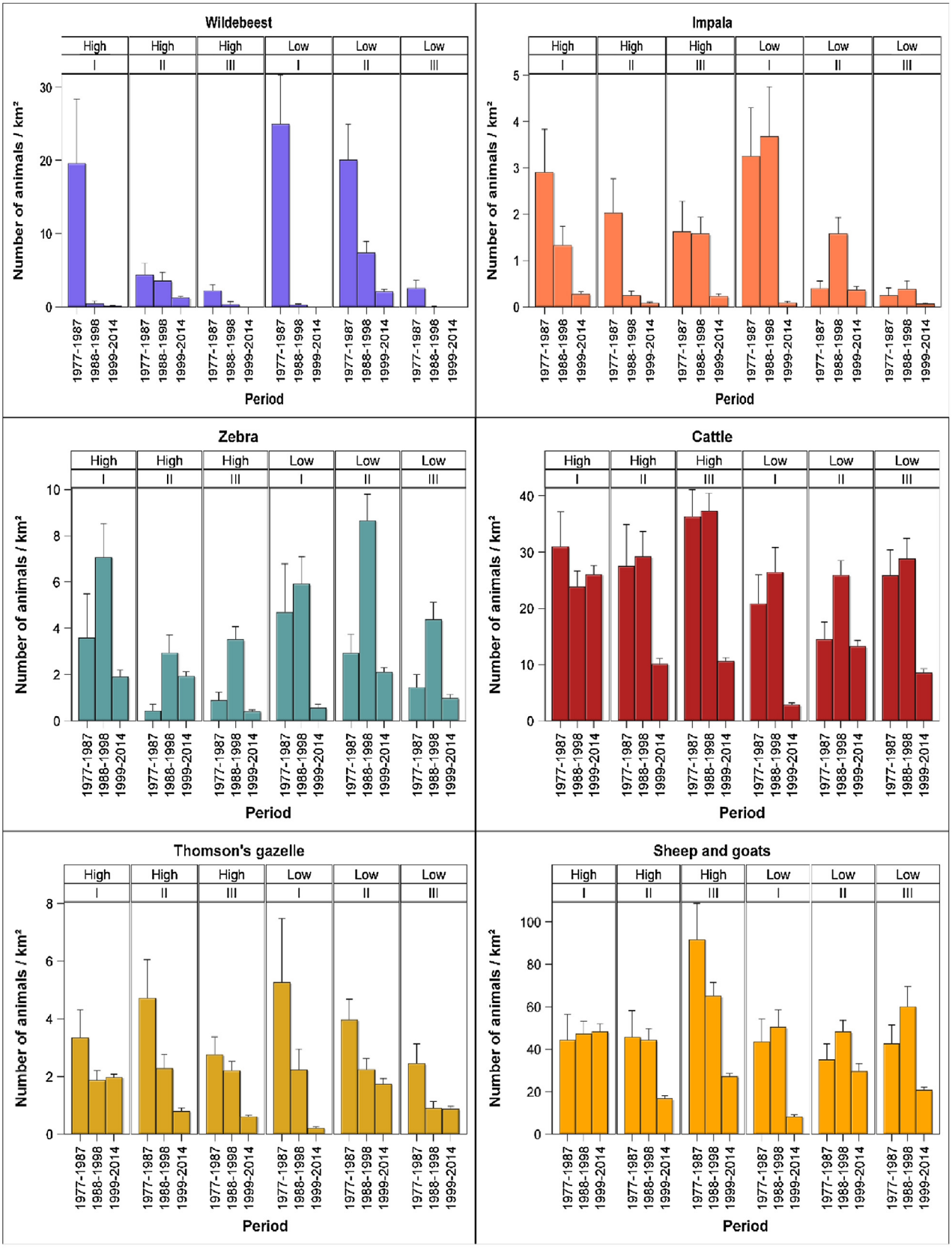

Fig. 3. Temporal trends in the density (animals/km^2) of wildebeest, zebra, Thomson's gazelle, impala, cattle, sheep and goats in areas of high (High) and low (Low) fence densities in Triangles I, II and III of the Athi-Kaputiei Plains in each survey during 1977–2014 averaged over 1977–1987 ($n = 6$ surveys), 1988–1998 ($n = 12$ surveys) and 1999–2014 ($n = 7$ surveys).

marginally in the sparsely fenced areas (10.8%) between 1977 and 1987 and 1999–2014 (Fig. 3). Impacts of land fragmentation and land use changes on the impala population were remarkably strong, resulting in marked range contractions in all the three Triangles (Fig. 4d).

