

# Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009

J. O. Ogutu<sup>1,2</sup>, N. Owen-Smith<sup>3</sup>, H.-P. Piepho<sup>1</sup> & M. Y. Said<sup>2</sup>

<sup>1</sup> Institute of Crop Science, Bioinformatics Unit, University of Hohenheim, Stuttgart, Germany

<sup>2</sup> International Livestock Research Institute, Nairobi, Kenya

<sup>3</sup> Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

## Keywords

ungulates; ostrich; population dynamics; land use change; Serengeti-Mara.

## Correspondence

Joseph O. Ogutu, Institute of Crop Science, Bioinformatics Unit, University of Hohenheim, Fruwirthstrasse 23, 70599 Stuttgart, Germany. Tel: +49 711 459 23022; Fax: +49 711 459 24345  
Email: jogutu2007@gmail.com

Editor: Andrew Kitchener

Received 8 December 2010; revised 4 March 2011; accepted 4 April 2011

doi:10.1111/j.1469-7998.2011.00818.x

## Introduction

Populations of many wildlife species have declined substantially inside and outside protected areas in Africa (Ogutu & Owen-Smith, 2003; Owen-Smith & Mills, 2006; Stoner *et al.*, 2006, 2007; Caro & Scholte, 2007; Bolger *et al.*, 2008; Harris *et al.*, 2009; Ogutu *et al.*, 2009; Western, Russell & Cuthill, 2009). Contributory causes include recurrent droughts (Ogutu *et al.*, 2007, 2008, 2009), expansion of large-scale cultivation and other land-use changes (Serneels, Said & Lambin, 2001; Thompson & Homewood, 2002; Ogutu *et al.*, 2009), growing human settlements (Lamprey & Reid, 2004; Norton-Griffiths *et al.*, 2009), illicit hunting (Mduma, Hilborn & Sinclair, 1998; Loibooki *et al.*, 2002) and livestock incursions into protected areas (Ogutu *et al.*, 2009).

The Mara region located in south-western Kenya exemplifies this pattern (Stelfox *et al.*, 1986; Broten & Said, 1995; Ogutu, 2000; Ottichilo *et al.*, 2000; Lamprey & Reid, 2004). It supports the greatest densities of both wild and domestic herbivores in Kenya, and provides dry season range for the migratory wildebeest *Connochetes taurinus* and zebra *Equus burchelli* moving northwards from the Serengeti region of Tanzania from late June until October. The future of this spectacular migration is critically dependent on the continued availability and productivity of this dry season refuge (Thirgood *et al.*, 2004). The high wildlife density and the

## Abstract

Populations of many wild ungulate species in Africa are in decline largely because of land-use changes and other human activities. Analyses that document these declines and advance our understanding of their underlying causes are fundamental to effective management and conservation of wild ungulates. We analyzed temporal trends in wildlife and livestock population abundances in the Mara region of Kenya. We found that wildlife populations in the Mara region declined progressively after 1977, with few exceptions. Populations of almost all wildlife species have declined to a third or less of their former abundance both in the protected Masai Mara National Reserve and in the adjoining pastoral ranches. Human influences appeared to be the fundamental cause. Besides reinforced anti-poaching patrols, the expansion of cultivation, settlements and fences and livestock stocking levels on the pastoral ranches need to be regulated to avoid further declines in the wildlife resource.

magnificent annual migration make the Masai Mara National Reserve (MMNR) one of the premier tourist attractions in Kenya (Akama, 2002).

Here, we extend earlier analyses of wildlife population trends in the Mara region of Kenya to span the 33-year period from 1977 to 2009. We document spatial distinctions in population trends among 14 common wildlife and four livestock species within both the MMNR and the adjoining group ranches. The wildlife species are wildebeest, zebra, Thomson's gazelle *Gazella thomsoni*, impala *Aepyceros melampus*, topi *Damaliscus lunatus korrigum*, African buffalo *Syncerus caffer*, Grant's gazelle *Gazella granti*, eland *Taurotragus oryx*, Coke's hartebeest *Alcelaphus buselaphus cokei*, warthog *Phacochoerus africanus*, giraffe *Giraffa camelopardalis*, African elephant *Loxodonta africana*, waterbuck *Kobus ellipsiprymnus* and ostrich *Struthio camelus masaiicus*, in decreasing order of numerical abundance. The livestock species are cattle, sheep and goats (lumped during aerial surveys as shoats) and donkeys.

We investigated distinctions in the spatial pattern of the wildlife species declines between the MMNR and adjoining pastoral ranches, as well as regional distinctions within MMNR potentially resulting from cattle incursions and illegal hunting extending into the protected area. We anticipated that population density would decline more within the ranches than within MMNR, which has a core area most

remote from human intrusions, while recognizing species that would be affected everywhere because of their wide ranging across the reserve and perhaps beyond, in particular the migratory species. We expected wildlife density to decline more at the edges of MMNR that experience greater livestock incursions and poaching than in its interior. Finally, we evaluated the relative significance of climatic variability relative to anthropogenic influences as the most likely causes underlying the observed wildlife population declines and range constrictions in the Mara region during 1977–2009.

## Material and methods

### Study area

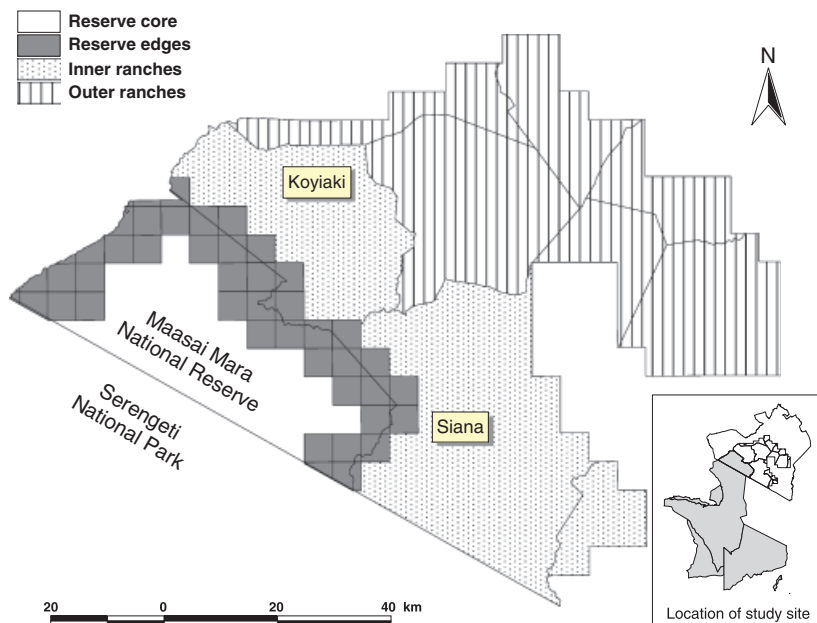
The Mara region is bounded by the Rift Valley in the east, the international border with Tanzania in the south and the Siria Escarpment in the west, extending between latitudes 1°00' and 2°00' S and longitudes 34°45' and 36°00' E. The MMNR encompasses 1530 km<sup>2</sup> and is a national conservation estate managed by the Narok and Transmara County Councils on behalf of the government of Kenya. Group-owned ranches adjoin MMNR in the north and east and cover 4870 km<sup>2</sup> (Fig. 1). The land uses in the ranches include traditional pastoralism, wildlife conservation, tourism, subsistence maize cultivation and commercial wheat cultivation. Wildlife conservation and tourism are the only land uses permitted within the reserve. Wildebeest, zebra and Thomson's gazelles migrate between MMNR and Loita Plains within the group ranches to the north-east of MMNR.

