BIOLOGICAL CONSERVATION 137 (2007) 461–472

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/biocon

Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time

Nicholas J. Georgiadis[a,*], *J.G. Nasser Olwero*[a,1], *Gordon Ojwang'*[b], *Stephanie S. Romañach*[c]

[a] *Mpala Research Centre, P.O. Box 555, Nanyuki 10400, Kenya*
[b] *Department of Resource Surveys and Remote Sensing, P.O. Box 47146, Nairobi, Kenya*
[c] *University of Zimbabwe, P.O. Box 167, Mount Pleasant, Harare, Zimbabwe*

ARTICLE INFO

Article history:
Received 1 November 2006
Received in revised form
14 January 2007
Accepted 12 March 2007
Available online 9 May 2007

Keywords:
Africa
Wildlife
Monitoring
Conservation
Non-protected areas

ABSTRACT

Ecosystem processes in African savannas can be better conserved if management is based on a mechanistic understanding of wildlife dynamics in livestock-dominated landscapes. For Laikipia District, a non-protected savanna region in northern Kenya, we used spatially explicit estimates of density to characterize factors influencing the dynamics of large herbivores on three land-use types: commercial ranches that favor wildlife, communal 'group ranches' practicing pastoralism, and the remainder ('transitional' properties). For 21-year time series of nine wild and two domestic species, linear model selection was used to ascribe between 45% (Grant's gazelle) and 95% (plains zebra) of observed variation in biomass density to land use, rainfall-dependence, density-dependence, and trends over time.

Strongly opposing patterns of variation across the landscape in wildlife and livestock densities affirmed the primacy of land use among factors influencing wildlife abundance in non-protected areas. Rainfall limited densities of only the dominant grazing species throughout the monitoring period (plains zebra and cattle), and of most other species while their densities were high. Regulating effects of density were detected only for the dominant wild grazing and browsing species (zebra and giraffe). All but two wild species (zebra and Grant's gazelle) declined on at least one land-use type, for reasons that varied among land uses.

Where favored, diverse and abundant wild herbivores (mean of 1.7 t km^{-2} on pro-wildlife ranches) can thrive even when sharing the landscape with a slightly higher biomass density of livestock (mean of 2.7 t km^{-2}). Where not favored, only a few resilient wild species (e.g. gazelles and plains zebra) persist with high densities of livestock (mean of 4.6 t km^{-2} on transitional ranches). Maintaining higher wild species diversity in the landscape will depend on the creation of a network of unfenced conservation areas in which livestock densities are persistently low or zero, which are sufficiently large to act as 'sources' of wild species that are prone to displacement by humans and livestock, and which generate benefits to community members that exceed opportunity costs.

---

[*] *Corresponding author*: Tel.: +254 62 32752; fax: +254 62 32750.
E-mail address: njg@mpala.org (N.J. Georgiadis).
[1] Present address: World Wildlife Fund – US, 1250 24th Street, NW, Washington, DC 20037-1193, USA.

0006-3207/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2007.03.005

1. Introduction

Recognition that protectionism alone is insufficient to sustain biodiversity has broadened the scope of conservation to target ecosystem processes, and to include human-occupied landscapes (Margules and Pressey, 2000). In Africa the rationale has long been compelling. Most protected areas are too small to host viable populations of large mammals (Western and Sesemakula, 1981; Western and Gichohi, 1993; Newmark, 1996). Many are smaller than the individual home ranges of such species as elephants and large predators (e.g. Armbruster and Lande, 1993; Grainger et al., 2005). Ecological processes within even the largest protected areas are influenced by humans and livestock in the surrounding matrix in ways that are only beginning to be documented (Woodroffe and Ginsberg, 1998; Harcourt et al., 2001). Much of the biodiversity remains outside protected areas, and would likely be lost without active conservation (Western, 1989). And few, if any, protected areas are large enough to be buffered against projected effects of climate warming and variability (e.g. Erasmus et al., 2002; Hannah et al., 2002). To the extent possible, fragmented landscapes must be actively managed as functionally intact ecosystems. In principle, addition of non-protected areas to a protected core should help to maintain ecosystem integrity and permit ecological community dynamics to remain as natural as possible.

Yet conserving large mammals is more challenging in non-protected than in protected areas, prescriptions are far less well defined, and it is too soon to know whether diverse wildlife communities can persist in human-occupied landscapes over the long term (Hackel, 1999; Goldman, 2003; Hutton et al., 2005). Active intervention is increasingly required – but not often provided – to manage non-protected wildlife towards stated conservation goals, compensate for the diminishing role played by natural ecological processes, and minimize conflict between humans and wildlife (Hoare and Du Toit, 1999; Prins et al., 2000; Woodroffe et al., 2005). These are more likely to be achieved when management is informed by a mechanistic understanding of the dynamics of wild species where they share landscapes with humans and livestock.

Over the last 15 years considerable effort and resources have been applied to conserving wildlife in Laikipia District, a semi-arid savanna region in northern Kenya. The importance of this region is that little of it is formally protected, yet wildlife abundance is second in Kenya only to the renowned Masai Mara National Reserve. Only 2.1% of the area is set aside exclusively for wildlife in (private) fenced reserves. Elsewhere wildlife share the largely unfenced landscape with varying densities of livestock. Over recent decades, land use and management practices have varied widely as patterns of land ownership, and attitudes to wildlife among landholders, have changed. The result is a mosaic of properties with contrasting histories, land uses, management attitudes and practices, and densities of livestock and wildlife (Fig. 1). Such diversity over time and space provides an instructive model for large-mammal conservation in human-occupied landscapes, and warrants scrutiny as such.

Wild and domestic ungulates have been censused across the entirety of Laikipia District 13 times since 1985 using systematic sample survey methods (but also see Denney,