In stark contrast to wildlife, livestock numbers were far higher, but likewise to wildlife, also declined strikingly between 1977 and 1987 and 1999–2014. In general, cattle were less abundant than sheep and goats in the AKP. Cattle density decreased in the sparsely fenced areas in Triangles I (86.4%), II (8.8%) and III (66.9%) as well as in the densely fenced areas in Triangles I (16%), II (63.3%) and III (70.8%) between 1977 and 1987 and 1999–2014 (Fig. 3). As with cattle, the density of sheep and goats decreased in the sparsely fenced areas in Triangles I (80.8%), II (15.7%) and III (51.6%). Furthermore, between 1977 and 1987 and 1999–2014 the density of sheep and goats increased slightly in the densely fenced areas in Triangle I (9%) but decreased in similar areas in Triangles II (63.3%) and III (70.4%) (Fig. 3). Despite the steep declines in the densities of cattle, sheep and goats, their range had not discernibly contracted in AKP (Fig. 4e and f).

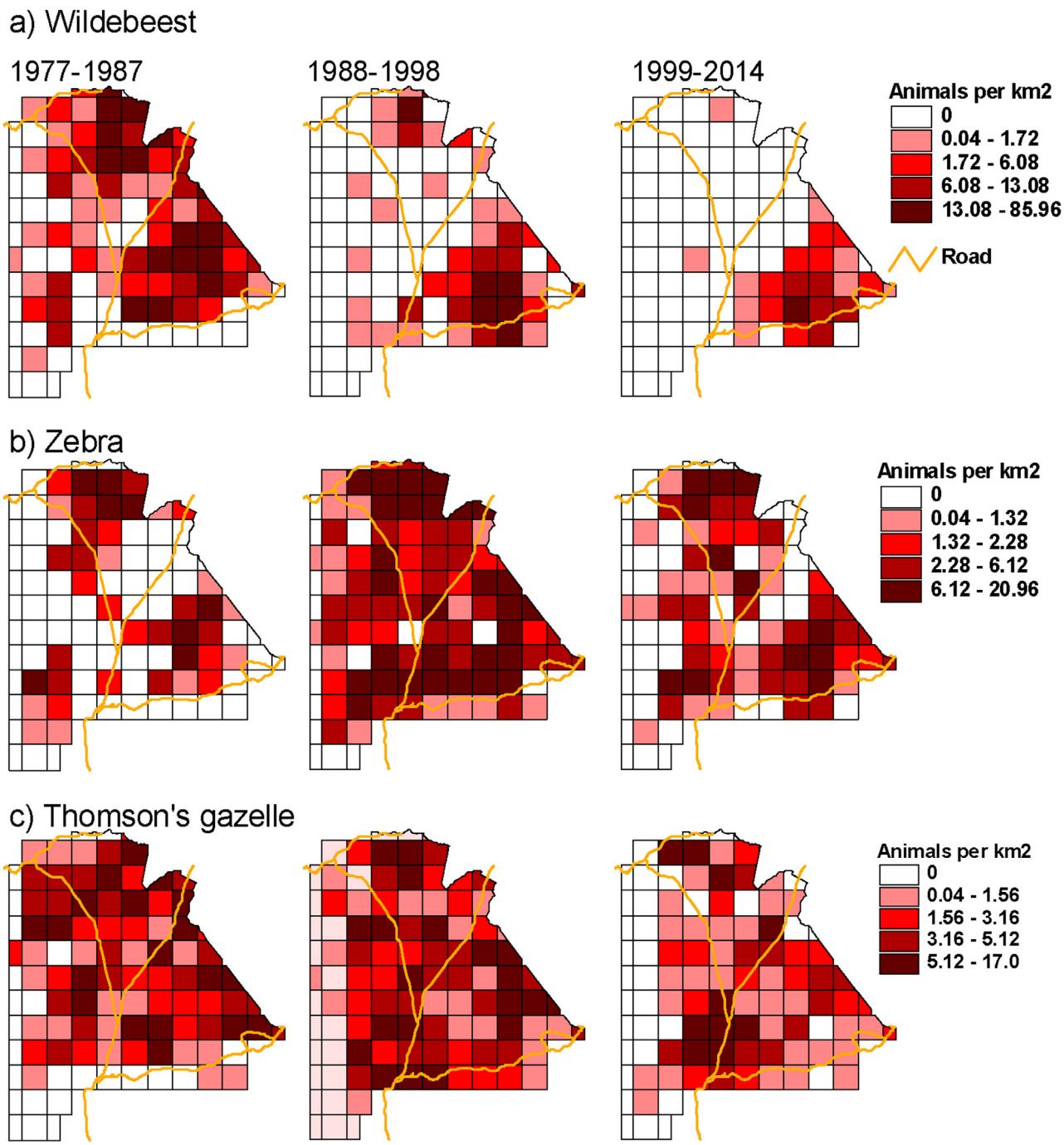

Fig. 4. The spatial distributions of the densities (number of animals per km^2) of (a) wildebeest, (b) zebra, (c) Thomson's gazelle, (d) impala, (e) cattle and (f) sheep and goats in Athi-Kaputiei Plains averaged over the 1977–1987, 1988–1998 and 1999–2014 periods.