Rainfall in the Mara region is bimodal with short rains falling during November–December and long rains during March–June. The dry season spans July–October (Norton-Griffiths, Herlocker & Pennycuik, 1975). Mean annual

rainfall increased from 877 mm at Ololaimutia Gate in the south-east to 1341 mm at Kichwa Tembo Lodge in the north-west, of which about 20% on average was received during the dry-season months. Recurrent droughts are associated with fluctuations in the El Niño–Southern Oscillation (Nicholson & Kim, 1997; Nicholson & Selato, 2000), and the Indian Ocean Dipole (Webster *et al.*, 1999; Hastenrath, Polzin & Mutai, 2007). Mean temperature levels have risen in the Mara region in recent decades leading to progressive habitat desiccation (Ogutu *et al.*, 2007). The Mara region also experienced recurrent severe droughts, the most noteworthy during 1977–2009 being in 1984, 1993 and 1999–2000 (Ogutu *et al.*, 2007) and during 2005–2006 and 2008–2009.

### Animal counts

Regular aerial reconnaissance surveys were carried out by the Kenya Rangeland Ecological Monitoring Unit, later renamed the Department of Resource Surveys and Remote Sensing (DRSRS), from 1977 to 2009 (Ottichilo, de Leeuw & Prins, 2001; Stelfox *et al.*, 1986; Broten & Said, 1995; Ottichilo *et al.*, 2000; Homewood *et al.*, 2001; Serneels *et al.*, 2001; Lamprey & Reid, 2004). The surveys were conducted less frequently in later than earlier years owing to financial constraints. Surveys undertaken by DRSRS followed the systematic flight protocol designed by Norton-Griffiths (1978). Transects oriented in an east–west or north–south direction were flown at 5 km intervals at a height of *c.* 90 m above ground level during 1977–1985 and *c.* 120 m thereafter (Ottichilo *et al.*, 2000). Two experienced and well-trained observers occupying the rear section of a high-wing aircraft (Cessna 185 or Partenavia) counted animals located between two rods attached to the wing struts. The field of vision between these rods projected a census strip that was calibrated by flying repeatedly across ground markers of



**Figure 1** A map of the Mara region of Kenya showing the Masai Mara National Reserve and its immediately adjoining pastoral ranches of Koyiaki plus Siana, together called the inner ranches and the remaining more outlying ranches, collectively called the outer ranches.

known spacing. The survey strip spanned a mean width of 263 m (range = 205–354 m), and the corresponding average sampling intensity (mean 4.8%, range = 2.1–5.6%) was determined for each flight. The numbers of animals within these strips were counted and recorded into tape recorders. Groups of more than 10 animals were photographed and later counted with the aid of a  $\times 10$  binocular microscope and an overhead projector (Stelfox *et al.*, 1986; Ottichilo *et al.*, 2000).

Each 5 km transect segment was treated as an observation. Animals counted were recorded spatially within the universal transverse mercator grid to the nearest 25 km<sup>2</sup> unit. Population estimates (PE) and standard errors (SE) were calculated using Jolly's Method 2 (Jolly 1969). PE is estimated as  $PE = N\bar{y}$  and its SE as  $SE = \sqrt{\frac{N(N-n)s^2}{n}}$  where  $\bar{y}$  is the sample mean,  $s^2$  is the sample variance,  $n$  is the sample size and  $N$  is the number of observations required to completely cover the study area. Empirical tests of visibility bias showed that on average 70–80% of wild herbivores and 80–90% of livestock are counted. Hence, count totals were corrected upward by about  $1.33 \times$  for wildlife and  $1.18 \times$  for livestock (Stelfox *et al.*, 1986). The estimated population sizes for the 14 most common large wild herbivore and four livestock species in the Mara Reserve and all the Mara ranches during 1977–2009 and their estimated SE are provided in the electronic supplementary material (supporting information Table S1).

## Statistical analysis

The entire Mara region encompasses MMNR and the adjoining group ranches. For some analyses, we partitioned the ranches between the inner ranches adjoining the MMNR (Koyiaki plus Siana) and the outer ranches. Because population counts are typically non-normally distributed, with the variance increasing with the mean, the frequency of counts varied over time, and the temporal trends in the counts were characteristically non-linear; a suitable model for the trends should allow for the non-normality and non-linearity of the counts and the varying frequency of surveys. We thus analyzed long-term trends in the estimated population sizes for resident species in each region using a flexible multivariate semiparametric generalized linear mixed model with a negative binomial error distribution and a log link function. The model smoothes the population trend of each species and correlations between trends for different species to reveal patterns shared by trends for the different species. More precisely, the model specified a cubic B-spline (Eilers & Marx, 1996) covariance structure with 20 equidistant interior knots placed on the running time of survey (January 1977, ..., October 2009) and random spline coefficients, with a cubic difference penalty on the B-spline coefficients. De Boor (2001) provides details about the computation and properties of B-splines. The smoother is based on the automatic smoother in Ruppert, Wand & Carroll (2003, Chapter 13.4–13.5). We used multiple continuous random spline effects (running time of survey) to obtain a multivariate smoother in the SAS GLIMMIX

procedure (SAS Institute Inc., 2010). One continuous random time effect modeled the trend common to all species and hence accounted for correlations among trends for all the species, while the others modeled trends specific to each species. Livestock trends were similarly modeled.