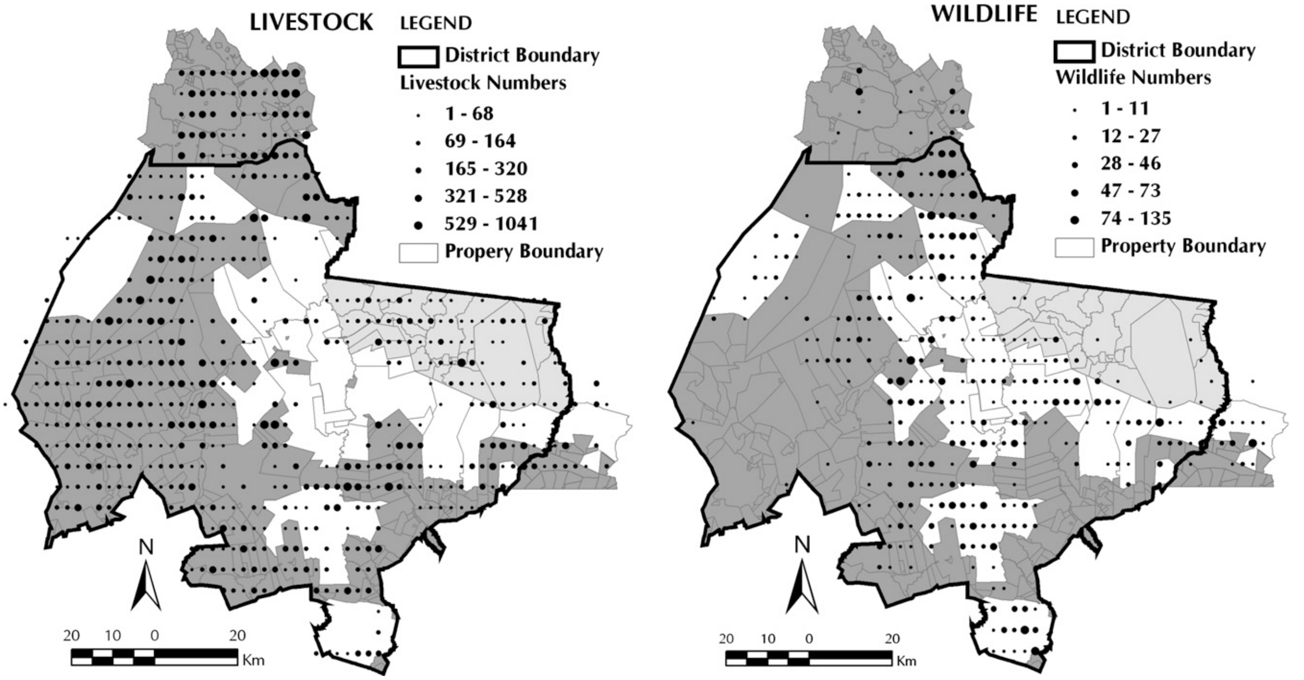

Fig. 1 – Distribution and relative abundance of livestock and wildlife in Laikipia District in February 2005, on three land-use types featured in this study: pro-wildlife (white), group ranch (light grey), and transitional (dark grey). Sections of this ecosystem are added to the north (Lerogi Plateau) and east (including Lewa Wildlife Conservancy) of Laikipia District. Data from these areas were not included in the analysis because they have only recently been added to the survey zone. Apparent absence of herbivores means that none were observed within transects.

1972). We used these time series to define and interpret the dynamics of wild herbivores that share the landscape with livestock and people. Objectives were to examine and compare differences in herbivore biomass over space, and to contrast their dynamics over time, on different land-use types. We assessed whether limitation by rainfall and regulation by density could be detected in time series derived from unevenly spaced sample surveys. Wild herbivore species were compared in their differing tolerance of, and degree to which they can coexist with, humans and livestock. Finally, we discuss the implications of these patterns and processes for persistence of wildlife in livestock-dominated landscapes over the longer term.

2. Methods

2.1. Study area

The larger study area spans a vast and geographically diverse region in northern Kenya, including the entirety of Laikipia District (9666 km^2) and parts of adjacent Samburu and Meru Districts to the north and east, respectively (Fig. 1; however, this study focuses only on the area within the boundary of Laikipia District). Steep elevation and thus climatic gradients are created by the presence of Mt. Kenya (5199 m) to the south east, and the Aberdare highlands (3999 m) to the south west. These uplands are drained to the north by many streams that ultimately combine to form two perennial rivers, the Ewaso Ny'iro and Ewaso Narok, which are confluent in the central 'Laikipia plateau', continuing to flow northward and then eastward through the Samburu, Buffalo Springs, and Shaba National Reserves. The climatic gradient is associated with marked land cover and land-use changes, from alpine moorlands, through protected montane rain forests, and an intensively cultivated moist zone, to relatively dry savanna grass- and bushlands at lower elevations. Rainfall increases at higher elevations in the south, and is weakly trimodal, falling in April–May, August, and November, with a pronounced dry season in January–March.

2.2. Land use types

In the context of this study, herbivore abundance and dynamics were compared among the three principal land-use categories, described below (Fig. 1).

Pro-wildlife properties (area covered was 3288 km^2, with 500–750 mm of rainfall annually). Following colonization in the early 1900s, much of Laikipia District was divided by the British administration into large-scale land holdings (2500–40,000 ha), with some of the smaller properties combined to make larger holdings later in the colonial period. Most of the larger ranches were acquired or leased by private landholders (three are now owned by the Kenya Government) and used for sport hunting and cattle ranching. Wild ungulates were shot in large numbers during WWII to feed troops and prisoners of war. Wild species that threatened ranching (mostly predators and plains zebras) were heavily suppressed, and income on most properties was supplemented from sale of wildlife skins and trophies (Denney, 1972).

Following a country-wide ban of consumptive use of wildlife in 1977, wild herbivore numbers increased to high densities in Laikipia District, especially plains zebras. Consequently, Laikipia was one of five areas in Kenya chosen to resume harvesting of wild ungulates on an experimental basis in 1992. The Laikipia Wildlife Forum, an association of landholders with a shared interest in conserving wildlife and ecosystem integrity, was established to manage wildlife harvesting. Although sustainably managed in Laikipia (Georgiadis et al., 2003), the scheme was suspended country-wide in 2003. From the late 1980s, growing awareness of the intrinsic value of wildlife and its economic potential sparked an enthusiastic conservation movement in Laikipia. The majority of private landholders continued to ranch livestock commercially, but at low to moderate densities, in order to favor wildlife (only two large-scale ranches continue to ranch cattle exclusively of wildlife). Consequently, there was a resurgence of wildlife, including elephants (*Loxodonta africana*) and predators, from the late-1980s. Seven reserves were established for rhino conservation.

Today more than 30 eco-tourist ventures depend on the wildlife and 'wilderness' resources in Laikipia and adjacent Districts (see www.laikipia.org). For this analysis, only those large-scale ranches that actively conserved and/or invested in wildlife from the early 1990s were classified as 'pro-wildlife'.

Group ranches (area covered was 1022 km^2, with 400–500 mm annual rainfall). In the 1970s, the drier north-east sector of Laikipia District was progressively sub-divided into unfenced 'group ranches' (2000–10,800 ha). These are properties for which title was registered to a limited number of families of mixed but largely pastoralist origin. They have mostly continued to use the land communally for pastoralism, although parts are now further subdivided and privately owned. Traditional attitudes to wildlife, which were more benign and less consumptive than in other cultures, have endured among some group ranch members, but high densities of livestock have long displaced most of the wildlife. The Mukogodo Forest was included in this category, an area of 295 km^2 in the east gazetted as a forest reserve, parts of which are used for dry season grazing (Fig. 1).

Transitional properties (area covered was 5357 km^2, 550–900 mm annual rainfall). Since the 1970s, large-scale ranches in the wetter south, south-east, and south-west, amounting to at least 17% of Laikipia District, have been subdivided into small plots (1–10 ha) and titles sold to thousands of smallholders. We refer to these as 'transitional' properties because only some of the plots have been occupied and cultivated when rainfall permits. Elsewhere, the land is heavily grazed, largely by pastoralists. Thus, a large area is in varying stages of transition from larger-scale ranching to small-scale holdings that are used in ways that have displaced or eliminated wildlife (Huber and Opondo, 1995; Thenya, 2001). Also included in this category are larger-scale farms and ranches that may or may not tolerate, but do not actively favor wildlife. Consequently, there is a wide range of wildlife densities on 'transitional' properties.