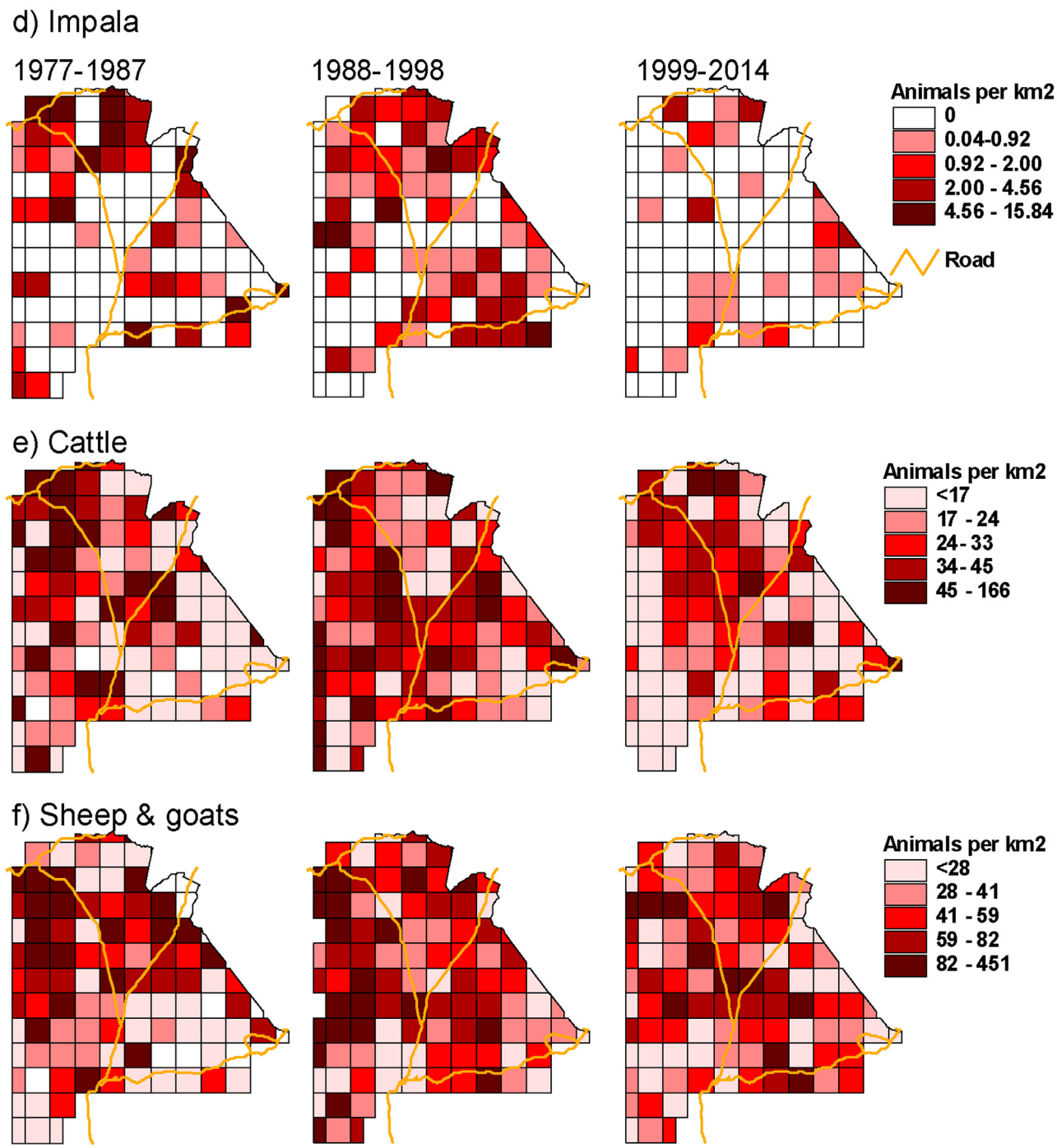

Fig. 4. (*Continued*)

4. Discussion

4.1. Spatial correlates of fragmentation

Human-created features indexed by distances to the nearest roads, boundary of Nairobi National Park, quarries and their interactions plus natural features such as distance to the nearest rivers and terrain slope were strongly correlated with the probability of occurrence of fences. A growing body of empirical evidence suggests that the impacts on biodiversity of human activities are exacerbated by the tendency to locate human settlements in areas of high biological value (Balmford et al., 2001; Ceballos & Ehrlich, 2002; Scharlemann, Green, & Balmford, 2004). This appeared to be the case in AKP, leading to dramatic local extirpations of once abundant large herbivores in areas of both low and high density of fences and hence settlements. The rapid land use changes that have occurred in the Athi-Kaputiei Plains in the last three decades have been heavily influenced by changing policy and legislation on land use, access and tenure arrangements (Rutten, 1992; Gichohi, 1996; Kimani & Pickard, 1998; Western et al., 2009), historical alienation of Maasailand (territories inhabited by the Maasai), coupled with proximity to the rapidly expanding Nairobi Metropolis, the associated infrastructure developments (Kimani & Pickard, 1998) and low land prices compared to Nairobi Metropolis. Demand for land due to population expansion in Nairobi has raised the monetary value of land in AKP, leading to particularly high prices near the park