The spline smoother we used exploits the connection between splines and mixed models (Ruppert *et al.*, 2003, p. 108) that enables a mixed model formulation of spline smoothing, which has the advantage that the smoothing parameter is selected 'automatically,' as a function of the covariance parameter estimates. We estimated the covariance parameters in the mixed model by the method of restricted log pseudo-likelihood in GLIMMIX. The nature of the spline coefficients also differs between the classical spline fitting and the mixed model smoothing variant that we used, in that the solutions for the spline coefficients in the classical framework are solutions of fixed effects but in the mixed model framework they are the solutions of random effects. As a consequence, the extra variation introduced by the random effects is accounted for explicitly in computing, for example, SE (SAS Institute Inc., 2010), such as those we computed for the predicted population counts in this study.

To distinguish the migratory influx of wildebeest and zebra from the Serengeti from resident populations of these species, we analyzed their trends separately for the wet (December–May) and dry (June–November) seasons. Ottichilo *et al.* (2000, 2001) showed that the wildlife declines were similar between the MMNR and the ranches during 1977–1997, and hence we performed a similar analysis to establish whether this similarity continued through 1998–2009. For each herbivore species, we calculated the difference in the average of the expected population size on the basis of the penalized B-splines during 2007–2009 from that during 1977–1979 to minimize the influence of stochastic variability on the counts and to reveal spatial (MMNR vs. ranches) distinctions in the extents of population declines.

We further analyzed spatial variation in distribution of herbivores between MMNR and the ranches by computing the density of each species found in each of these regions during each survey and the variation in this density during 1977–2009. The density and proportion of each region occupied by each species were averaged over four periods spanning 1977–1979, 1980–1989, 1990–1999 and 2000–2009 to minimize the influence of stochastic variation in the count totals. To assess the role of edge effects on wildlife population trends, we compared trends in livestock and resident wildlife densities at the edges and in the interior of MMNR during each of the preceding four periods. The edges of MMNR were defined as all  $5 \times 5$  km<sup>2</sup> grid cells with at least one side located within 5 km of the boundary between MMNR and group ranches in the east, north and west.

## Results

### Trends in abundance during 1977–2009

Most resident wildlife species declined almost as severely within MMNR as in the adjoining ranches between 1977 and

2009 (Figs 2 and 3). Only the two gazelle species plus impala and giraffe remained numerically more abundant in the ranches than in the reserve. Buffalo were effectively eliminated from the group ranches (Fig. 3). Almost no wildebeest were resident in MNRR during the wet season, although several thousand remained in the group ranches, and few of the migrant wildebeest augment the resident animals in the ranches in the dry season (Fig. 4). Zebra showed a very similar pattern (Fig. 4). Cattle numbers in the ranches changed little, while the number of sheep and goats almost tripled between 1977 and 2009. The numbers of both of these domestic livestock counted within the reserve increased hugely over this period (Fig. 4).

### Spatial contrasts in density during 1977–2009

Most species declined uniformly in density in all subdivisions of the Mara region, the exceptions being eland, ostrich and shoats (Fig. 5). Nevertheless, Thomson's gazelle, impala, eland and giraffe still occurred at higher densities in the ranches than in MMNR. Moreover, Grant's gazelle, ostrich, resident wildebeest and zebra were more abundant in the outer ranches than in MMNR. The contribution of all wildlife resident in the Mara region in the wet season to the overall biomass of wildlife and livestock declined by 50% during 1977–2009 from 63.8% in the 1970s to 55.6% in the 1980s, 46.3% in the 1990s and 34.7% in the 2000s, demonstrating progressive replacement of wildlife by livestock in the Mara. Declines in wildlife numbers were no less dramatic in the interior than at the edges of the MMNR (Fig. 5). Despite higher livestock density at the edges than in the interior of MMNR, the densities of Thomson's gazelle, impala, topi and buffalo were higher at the edges than in the interior of MMNR (Fig. 5). However, ostrich and eland numbers increased during 2000–2009 in the interior, but not at the edges of MMNR (Fig. 5).