Fences and migration. An important feature of this landscape is that fences are generally lacking that would prevent wildlife moving within or between land use types. The few exceptions are in the south-east, south, and far west of the District, where electrified barriers have been installed between pro-wildlife and transitional properties, largely to reduce crop raiding by elephants. This is the only wild species known to regularly migrate out of the District, mostly to the lowlands in Samburu District to the north-east during wet seasons. In the past, wildlife, mostly plains zebras, moved locally across the District boundary to the north, from Laikipia to the Lerogi Plateau in southern Samburu District (Fig. 1). Today, however, wildlife has been largely displaced from that area by pastoralist livestock. Other than for elephants, therefore, Laikipia District is a relatively closed system for wildlife, but not for pastoralist livestock (discussed below).

2.3. *Aerial sample surveys*

Dynamics of the abundant herbivore species, 10 wild and two domestic, as well as human attributes such as cultivation and habitation, have been monitored across the entirety of Laikipia District since 1985 by the Department of Resource Surveys and Remote Sensing (DRSRS; Ministry of Environment and Natural Resources, Government of Kenya) using systematic aerial sample survey methods (Norton-Griffiths, 1978). Domestic species include cattle, and sheep and goats, the latter two treated as a single 'species' because they cannot be distinguished from the air. Elephants were omitted from this analysis because they are highly mobile, and tend to unduly skew biomass densities where they are encountered during surveys.

Since 1997 surveys have been designed and analyzed in collaboration with the Mpala Research Centre (MRC). Topographic sheets of scale 1:250,000 were used in flight planning to define the survey area boundary, and the location of transects. Transects were oriented north–south, with a flying speed of about 190 km/h, at a height above ground of about 122 m (400 ft), maintained with a radar altimeter. Transects were subdivided into 5 km sections using GPS. Transect strip widths had been empirically calibrated at 150 m on each side, yielding sampling fractions of about 6% for lower resolution surveys, to 12% for higher resolution surveys. The aircraft used was a high-wing, twin-engined Partenavia P68. A crew of four consisted of the pilot, Front Seat Observer (FSO), and two Rear Seat Observers (RSO). Herds of 10 or fewer animals were counted directly. Herds exceeding 10 animals were estimated, and obliquely photographed using 35 mm cameras for subsequent counting.

Undercounting is a well-known bias in aerial surveys (East, 1998, pp. 91–92; Redfern et al., 2002), but no attempt was made to correct for undercounting bias. Rather, consistency in counting methodology was maintained, such that the change in bias would be minimized. Season was potentially a confounding factor in these time series, because background vegetation colour and density affect the visibility of different species in different ways. Six of seven surveys after 1996 were conducted in the driest month, February (to maximize visibility, and minimize visibility variation between surveys), whereas none of the six surveys prior to 1995 was conducted in February. Effect of season on herbivore numbers and distributions was tested by conducting two surveys in 1997, the first in February, the second only 5 months later in June. February 1997 was dry, in that no rain fell, and a mean of only 20.2 mm of rain had fallen in the preceding two months. By contrast, June 1997 was wet, with a mean of 71.8 mm recorded in that month, and 327.3 mm falling in the preceding two months.

Since Laikipia District is effectively a closed system for the wild species featured here, differences in total population estimates between February and June 1997 would more likely reflect visibility bias than actual population change. Total population estimates for wild herbivores did not differ significantly between the February and June surveys of 1997 (Fig. 3a). Similarly, there was no overall change in wildlife density estimates on individual properties within each land use type with season (Fig. 3b), suggesting that net seasonal movements of wild species were limited. The same was true of livestock on pro-wildlife properties (Fig. 3c), but not of livestock on transitional properties, where estimates in June were about one fifth of estimates in February, or on group ranches, where wet and dry season estimates bore no resemblance to each other (Fig. 3c). These patterns reflect movements by pastoralists between group ranch and transitional properties, and between Districts, on a seasonal basis. We conclude that season was not a confounding factor for wildlife, or for livestock on pro-wildlife properties, but was for livestock on group ranch and transitional properties.

Survey sampling resolution was also a potentially confounding factor in these time series, because all surveys but one prior to 1997 were conducted at 'low' resolution (5-km transect spacing), and all surveys following that date were at 'high' resolution (2.5-km spacing). Indeed, a pattern of fluctuation prior to 1997, followed by decline, was repeated in some species, suggesting fluctuations to have been an attribute of low survey resolution, and/or low density estimates an attribute of higher survey resolution. This could be discounted by three observations. First, species that did not decline (plains zebras, Grant's gazelle, and impala) continued to fluctuate in the latter half of the period. Second, the 1991 survey, which was conducted at high resolution, yielded among the highest total biomass estimates in the entire series (Fig. 4), so high-resolution surveys did not necessarily yield low density estimates. Third, re-analysis following omission of alternating transects from high-resolution survey data (turning them into low-resolution surveys) yielded similar, although slightly 'noisier' declines. We inferred that observed fluctuations and declines were real.

2.4. *Spatial data analysis*

Each property was assigned to one of three land-use types (pro-wildlife, group ranch, or transitional), based on the livestock management regime, attitude to wildlife, and the presence or absence of cultivation (Fig. 1). GIS was used to estimate biomass densities of each species on each of the three land-use types in Laikipia District. It was first assumed that the density of each species within each 'subunit' of the survey grid (either 2.5 km × 5 km, or 5 km × 5 km, depending on survey resolution) was the same as densities estimated within transects. A 100 m raster grid was then overlaid on the survey subunit grid, and each raster grid unit given the density value of the survey subunit grid on which it overlaid. Finally, the property boundary layer was overlaid on the raster grid, and the mean density of each species on each land-use type was calculated from values in raster grids falling within property boundaries.

2.5. Cumulative rainfall index

Rainfall records covering 40 years from five gauging stations scattered across the study area were used in this study (Fig. 2). Correlations between stations in amounts of rain falling monthly ranged between 0.37 and 0.73 (Table 1). Monthly totals were used to provide an index of the degree to which rain falling between one survey and the next was below or above average. This cumulative Rainfall Deficit Index, R, was calculated as:

$$R = \left(\sum (r_i/\overline{r_i})\right)/n$$

where r is the rainfall in a given calendar month i, $\overline{r_i}$ the long-term mean rainfall for calendar month i, and n is the number of months between surveys. This gave a normalized index of cumulative rainfall deficit (<1) or surfeit (>1) between one survey and the next.