(around $10,700 per acre by 2005) and near the major roads, while far away from the tarmacked roads, land prices averaged about $530 per acre by 2005 (ACC, 2005). In AKP land value had appreciated at over 11% per annum over the 10 years spanning 2000–2009, which compared well with the average ten-year returns from Treasury bills issued by the Central Bank of Kenya over the same period (Norton-Griffiths & Said, 2010). This has encouraged land speculators to buy land in AKP due to its proximity to Nairobi. The land use changes are rapidly and extensively disrupting the ecosystem structure and functions that require spatial connectivity, including wildlife migrations and extensive pastoral livestock production, thus compromising the long-term sustainability of the regional pastoral economies (Reid et al., 2008) and wildlife conservation endeavours (Gichohi, 1996). More precisely, the land use changes progressively degrade and truncate the AKP, excluding wildlife and livestock from parts of the ecosystem, besides constraining their movements.

4.2. Effects of fencing on wildlife and livestock population trends and distribution

Wildlife have declined sharply and significantly in the AKP over the last 40 years, and their range has contracted, reflecting the progressive habitat deterioration and loss due to human population growth, densification of settlements and fences and development of infrastructure (Gichohi, 2000; Imbahale, Githaiga, Chira, & Said, 2008; Ogutu et al., 2013; Reid et al., 2008). Perhaps most importantly, land fragmentation through fencing and settlements was contemporaneous with the declining numbers of both migratory and resident wildlife species and livestock. Most notably, the migratory wildebeest exhibited the greatest declines coincident with land fragmentation and were extirpated from vast parts of their former range. These declines reveal a greater sensitivity of the migratory species, especially wildebeest, to habitat fragmentation and land transformations (Homewood et al., 2001; Ottichilo, de Leeuw, Skidmore, Prins, & Said, 2001; Serneels & Lambin, 2001). Ogutu et al. (2013) report a collapse of the wildebeest migration in AKP. In the decade between 2001 and 2011, the highest wildebeest numbers counted in the park was 799 animals in December 2005, while during the last five years spanning 2007–2011 less than 520 wildebeest crossed into the park (Ogutu et al., 2013). More recently, from 2012 to 2015 wildebeest numbers entering the park averaged a mere 123 ± 155 animals and ranged between 0 and 337 individuals. This finding is further reinforced by information generated from line transects and by GPS collared wildebeest in AKP, indicating that wildebeest are not moving from Triangle II to I and into the park as a result of being constrained mainly by the fences along the main road and avoiding the main roads even in the absence of fences (Stabach, Wittemyer, Boone, Reid, & Worden, 2016). In contrast to wildebeest, the number of zebra entering the park between 2012 and 2015 remained relatively higher, averaging 761 animals (range 0–1387). The density of fences was far higher closer to the major roads and towns, implying that proximity to these roads and towns was an influential determinant of the location of fences and buildings. This interaction complicates separation of the role of roads and towns from that of fences in influencing the wildlife and livestock population declines without direct assessment of the role of towns and roads, including traffic volumes on the roads.

Migratory wildlife species are especially vulnerable to land use changes because they require multiple habitats and widely spatially separated resources throughout their annual migratory cycle (Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009; Morrison & Bolger, 2012; Morrison & Bolger, 2014). However, zebra appeared less sensitive to land use changes in AKP than wildebeest probably owing to their non-ruminant, bulk feeding style, enabling them to subsist on poor-quality diets (Owaga 1975). Their population increase during 1988–1998 was associated with elevated rainfall during this period (average $734\,\text{mm} \pm 26$) compared to 1977–1987 ($577\,\text{mm} \pm 11$) and 1999–2014 ($627\,\text{mm} \pm 20$). Similar resilience to anthropogenic changes in human-dominated pastoral rangelands has been noted for zebra populations in the Laikipia (Georgiadis, Olivero, Ojwang, & Romanasch, 2007) and Maasai Mara (Ogutu et al., 2011) regions of Kenya. The steep decline in impala numbers and the increasing patchiness of their distribution during 1999–2014 reflects, in part, the ongoing intensification of land fragmentation, especially in Triangle III due to conversion of rangelands to cropland and fencing. As landscapes become increasingly fragmented, species disappear faster, as the rate of extinction is inversely related to habitat area (Newmark, 1996; Rosenzweig, 2003). This is already evident for some species such as the wildebeest in large parts of its former range in the AKP (Ogutu et al., 2013) and more generally in Kajiado County within which the Athi-Kaputiei Ecosystem is located (Ogutu et al., 2014).

