

Dynamics of Mara–Serengeti ungulates in relation to land use changes

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Abstract

Animal population dynamics can be driven by changing climatic forcing, shifting habitat conditions, trophic interactions and anthropogenic influences. To understand these influences, we analyzed trends in populations of seven ungulate species counted during 15 years (1989–2003) of monthly monitoring using vehicle ground counts in the Maasai Mara National Reserve, Kenya. Abundance of six species declined markedly and persistently throughout the reserve during this period. The declines were contemporaneous with progressive habitat deterioration due to changing land use in pastoral ranches bordering the reserve, habitat desiccation due to rising temperatures, recurrent severe droughts and an exceptional ENSO flood in 1997–1998. The effect of progressive habitat deterioration was accentuated by illicit harvest, competition with livestock and elevated predation. After factoring out the influence of rainfall, ungulate populations declined more markedly in sections of the reserve experiencing greater livestock incursions and poaching. The declines were significantly correlated with increasing number of settlements and people in the pastoral ranches for five species. Heightened predation following a crash in the buffalo *Syncerus caffer* population during a severe drought in 1993 had little support as the primary cause of the declines.

Introduction

Animal population dynamics can be driven by shifting climatic forcing, habitat conditions, trophic interactions, anthropogenic influences and their interactions. Rainfall drives population dynamics of African savanna ungulates through its controlling influence on vegetation growth, food sufficiency and availability of surface water. Consequently, fluctuations in rainfall underpin ungulate population dynamics in Kruger Park, South Africa (Mills, Biggs & Whyte, 1995; Ogutu & Owen-Smith, 2003; Owen-Smith & Mills, 2006), Mara–Serengeti ecosystem (Mduma, Sinclair & Hilborn, 1999; Ogutu *et al.*, 2008) and Laikipia district of Kenya (Georgiadis, Hack & Turpin, 2003; Georgiadis *et al.*, 2007). Trophic interactions can also centrally influence ungulate population dynamics through predation (Owen-Smith & Mills, 2006, 2008) and competition (Dublin *et al.*, 1990).

Human population growth and land transformations also influence ungulate population dynamics through the destruction and loss of their natural habitats and accelerated exploitation (Sinclair & Wells, 1989; Western, 1989; Sinclair *et al.*, 1995). The long-term viability of wildlife in the Mara

region of Kenya, where pastoral landscapes are shared by wildlife, people and livestock, is threatened by land transformations due to rapid (1) human population growth (Homewood *et al.*, 2001; Coast, 2002; Thompson & Homewood, 2002); (2) demographic, socio-cultural, economic, policy, political and institutional changes (Sereneels, Said & Lambin, 2001; Coast, 2002; Thompson & Homewood, 2002; Sitati, 2003; Lamprey & Reid, 2004); (3) expansion of settlements (Lamprey & Reid, 2004) and agriculture (Sereneels *et al.*, 2001; Sitati, 2003); (4) transition from semi-nomadic pastoralism to a sedentary lifestyle and from communal to private and corporate land tenure to secure legal title to land and user rights (Campbell & Axinn, 1980; Kimani & Pickard, 1998; Campbell *et al.*, 2000). The transformations are associated with habitat alteration (Boydston *et al.*, 2003), including declining woodland cover (Dublin, 1995; Lamprey & Reid, 2004), increasing competition between wildlife and livestock, harassment and displacement of wildlife (Mukinya, 1973) and illicit harvest, resulting in marked declines in wildlife numbers (Ottichilo *et al.*, 2000).

Economic diversification from livestock herding to trade, tourism development, conservation, cultivation and land

use intensification to increase productivity and return to capital investment (Campbell *et al.*, 2000; Coast, 2002; Thompson & Homewood, 2002; Lamprey & Reid, 2004) also threaten wildlife conservation in the Mara ranches. These incongruent land uses engender intense competition and conflicts (Campbell *et al.*, 2000). Also, rapid changes in customary perceptions, values and aspirations of young Maasai are undermining the traditional symbolic attributes and social institutions that historically protected wildlife and their environment in the pastoral lands of the Mara.

These changes, particularly individualization of land ownership, land subdivision and proliferation of permanent settlements, fences and cultivation (Thompson & Homewood, 2002) are occurring at alarming rates, threatening the future of wildlife conservation. The area of cultivated land has increased tremendously in the Mara ranches since 1975 (Serneels *et al.*, 2001; Sitati, 2003), advancing cultivation right up to the boundary of the Mara Reserve in Ololaimutia. Development of major trading centers and settlements near the main gates of the reserve and in parts of the ranches (Thompson & Homewood, 2002; Lamprey & Reid, 2004) further exclude wildlife or restrict their movements.

Here we analyze trends in numbers of seven ungulate species monitored monthly in the Maasai Mara National Reserve (MMNR) for 15 years. The data cover 5 years beyond the period covered by earlier analyses of annual aerial survey data (Brotten & Said, 1995; Ogutu, 2000; Ottichilo *et al.*, 2000). We assess the influence of land use on ungulate population trends, specifically poaching, competition from cattle, range contraction and deterioration. We evaluate evidence for spatial distinctions in trends, related to regional differences in cattle incursions and

poaching in the reserve, after factoring out temporal variability in trends related to rainfall. We use prevalence of poaching, illegal livestock grazing in the reserve, range contraction and human population growth in the ranches as indices of anthropogenic impacts. We test predictions of hypotheses relating to bottom-up (H1 and H3) and top-down (H2 and H4) processes (Table 1).

Materials and methods

Study area

The MMNR (1°13'–1°45'S, 34°45'–35°25'E) covers some 1530 km² in south-western Kenya. It is the northern-most section of the Mara–Serengeti ecosystem, covering some 25 000 km². It is bounded by the Serengeti Park to the south, the Siria escarpment to the west and Maasai pastoral ranches to the north, east and west. Rainfall in the ecosystem increases markedly along a south-east–north-west gradient (Norton-Griffiths, Herlocker & Pennycuik, 1975), varies strikingly in space and time, and is markedly bimodal. The Sand, Talek and Mara are the major rivers draining the reserve. Shrubs and trees fringe most drainage lines and cover hillslopes and hilltops.

Wildebeest *Connochaetes taurinus*, zebra *Equus burchelli* and Thomson's gazelle *Gazella thomsoni* migrate into and occupy the Mara reserve from the Serengeti plains to the south and Loita plains in the pastoral ranches to the north-east from July to October or later. Herds of all three species are also resident in the reserve.