2.6. Unit weights

Unit weights (m in kg), given for each species in Table 2, were calculated as a function of the mean body weight of adult males and females (M in kg), using a power equation which accounts for population age structure and allometric growth

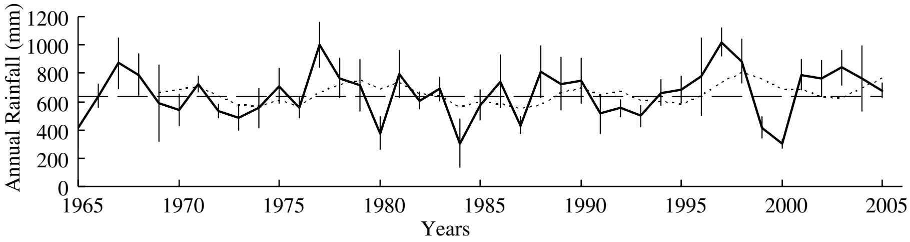

Fig. 2 – Mean annual rainfall over 40 years from five gauging stations scattered across the study area (bold black line, with standard deviations). The 5-year moving average (dotted line) and long-term mean (639 mm; dashed line) are also given.

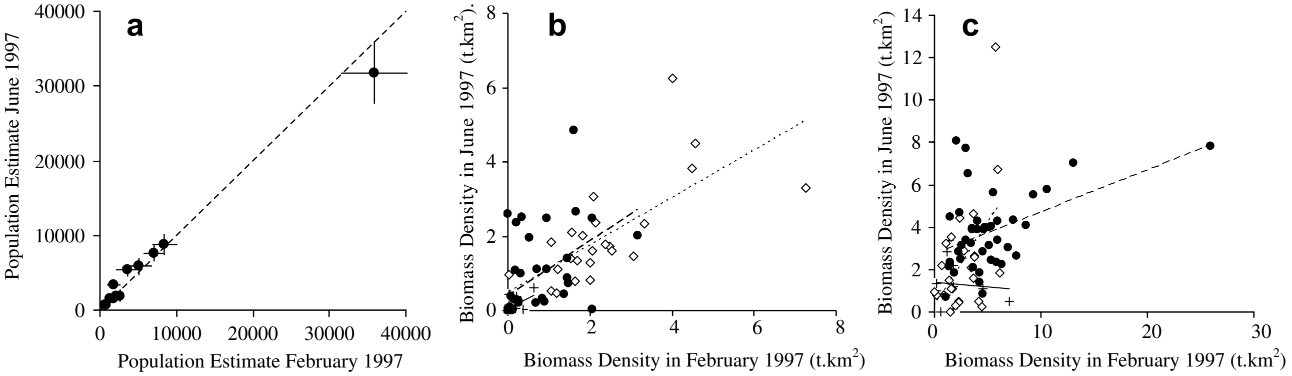

Fig. 3 – (a) Sample surveys in February and June 1997 yielded similar population estimates for wild herbivore species in Laikipia District, of which the most abundant was plains zebra. Error bars are standard errors; the dotted line is $x = y$. (b) Estimates of total wild herbivore biomass density in February and June 1997 on pro-wildlife properties (dotted line and open diamonds, $y = 0.64x + 0.47$; $r = 0.71$, $n = 22$, $P < 0.001$), transitional properties (dashed line and filled circles, $y = 0.74x + 0.38$; $r = 0.5$, $n = 52$, $P < 0.001$), and group ranches (solid line and filled triangles, $y = 0.52x + 0.07$; $r = 0.69$, $n = 15$, $P < 0.01$). (c) Estimates of total livestock biomass density in February and June 1997 on pro-wildlife properties (line types and symbols as in (b); $y = 0.78x + 0.28$; $r = 0.51$, $n = 22$, $P < 0.05$), transitional properties ($y = 0.20x + 2.75$; $r = 0.46$, $n = 52$, $P < 0.01$), and group ranches ($y = -0.04x + 1.39$; $r = 0.10$, $n = 15$, $P \gg 0.05$).

Table 1 – Forty year annual rainfall means (leading diagonal), correlation coefficients for monthly rainfall totals between pairs of gauging station during the study period (1985–2004; $n = 228$ for all except Ol Pejeta for which $n = 204$; above diagonal), and distances between gauging stations (km; below diagonal)

	El Karama	Ol Naishu	Mugie	Ol Maisor	Ol Pejeta
El Karama	722 mm	0.66	0.67	0.72	0.59
Ol Naishu	28	603 mm	0.68	0.67	0.37
Mugie	67	92	604 mm	0.73	0.50
Ol Maisor	39	66	34	620 mm	0.57
Ol Pejeta	21	40	77	72	722 mm

Table 2 – Mean biomass densities of wildlife and livestock ($t\ km^{-2}$), and their ratios on different land-use types in Laikipia District between 1985 and 2005

	Unit weight (kg)	Mean biomass density ($t\ km^{-2}$)		
		Group ranches	Transitional ranches	Pro-wildlife ranches
Plains zebra	166.3	0.032 a	0.454 b	0.792 c
Thomson's gazelle	21.0	0.001 a	0.014 b	0.013 b
Giraffe	735.9	0.032 a	0.036 a	0.302 b
Hartebeest	110.2	0.002 a	0.014 a	0.041 b
Eland	295.3	0.027 a	0.058 a	0.210 b
Buffalo	388.6	0.017 a	0.020 a	0.262 b
Impala	41.9	0.007 a	0.018 a	0.058 b
Waterbuck	158.1	0.002 a	0.002 a	0.018 b
Grant's gazelle	43.4	0.010 a	0.020 a	0.042 b
Total wild herbivores	–	0.112 a	0.636 b	1.738 c
Sheep and goat	19.0	0.522 a	0.659 a	0.271 b
Cattle	207.0	2.060 a	3.927 b	2.459 a
Total livestock	–	2.582 a	4.586 b	2.730 a
Total	–	2.694 a	5.223 b	4.459 b
Ratio livestock/wild herbivores	–	23.0536	7.2107	1.5708

Letters denote levels of significance using Tukey's paired contrasts.

patterns (smaller-bodied ungulates spend a greater proportion of their lifespan at adult size than do larger-bodied ungulates; Georgiadis, 1985, and unpublished data): $m = 1.29 \cdot M^{0.89}$ ($n = 12$, $r^2 = 0.99$, $P < 0.001$).

2.7. *Model definition, fitting, and selection*

Modeling was based on biomass-density estimates for each species on each land-use type. Following the approach of Ogutu and Owen-Smith (2003), and Owen-Smith and Ogutu (2003), a general linear model featuring four factors (land use, rainfall deficit, density, and time), with interactions between land use and time, was used to model observed time series. Time was included as an independent variable to detect statistically supported trends in density on different land use types. The model had the form:

$$D_t = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot Y + \beta_3 \cdot T + \beta_4 \cdot P + \beta_5 \cdot D_{t-1} + \beta_6 \cdot Y \cdot T + \beta_7 \cdot Y \cdot P + e$$

where D_t is the biomass density at the current time (log-transformed), R the rainfall deficit index (log-transformed), Y the time in years (log-transformed), T a dummy variable denoting transitional land use, P a dummy variable denoting pro-wildlife land use, and D_{t-1} is the biomass density of the focal species at the time of the previous census (log-transformed).