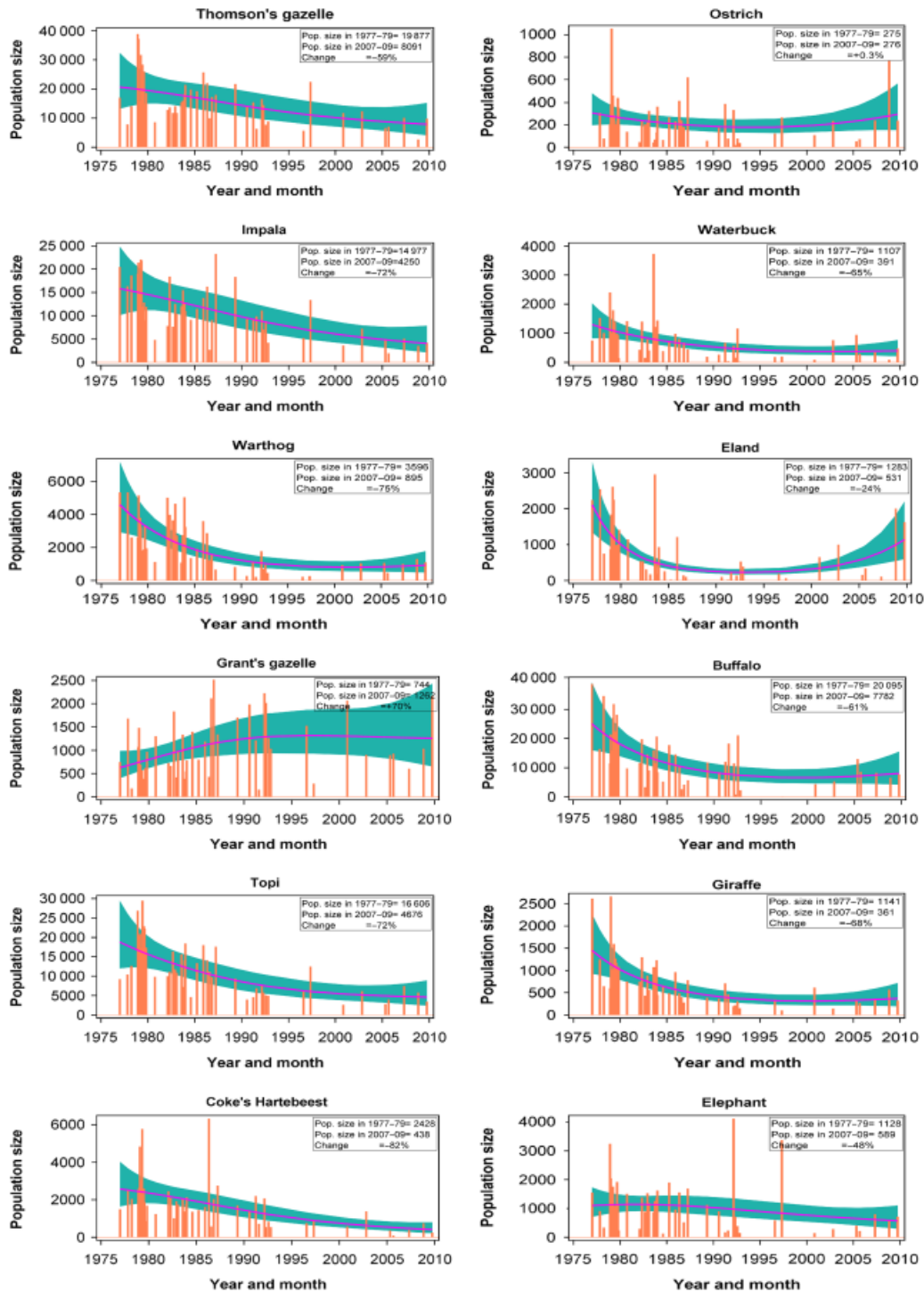
### Discussion

Most wildlife species have declined toward a third or less of their previous abundance within the overall Mara region between 1977 and 2009, with these decreases being almost as severe within the reserve as in the adjoining ranches. Hence, the earlier downward population trends of most wildlife species (Brotten & Said, 1995; Ogutu, 2000; Ottichilo *et al.*, 2000, 2001; Serneels & Lambin, 2001) have continued. Not only have resident populations decreased, but the numbers of migratory wildebeest and zebra entering the Mara region during the dry season have also shrunk, although no change in the source populations in the Serengeti ecosystems has been recorded (Sinclair *et al.*, 2007). The biomass of livestock as a per cent of total livestock and wildlife biomass recorded within the reserve boundaries increased from an average of 2% in the 1970s to 23% in the 2000s and now greatly exceeds that of any resident wildlife species, except buffalo. The numbers of the small livestock (shoats) have increased hugely within the ranches, although relatively few

enter the reserve. The wild ungulates that seem best able to survive alongside the livestock within the ranches are impala and Thomson's gazelle. Our findings on the basis of the aerial surveys are consistent with those from independent aerial monitoring of buffalo and elephant numbers (H.T. Dublin & J.O. Ogutu, in prep.; Kenya Wildlife Service, unpub. data) and with monthly ground monitoring of seven ungulate species conducted from vehicles in MNRR and in slivers of the inner ranches from July 1989 to December 2003 (Ogutu *et al.*, 2009). Notably, however, the Mara ranches now support higher densities of some wildlife species than the protected area, especially Koyiaki (impala and giraffe) and the outer ranches (Grant's gazelle, resident wildebeest and zebra).

The disappearance of buffalo from the ranches and severe reduction in its numbers within MNRR suggests competitive displacement by cattle, possibly exacerbated by drought conditions when remaining forage became inadequate to support both bulk grazers with similar forage needs. Nevertheless, heavy grazing by livestock within the ranches promotes short nutritious grass favored by smaller grazers or mixed feeders (Hobbs & Swift, 1988), like impala and gazelles. The reduction in grass biomass and hence fuel for fires also enhances the regeneration of the trees and shrubs supporting browsing giraffe. Illegal hunting probably contributed to the extirpation of the roan antelope *Hippotragus equinus* in MMNR in the 1970s, near extirpation of the black rhino *Diceros bicornis* and severe reductions in elephant numbers in the Serengeti-Mara ecosystem (Darling, 1960; Hofer *et al.*, 1996; Walpole *et al.*, 2001). Escalated illegal hunting along the western border of the northern Serengeti Park and adjoining Mara Triangle (Hofer *et al.*, 1996; Mduma *et al.*, 1998; Loibooki *et al.*, 2002; Ogutu *et al.*, 2009) was associated with dramatic reductions in numbers of topi, waterbuck, buffalo and giraffe (Hofer *et al.*, 1996; Metzger *et al.*, 2010). The drastic wildlife declines typify a more widespread pattern in Kenya and in the rest of Africa (Caro & Scholte, 2007; Western *et al.*, 2009; Craigie *et al.*, 2010).

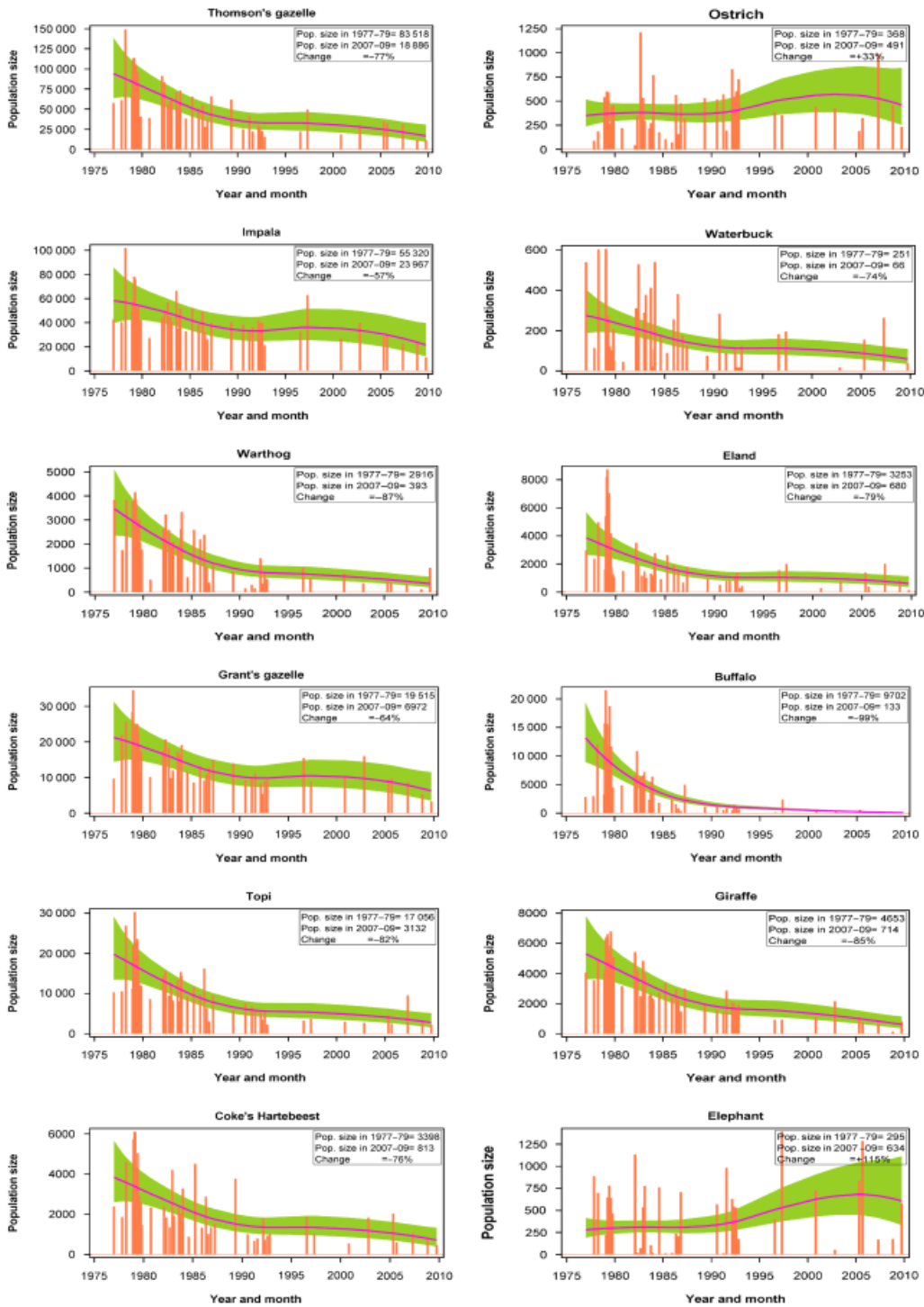
Despite recurrent droughts, there was no persistent change in regional rainfall that might have explained the persistent wildlife decline (Ogutu *et al.*, 2007). The declines in the Mara region during 1977–2009 were contemporaneous with habitat degradation, fragmentation and loss through large-scale commercial mechanized wheat cultivation in the Loita Plains, subsistence maize cultivation and expansion of settlements (Ottichilo *et al.*, 2000, 2001; Home-wood *et al.*, 2001; Serneels *et al.*, 2001; Thompson & Home-wood, 2002; Lamprey & Reid, 2004), high and unregulated livestock stocking levels, poaching and illegal livestock grazing in MMNR (Butt, Shortridge & WinklerPrins, 2009; Ogutu *et al.*, 2009). A high level of poaching activity was documented in the western triangle of MMNR (Ogutu *et al.*, 2009) and was probably more widespread. Given the rising number of sheep and goats, and the expanding distribution of cattle, sheep and goats in the Mara ranches, we expect the competition between livestock and wildlife to further intensify over time.