To capture spatial heterogeneity in population changes, the reserve was partitioned into three blocks (Ogutu *et al.*,

Table 1. Theoretical predictions of the effects of anthropogenic influences and trophic interactions on ungulate population trends in the Mara Reserve, Kenya, during 1989–2003 and previous studies related to the hypothesized mechanisms

Causal agent	Mechanism	Predictions	Previous studies in the Mara
Anthropogenic influences	H1: Reduced spatial heterogeneity and exclusion from the ranches	Declining population of grazers and browsers in all blocks independent of rainfall	Brotten & Said (1995), Ogutu (2000), Ottichilo <i>et al.</i> (2000), Homewood <i>et al.</i> (2001), Ogutu <i>et al.</i> (2005), Serneels <i>et al.</i> (2001), Serneels & Lambin (2001)
	H2: Illegal harvest of wildlife within the reserve	Declining population of grazers and browsers independent of rainfall and livestock numbers in block 1	Darling (1960), Talbot & Talbot (1963), Walpole <i>et al.</i> (2001)
	H3: Increased illegal livestock grazing in the reserve	Declining population of grazers correlated with livestock numbers using the reserve in blocks 2 and 3. This should affect long more than short grass feeders and have no direct effect on browsers	Mukinya (1973), Boydston <i>et al.</i> (2003)
Trophic interactions			
Predation	H4: Heightened lion predation after 1993–1994 when the population of the major lion prey in the wet season, buffalo, crashed by 75% from 13 000 to 3220.	Declining population after 1993 and no recovery thereafter for both grazers and browsers except for giraffe that are largely free of lion predation in all blocks	H. T. Dublin (unpubl. data)

2008). Block 1 is a low lying and open grassland that receives the highest amount of rainfall and hence is prone to water-logging in the wet season. Hills and ridges cover the southern and western sections of block 1. Block 2 has a high elevation and receives intermediate rainfall. Large, open and rolling grass plains interspersed with shrub and woodland mosaics occur in block 2. Hills and ridges are found in the southern, eastern and western edges of block 2. Block 3 receives the lowest rainfall, has several hills and ridges covered by forests and thickets, and a few grass plains. This block has the highest average elevation.

Animal counts

Four resident grazers comprising topi *Damaliscus korrigum*, kongoni or Coke's hartebeest *Alcelaphus busephalus cokii*, waterbuck *Kobus ellipsyprimmus* and warthog *Phacocoerus africanus*; zebra a migratory grazer, impala *Aepyceros melampus*, a resident mixed feeder and giraffe *Giraffa camelopardalis*, a resident pure browser, were counted monthly in the MMNR by the Maasai Mara Ecological Monitoring Program (MEMEP) from July 1989 to December 2003. A monthly interval was chosen to capture seasonal effects and reliably detect and link the timing, direction and extent of changes in abundance to the underlying causal agents.

Illicit harvest, livestock incursions, settlements and human population growth

Poaching was most prevalent in block 1 based on recorded numbers of arrested poachers and snares recovered during anti-poaching ranger patrols and numbers of carcasses of wildlife killed by poachers and sighted during the patrols

from August 2001 to July 2004 (Table 2). Interviews of key informants suggested negligible or no poaching in blocks 2 and 3. Livestock grazing is prohibited in the reserve but was common in block 3 followed by block 2 but negligible in block 1. The contrasting levels of poaching and livestock grazing among blocks were used as treatments. Thus we contrasted trends between the three blocks distinguished by poaching and no livestock grazing (block 1), no poaching and low livestock grazing (block 2) and no poaching and heavy livestock grazing (block 3).

The wild ungulates can compete with or be displaced by livestock, hence we used estimates of absolute population sizes of livestock (cattle, donkey, sheep and goats) from aerial sample surveys conducted by the Department of Resource Surveys and Remote Sensing of Kenya (DRSRS) in the reserve during 1977–2002 to assess indirect evidence for competition, harassment or displacement of wildlife by livestock and herders (Mukinya, 1973; Boydston *et al.*, 2003). The DRSRS conducted 44 surveys in the Mara from 1977 to 2002, with at least one survey conducted each year except in 1981, 1988, 1995, 1998, 1999 and 2001. Norton-Griffiths (1978) comprehensively describes the details of counting and population estimation procedures used by DRSRS.

Using the DRSRS counts and unit weights in Coe, Cumming & Phillipson (1976) the combined biomass of livestock was calculated, log transformed and lagged by 1 year. Densities of cattle and buffalo were likewise transformed and lagged. The density of buffalo was used as a proxy for lion *Panthera leo* predation pressure falling on alternative prey species (cf. Owen-Smith & Mills, 2008), assuming the number of buffalo determined that of lions before the buffalo population crash. The number of pastoral settlements (bomas) in the adjacent Koyiaki ranch indexed land use change while the total number of huts in the bomas

Table 2. The number of arrested poachers and recovered snares during ranger patrols in the Mara Triangle (block 1) from August 2001 to July 2004

Month	2001		2002		2003		2004	
	Arrests ^a	Snares	Arrests	Snares	Arrests	Snares	Arrests	Snares
January					10	11	0	84
February			1	0	11	5	9	76
March			13	95	9	8	4	0
April			6	0	12	12	1	0
May			10	80	4		1	0
June			12	33	2	44	1	0
July			6	10	10	25	2	22
August	10	60	17	113	6	2		
September	0	140	26	107	9	20		
October	3	68	5	0	10	31		
November	7	17	30	64	22	53		
December	4	0	1	12	4	9		
Total	24	285	127	514	109	220	18	182

^aThe arrested poachers were found with a total of 1200 kg of wildlife meat, spears, bows, arrows and dogs and potassium cyanide crystals used to poison wildlife. Arrested poachers were also found with carcasses of three buffaloes, 27 Thomson's gazelles, three warthogs, 13 zebras, 41 wildebeests, one eland, two impalas, one reedbuck and one waterbuck.

indexed human population growth, as the number of huts is directly proportional to human population size (Lamprey & Reid, 2004). The numbers of bomas and huts were obtained from Lamprey & Reid (2004) and lagged by 1 year. A semiparametric generalized linear mixed model (SGLMM) was used to interpolate missing aerial counts, number of bomas and huts.