Gardner, Milne, Turner, and O'Neill, (1987) predicted that the ease of movement of animals through a connected landscape is rapidly lost when 30–50% of the landscape has been converted to uses incompatible with animal movement. In AKP 20% of the land surface was fenced by 2009, meaning a marked loss of connectivity and hence ease of movements. Many of the traditional migratory pathways in AKP have been blocked by fences, settlements, roads and other infrastructure. Also, the spatial distribution maps showed widespread local extirpations of wildlife populations, associated with habitat deterioration and exclusion by fences and settlements. For wildebeest, more animals were found in Triangle II and few in Triangle I in the latter part of the study period likely due to fencing.

The disruption of migratory routes makes it difficult for migrants to efficiently exploit seasonally available forage and water (Morrison & Bolger, 2012; Morrison & Bolger, 2014; Williamson & Williamson, 1985), leading to population declines or collapse. Thus, long-term wildlife population trends in the Athi-Kaputiei Ecosystem reveal that the migration of wildebeest between the Nairobi National Park and AKP collapsed from 5000–10000 animals during 1989–2000 to fewer than 800 animals during 2001–2011 (Ogutu et al., 2013) due to the ongoing land use changes in the APK. Recent bimonthly censuses show that the population of wildebeest entering Nairobi Park remained under 350 animals throughout 2012 to 2015. The extreme loss of wildlife and contraction of their distributional ranges in AKP mirror the catastrophic loss of wildlife in the rest of Kajiado County in which AKP is located (Ogutu et al., 2014), Masai Mara (Ogutu et al., 2011) and other rangelands of Kenya (Ogutu et al., 2016) between 1977 and 2016.

In conclusion, the Athi-Kaputiei ecosystem of Kenya exemplifies an ecosystem experiencing extreme landscape fragmentation due to expansion of fences, settlements, roads, farms and other developments. The location of this ecosystem so close to a rapidly expanding major city where undeveloped land is becoming increasingly scarce and expensive, has made it a strong magnet for those seeking relatively cheap land for settlement, industrial and other developments. Correspondingly, there is massive expansion in infrastructure supporting the expanding developments and human population. Wildlife and pastoral livestock are being displaced by these changes and their remaining habitats degraded. The corridors for migratory wildebeest, zebra and eland populations in this ecosystem have either become severely restricted or completely blocked. As a result, the range and population size of the once spectacular wildlife populations in this ecosystem have been dramatically reduced. These processes will continue to endanger both the ecological integrity of the ecosystem and the wildlife and livestock populations that it supports, if no appropriate interventions are instituted immediately. Interventions currently being undertaken to counteract the range contractions and population losses

are disjointed, underfunded or too limited in their spatial extents to even save the few remaining critical parts of the ecosystem still supporting wildlife and livestock in the long-term. Establishing a community wildlife conservancy whose status is secured by law would be one potential option for protecting parts of the ecosystem still supporting wildlife. Far-sighted land use plans and faithful implementation of such plans are thus necessary to steer other similar ecosystems away from the trajectory followed by the Athi-Kaputiei ecosystem resulting in its current extreme fragmentation and imminent collapse of its functional integrity.

Acknowledgments

We are grateful to the Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS) for permission to use the animal counts. We are grateful to Timothy Kavithi and Lucy Njino for the entry, quality control and processing of the aerial survey data. We thank two anonymous reviewers and the editor for insightful comments and suggestions that helped improve this paper. The Belgian Government (DGIC BEL011) and USAID funded the mapping of fences in the Athi-Kaputiei Plains through grants to the International Livestock Research Institute (ILRI) and the African Wildlife Foundation (AWF). The National Science Foundation of America (NSF) supported MYS and JOO through Grant No: BCS 0709671. JO Ogutu was also supported by the German Research Foundation (DFG, Grant # OG 83/1-1) and MYS by the Pathways to Resilience in Semi-Arid Economies (PRISE) Project. The following members of Kitengela Community carried out the mapping of fences: D. Isa, K. Makui, D. Sorimpan, N. Parmisa, W. Suiyanka, F. Karaine, L. Kiranto, S. Lekuik, M. Moipa, E. Sankaire, D. Toilimo, S. Roika, B. Shankah, A. Kinaiya, M. S. Kuyo, J. Tuleto, J. Kimiti, F. Kitende, W. Ntayia, J. Seneyioi, D. Semankur, S. Peria, J. Roika and E. Kaloi.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2016.10.005.