Some zero density values, resulting from no individuals being detected within transects, were found on group ranches for all species except plains zebra and Grant's gazelle (data points on baselines in Fig. 4). These were omitted from the analysis, with results and conclusions not appreciably different from analyses including all data, with the value 1 added before log-transformation. Models were fit using the linear model fitting procedure in JMP statistical software (version 5.1), allowing candidate models to be selected by minimizing the corrected Akaike Information Criterion (AICc; Burnham and Anderson, 2002; Johnson and Omland, 2004). Projections of models defined in Table 3 were depicted in Fig. 4.

3. Results

3.1. *Observed biomass densities on different land-use types*

Livestock dominated wild herbivore biomass by a mean factor of 3.9 across the entire District, but to the greatest extent on group ranches (23.1), and to the least extent (1.7) on pro-wildlife properties (Table 2). Livestock and wildlife were inversely distributed across this landscape (Fig. 1). Wild herbivores were most abundant on pro-wildlife ranches, and least abundant on group ranches, but differences between land-use types varied among species (Table 2). Thomson's gazelle was the only species with similar biomass densities on transitional and pro-wildlife ranches. Giraffe biomass densities were equally low on group and transitional properties.

Time series of wild herbivore populations (data points in Fig. 4) showed plains zebras increasing initially on both pro-wildlife and transitional properties, then fluctuating with no apparent trend. In all wild species except plains zebra, Grant's gazelle and impala, variation in density on pro-wildlife properties was greater in the first half of the series, and declined with dampened fluctuations in the latter half. Declining trends were evident on both pro-wildlife and transitional properties in Thomson's gazelle, eland, waterbuck, buffalo, and hartebeest.

Total livestock biomass densities were similar on group and pro-wildlife ranches, but the value on transitional properties was, on average, greater by a factor of almost two. Summing values for wildlife and livestock, total herbivore biomass density on pro-wildlife ranches increased to levels approaching those on the livestock-dominated transitional properties. This applied until after a major drought in 1999–2001, when livestock on transitional properties and group ranches increased dramatically, but remained stationary or declined on pro-wildlife ranches.

Thus, two features of these time series were readily apparent upon visual inspection. First, there were marked and

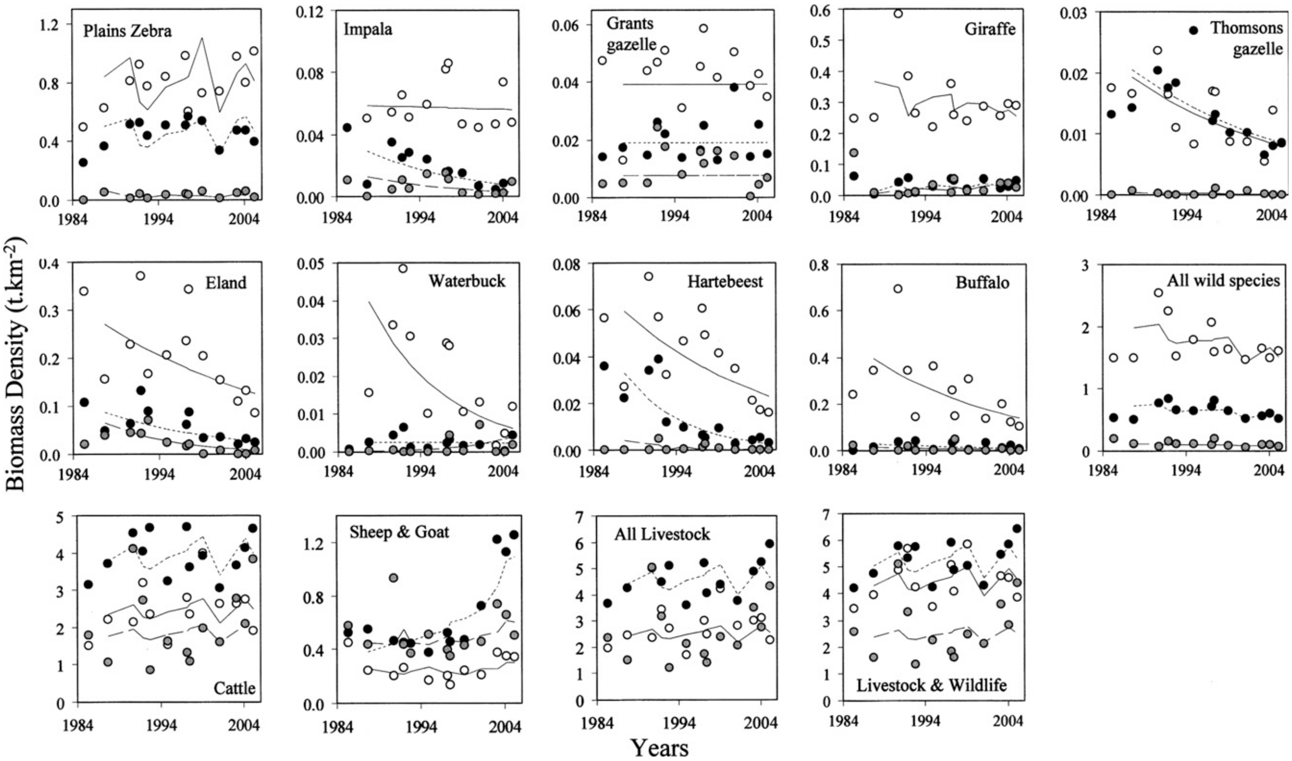

Fig. 4 – Biomass density time series and projections of models given in Table 3 for wildlife and livestock species in Laikipia District between 1985 and 2005, on three land-use types: pro-wildlife (open circles, solid line), transitional (black circles, dotted line) and group ranches (grey circles, dashed line).

opposing differences in biomass density of livestock and wildlife among land-use types. Second, on transitional properties, and to an even greater extent on pro-wildlife ranches, some species declined in the latter half of the series (Thomson's gazelle, eland, waterbuck, hartebeest, buffalo), while others did not (plains zebra, Grant's gazelle, impala, and giraffe).

3.2. *Model selection*

Model selection was used to examine effects of four factors (land use, rainfall, density, and time) on the biomass density dynamics of each species separately, and of their combinations. Coefficients associated with parameters remaining after model selection (Table 3) showed that biomass density of all species differed markedly among land-use types. Compared to group ranches, biomass densities of all wild herbivores except Thomson's gazelle were greater on transitional properties, and greater still on pro-wildlife ranches. Giraffe and buffalo densities were similarly low on group and transitional properties.

Livestock and wild species displayed opposing patterns of biomass density variation among land-use types. Sheep and goats maintained lowest densities on pro-wildlife ranches throughout, and at least initially their densities were similar on group and transitional properties. Following the drought in 1999–2001, sheep and goat densities more than doubled on transitional properties. Cattle biomass density was lowest on group ranches, and highest on transitional properties, but showed no trend over time. Total biomass density of livestock was indistinguishable on group and pro-wildlife ranches, but greater on transitional properties by a factor of almost two.