**Figure 2** Temporal trends in resident wildlife numbers in the Masai Mara National Reserve during 1977–2009. The shaded bands are the point wise 95% confidence limits.

Similarly persistent patterns of wildlife declines have been reported for other pastoral lands experiencing major land-use changes and other anthropogenic activities similar to the Mara region, including the Kenyan Athi-Kaputiei Plains (Reid *et al.*, 2008), Amboseli basin (Western *et al.*,

2009), Laikipia District (Georgiadis *et al.*, 2007) and the Tanzanian Tarangire–Simanjiro ecosystem (Msoffe *et al.*, 2011). However, comparable wildlife declines have not occurred in the adjoining Serengeti National Park, except for the northern extension adjoining the Mara



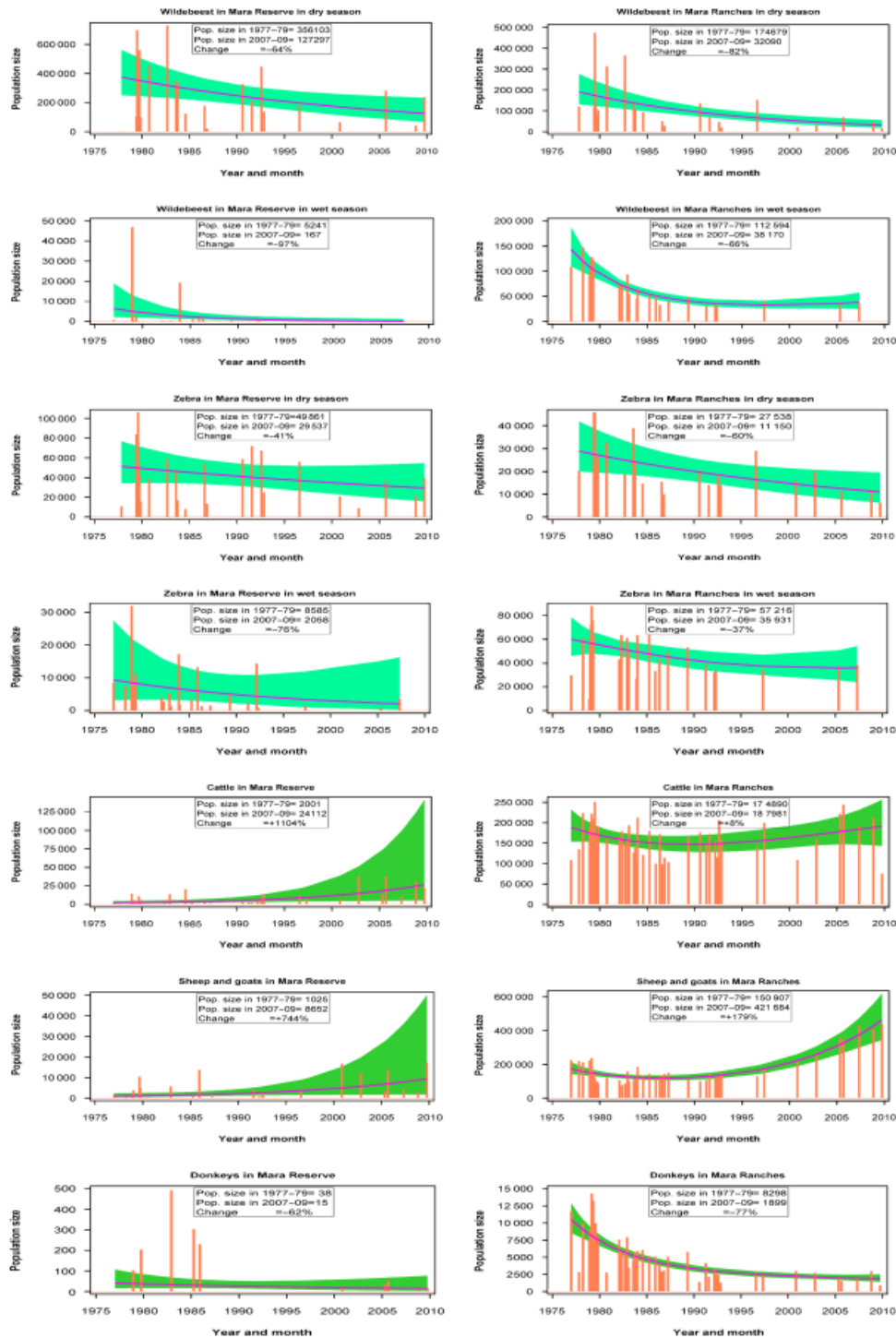
**Figure 3** Temporal trends in resident wildlife numbers in all the pastoral ranches of the Mara during 1977–2009. The shaded bands are the point wise 95% confidence limits.

triangle where poaching was clearly involved (Metzger *et al.*, 2010).

