Seasonal interactions of pastoralists and wildlife in relation to pasture in an African savanna ecosystem

Samantha Russell[a,b,*], Peter Tyrrell[a], David Western[b]

[a] South Rift Association of Landowners, P.O. Box 15289, Nairobi 00509, Kenya
[b] African Conservation Centre, P.O. Box 15289, Nairobi 00509, Kenya

A B S T R A C T

Wildlife and livestock have coexisted across East African rangelands for millennia, tracking seasonal forage availability across large landscapes. More recently however, free-ranging movements have been increasingly restricted by land use changes, reducing the ability of livestock and wildlife to access necessary grazing resources, leading to both homogenization and degradation of the rangeland. This in turn has led to losses in productivity of both livestock and wildlife. This study describes wildlife and livestock interactions in response to pasture in one of the few remaining areas of mixed wildlife-livestock use with unrestricted movements. We ask if pastoral management systems can create and maintain spatial and temporal heterogeneity of pasture, through the seasonal movement of livestock. Furthermore, does this heterogeneity create a diverse, productive and resilient assemblage of both domestic and wild ungulates? Our results provide evidence to support the notion that traditional pastoral systems which continue to manage for heterogeneity of pasture can still support not only livestock but also substantial numbers of wildlife. The results highlight the need for wildlife and livestock to retain both mobility and access to both wet and dry season areas to maintain ecosystem resilience and promote coexistence in mixed livestock-wildlife landscapes.

1. Introduction

Sub-arable rangelands lands cover 60% of East Africa (Bourn and Blench, 1999) and have been dominated by subsistence pastoralists for the past three to four millennia (Williamson, 2000). Although best known for the abundance of wildlife, livestock make up 60–90% of the large mammal biomass in the African savannas (Ogutu et al., 2016; du Toit and Cumming, 1999).

Until the last two to three decades, wildlife and livestock coexisted over most of the rangelands and moved freely with the seasons, driven largely by rainfall, pasture availability and water (Coughenour et al., 1990; Western, 1982, 1975). Two thirds of Kenya's wildlife is still spread across the rangelands in community lands, group and private ranches (Western et al., 2009b). A rising human population, land pressure and subdivision of land has resulted in a 40%–70% percent loss of wildlife in the past forty years (Ogutu et al., 2016). Wildlife losses in parks match the country-wide losses (Western et al., 2009b). Large wildlife losses have also occurred in Tanzania (Estes et al., 2006) and in other Eastern and Southern African protected areas (Craigie et al., 2010).

Evidence also points to a steady loss of pastoral productivity in much of the rangelands, resulting from subdivision, range compression, loss of seasonal resources, mobility to access these resources, collapse of traditional grazing management systems and pasture degradation (Bhola et al., 2012; Boone, 2005; Groom and Western, 2013; Hobbs et al., 2008). The importance of the pastoral lands in maintaining wildlife has been highlighted in Kenya by the success of community and private wildlife conservation initiatives since the 1990s. More wildlife is now supported in the community and private conservation lands (conservancies) than within nationally protected areas, and the populations are holding steadier (Western et al., 2006). The conservancies are also proving important in restoring and sustaining pasture and livestock health (Glew, 2012).

The growing importance of conservancies underscores the need to understand the factors governing the productivity, diversity and resilience of savannas in order to sustain free-ranging populations of wildlife and livestock in the rangelands. The focus on wildlife studies in protected areas and lack of research into interacting livestock and wildlife populations within traditional pastoral systems has hampered the application of research to conservation planning in the rangelands areas (Butt and Turner, 2012).

Research studies into African savanna ecosystems point to the

importance of rainfall and seasonality as the main drivers of the pasture quality, quantity and spatial heterogeneity governing wildlife and livestock abundance and movements (Coughenour et al., 1990; Illius and O'Connor, 2000; Mose et al., 2013). Water availability (Western, 1975), topography (Coughenour et al., 1990), geology (Cole, 1982), disturbance (McNaughton, 1983) and human activity (Turner and Hiernaux, 2002) modify the influence of rainfall and seasonality. In Eastern Africa the biannual rainfall supports a higher livestock biomass and a more milk-dependent pastoral system than the single season rainfall of Southern Africa (Western and Finch, 1986).

Subsistence pastoralists around the world have developed ecological and social strategies to maximize production, lower risk and take advantage of the spatial and temporal variation of pasture (McAllister et al., 2006; Müller et al., 2007; Western, 1982). Mobility in pastoral and wildlife herds is important in reducing the effect of seasonality, avoiding droughts and taking advantage of landscape heterogeneity (Niamir-Fuller, 1999). Free-ranging herds are able to track seasonal pastures and maximize digestible intake by optimizing trade-offs between pasture quantity and quality (Illius and Gordon, 1992; Mose et al., 2013) within range of permanent water (Western, 1975).