Statistical modelling and analyses

A suitable statistical model for long-term trends in the monthly counts should accommodate possibly nonlinear and disparate trends for different blocks. The model should further allow for non-normality of counts, many zeros and missing counts. We thus fitted a SGLMM to the time series of counts to allow for disparate trend curves for different blocks.

Modelling trends in monthly counts

We analyzed long-term trends in the monthly counts using a SGLMM with a negative binomial error distribution and a log link function. The trend model included census block as a fixed effect and a radial basis smoothing spline covariance structure (Ruppert, Wand & Carroll, 2003). This model is equivalent to a semiparametric regression model, allowing significance testing for the effects of block and spline smoothing of the time series of counts. The radial smoother covariance structure is equivalent to an approximate low-rank thin-plate spline based on the automatic smoother in Ruppert *et al.* (2003, chapter 13.4–13.5). We used the k-d tree method for knot construction and tried different choices to select a suitable bucket size. The total variance for each species was partitioned into two components corresponding to the correlations between temporal trends in counts across all blocks and serially correlated residual error. This was achieved by fitting the one-way model with block as a factor and assigning a separate spline component to the intercept.

Counts were offset by the logarithm of the area sampled in each block to obtain numerical relative densities. The running months were divided by 100 to obtain variance components of similar magnitude and accelerate convergence. The model assumed that missing counts were missing at random (Verbeke & Molenberghs, 2000) and was fitted by maximizing the residual log pseudo-likelihood with expansion about the current selections of the best linear unbiased predictors of the random effects (Wolfinger & O'Connell, 1993). The denominator degrees of freedom were synthesized using the method of Kenward & Roger (1997) and the model fitted by restricted pseudo-likelihood in the SAS procedure GLIMMIX (SAS Institute, 2006), which automatically computed the scale and overdispersion parameters of the negative binomial model. We also fitted a multivariate SGLMM to the counts of all species aggregated over each block. This model allowed for serial autocorrelation in the counts of each species and correlations between trends for

different species to establish patterns shared by trends for the different species.

Relating density to livestock, settlements, predation and human population growth

The influences of livestock and buffalo populations, expansion of bomas and human population growth on the density of each species were assessed by regressing LN (count/area) against linear terms in the predictor variables. Serial autocorrelation in animal abundance was accounted for using the spatial generalization of the autoregressive model, particularly the exponential model. The Akaike information criterion (AIC_c , Burnham & Anderson, 2002) was used to select the best model. The models were fitted in a general linear mixed model framework by maximum likelihood assuming a normal distribution in the SAS MIXED procedure (SAS Institute, 2006). The amount of variance explained by these models was assessed by regressing the observed against predicted counts assuming equality and calculating conventional R^2 .

Results

Illicit harvest, livestock, settlements and human population growth

The numbers of arrested poachers, the weapons they used and the species of animals they killed in block 1 from August 2001 to July 2004 revealed heavy illicit harvest of wildlife in block 1 (Table 1). Overall, 278 poachers were arrested and 1201 snares and 1200 kg of wildlife meat, belonging to at least nine different species, recovered during anti-poaching operations spanning the 30-month period (Table 2). Although substantial organized poaching operations based on dogs, poisoned arrows and snares and thus targeting a broad spectrum of species occurred in block 1, poaching was negligible in blocks 2 and 3.

Human population size increased rapidly in the Mara ranches (Fig. 1). The number of bomas increased exponentially from four in 1950 to 368 in 2003 as did the number of huts from 44 in 1950 to 2735 in 2003 (Fig. 2). The biomass of livestock grazing in the reserve increased strikingly from 1980 to 2003 and almost all occurred in blocks 2 and 3, with block 3 used more intensively than block 2 (Fig. 2). Buffalo numbers declined precipitously in the 1993 drought (see Table 1). Temporal patterns in climatic variables are reported in Ogutu *et al.* (2007).

Heavy illicit livestock grazing also occurred in the reserve (Fig. 2), implying intensifying competition between wildlife and the large number of livestock grazing in the reserve. Besides the exponential increase in the number of pastoral settlements, expanding crop cultivation and human population growth (Fig. 2) and intensification of land use due to progressive sedentarization of Maasai pastoralists likely caused progressive fragmentation and loss of wildlife habitat, reduced habitat heterogeneity and gradual

Trends in human population size in the Mara area of Kenya

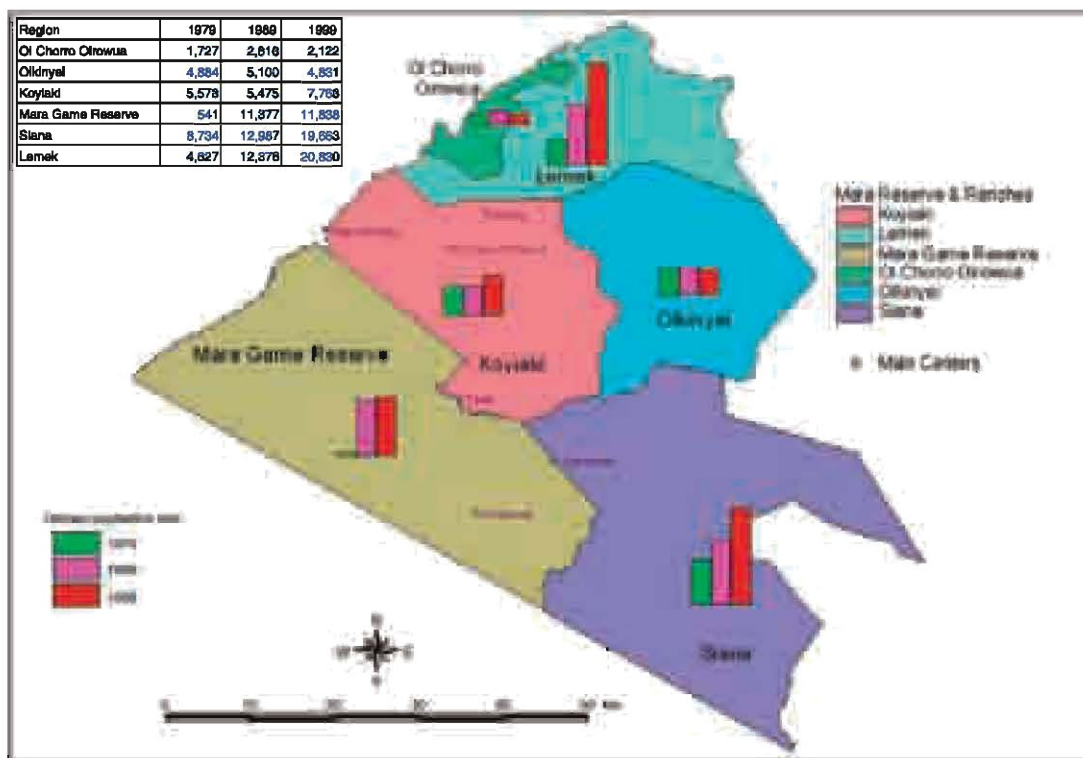


Figure 1 Trends in human population size in the Mara region from 1979 to 1999 based on decadal national census data compiled by the Central Bureau of Statistics of Kenya.

exclusion of wildlife from the pastoral lands adjoining the reserve.