The basic cause of the wildlife population declines seems to be the expanding human population in the ranches along

with livestock influences spreading into the nominally protected area. However, the regional numbers of some wildlife species would be greatly reduced if they were excluded from the ranches. Movements of some of the grazers between the

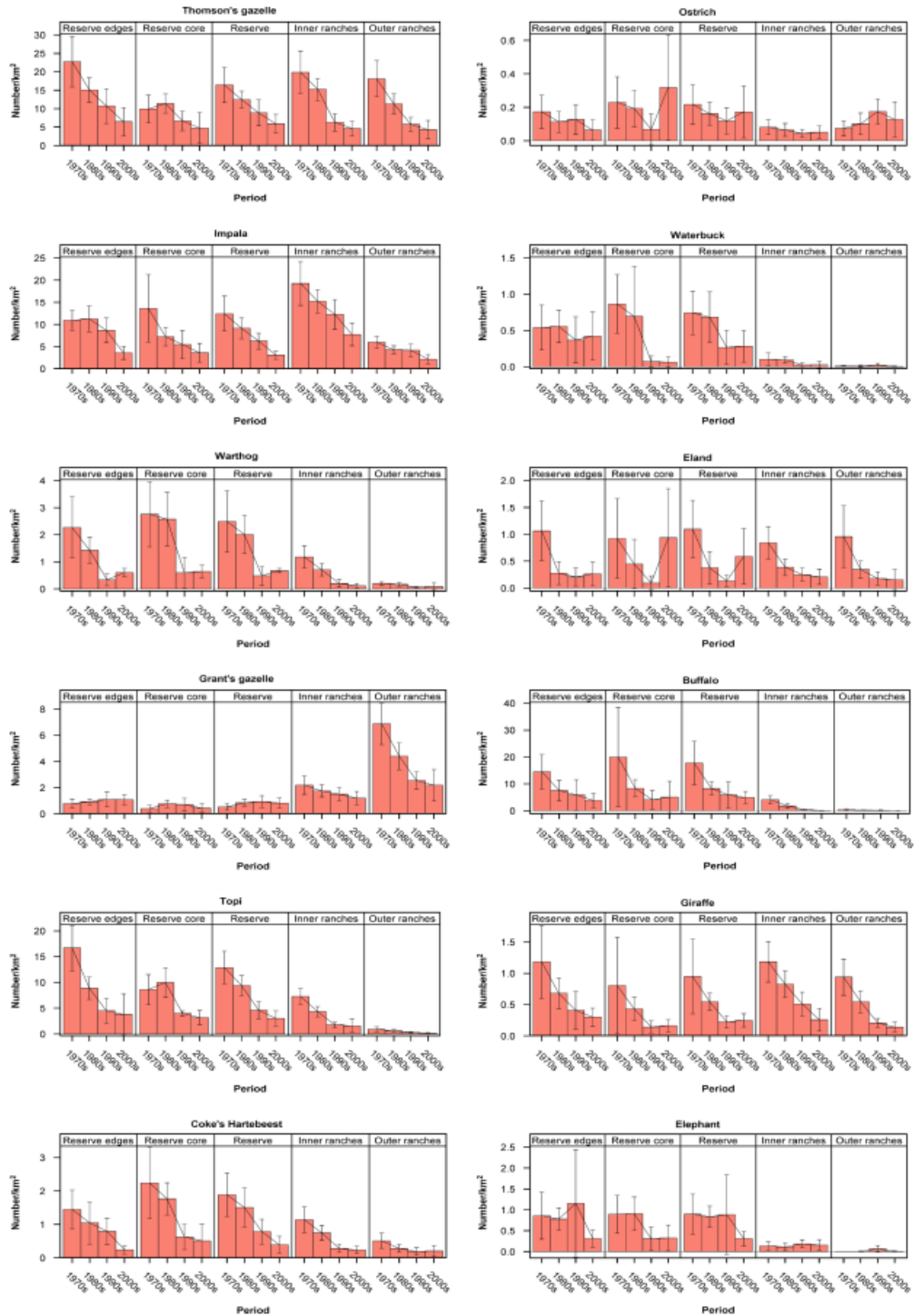




**Figure 4** Temporal trends in resident (wet season) and migratory (dry season) wildebeest and zebra numbers and in livestock numbers in the Masai Mara National Reserve and all the adjoining pastoral ranches during 1977–2009.

reserve and adjoining ranches have been noted, apart from the large influx of migratory wildebeest and zebra into the reserve during the dry season (Stelfox *et al.*, 1986). Hence, fencing the reserve boundary to block livestock incursions would not be helpful for wildlife conservation in these

circumstances. Instead, the urgent need is to promote land-use patterns in the ranches that would enable owners to benefit from the presence of wildlife alongside livestock. Such developments have indeed been initiated through the establishment of conservancies, whereby some sections of



**Figure 5** Temporal trends in the density (number per km<sup>2</sup>) of individuals of each species occupying each region of the Mara in each survey during 1977–2009 averaged over 1977–1979 (1970s, *n* = 15 surveys), 1980–1989 (1980s, *n* = 18), 1990–1999 (1990s, *n* = 9) and 2000–2009 (2000s, *n* = 7).

the ranches have been leased out for ecotourism activities (Ogutu *et al.*, 2009). At the same time, the coverage and intensity of the anti-poaching patrols need to be stepped up to reduce the currently high rates of poaching and snaring,

especially within the western region of MMNR. Further expansion of cultivation, settlements and fences and live-stock stocking levels on the pastoral ranches should be regulated. The solution to wildlife conservation within