Typically, wildlife and livestock in the savannas migrate seasonally between higher quality wet season ranges unconstrained by water and dry season lower quality higher biomass areas near permanent water (Fryxell et al., 2005; Müller et al., 2007; Western, 1975).

Since the beginning of the 20th Century there have been negative perceptions towards pastoral grazing practices, including seasonal movements of livestock in Kenya, with pastoralists blamed for both rangeland degradation and for loss of wildlife (Mwangi and Ostrom, 2009). Here we follow on previous work that has shown that there is coexistence between livestock and wildlife in the Shompole and Olkiramatian ecosystem (Schuette et al., 2013), and provide evidence that pastoral governed rangelands can indeed promote sustainable coexistence of wildlife and livestock.

Important as it is to understand the ecological dynamics of free-ranging wildlife and pastoral livestock systems in light of its growing significance for rangelands productivity, sustainability and wildlife conservation, few areas remain where traditional seasonally governed movements remain. Exceptions include the Shompole and Olkiramatian group ranches in southern Kenya. Here, the Maasai still sustain seasonal movements and traditional grazing practices alongside a large population of wildlife, with a full complement of herbivore and carnivore species, except for black and white rhinoceros (Schuette et al., 2013). The two group ranches remain as intact land parcels held under communal title, with none of sub-division or fragmentation into smaller parcels which is occurring across much of the East African rangelands (Homewood et al., 2009). Here we draw on long-term ecological data to describe the seasonal dynamics of this South Rift ecosystem, focusing on trends in pasture availability and the densities and distributions of wildlife and livestock.

Using this case study, we ask if pastoral management systems can maintain and create spatial and temporal heterogeneity of pasture through the seasonal movement of livestock. Does this heterogeneity in turn create a diverse, productive and resilient assemblage of both domestic and wild ungulates? We hypothesize that this community management system will help create and maintain a temporally and spatially heterogenous pasture resource base (quantified as grass biomass, grass height, percentage grazed and percentage green). In addition, we expect that productive populations of wildlife and livestock are distributed across this landscape in relation to this pasture resource base, which is dictated by the underlying management regime and the metabolic requirements of each specific species.

2. Materials and methods

2.1. Study area

Located at the western edge of Great Rift Valley on the international border between Kenya and Tanzania, the study area borders the Nguruman Escarpment and Loita Hills to the West, the alkaline Lake Magadi to the East, and the alkaline Lake Natron to the South. The area has an altitude of 600–700m and high temperatures ranging from 18 °C at night to 45 °C during the day (SORALO, unpublished data). This area is classified as Agroclimatic Zones V (Bekure and International Livestock Centre for Africa, 1991), which is semi-arid land, with erratic rainfall that is scattered across the area, averaging 400–600 mm yr^{-1} (SORALO, unpublished data; Agnew et al., 2000), and with percentage variation of annual rainfall over 33% (Agnew et al., 2000). High evapotranspiration rates and low rainfall ensures there is little standing water outside the rainy season. A perennial river, the Ewaso Ngiro, runs through the study area, along with some small streams from the Nguruman Escarpment, these representing the only permanent water sources available in the area. The Ewaso Ngiro river flows through the Shompole swamp before ending up in Lake Natron.

Historical Rift Valley down-faulting and up-thrusting has created steep elevation gradients, a range of habitats from arid soda flats to montane forest, and one of the richest vertebrate assemblages in Africa (MEWNR, 2015). Despite the semi-arid climate, combinations of topography, river and spring discharge through the area creates a mosaic of habitats and seasonal pasture fluxes which in turn support a high density of migratory grazing herds of wildlife and livestock and resident browsing species. The ecology and seasonal dynamics mirrors other pastoral and livestock systems in East Africa that have now largely been fragmented and ecologically uncoupled by land use changes (Hobbs et al., 2008).

The area is covered by two group ranches which are, however, used as a single management area. A group ranch is a jointly owned freehold land title given to the customary occupants of communal lands (Kimani and Pickard, 1998). The occupants of Olkiramatian and Shompole number roughly 20,000 people (Agnew et al., 2000) in an area of approximately 1000 km^2 (Fig. 1).