Density-dependence was detected only in the dynamics of plains zebra and giraffe. Sheep and goats showed a positive effect of density, but this was due to autocorrelation caused by a persistent increase over time. Among wild species, a limiting effect of rainfall was detected only in plains zebra, and in the biomass dynamics of all wild herbivores combined, largely because of the dominance of plains zebra. A weak rainfall signal was detected in the series of cattle, total livestock and total herbivore biomass.

The only wild species to show no trends over time were plains zebra and Grant's gazelle. Only giraffe showed a minor increase on group ranches and transitional properties, but declined, at least initially, on pro-wildlife ranches (interaction terms in Table 3). All other species declined on at least two land use types. Hartebeest declined less steeply, and waterbuck more steeply, on pro-wildlife than on transitional ranches. Impala declined on group ranches and transitional properties, but not on pro-wildlife properties. Declining trends were evident in total wild herbivore biomass on all land use types.

In absolute terms, fluctuations in biomass of wild species on pro-wildlife properties were greater initially, when densities were high, than later, when most species had declined. Initial fluctuations may have been due to rainfall limitation that was not detected by the full model because degrees of freedom were insufficient to include interactions between

Table 3 – Coefficients (with probability values in parenthesis) associated with log-transformed model parameters remaining after model selection

Species or total	Intercept	Main effects					Interactions		DFE	Adj. r^2
		Transitional	Pro-wildlife	Years	Rainfall	Density dependence	Transitional * years	Pro-wildlife * years		
Plains zebra	−4.70	3.691	4.411		0.644	−0.318			31	0.95
Equus burchelli		(0.001)	(0.001)		(0.001)	(0.001)				
Thomsons gazelle	762.50	4.050	3.984	−101.4					22	0.94
Gazella thomsoni		(0.001)	(0.001)	(0.001)						
Giraffe	−557.19	0.425	3.601	72.6		−0.339		−166.1	28	0.85
Giraffa camelopardalis		(0.081)	(0.001)	(0.017)		(0.015)		(0.030)		
Hartebeest	1613.20	2.068	3.483	−213.2				178.2	24	0.89
Alcelaphus buselaphus		(0.001)	(0.001)	(0.001)				(0.042)		
Eland	1085.15	0.761	2.139	−143.3			100.4	150.7	26	0.81
Taurotragus oryx		(0.003)	(0.001)	(0.001)			(0.190)	(0.055)		
Buffalo	896.62	0.739	3.371	−118.6					25	0.75
Syncerus caffer		(0.118)	(0.001)	(0.057)						
Impala	816.72	0.856	2.336	−108.2				158.9	29	0.76
Aepyceros melampus		(0.002)	(0.001)	(0.010)				(0.057)		
Waterbuck	462.07	0.997	2.840	−61.7			−365.7	−574.1	19	0.64
Kobus kob		(0.090)	(0.001)	(0.060)			(0.138)	(0.021)		
Grants gazelle	−4.90	0.931	1.658						33	0.45
Gazella grantii		(0.004)	(0.001)							
Total wild herbivores	277.41	1.862	2.864	−36.8	0.249				31	0.97
		(0.001)	(0.001)	(0.021)	(0.131)					
Sheep and goat	−389.18	0.171	−0.504	51.1		0.293	66.7		30	0.69
Ovis aries and *Capra hircus*		(0.129)	(0.004)	(0.015)		(0.077)	(0.114)			
Cattle	0.622	0.760	0.289		0.309				32	0.47
Bos taurus and *B. indicus*		(0.001)	(0.041)		(0.164)					
Total livestock	0.94	0.597			0.291				33	0.48
		(0.001)			(0.149)					
Total	1.00	0.750	0.594		0.281				32	0.60
		(0.001)	(0.001)		(0.116)					

Coefficients associated with ‘transitional’ and ‘pro-wildlife’ land use types indicate the difference in biomass density compared to ‘group ranches’. DFE is degrees of freedom for error.

Table 4 – A decline in rainfall limitation among wild herbivores on pro-wildlife properties was indicated by higher correlation coefficients between change in biomass density and rainfall deficit between surveys conducted between 1985 and 1997, as compared to surveys conducted after that date (significant values of r using a one-tailed test are given in bold font for $\alpha = 0.01$, $n = 6$ in all cases)

	Zebra	Harte-beest	Giraffe	Thomson's gazelle	Grant's gazelle	Impala	Buffalo	Eland	Waterbuck
1987–February 1997	0.63	**0.91**	**0.94**	**0.93**	0.53	0.51	0.68	0.43	0.46
June 1997–2005	−0.20	−0.04	−0.32	0.04	−0.36	−0.03	0.60	0.03	−0.45

rainfall deficit, land use, and time. Rainfall-dependence for each wild species on pro-wildlife ranches was therefore further tested by dividing the series in half, and correlating changes in density with rainfall deficit between the first six surveys (1985–February 1997), and again between the last six surveys (June 1997–2005). For the former, such relationships were strongly positive for all nine species (an unlikely result by chance: $p = 0.5^9 = 0.002$), significantly so for hartebeest, giraffe, and Thomson's gazelle (Table 4). Thereafter (1997–2005), the correlation between density change and rainfall deficit declined in all species, being greater than 0.04 only for buffalo ($r = 0.60$), and none was significant. These patterns imply that herbivore densities on pro-wildlife properties were close to rainfall-defined carrying capacities prior to 1997, and that the influence of rainfall on herbivore dynamics diminished thereafter as densities declined for reasons other than rainfall limitation.

4. Discussion

Linear model analysis of spatially explicit data derived from aerial sample surveys provided mechanistic insights about factors influencing wild and domestic herbivore abundance and dynamics. Strongly opposing patterns in wildlife and livestock density on different property types affirmed the primacy of land use among factors influencing wildlife abundance in non-protected areas. Rainfall limited densities of the most abundant grazing species throughout (plains zebra and cattle), and of most other species while their densities were high. Regulating effects of density were detected only in the most abundant wild grazing and browsing species (zebras and giraffe).

A previous study showed that observed variation in the (total) Laikipia zebra population between 1985 and 1999 could be adequately imitated using a simulation model driven solely by rainfall and zebra density (Georgiadis et al., 2003). Since 1999 the model has provided independent predictions of plains zebra numbers that have continued to correspond closely with sample survey estimates (unpublished data), increasing our confidence that the principal factors controlling plains zebras in Laikipia (rainfall and density) have not changed in two decades. Linear modeling affirmed these conclusions for zebras.

In contrast to plains zebras, rainfall-dependence was only weakly apparent in the dynamics of cattle, and did not feature at all in the dynamics of sheep and goats. In fact, livestock are strongly rainfall-limited in this region, with large numbers dying during droughts, particularly pastoralist cattle. The rainfall signal in livestock data may have been weakened for two reasons. First, cattle on pro-wildlife properties are managed at relatively low densities, and many are fed dietary supplements during droughts. Second, pastoralist livestock move between group ranches and transitional properties, seeking grazing on a seasonal basis (see Section 2). During droughts, pastoralist livestock move longer distances both into and out of the District. Immigration from the north contributed to the dramatic increase of sheep and goats on transitional properties following the drought in 2001.