Trends in wildlife abundance

Kongoni, warthog, topi, impala, giraffe and waterbuck, in decreasing order, decreased substantially during the monitoring period (Fig. 3). All the species but zebra decreased in abundance to lower than the 1984–2003 average during the 1993 drought, increased to above average during the good rainfall period in 1995–1996, decreased further during the drought of 1997, remained low through the exceptional El Niño floods of 1997–1998 and the La Niña drought of 1999–2000 and increased again to above average during 2001–2003, when wet season rainfall was high (Fig. 3). Migratory zebra became more numerous in the reserve during the rainy years of 1995–1996 and thereafter, with a minor decrease in numbers during the ENSO floods (1997–1998) and an increase in numbers during the prolonged drought of 1999–2000 and the good rains of 2002–2003 (Fig. 3). Waterbuck numbers increased during the ENSO floods (Fig. 3).

Regional distinctions in trends were evident for all species but warthog. Topi abundance decreased strikingly and persistently in blocks 1 and 3 throughout 1989–2003 but decreased only slightly before 1995 and then increased markedly during 1995–1996 and April–May 1999 only in

block 2, following the 1997–1998 ENSO floods (Fig. 4a). Kongoni numbers also declined markedly in all blocks only in block 2 during 1995–1996 and January–August 1997. Warthog numbers declined sharply and uniformly across all blocks throughout 1989–2003. Waterbuck numbers also declined more severely in blocks 1 and 3 than block 2, with successful recruitment apparent during the high rainfall periods in 1997–1998 and 2003 (Fig. 4a). Impala numbers first decreased from 1989 to a low during the drought of 1993, increased to a peak in 1995 and decreased again till 2000 before increasing thereafter in all blocks. The increase in impala numbers in block 1 was less pronounced than in blocks 2 and 3 (Fig. 4b). Giraffe abundance decreased sharply during 1989–2003 in blocks 1 and 3 but only slightly during 1989–1997 and increased later in block 2. Zebra abundance hardly changed in block 1 but increased in blocks 2 and 3 after the 1993–1994 drought (Fig. 4b).

Influences of livestock, predation, settlements and human population growth

The number of settlements and cattle were better predictors of variation in abundance than buffalo abundance (Table 3). Abundances of all the species but waterbuck and zebra decreased significantly as the number of bomas or huts increased (Table 4).

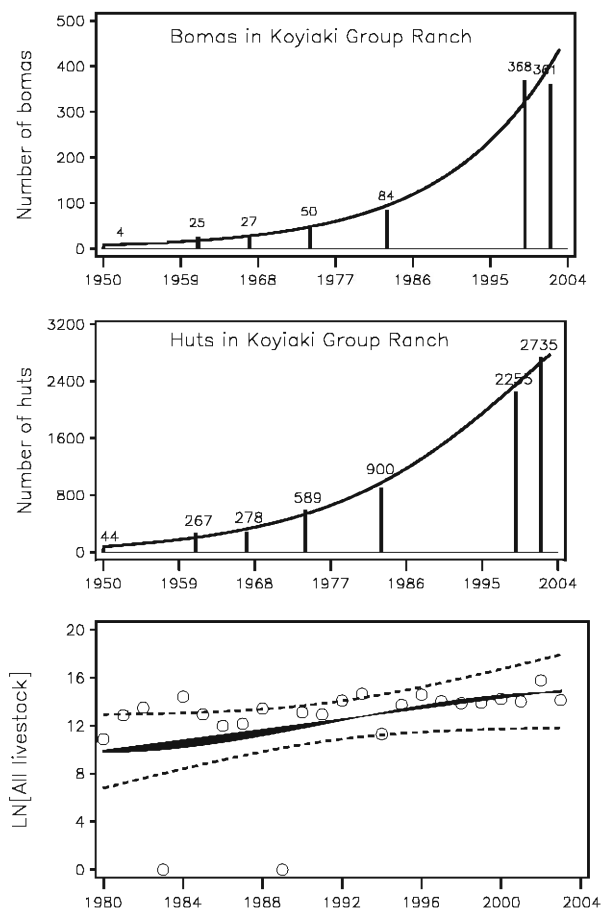


Figure 2 Temporal patterns in the number of pastoral settlements (bomas) and huts in Koyiaki pastoral ranch and the combined biomass of livestock (cattle, donkeys, sheep and goats) using the Maasai Mara National Reserve from 1980 to 2003.

Discussion

Trends in wildlife abundance

The declines in overall abundance of the four resident grazers portray the role of some broadly acting factor besides the background controlling influence of rainfall, poaching in block 1 and competition with livestock in block 3. The trends confirm drastic declines in wildlife numbers reported by earlier analyses (Brotten & Said, 1995; Ogutu, 2000; Ottichilo *et al.*, 2000). Pronounced non-linearity characterized the population trends, reflecting herbivore responses to sequential episodic perturbations, especially recurrent droughts.