References

ACC. (2005). *Will Kitengela die?* Nairobi Kenya: Fact Sheet 1 African Conservation Centre.
Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.
Balmford, A., Moore, J. L., Brooks, T., Burgess, N., Hansen, L. A., Williams, P., et al. (2001). Conservation conflicts across Africa. *Science*, *291*, 2616–2619.
Bedelian, C., Nkedianye, D., & Herrero, M. (2006). Maasai perception of the impact and incidence of malignant catarrhal fever (MCF) in southern Kenya. *Preventive Veterinary Medicine*, *78*, 296–316.
Berger, J. (2004). The last mile: How to sustain long-distance migrations in mammals. *Conservation Biology*, *18*, 320–331.
Berry, H. H. (1997). Aspects of wildebeest Connochaetes taurinus ecology in the Etosha National Park—A synthesis for future management. *Modoqua*, *20*, 137–148.
Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, *11*, 63–77.
Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.
Campbell, D., Gichohi, H., Mwangi, A., & Chege, L. (2000). Land use conflict in South East Kajiado District, Kenya. *Land Use Policy*, *17*, 337–348.
Cayuela, L., Golicher, D. J., Benayas, J., Gonzalez-Espinosa, M., & Ramirez-Marcial, N. (2006). Fragmentation: Disturbance and tree diversity conservation in tropical montane forests. *Journal of Applied Ecology*, *43*, 1172–1181.
Ceballos, G., & Ehrlich, P. R. (2002). Mammal population losses and the extinction crisis. *Science*, *296*(5569), 904–907.
Debinski, D. M., & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, *14*, 342–355.
Dunning, J. B., Stewart, J., Danielson, D. J., Noon, B. R., Root, T. L., Lamberson, R. H., et al. (1995). Spatially explicit population models: Current forms and future uses. *Ecological Applications*, *5*, 3–11.
Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, *34*, 487–515.
Foster, J. B., & Coe, M. J. (1968). The biomass of game animals in nairobi national park, 1960–1966. *Journal of Zoology*, *155*, 413–425.
Foster, J. B., & Kearney, D. (1967). Nairobi National Park game census, 1966. *East African Wildlife Journal*, *5*, 112–120.
Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Endangered Species Research*, *3*, 237–241.
Galvin, K. A., & Reid, R. S. (Eds.). (2007). *Fragmentation in semi-arid and arid landscapes: Consequences for human and natural systems*. Dordrecht: Springer.
Gardner, R. H., Milne, B. T., Turner, M. G., & O'Neill, R. V. (1987). Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology*, *1*, 19–28.
Garrison, B. A. (2005). Fragmentation of terrestrial habitat: An overview for wildlife biologists. *Transactions of the Western Section of the Wildlife Society*, *41*, 42–58.
Georgiadis, N. J., Olivero, J. G. N., Ojwang, G., & Romanasch, S. S. (2007). Savanna herbivore dynamics in a livestock-dominated landscape. I. Dependence on land use, rainfall, density and time. *Biological Conservation*, *137*, 461–472.
Gichohi, H. W. (1996). *The ecology of a truncated ecosystem—The Athi-Kapiti Plains. PhD Thesis*. Leicester: University of Leicester.
Gichohi, H. (2000). Functional relationships between parks and agricultural areas in East Africa: The case of Nairobi National Park. In H. H. T. Prins, J. G. Grootenhuis, & T. T. Dolan (Eds.), *Wildlife conservation by sustainable use* (pp. 141–168). Dordrecht: Kluwer.
Harris, G., Thirgood, S., Hopcraft, J. C. G., Cromsigt, J. P. G., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, *7*, 55–76.
Hillman, J. C., & Hillman, A. K. K. (1977). Mortality of wildlife in Nairobi National Park during the drought of 1973–1974. *African Journal of Ecology*, *15*, 1–18.
Homewood, K., Lambin, E. F., Kariuki, A., Kikula, I., Kivelia, J., Said, M. Y., et al. (2001). Long term changes in Serengeti-Mara wildebeest and land cover: Pastoralism, population or policies? *Proceedings of the National Academy of Science of the United States of America*, *22*, 12544–12549.
Imbahale, S. S., Githaiga, J. M., Chira, R. M., & Said, M. Y. (2008). Resource utilization by large migratory herbivores of the Athi-Kapiti ecosystem. *African Journal of Ecology*, *46*, 43–51.
Johnson, A. R., Wiens, J. A., Milne, B. T., & Crist, T. O. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, *7*, 63–75.
Jolly, G. M. (1969). Sampling methods for aerial censuses of wildlife populations. *East African Agricultural and Forestry Journal*, *34*, 46–49.
Kimani, K., & Pickard, J. (1998). Recent trends and implications of group ranch sub-division and fragmentation in Kajiado District, Kenya. *Geographical Journal*, *164*, 202–213.
Kristjanson, P., Radeny, M., Nkedianye, D., Kruska, R., Reid, R., Gichohi, H., et al. (2002). *Valuing alternative land-use options in the Kitengela wildlife dispersal area of Kenya*. Nairobi: International Livestock Research Institute (ILRI).
Leblois, R., Estoup, A., & Streiff, R. (2006). Genetics of recent habitat contraction and reduction in population size: Does isolation by distance matter? *Molecular Ecology*, *15*, 3601–3615.
Martensen, A. C., Ribeiro, M. C., Banks-Leite, C., Prado, P. I., & Metzger, J. P. (2012). Associations of forest cover fragment area, and connectivity with neotropical understory bird species richness and abundance. *Conservation Biology*, *26*, 1100–1111.
McAlpine, C. A., Rhodes, J. R., Callaghan, J. G., Bowen, M. E., Lunney, D., Mitchell, D. L., et al. (2006). The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: a case study of koalas in Queensland, Australia. *Biological Conservation*, *132*, 153–165.
McGarigal, K., & Cushman, S. A. (2002). Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, *12*, 335–345.
Moenga, B. O., Muchemi, G. M., Kang'ethe, E. K., Kimenju, J. W., Mutiga, E. R., & Matete, G. O. (2013).. *The impact of climate change on the incidence of cattle diseases in a pastoral area of Kenya* (Vol. 25) Livestock Research for Rural Development. Article #67. Retrieved on 17.09.16, from http://www.lrrd.org/lrrd25/4/moen25067.htm
Morrison, T. A., & Bolger, D. T. (2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*, *81*, 543–552.
Morrison, T. A., & Bolger, D. T. (2014). Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. *Oryx*, *48*, 613–621.
Mudsprings Inc. (1999). Downloaded meta data from www.mudsprings.com.
Mutune, M., Waruiru, W., & Kilelu, E. S. (2003). Rift Valley fever virus in Kenya: Kajiado district. Serological analysis of antibody titres. *Kenya Veterinary Journal*, 29–39.
Mwacharo, J. M., Otieno, C. J., & Okeyo, A. M. (2002). Genetic variations between indigenous fat-tailed sheep populations in Kenya. *Small Ruminant Research*, *44*, 173–178.
Newmark, W. D. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology*, *10*, 1549–1556.
Newmark, W. D. (2008). Isolation of African protected areas. *Frontiers in Ecology and Environment*, *6*, 321–328.
Nkedianye, D., Radeny, M., Kristjanson, P., & Herrero, M. (2009). Assessing returns to land and changing livelihood strategies in Kitengela. In K. Homewood, P. C. Trench, & P. Kristjanson (Eds.), *Staying maasai?: Livelihoods, conservation and development in east african rangelands* (pp. 115–149). New York: Springer.
Nkedianye, D., de Leeuw, J., Ogutu, J. O., Said, M. Y., Saidimu, T. L., Kifugo, S. C., et al. (2011). Mobility and livestock mortality in communally used pastoral areas: The impact of the 2005–2006 droughts on livestock mortality in Maasailand. *Pastoralism: Research, Policy and Practice*, *1*, 17.