Mean values of total herbivore biomass density (livestock + wildlife) increased with mean annual rainfall from group ranches to pro-wildlife ranches to transitional properties (Table 2 and Fig. 4), agreeing with the well-documented limitation by rainfall of herbivore biomass in African savannas (e.g. Fritz and Duncan, 1994). Assuming mean annual rainfall values of 450, 625, and 775 mm for group ranch, pro-wildlife, and transitional properties (these are mid-points of the range of values given for each land use type in Section 2), total herbivore biomass densities were predicted by the moderate soil nutrient availability equation of Fritz and Duncan (1994) to be 2.53, 4.54, and 6.65 t km^{-2}, respectively. The equivalent observed values closely matched these predictions: 2.69, 4.46, and 5.22 t km^{-2}, respectively. Although these figures omit elephants, and values on transitional properties were reduced by the presence of cultivation, total herbivore biomass density in Laikipia District is predominantly rainfall-limited on all land use types.

All but two wild species (zebra and Grant's gazelle) declined on at least one land-use type. Giraffe, hartebeest, eland, impala and waterbuck declined at different rates on different land-use types (interaction terms in Table 3), suggesting declines were influenced by different factors, or by different intensities of the same factors, among land-use types. Anthropogenic factors were likely contributors to wildlife declines on transitional properties, particularly the dramatic increase in the density of sheep and goats following the drought in 2001, but also the spread of cultivation and habitation over time, as well as bushmeat hunting. Similarly, high livestock densities (given low annual rainfall) were responsible for the displacement of wildlife on group ranches well before the first survey in 1985.

However, these anthropogenic factors were unlikely to have caused wild herbivore declines on pro-wildlife properties, because livestock densities remained low (Fig. 4), and habitation and cultivation remained negligible throughout (Fig. 1 in Georgiadis et al., 2003). Scrutiny of seven additional factors that could have caused selective wild herbivore declines on pro-wildlife properties implicated the restoration of predators in this landscape as the most likely factor (Georgiadis et al., this issue). Beginning in the late 1980s, a relatively intact predator community was restored, following a change in land use on pro-wildlife properties from ranching, under which predators were heavily suppressed, to eco-tourism and wildlife conservation. This created a demand for living predators. Dispersing predators from pro-wildlife properties may have contributed to herbivore declines on adjacent transitional properties supporting high wildlife densities.

4.1. *Conservation implications for non-protected areas*

Diverse and abundant wildlife communities can clearly thrive where wildlife is favored, even when sharing the landscape with a higher biomass density of livestock (mean for wild herbivores on pro-wildlife ranches was 1.7 t km^{-2} and for livestock was 2.7 t km^{-2}; Table 2). While this affirms that mixed systems can provide an ecologically viable land use option for conservation, the economic viability of mixed systems can be compromised (Heath, 2000). On many of the larger pro-wildlife properties in Laikipia District, income from ranching is sufficient only to defray costs in years of adequate rainfall, while costs in dry years are met by external sources (in this sense, therefore, conservation is subsidized). This 'pro-wildlife model', which entails private ownership of large-scale properties supporting both livestock and wildlife, has been effective in conserving wildlife in Laikipia District, but has potential for wider application only where external subsidy is available.

On transitional and group ranch properties, wild species have been displaced largely by livestock and to a lesser extent by cultivation, within ecological limits set by rainfall and habitat. But wild species have not been displaced entirely, or equally. Low diversities and densities of wild ungulates on transitional properties and group ranches, chiefly plains zebras and gazelles, reflect an increasingly familiar impression of wildlife in non-protected drylands of Kenya today. Gazelles, especially Grant's, are largely independent of water, and thrive in areas too far from surface water to be grazed heavily by livestock. Grant's gazelle was the only wild species for which neither rainfall-dependence nor time had a detectable effect, and they survive better than any other species on group ranches, where the driest and most heavily grazed habitats in the study area are found. Thomson's gazelle was the only species with comparable biomass densities on pro-wildlife and transitional properties. The diets of gazelles include forbs and shrubs that flourish on disturbance by livestock. Plains zebras persist in livestock-dominated landscapes (see also de Leeuw et al., 2001) partly because they are not territorial, and are therefore resilient to being frequently displaced by humans and livestock without disrupting social structure. Zebras often access water at night when livestock are impounded, are not a preferred source of bushmeat, and tend to occupy open areas lacking the trees that are suitable for snaring.

Resilient species like plains zebra and grants gazelle are more likely to persist in the 'matrix' of livestock-dominated landscapes than are other wild ruminant species (in this case eland, hartebeest, impala, giraffe, waterbuck and buffalo), which are more susceptible to human disturbance, prone to displacement by livestock, and all except waterbuck are preferred by humans as a source of bushmeat. They tend to occupy woody habitats where they are vulnerable to snaring, or, where trees have been cleared for charcoal production, to habitat loss. Buffalo present a danger to humans and are often quickly removed. These species can be expected to persist in the landscape only where livestock densities are far lower than is typical on group ranch and communal properties, but not necessarily zero. Since fences that would prevent dispersal by wildlife between pro-wildlife and group ranches are generally lacking in Laikipia District, the persistence on group ranches of wild species that are sensitive to displacement by livestock may be partly due to source–sink dynamics, with the pro-wildlife properties providing a source.

In the drier, communal sectors of this landscape, unfenced conservation areas have been established or are planned as a way of justifying space for wildlife, and promoting landscape 'connectivity', by providing incomes to communities. They are expected to endure only if benefits from wildlife to community members exceed opportunity costs (Kiss, 2004; Walpole and Thouless, 2005). The ecological viability of these conservation areas may not depend on total exclusion of livestock, but this is often necessary for economic and aesthetic reasons, for example, if the primary use is eco-tourism. However, community conservancies are sometimes further justified by serving as 'grass banks' for livestock during droughts. Since this is when displacement of wildlife by livestock is most severe, use of conservation areas as grass banks may compromise the viability of wildlife, and thus enterprises based on wildlife.

The viability and diversity of wild species in non-protected landscapes, particularly those less resilient to displacement by humans and livestock, will also depend on size and degree of isolation of conservation areas. They should be sufficiently large and free of livestock to support viable populations of sensitive wild species. By definition, they must effectively act as 'sources' of these species (as opposed to 'sinks') in the landscape, for if they fail in this regard, neither landscape connectivity nor economic viability are likely to be achieved. Existing national reserves at Samburu, Buffalo Springs and Shaba provide models in this region of conservation areas which generate sufficient income to compete effectively with other land uses (although income goes primarily to county councils). Further study is needed to examine for which wild species conservation areas act as 'sources' in the landscape. The critical size and density of conservation areas in this landscape that would be sufficient to maintain species diversity and landscape connectivity remains to be determined.