In Shompole and Olkiramatian the traditional seasonal livestock movements and herding practices are formalized by group ranch grazing plans governed by local committees. The wet season grazing areas in both group ranches are termed 'livestock zones.' The dry season grazing areas have been retained as a 'grass banks' for livestock and since 2000 have been established as wildlife conservancies used for ecotourism. In both group ranches livestock rearing occurs to the East of the Ewaso Ngiro river, grass banks and the wildlife conservancy to the West of the Ewaso Ngiro river, and the area North West of the group ranch in Olkiramatian and the South West in Shompole for crop farming. Seasonally the communities of both group ranches move their livestock between the livestock rearing zone in the wet season and the grass bank in the dry season when regional grass biomass and quality decline. See Fig. 1 below for a map of these land use zones.

In 2007 a long-term ecological monitoring programme was established on Shompole and Olkiramatian group ranches, modeled on the Amboseli ecological monitoring program (Western et al., 2015). The Shompole-Olkiramatian monitoring program is run by the South Rift Association of Landowners (SORALO), which has also set up the Lale'enok Resource Centre and trained local resource assessors to conduct the regular monitoring activities.

2.2. Vegetation characteristics

Pasture characteristics were measured using the pin – intercept methodology (McNaughton, 1983; Mwangi and Western, 1998) which counts the number of plant 'hits' on ten thin metal pins. Twenty-five plots, measuring 314.16 m^2, have been regularly sampled across the
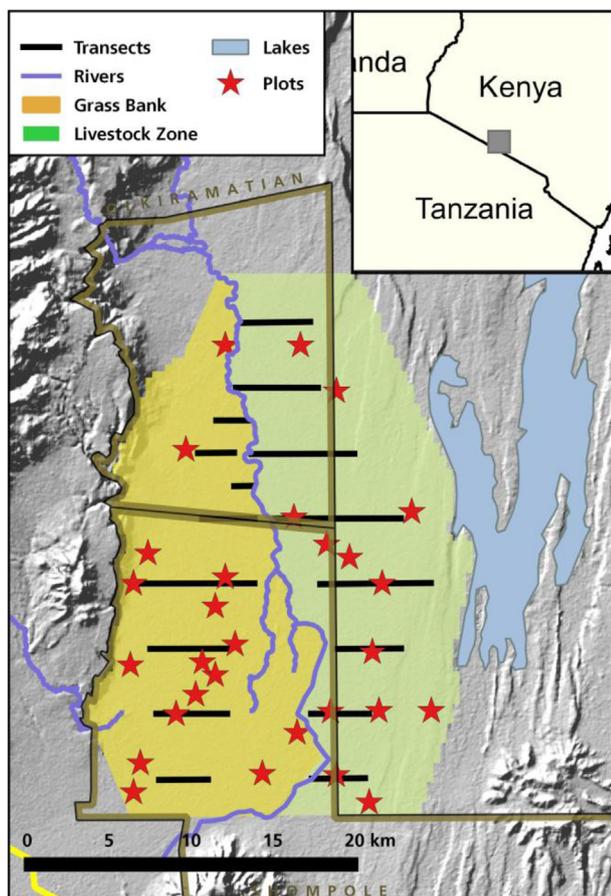
Fig. 1. Map of the study area covering both Olkiramatian and Shompole group ranches in southern Kenya showing the location of both grazing zones and the overlay of transects and plots for data collection.

ecosystem since 2008 (Fig. 1). These plots represent all major habitat types except the swamp where accessibility is difficult. They were selected from an original random sample of 80 plots, with 25 representing the least numbers of plots required to have for accurate regional biomass estimates. The most significant output from this method is the mean number of hits per pin at each plot. Through measurement of dry biomass at clipped plots we converted mean hits per pin into biomass in g/m^2 (Groom and Western, 2013). Previous calibration experiments have shown regional variation in converting mean hits per pin to biomass (McNaughton, 1983; Mwangi and Western, 1998; Groom and Western, 2013), and a local calibration exercise was conducted. We measured hits per pin and collected and dried plant material at 40, 1 m^2 plots which were randomly selected in the study area. A simple linear regression was calculated to predict grass biomass (g/m^2) based on the mean hits per pin. A significant regression was found (F $(1,38) = 21.23$, p < 0.001), with an R^2 of 0.359. The resulting equation was: $y = 48.63x + 13.16$ where x represents mean hits per pin, and y is grass biomass in g/m^2, which is similar to other relationships for this method in the region (Jensen, 1982 (Unpublished); Strum et al., 2015). The percentage of grazed to non-grazed and green to brown plant material is also calculated from the number of hits per pin of each type.