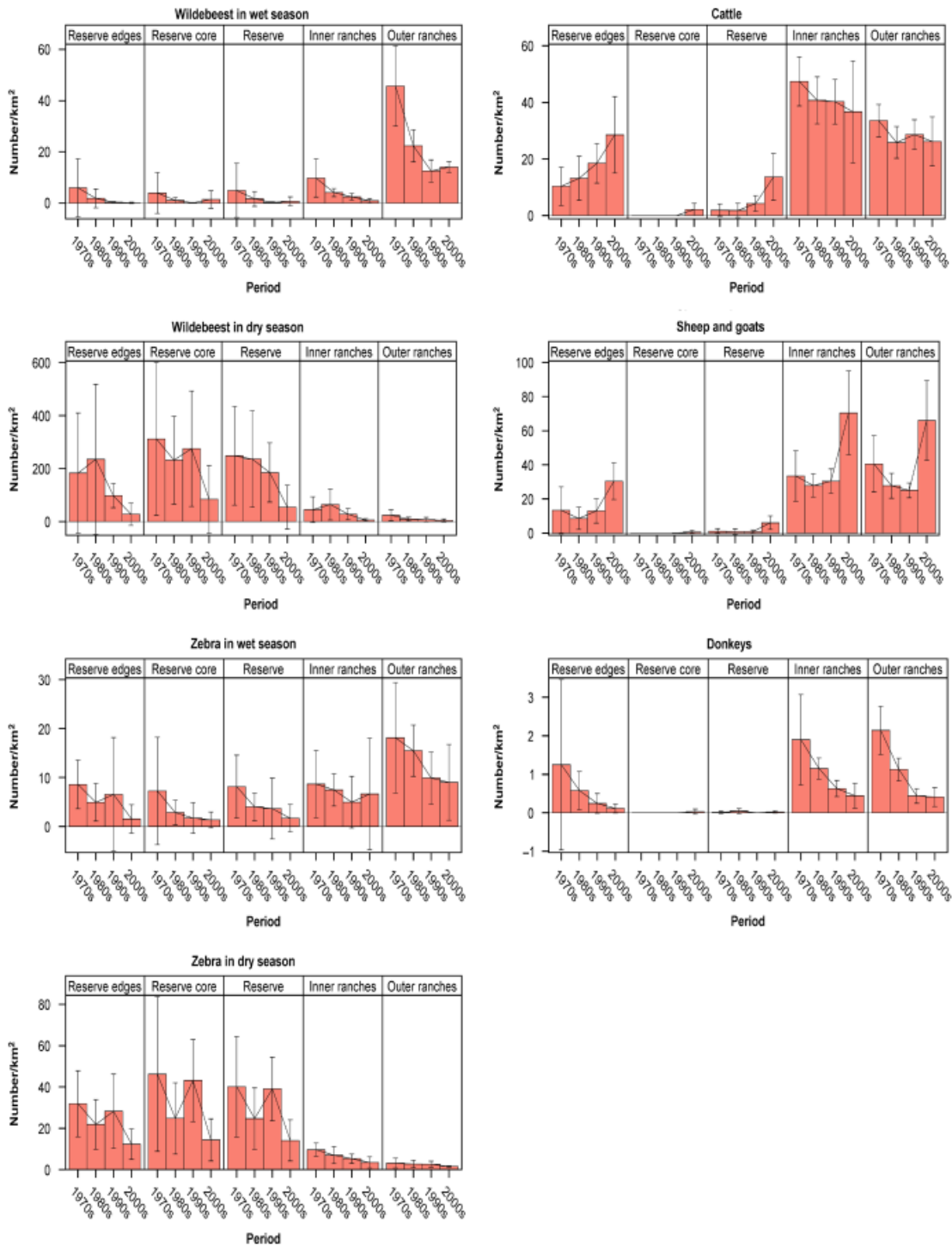


Figure 5 Continued.

the Mara region rests on the land-use arrangements outside the protected area.

**Acknowledgements**

We thank the DRSRS for permission to use their data.

**References**

Akama, J.S. (2002). The role of government in the development of tourism in Kenya. *Int. J. Tourism Res.* **4**, 1–13.  
 Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008). The need for integrative approaches to under-

- stand and conserve migratory ungulates. *Ecol. Lett.* **11**, 63–77.
- de Boor, C (2001). *A practical guide to splines*, Revised edition. New York: Springer-Verlag.
- Broten, M.D. & Said, M. (1995). Population trends of ungulates in and around Kenya's Maasai Mara Reserve. In *Serengeti II: dynamics, management and conservation of an ecosystem*: 169–193. Sinclair, A.R.E. & Arcese, P. (Eds). Chicago: University of Chicago Press.
- Butt, B., Shortridge, A. & WinklerPrins, A.M.G.A. (2009). Pastoral herd management, drought coping strategies, and cattle mobility in southern Kenya. *Ann. Assoc. Am. Geogr.* **99**, 309–334.
- Caro, T. & Scholte, P. (2007). When protection falters. *Afr. J. Ecol.* **45**, 233–235.
- Craigie, D.I., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E. & Hutton, J.M. (2010). Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228.
- Darling, F.F. (1960). *An ecological reconnaissance of the Mara Plains in Kenya colony. Wildlife Monographs No. 5*. Kansas: Allen Press, 41pp.
- Eilers, P.C. & Marx, B.D. (1996). Flexible smoothing with B-splines and penalties. *Stat. Sci.* **11**, 89–121.
- Georgiadis, N.J., Olwero, J.G.N., Ojwang, G. & Romañach, S.S. (2007). Savanna herbivore population dynamics in a livestock-dominated landscape: I. dependence on land use, rainfall, density and time. *Biol. Conserv.* **137**, 461–472.
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Crooms, J.P.G.M. & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endang. Species Res.* **7**, 55–76.
- Hastenrath, S., Polzin, D. & Mutai, C. (2007). Diagnosing the 2005 drought in Equatorial East Africa. *J. Clim.* **20**, 4628–4637.
- Hobbs, N.T. & Swift, D.M. (1988). Grazing in herds: when are nutritional benefits realized? *Am. Nat.* **131**, 760–764.
- Hofer, H., Campbell, K.L.I., East, M.L. & Huish, S.A. (1996). The impact of game meat hunting on target and non-target species in the Serengeti. In *The exploitation of mammal populations*: 117–146. Taylor, V.J. & Dunstone, N. (Eds). London: Chapman and Hall.
- Homewood, K., Lambin, E.F., Coast, E., Kariuki, A., Kikula, I., Kivulia, J., Said, M., Serneels, S. & Thompson, M. (2001). Long-term changes in Mara-Serengeti wildlife and land cover: pastoralists, population or policies? *Proc. Nat. Acad. Sci.* **98**, 12544–12549.
- Jolly, G.M. (1969). Sampling methods for aerial census of wildlife populations. *East Afr. Agric. For. J.* **34**, 46–49.
- Lamprey, R.H. & Reid, R.S. (2004). Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *J. Biogeogr.* **31**, 997–1032.
- Loibooki, M., Hofer, H., Campbell, K.L.I. & East, M.L. (2002). Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environ. Conserv.* **29**, 391–398.
- Mduma, S.A.R., Hilborn, R. & Sinclair, A.R.E. (1998). Limits to exploitation of Serengeti wildebeest and implications for its management. In *Dynamics of tropical communities*: 243–265. Newbury, D.M., Prins, H.H.T. & Brown, N. (Eds). Oxford: Blackwell Science.
- Metzger, K.L., Sinclair, A.R.E., Hilborn, R., Hopcraft, J.G.C. & Mduma, S.A.R. (2010). Evaluating the protection of wildlife in parks: the case of African buffalo in Serengeti. *Biodivers. Conserv.*, **19**, 3431–3444.
- Msoffe, F.U., Kifugo, S.K., Said, M.Y., Neselle, M.O., van Gardingen, P., Reid, R.S., Ogutu, J.O., Herero, M. & de Leeuw, J. (2011). Drivers and impacts of land-use change in the Maasai Steppe of northern Tanzania: an ecological-social-political analysis. *J. Land Use Sci.* Online DOI: 10.1080/1747423X.2010.511682.
- Nicholson, S.E. & Kim, J. (1997). The relationship of the El Niño–southern oscillation to African rainfall. *Int. J. Climatol.* **17**, 117–135.
- Nicholson, S.E. & Selato, J.C. (2000). The influence of La Nina on African Rainfall. *Int. J. Climatol.* **20**, 1761–1776.
- Norton-Griffiths, M. (1978). *Counting animals. Handbook No. 1*, 2nd edn. Nairobi: Africa Wildlife Leadership Foundation.
- Norton-Griffiths, M., Herlocker, D.J. & Pennycuik, L. (1975). The patterns of rainfall in the Serengeti ecosystem. *E. Afr. Wildl. J.* **13**, 347–374.
- Norton-Griffiths, M., Said, M.Y., Serneels, S., Kaelo, D.S., Coughenour, M., Lamprey, R.H., Thompson, D.M. & Reid, R.S. (2009). Land use economics in the Mara area of the Serengeti ecosystem. In *Serengeti III: human wildlife interactions*: 379–416. Packer, C. & Sinclair, A.R.E. (Eds). Chicago: University of Chicago Press.
- Ogutu, J.O. (2000). *Herbivore dynamics in the Mara Area of Kenya: the influence of land use change, climate and predators*. Aachen: Shaker Verlag.
- Ogutu, J.O. & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol. Lett.* **6**, 412–419.
- Ogutu, O.J., Piepho, H.-P., Dublin, H.T., Bhola, N. & Reid, R.S. (2007). ENSO, rainfall and temperature fluctuations in the Mara-Serengeti ecosystem. *Afr. J. Ecol.* **46**, 132–143.
- Ogutu, J.O., Piepho, H.-P., Dublin, H.T., Bhola, N. & Reid, R.S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *J. Anim. Ecol.* **77**, 814–829.
- 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. *J. Zool. (Lond.)* **278**, 1–14.
- Ottichilo, W.K., De Leeuw, J., Skidmore, A.K., Prins, H.H.T. & Said, M.Y. (2000). Population trends of large non-migratory wild herbivores and livestock in the Maasai Mara ecosystem, Kenya, between 1977 and 1997. *Afr. J. Ecol.* **38**, 202–216.