Trends in regional abundances of all species but impala did not match fluctuations in rainfall, with numbers declining persistently even during periods of good annual rainfall (1989–1992, 1995–1996, 2001–2003), floods (1997–1998) or droughts (1993, 1997, 1999–2000). However, temporal variation in abundance tracked variation in rainfall more in block 2 than in blocks 1 and 3. Hence we reject H4. The

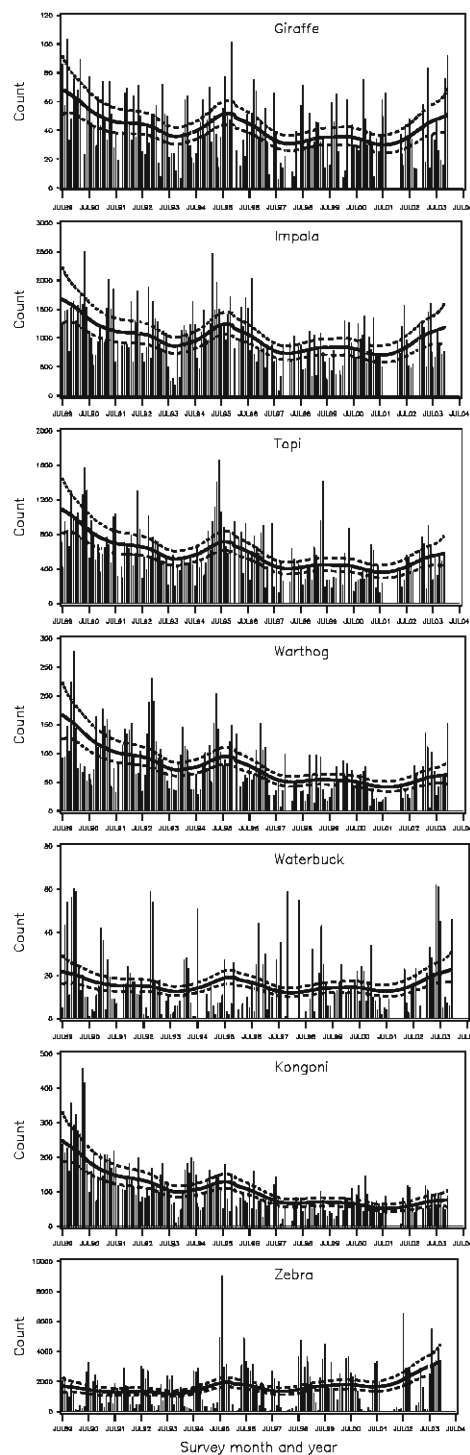


Figure 3 Trends in monthly counts for the seven ungulate species aggregated over all census blocks in the Mara Reserve during 1989 to 2003. Fitted trend curves and the associated 95% confidence bands are based on the multivariate semiparametric generalized linear mixed model incorporating all the seven species simultaneously.

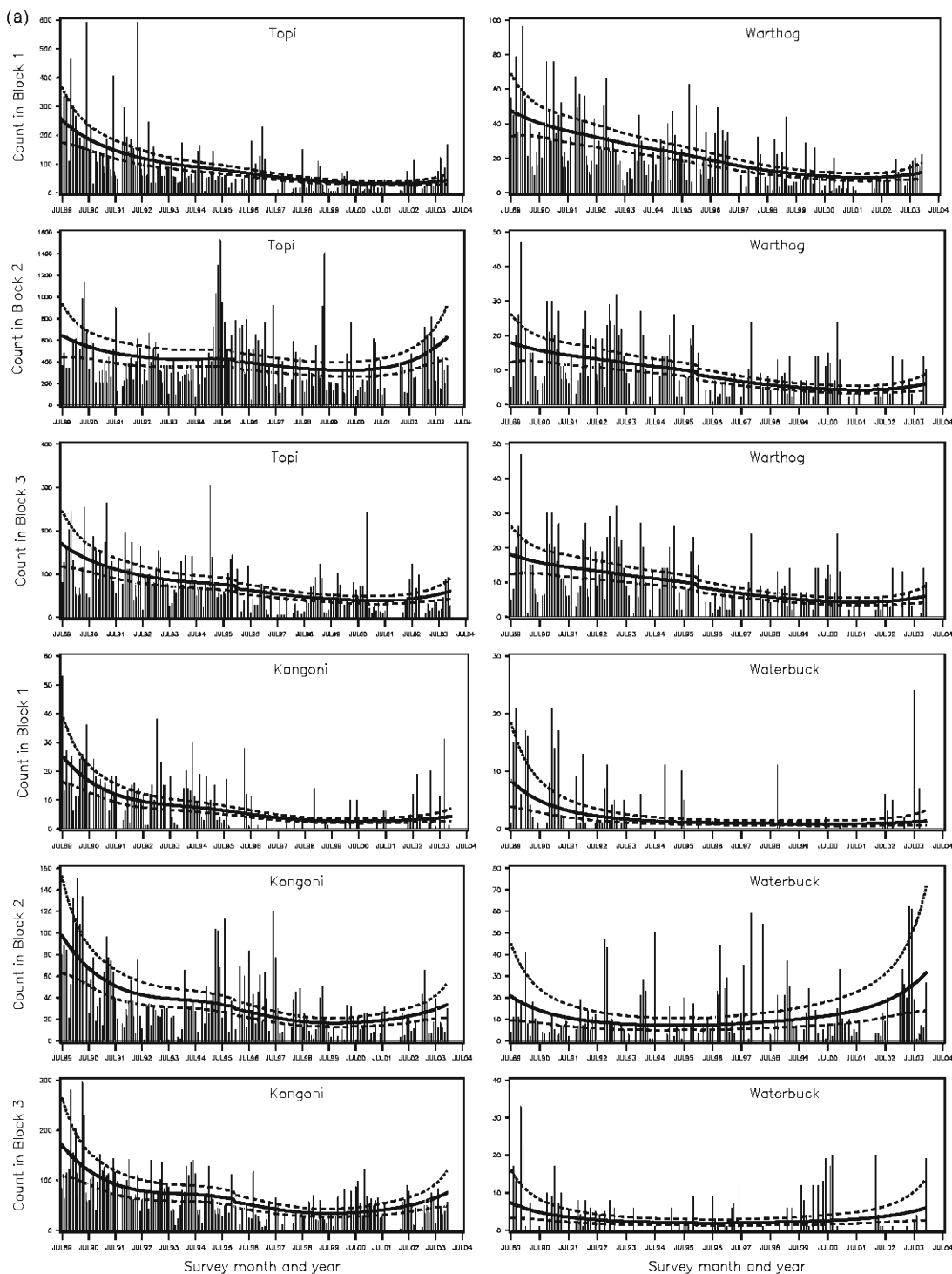


Figure 4 Trends in monthly total counts for (a) topi *Damaliscus korrigum*, warthog *Pharacoceerus africanus*, kongoni and waterbuck *Kobus ellipsyprimmus* and (b) impala *Aepyceros melampus*, giraffe *Giraffa camelopardalis* and zebra *Equus burcheli* by census block. The fitted trend curves and the associated 95% confidence bands are computed using the semiparametric generalized linear mixed model separately for each species.

regional disparities in trends, implicate differential mortality among regions, consistent with the high level of poaching in block 1 and livestock grazing in block 3. Hence H2 and H3 but not H1 are supported for topi, kongoni, waterbuck,

impala and giraffe. Zebra numbers increased in blocks 2 and 3 after the 1993–1994 drought, reflecting deteriorating habitat conditions in, and exclusion from, the ranches. Thus H1 is supported for zebra but H2 and H3 are not.