2.3. Season categories

To compare pasture properties, including grass biomass, percentage green, percentage grazed and grass height, across season and land use (grazing area), we allocated seasonal classifications to each month during data collection. Following methodology of Groom and Western

(2013), Western et al. (2015) and Mwangi and Western (1998), we used deviation in grass biomass and percentage green to separate months into three seasons: wet, dry and drought. Any month with greater than average biomass, and over 25% green was labeled as wet. Drought months had lower biomass than the overall mean minus half the standard deviation of biomass over the sampling period. Dry months were those not classified in either of these categories. Classification of months can be found in Table A.1.

2.4. Analysis of pasture data

Mean hits per pin was converted into grass biomass using the linear relationship from calibration. Following exploratory data analysis, it was determined that vegetation data would be analyzed using non-parametric tests, including Mann-Whitney U tests, Sign Ranked Mann-Whitney *U* test, and Kruskall Wallis tests (Groom and Western, 2013). This was justified because percentage grazed and green have a large number of 0 and 1 values, and thus cannot be analysed using parametric tests. In addition, distributions of both grass biomass and grass height across both land use types are considerably skewed. We used various tests and metrics to test the differences in pasture heterogeneity between the grass bank and livestock zone and within these grazing areas.

We also calculated the linear relationship between regional biomass and antecedent rainfall. Antecedent rainfall was defined as the sum of rainfall in the two months prior to data collection. Rainfall data was provided by Lale'enok Resource Centre (SORALO, unpublished).

This analysis was conducted using the free statistical software R version 3.2.2 (R Development Core Team, 2008).

2.5. Wildlife and livestock line transects

Sixteen line transects were sampled on 22 occasions between May 2008 and April 2011, at roughly six-week intervals. Transects were surveyed during the day. All transects originated as near to the river as possible and continued as far as possible before reaching impassable geographic features (other rivers, ridges, thick forest and the escarpment), and were oriented in an east to west direction. Transects were spaced at 4 km intervals with the exception of the northernmost three in the dry season grazing area which were spaced at 2 km apart due to their limited length. There were an equal number within the dry and wet season grazing areas. In total, the combined transect length was 69.2km, with the longest transect being 7.8km and the shortest 1.1km (Fig. 1).

Transects were driven using a four-wheel drive vehicle at 10 km/h following programmed GPS routes. Two observers sitting on the roof of the car scanned for animals. On sightings of animals the vehicle was stopped and sighting information was recorded. The species detected was recorded, and the number of animals were counted as clusters to avoid pseudo-replication (Buckland et al., 1993). Straight-line distance (r_i) and angle (θ_i) to the centre of the cluster were recorded, along with cluster size. Perpendicular distance (x_i) from the transect was found using $x_i = r_i \sin \theta_i$. Distance was recorded using laser rangefinders (Leica Optics, Germany) and angle was found using the GPS compass.

2.6. Transect analysis

Transect data was analyzed using Distance 6.2 software (Thomas et al., 2010). Our analysis focused on the nine species with greater than 60 detections, which was considered a reasonable limit to develop reliable detection functions (Buckland et al., 2001). This consisted of three types of livestock: cattle (*Bos indicus*); shoats, consisting of sheep and goats due to the difficulty in distinguishing the two species in large mixed herds (*Ovis aries*, and *Capra aegagrus hircus*); and donkeys (*Equus africanus asinus*). Wildlife species included: zebra (*Equus burchelli*); wildebeest (*Connochaetes taurinus*); Grant's gazelle (*Gazelle granti*);

impala (*Aepyceros melampus*); ostrich (*Struthio camelus*); and giraffe (*Giraffa camelopardalis*). Other species detected during the transects are listed in Table A2.

For each species a global detection function was fitted. Data was right truncated to maximize model fit (Buckland et al., 2001). Truncation was based on exploratory analysis and exploration of the initial detection functions in Distance. Truncation distances are given in Table 2. Mean cluster size was corrected for bias at larger distances by regressing the log of cluster size against detection probability (Buckland et al., 2001).

Exploratory data analysis suggested variation in detection distance based on land use (grass bank and livestock zone) and across season (dry, drought and wet). This merited the use of multiple covariate distance sampling (MCDS) alongside conventional distance sampling (CDS), treating season and land use as factor covariates. The seasonal definition was provided by the methodology described above. MCDS accounts for changes in detection functions based on these sampling covariates, potentially increasing model precision (Marques et al., 2007, Thomas et al., 2010).