- Ottichilo, W., de Leeuw, J. & Prins, H.H.T. (2001). Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Maasai Mara ecosystem, Kenya. *Biol. Conserv.* **97**, 271–282.
- Owen-Smith, N. & Mills, M.G.L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecol. Monogr.* **76**, 73–92.
- Reid, R.S., Gichohi, H., Said, M.Y., Nkedianye, D., Ogutu, J.O., Kshatriya, M., Kristjanson, P., Kifugo, S.C., Agatsiva, J.L., Andanje, S.A. & Bagine, R. (2008). Fragmentation of a peri-urban savanna, Athi-Kaputiei Plains, Kenya. *Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems*: 195–224. Galvin, K.A., Reid, R.S., Behnke, R.H. & Hobbs, N.T. (Eds). Dordrecht: Springer.
- Ruppert, D., Wand, M.P. & Carroll, R.J. (2003). *Semiparametric regression*. Cambridge: Cambridge University Press.
- SAS Institute Inc. (2010). *SAS system for windows, version 9.2*. Cary: SAS Institute Inc.
- Serneels, S. & Lambin, E.F. (2001). Impact of land use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. *J. Biogeogr.* **28**, 391–407.
- Serneels, S., Said, M.Y. & Lambin, E.F. (2001). Land cover changes around a major east African wildlife reserve: the mara ecosystem (Kenya). *Int. J. Remote Sens.* **22**, 3397–3420.
- Sinclair, A.R.E., Mduma, S.A.R., Hopcraft, J.G.C., Fryxell, J.M., Hilborn, R. & Thirgood, S. (2007). Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conserv. Biol.* **21**, 580–590.
- Stelfox, J.G., Peden, D.G., Epp, H., Hudson, R.J., Mbugua, S.W. & Agatsiva, J.L. (1986). Herbivore dynamics in Southern Narok, Kenya. *J. Wildl. Mgmt.* **50**, 339–347.
- Stoner, C., Caro, T., Mduma, S., Mlingwa, C., Sabuni, G. & Borner, M. (2007). Assessment of effectiveness of protection strategies in Tanzania based on a decade of survey data for large herbivores. *Conserv. Biol.* **21**, 635–646.
- Stoner, C., Caro, T., Mduma, S., Mlingwa, C., Sabuni, G., Borner, M. & Schelten, C. (2006). Changes in large herbivore populations across large areas of Tanzania. *Afr. J. Ecol.* **45**, 202–215.
- Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A.R.E. & Borner, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Anim. Conserv.* **7**, 113–120.
- Thompson, M. & Homewood, K. (2002). Entrepreneurs, elites and exclusion in Maasailand: trends in wildlife conservation and pastoralist development. *Hum. Ecol.* **30**, 107–138.
- Walpole, M.J., Morgan-Davies, M., Milledge, S., Bett, P. & Leader-Williams, N. (2001). Population dynamics and future conservation of a free-ranging black rhinoceros (*Diceros bicornis*) population in Kenya. *Biol. Conserv.* **99**, 237–243.
- Webster, P.J., Moore, A.M., Loschnigg, J.P. & Leben, R.R. (1999). Coupled ocean atmosphere dynamics in the Indian Ocean during 1997–1998. *Nature* **401**, 356–360.
- Western, D., Russell, S. & Cuthill, I. (2009). The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE* **4**, e6140. Online DOI: 10.1371/journal.pone.0006140.

## Supporting Information

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

**Table S1.** The estimated population sizes for the 14 most common large wild herbivore species and 4 livestock species in the Mara region of Kenya and each of its subdivisions during 1977–2009. The estimated population standard errors for aerial sample surveys covering 1977–2009 are also provided. Early aerial counts covering 1958, 1961 and 1974 were attempted total counts and so lacked estimates of standard errors. As a result, the early counts were not used in this study but have been provided here for the sake of completeness.

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