Norton-Griffiths, M., & Said, M. Y. (2010). The future for wildlife on Kenya's rangelands: An economic perspective. In J. du Toit, R. Kock, & J. Deutsch (Eds.), *Wild Rangelands: Conserving wildlife while maintaining livestock in semi-arid ecosystems* (pp. 367–392). Chichester (UK): Wiley-Blackwell.

Norton-Griffiths, M., Said, M. Y., Serneels, S., Kaelo, D. S., Coughenour, M., Lamprey, R. H., et al. (2008). Land use economics in the Mara area of the Serengeti ecosystem. In A. R. E. Sinclair, C. Packer, S. A. R. Mduma, & J. Fryxell (Eds.), *Serengeti III: Human wildlife interactions* (pp. 379–416). Chicago: University of Chicago Press.

Norton-Griffiths, M. (1978). *Counting animals*. Nairobi: Africa Wildlife Leadership Foundation.

Ogutu, J. O., Piepho, H.-P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*, *278*, 1–14.

Ogutu, J. O., Owen-Smith, N., Piepho, H.-P., & Said, M. Y. (2011). Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *Journal of Zoology*, *285*, 99–109.

Ogutu, J. O., Owen-Smith, N., Piepho, H.-P., Said, M. Y., Kifugo, S., Reid, R. S., et al. (2013). Changing wildlife populations in Nairobi National Park and adjoining Athi-Kaputiei Plains: Collapse of the migratory wildebeest. *The Open Conservation Biology Journal*, *7*, 11–26.

Ogutu, J. O., Piepho, H.-P., Said, M. Y., & Kifugo, S. C. (2014). Herbivore dynamics and range contraction in Kajiado County Kenya: Climate and land use changes, population pressures, governance, policy and human-wildlife conflicts. *Open Ecology Journal*, *7*, 9–31.