4.2. *Utility of sample surveys for monitoring herbivore dynamics*

Mechanistic insights into large herbivore population dynamics gained from this analysis affirm the sufficiency of aerial sample surveys for monitoring, understanding, and conserving large-scale processes in non-protected savannas. Factors that served to improve data quality include consistency in as many technical aspects as possible: the survey crews have long experience in counting animals; surveys are conducted in the same season when visibility was greatest, using the same aircraft, instruments, calibrated strip markers, and, to the extent possible, the same crews. Changing one or more of these factors introduces errors that can diminish the ecological signal in population time series.

Surveys conducted at higher resolution (2.5-km transect spacing) not only improved the precision of the population estimates, and admitted rarer species into the pool for which data are meaningful, but also increased spatial resolution of potentially conflicting factors, such as distributions of cultivation and wildlife. Although annual surveys are preferable, increasing fuel costs make this ever less affordable. This study showed that interpolation between unevenly spaced surveys is possible using composite variables such as an index of cumulative rainfall deficit. Succeeding estimates of density can also be informative about density-dependence across more than one year (but probably not more than 2 years). When a choice is forced, therefore, higher resolution surveys done less frequently provide a superior record to lower resolution surveys done frequently. The goals of landscape conservation will more likely be achieved by propagation of these approaches in non-protected landscapes elsewhere.

Acknowledgements

The quality of the data used in this analysis attests to the expertise and consistency of the aerial survey crews at the Department of Range Survey and Remote Sensing, Nairobi. Support for sample surveys came from the Mpala Wildlife Foundation, the African Wildlife Foundation, and the Kenya Wildlife Service. M. Stanton, J. Goheen, M. Norton-Griffiths, R. Sensenig, R. Pringle, T. Young and N. Owen-Smith gave helpful comments. Thanks to G. Grant, C. Mortensen, C. Burt, R. Vigne and J. Evans for rainfall data.

REFERENCES

Armbruster, P., Lande, R., 1993. A population viability analysis for African elephants (*Loxodonta africana*): how big should reserves be? Conservation Biology 7, 602–610.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer, New York. pp. 496.

de Leeuw, J. et al, 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. Biological Conservation 100, 297–306.

Denney, R.N., 1972. Relationships of wildlife to livestock on some developed ranches on the Laikipia Plateau, Kenya. Journal of Range Management 25, 415–425.

East, R., 1998. Africa Antelope Database 1998. IUCN/SSC Antelope Specialist Group Report, IUCN.

Erasmus, B.F.N., van Jaarsveld, A.S., Chown, S.L., Kshatriya, M., Wessels, K.J., 2002. Vulnerability of South African animal taxa to climate change. Global Change Biology 8, 679–693.

Fritz, H., Duncan, P., 1994. On the carrying capacity for large ungulates of African savanna ecosystems. Proceedings of the Royal Society of London B 256, 77–82.

Georgiadis, N.J., 1985. Growth patterns, sexual dimorphism and reproduction in African ruminants. African Journal of Ecology 23, 75–88.

Georgiadis, N.J., Hack, M., Turpin, K., 2003. The influence of rainfall on zebra population dynamics: implications for management. Journal of Applied Ecology 40, 125–136.

Georgiadis, N.J., Ihwagi, F., Olwero, N., Romañach, S.S., this issue. Savanna herbivore dynamics in a livestock-dominated landscape: II. Ecological, conservation, and management implications of predator restoration. Biological Conservation 137, 473–483.

Goldman, M., 2003. Partitioned nature, privileged knowledge: community-based conservation in Tanzania. Development and Change 34, 833–862.

Grainger, M., van Aarde, R., Whyte, I., 2005. Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. African Journal of Ecology 43, 369–375.

Hannah, L., Midgley, G.F., Millar, D., 2002. Climate change-integrated conservation strategies. Global Ecology and Biogeography 11, 485–495.

Hackel, J.D., 1999. Community conservation and the future of Africa's wildlife. Conservation Biology 13, 726–734.

Harcourt, A.H., Parks, S.A., Woodroffe, R., 2001. Human density as an influence on species/area relationships: double jeopardy for small African reserves? Biodiversity and Conservation 10, 1011–1026.

Heath, B., 2000. Ranching: an economic yardstick. In: Prins, H.T., Grootenhuis, J.G., Dolan, T.T. (Eds.), Wildlife Conservation by Sustainable Use. Kluwer Academic Publishers, Boston, Dordrecht, London.

Hoare, R.E., Du Toit, J.T., 1999. Coexistence between people and elephants in African Savannas. Conservation Biology 13, 633–639.

Huber, M., Opondo, C.J., 1995. Land use Change Scenarios for Subdivided Ranches in Laikipia District, Kenya. Group for Development and Environment, Institute of Geography, Berne, Switzerland.

Hutton, J., Adams, W.M., Murombedzi, J.C., 2005. Back to barriers? Changing narratives in biodiversity conservation. Forum for Development Studies, No. 2. (http://www.frameweb.org/ev.php?ID=14432_201andID2=DO_TOPIC).

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19, 101–108.

Kiss, A., 2004. Is community-based ecotourism a good use of biodiversity conservation funds? Trends in Ecology and Evolution 19, 232–237.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Newmark, W.D., 1996. Insularization of Tanzanian Parks and the local extinction of large mammals. Conservation Biology 10 (6), 1549–1556 (special issue).

Norton-Griffiths, M., 1978. Counting Animals. African Wildlife Foundation, Nairobi.

Ogutu, J.O., Owen-Smith, N., 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecology Letters 6, 412–419.

Owen-Smith, N., Ogutu, J., 2003. Rainfall influences on ungulate population dynamics. In: du Toit, J.T., Rogers, K.H., Biggs, H. (Eds.), The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, 1718 Connecticut Avenue, N.W., Suite 300, Washington, DC 20009, pp. 310–331.

Prins, H.T., Grootenhuis, J.G., Dolan, T.T., 2000. Wildlife Conservation by Sustainable Use. Kluwer Academic Publishers, Boston, Dordrecht, London.

Redfern, J.V., Viljoen, P.C., Kruger, J.M., Getz, W.M., 2002. Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. South African Journal of Science 98, 455–461.

Thenya, T., 2001. Challenges of conservation of dryland shallow waters, Ewaso Narok swamp, Laikipia District, Kenya. Hydrobiologia 458, 107–119.

Walpole, M.J., Thouless, C.R., 2005. Increasing the value of wildlife through non-consumptive use? Deconstructing the myths of ecotourism and community–based tourism in the tropics. In: Woodroffe, R., Thirgood, S.J., Rabinowitz, A. (Eds.), People and Wildlife: Conflict or Coexistence? Cambridge University Press, Cambridge, UK, pp. 122–139.

Western, D., 1989. Conservation without parks: wildlife in rural landscapes. In: Western, D., Pearl, M.M. (Eds.), Conservation for the Twenty-first Century. Oxford University Press, Oxford, UK, pp. 158–165.

Western, D., Sesemakula, J., 1981. The future of savanna ecosystems: ecological islands or faunal enclaves. African Journal of Ecology 19, 7–19.

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

Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128.

Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. People and Wildlife: Conflict and Coexistence. Cambridge University Press, Cambridge, UK.