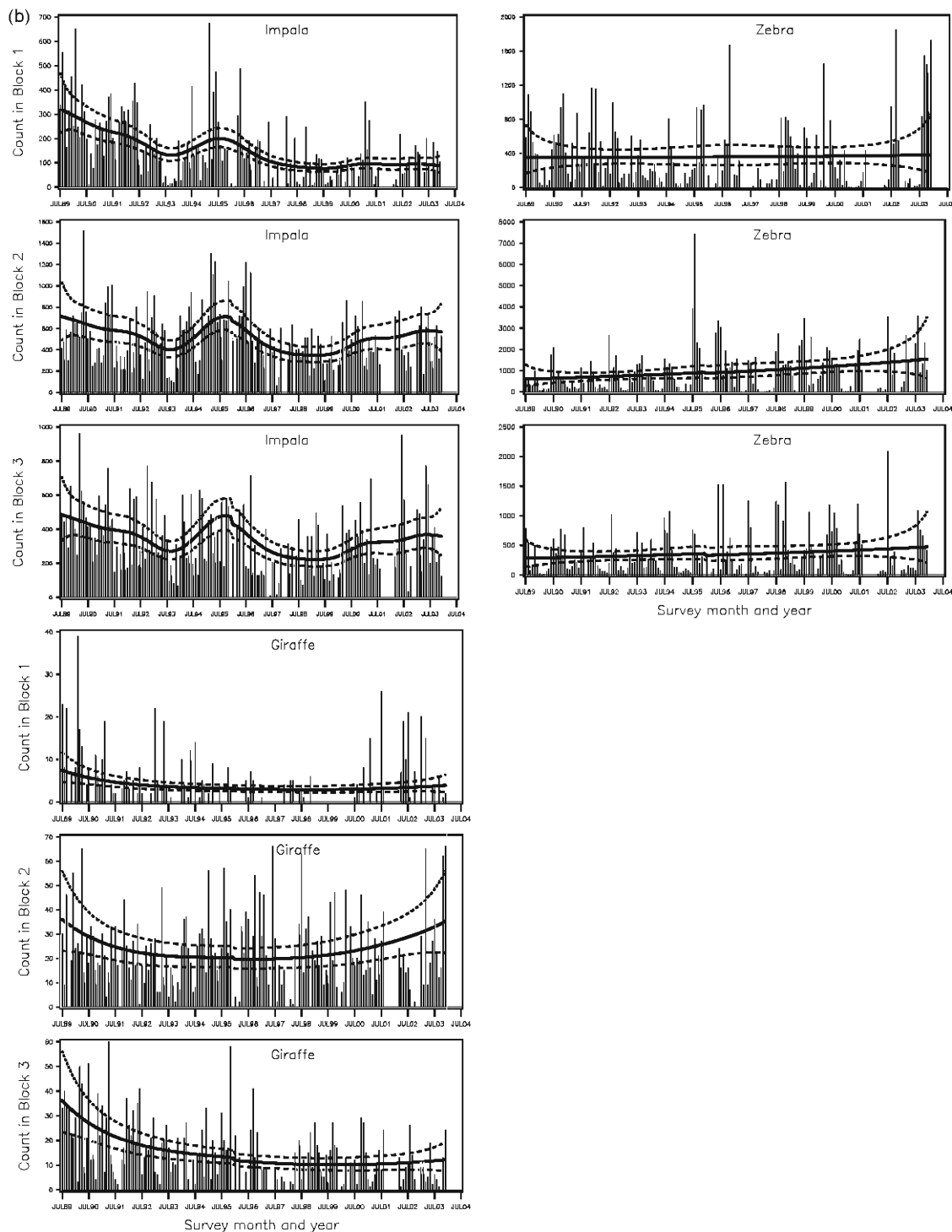


Figure 4 (Continued)

Periodic estimates of wildlife numbers were made in the Mara, or in parts of the region, using aerial and ground counts between 1958 and 1974 (Darling, 1960; Talbot & Talbot, 1963; Talbot & Stewart, 1964) but were replaced by regular monitoring of wildlife and livestock numbers in 1977

by DRSRS. Several analyses of changes in wildlife numbers have been undertaken using the DRSRS data. Stelfox *et al.* (1986) described annual migrations, seasonal dispersal movements and habitat selection by ungulates in the Mara during 1978–1979. Severe declines in wildlife populations in

Table 3. Selection of factors influencing variation in ungulate density in the Maasai Mara National Reserve during 1989–2003 using AIC_c

Effect	Giraffe	Impala	Kongoni	Topi	Warthog	Waterbuck	Zebra
Bomas	260.25	202.37	254.35	213.58	265.72	485.25	467.18
Huts	260.70	202.11	252.93	216.23	264.66	485.33	467.14
Cattle	260.17	201.86	264.57	217.34	277.18	485.36	467.02
All livestock	261.92	203.50	266.61	222.02	278.10	485.23	466.90
Buffalo	262.82	203.36	257.29	224.71	270.48	485.36	467.16
R^2 (obs vs. fitted)	0.952	0.693	0.889	0.212	0.914	0.917	0.274

The proportion of variance explained by the best model is indicated in terms of the R^2 obtained by regressing the observed against predicted log density R^2 (obs vs. fitted).

AIC_c, Akaike information criterion.