Ogutu, J. O., Piepho, H.-P., Said, M. Y., Ojwang, G. O., Njino, L. W., Wargute, P. W., et al. (2016). Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PloS One*, *11*(9), e0163249.

Ottichilo, W. K., & Khaemba, W. M. (2001). Validation of observer and aircraft calibration for aerial surveys of animals. *African Journal of Ecology*, *39*, 45–50.

Ottichilo, W. K., de Leeuw, J., Skidmore, A. K., Prins, H. H. T., & Said, M. Y. (2001). Population trends of large non-migratory wild herbivores and livestock in the Maasai Mara ecosystem, Kenya 1977–1997. *African Journal of Ecology*, *38*, 202–216.

Owaga, M. L. A. (1975). The feeding ecology of wildebeest and zebra in Athi-Kaputei Plains. *African Journal of Ecology*, *13*, 375–383.

Petersen, J. C. B., & Casebeer, R. L. (1972). *Distribution, population status and group composition of wildebeest (Connochaetes taurinus Burchell) and zebra (Equus burchelli Gray) on the Athi-Kapiti plains, Kenya. Project Working Document 2. Wildlife Management Project in Kenya*. Nairobi, Kenya: FAO.

Reid, R. S., Thornton, P. K., & Kruska, R. L. (2004). Loss and fragmentation of habitat for pastoral people and wildlife in East Africa: Concepts and issues. *South African Journal of Grass and Forage Science*, *21*, 171–181.

Reid, R. S., Gichohi, H., Said, M. Y., Nkedianye, D., Ogutu, J. O., Kshatriya, M., et al. (2008). Fragmentation of a peri-urban savanna in the Athi-Kaputiei Plains. In K. A. Galvin, R. S. Reid, R. H. Behnke, & N. T. Hobbs (Eds.), *Fragmentation of semi-arid and arid landscapes: Consequences for human and natural systems* (pp. 195–224). Dordrecht: Springer.

Ricketts, T., & Imhoff, M. (2003). Biodiversity, urban areas, and agriculture: Locating priority ecoregions for conservation. *Conservation Ecology*, *8*, 1.

Rosenzweig, M. L. (2003). *Win–win ecology: How earth's species can survive in the midst of human enterprise*. New York: Oxford University Press.

Rutten, M. M. E. M. (1992). *Selling wealth to buy poverty: The process of individualization of land ownership among the Maasai pastoralists of Kajiado District, Kenya, 1890–1990*. Saarbrucken: Breitenbach Publishers.

SAS Institute. (2016). *SAS system for windows, version 9.4*. Carey, NC: SAS Institute Inc.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.

Scharlemann, J. P., Green, R. E., & Balmford, A. (2004). Land-use trends in Endemic Bird Areas: Global expansion of agriculture in areas of high conservation value. *Global Change Biology*, *10*, 2046–2051.

Serneels, S., & Lambin, E. F. (2001). Proximate causes of land-use change in Narok District, Kenya: A spatial statistical model. *Agriculture, Ecosystems and Environment*, *85*, 65–81.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The principles and practice of statistics in biological research* (3rd ed.). New York: Freeman.

Spinage, C. A. (1992). The decline of the Kalahari wildebeest. *Oryx*, *26*, 147–150.

Stabach, J. A., Wittemyer, G., Boone, R. B., Reid, R. S., & Worden, J. S. (2016). Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. *Ecosphere*, *7*(8), e01428. http://dx.doi.org/10.1002/ecs2.1428

Swift, T. L., & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: A review of the concepts evidence, and applications. *Biological Reviews*, *85*, 35–53.

Tambling, C. J., & Du Toit, J. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441.

Western, D., & Gichohi, H. (1993). Segregation and the impoverishment of savanna parks: The case for ecosystem viability analysis. *African Journal of Ecology*, *31*, 269–281.

Western, D., Groom, R., & Worden, J. (2009). The impact of subdivision and sedenterization of pastoral lands on wildlife in an African savanna ecosystem. *Biological Conservation*, *142*, 2538–2546.

Western, D. (2010). Worst drought. Tipping or turning point? East African wildlife society. *Swara*, *3*, 17–22.

Whyte, I. L., & Joubert, S. C. J. (1988). Blue wildebeest population trends in the Kruger National Park and the effects of fencing. *South African Journal of Wildlife Research*, *18*, 78–87.

Wiens, J. A. (1990). Habitat fragmentation and wildlife populations: The importance of autecology, time and landscape structure. In *Trans. 19th IUGB congress* (pp. 381–391).

Williamson, D., & Williamson, J. (1985). Botswana's fences and the depletion of Kalahari wildlife. *Parks*, *10*, 5–7.