Table 4. Linear regression coefficients for the relationships between animal density (log-transformed) and the number of huts in Koyiaki pastoral ranch (log-transformed)

Species	Coefficient	Estimate	LCL	UCL	d.f.	<i>T</i>	<i>P</i> > <i>T</i>
Giraffe	Int	1.87	-2.12	5.87	37.9	0.95	0.3482
Giraffe	Huts	-0.57	-1.10	-0.05	38.0	-2.20	0.0340
Impala	Int	4.61	0.49	8.73	33.4	2.28	0.0293
Impala	Huts	-0.51	-1.06	0.03	33.4	-1.92	0.0631
Kongoni	Int	11.95	6.60	17.31	27.0	4.58	0.0001
Kongoni	Huts	-1.79	-2.50	-1.09	27.0	-5.20	0.0000
Topi	Int	7.19	3.47	10.91	36.7	3.91	0.0004
Topi	Huts	-0.93	-1.42	-0.44	36.8	-3.83	0.0005
Warthog	Int	9.05	3.80	14.31	30.0	3.52	0.0014
Warthog	Huts	-1.45	-2.15	-0.76	30.0	-4.27	0.0002
Waterbuck	Int	-5.03	-13.15	3.09	42.6	-1.25	0.2183
Waterbuck	Huts	0.17	-0.91	1.24	42.7	0.31	0.7547
Zebra	Int	2.03	-11.86	15.92	21.7	0.30	0.7643
Zebra	Huts	-0.17	-2.00	1.67	21.8	-0.19	0.8502

The coefficients are the intercept (Int), slope (Huts), lower (LCL) and upper (UCL) 95% confidence limits.

the reserve and adjoining pastoral ranches during 1975–2000 (Brotten & Said, 1995; Ogotu, 2000; Ottichilo *et al.*, 2000; Homewood *et al.*, 2001; Ottichilo, de Leeuw & Prins, 2001; Serneels & Lambin, 2001; Piepho & Ogotu, 2002; Lamprey & Reid, 2004) have been vaguely attributed to land use and cover changes, most notably the expansion of mechanized large-scale wheat farming in the Loita plains. On the Tanzanian side of the Mara–Serengeti ecosystem, substantial changes in herbivore numbers have been reported in the Serengeti Park (Campbell & Borner, 1995) and Ngorongoro Crater (Runyoro *et al.*, 1995). However, these analyses have mainly described trends rather than establishing their underlying causes. Nevertheless, the marked population declines in the Mara reserve are consistent with similar declines in wildlife abundance and diversity since the 1970s around the reserve and other protected areas, or open rangelands across Kenya (Western, Russell & Mutu, 2006) and parts of Tanzania (Stoner *et al.*, 2007).

Predation

Lion and hyena *Crocuta crocuta* are the major predators of large herbivores in the Mara–Serengeti. Buffalo and warthog are the primary prey for lions in the wet season (Scheel & Packer, 1995). The abrupt and precipitous decline

in buffalo numbers in the Mara in 1993 thus could have accentuated the amount of predation falling on the resident herbivores in the wet season, when the migrants are absent from the reserve. The elevated predation pressure could suppress ungulate population growth even in years with sufficient rainfall and their population rebound after droughts.

We expected lion predation to be density dependent and to have much larger effect on other resident species after the buffalo population crash in 1993 because lions are limited by territoriality. Packer *et al.* (1999) reported massive declines in lion numbers in northern Serengeti due to an outbreak of canine distemper epizootic in 1993 but Kock *et al.* (1998) did not find evidence for a significant impact of this disease outbreak on the Mara lions. Ogotu, Bhola & Reid (2005) also found that lion and hyena numbers probably changed little in the Mara reserve between 1991 and 2003.

If lion and hyena numbers remained high after the buffalo population crash in 1993 then we expected the herbivore populations not to recover after the drought. However, declining trends for all species but impala in all blocks that began before 1993 and persisted till 2003, despite intermittent improvements in rainfall conditions, and recovery of the impala population in all blocks during 2001–2003 suggest that heightened lion predation after 1993 was not

the primary cause of population declines but could have been an important source of mortality. Thus we reject H4.

Predation on resident ungulates is highly reduced in the dry season when enormous herds of migratory ungulates are present in the Mara. Clearly, an increase in numbers of migrants in the reserve would reduce predation of residential herbivores and their food supply. Despite the increase in zebra numbers in blocks 2 and 3 after 1993–1994, numbers of resident grazers continued to decline, suggesting heightened interspecific competition with migratory zebra and livestock.

Anthropogenic influences

Livestock grazing in the reserve

The marked increase in livestock incursions in the reserve during 1980–2003, indicates habitat deterioration and intensification of livestock grazing due to sedentization of the Maasai in the ranches. This increase and the greater declines in herbivore numbers in block 3 than block 2 support H3. The decline in giraffe numbers in block 3 indicates disturbance and displacement by illicit livestock grazing.

Establishment of permanent settlements near the main entrances into the reserve from the late 1980s through 1990s coincided with increased livestock use of the reserve, which likely accentuated the effect of droughts on wild herbivores through elevated competition for forage and water. Similarly, the increase in livestock numbers using the reserve was probably also partially due to increasing habitat desiccation in the ranches (Ogutu *et al.*, 2007), exacerbated by sedentization of the Maasai, intensification of land use and increasing density of settlements, driven by rapid human population growth. However, range contraction due to habitat fragmentation, degradation and loss in the pastoral ranches probably increased the vulnerability of ungulates to rainfall variability on food production and habitat conditions, competitor impacts and heightened lion predation.

The Maasai pastoralists build their herds to very large numbers during good years because those with larger herds are more likely to retain larger herds after drought losses compared with those with smaller ones. This enables herders with many animals to rapidly rebuild their stocks after droughts. This intensifies competition between livestock and wildlife in dry periods and delays natural vegetation recovery after droughts. Cattle are regularly grazed in the MMNR along most of its eastern and northern boundaries, particularly in Talek, Ololaimutia, Sekenani and Enkikwei. This increases competition between livestock and wildlife, especially the long grass feeders (topi and kongoni). Also, sheep and goats crop grass to the ground, accelerating habitat desiccation in dry periods because exposed ground heats up more rapidly. The short grass excludes tall grass feeders. Land use change and fluctuations in rainfall also contributed to population declines by ungulates in Laikipia District of Kenya (Georgiadis *et al.*, 2007).

Poaching

Although the numbers of arrested poachers or poacher snares were available only from August 2001 to July 2004, thus precluding formal statistical testing, the many poachers in the reserve imply that many animals were taken, so the number of arrested poachers indexes intensity of poaching. Thus when more poachers are arrested, there are fewer left to poach. The high levels of poaching and decline in herbivore numbers in block 1 support H2. Block 1 was the hardest hit by poaching, a persistent pattern already apparent in the late 1950s (Darling, 1960; Talbot & Talbot, 1963). Intensified anti-poaching patrols were inaugurated by a bilateral pact between the Kenyan and Tanzanian governments allowing rangers to pursue poachers across their common border in mid 1990s. Further intensification of ranger patrols in block 1 started after 2000 and resulted in unprecedented arrests of poachers and removal of snares. Previously, rangers had limited logistical and financial support for regular and effective law enforcement patrols and were also hampered by limited accessibility in the wet season due to poor roads.

Most poachers in the Mara–Serengeti ecosystem are poor subsistence farmers dependent on bushmeat for protein nutrition and income in north-western Serengeti (Arcese, Hando & Campbell, 1995; Campbell & Hofer, 1995; Loibooki *et al.*, 2002), where they have greatly reduced populations of residential herbivores (Campbell & Hofer, 1995). Specifically, bushmeat hunting caused a 90% decline in the buffalo population in northern and western Serengeti (Dublin *et al.*, 1990), whereas illegal hunting for its horn caused the near extinction of the black rhinoceros *Diceros bicornis* population (Walpole *et al.*, 2001) and major reductions in elephant numbers (Dublin *et al.*, 1990). Illegal hunting was also largely responsible for the extinction of the roan antelope *Hippotragus equinus* and greater kudu *Tragelaphus strepciceros* in the Mara reserve in the 1970s. Wire snares are the most widely used method of capturing wildlife in the Mara–Serengeti (Arcese *et al.*, 1995). Snares are unselective and negatively affect populations of many non-target wildlife species (Hofer, East & Campbell, 1993; Arcese *et al.*, 1995; Hofer & East, 1995), even though most of the illegal bushmeat harvest consists of migratory wildebeest and zebra (Campbell & Hofer, 1995). About 160 000 resident and migratory herbivores (Hofer *et al.*, 1996), including about 40 000 wildebeest (Mduma, Hilborn & Sinclair, 1998), are illegally harvested annually in the Mara–Serengeti.

Land use change and human population growth

Cultivation is a major cause of loss of wildlife habitats in the Mara ranches. The cultivated acreage in pastoral ranches to the north of the reserve increased by 319% from 1975 (73.7 km²) to 1996 (308.6 km²) (Sitati, 1997). In the ranches east of the reserve the corresponding rate of increase in cultivated land from 1975 (0.08 km²) to 1997 (80.98 km²)

was 1011% (Kimanzi, 1999), while in the ranches bounding the reserve to the west, the rate of increase from 1975 (117.3 km²) to 2000 (1101.5 km²) was 839% (Sitati, 2003).

Declining woodland cover in the reserve (Dublin, 1995; Lamprey & Reid, 2004) is associated with expansion of settlements (Lamprey & Reid, 2004), cultivation (Sitati, 2003) and human population growth (Coast, 2002). Thus progressive habitat loss and fragmentation in the pastoral ranches also contributed to declines in wildlife abundance. Declining woodland cover in the Mara is consistent with the declining giraffe numbers in the Mara reserve and ranches (Ogutu, 2000; Ottichilo *et al.*, 2000).

The effects of land use and cover change in the ranches on wildlife were exacerbated by recurrent severe droughts and rising temperatures (Ogutu *et al.*, 2007). Reduced spatial habitat heterogeneity due to widespread clearance of woodland cover for settlements, cultivation, fuelwood, fencing and construction materials in the ranches (Serneels *et al.*, 2001; Thompson & Homewood, 2002; Lamprey & Reid, 2004) displaced or excluded wildlife from the ranches and compressed them into the reserve, as evidenced by zebra after 1993–1994. The exclusion constrains wildlife access to water, seasonal dispersal and migratory movements.

Since seasonal movements (Stelfox *et al.*, 1986) allow them to optimally use seasonally variable forage and water, restrictions on wildlife movements by land use changes constrain their exploitation of the pastoral buffer zones. Reduced flexibility and mobility due to progressive habitat loss in the ranches amplifies the vulnerability of wildlife to recurrent climatic extremes, exacerbating population declines. Not surprisingly, massive declines have occurred in wildlife numbers in areas under extensive commercial wheat cultivation in the Mara ranches (Homewood *et al.*, 2001; Ottichilo *et al.*, 2001; Serneels & Lambin, 2001). The impact of commercial cultivation in the Loita plains on population declines is accentuated by degradation of the hydrology of the entire northern Mara–Serengeti ecosystem through spiralling extraction of water from the Mara river for large commercial cultivation and small but intensive areas of irrigated cultivation (Wolanski *et al.*, 1999; Wolanski & Gereta, 2001; Gereta, Wolanski & Chiomba, 2003).

Disease outbreaks are associated with droughts and floods in Eastern Africa but the field team did not observe increased frequency of epizootics. However, contracting range increases contacts and risks of disease transmission between wildlife and livestock in the ranches. The threat of disease transmission between livestock and wildlife is growing due to an increasing number of domestic dogs and adoption of exotic breeds of livestock by some pastoralists. Habitat fragmentation increases exposure of wildlife to domestic dogs, which act as disease reservoirs for many zoonotic diseases. Transmission of infectious diseases is likely to escalate and was probably responsible for the extinction of local wild dog *Lycaon pictus* packs.

Settlements are expanding faster nearer the reserve than further away, attracted by enhanced economic activities and opportunities inside and near the reserve (Norton-Griffiths *et al.*, 2008). This plus the intensifying competition and

conflicts between the incongruent land uses, people and wildlife (Omondi, 1994; Sitati, 2003) pose a serious threat to the long-term viability of wildlife populations and pastoralism in the Mara. Already, killing of wildlife in retaliation for destruction of fences, degradation of water quality, crop damage (Sitati, 2003), livestock depredation, human injuries and fatalities is common and increasing (Karani, 1994; Mwangi, 1997; Sitati, 2003). This could portend grave consequences for the future of wildlife conservation, as most wildlife in the Mara occur in the ranches or move seasonally between the ranches and the reserve. Recent and ongoing formation of private conservancies and tourism concerns on formerly Masai group ranch land in Koyiaki, Lemek and Siana, involving partnerships between groups of neighboring private land owners and outside investors, in which land owners voluntarily vacate their land for wildlife in exchange for land rents, if encouraged, would promote recovery of wildlife populations in the ranches.

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