Candidate models included the half-normal key with cosine adjustments; half-normal key with hermite polynomial adjustments; and hazard-rate key with simple polynomial adjustments (Thomas et al., 2010). The series adjustment terms were limited to two for the MCDS models (Marques et al., 2007), and up to five for the CDS models (Buckland et al., 2001). The series adjustment terms were selected sequentially using the Akaike information criterion (AIC). MCDS analysis tested two covariates: land use with two levels, grass bank and livestock zone; and season, with three levels, dry, drought and wet. This produced twelve candidate models for each species: three CDS and nine MCDS models. The model fit was examined by visual observation of histograms, q-q plots, and using the statistical tests provided by distance: χ^2 goodness-of-fit, Kolmogorov–Smirnov and Cramer–von Mises family tests. If there was no reason to reject models based on these tests, then the AIC and likelihood ratio scores were used to choose the model with the best fit. This model was then used to create density estimates for the entire sampling period.

The best fitting models for each species were then post-stratified by land use type to obtain density estimates for the grass bank and livestock zones. Cluster size was estimated independently for each stratum due to expected changes in both wildlife and livestock group size across spatial scales. Density estimates for livestock and wildlife were produced by summing the applicable species groups and calculating confidence intervals following methodology from Buckland et al. (2001:77). We tested differences in density estimates between the two grazing areas by first using the delta method to find the variance of the density estimates being compared (Buckland et al., 2001:84), then we used the Z-statistic to test for significant differences (Buckland et al., 2001:84).

Another metric, production, was calculated from the density estimate. Production takes into account the difference in metabolism and turnover rates found between species to give a common energetic equivalence per unit area for all species sampled (Western, 1983). We used the equation $P = N\,13.8M_s^{0.67}$ where M_s represent the mean kcal equivalent of adult mass (this is given by multiplying adult body mass by the average mammalian calorific content of 1.5 kcal/g), and N represent population density (Groom and Western, 2013). We used body mass figures from the Amboseli Conservation Project (ACP, unpublished).

3. Results

3.1. Pasture conditions

3.1.1. Heterogeneity between grazing areas

Fig. 2 shows descriptive statistics and the results of a Mann-Whitney *U* test for pasture conditions across the two land use types through all

three seasons; dry, drought and wet. These seasonal results show that for all seasons there is significantly more grass biomass and taller grass in the grass bank than the livestock zone. This includes drought months, despite only a small absolute difference of means (grass bank 14.26g/m², 0.4cm; livestock zone 15.35 g/m², 1.78 cm). Only during the wet season months are there significant differences between grazing pressure, with a larger percentage grazed within the livestock zone. There is no significant difference in percentage green between the grazing areas in any season.

Mean monthly biomass was generally higher, surged faster and rose higher in the grass bank than the livestock zone (Sign Ranked Mann-Whitney-U test: V = 21, p-value < 0.001, Fig. 3).

3.1.2. Heterogeneity within grazing areas

Overall, monthly variation in grass biomass for both land use types decreases with season, from wet to dry to drought. Across all the seasons the grass bank showed higher monthly grass biomass standard deviation than the livestock zone (Fig. 3). This difference is significant for wet months (Paired Sign Ranked Mann-Whitney *U* test: V = 28, p-value < 0.008) and dry months (Paired Sign Ranked Paired Mann-Whitney *U* test: V = 45, p-value < 0.002) and marginal for drought months (Paired Sign Ranked Mann-Whitney *U* test: V = 69, p-value < 0.056). For both land use types, coefficient of variation increases with biomass (Fig. 4).

Within both grazing areas there was a significant difference in monthly grass biomass between the plots (Kruskall Wallis Test: H (2) = 82.69, p < 0.001; H(2) = 83.73, p < 0.001; for the livestock zone and grass bank areas respectively). This relationship was also significant across all seasons for both land use types (Table 1).

3.2. Animal densities and distributions

In total, 31 species were recorded on transect counts, but only 9 had sufficient detections to warrant model fitting (see Table A.2). Based on the AIC, likelihood ratio scores, and assessment of the model fit, detection models were selected for the nine focal species, as shown in Table 2.

Post stratification by land use created individual estimates of expected cluster size for each species within each land use, which was used to calculate density from the local encounter rate and global detection function. The results are shown below in Fig. 5. The comparison of density estimates through the use of the delta method and creation of a Z statistic, and associated p-values are also shown. These results show that zebra, wildebeest and Grant's gazelle are found in significantly higher densities within the grass bank than the livestock zone. Shoats and donkeys are found at significantly higher densities within the livestock zone. Ostrich, giraffe and cattle do not differ significantly in their densities between the two areas.

Density estimates were then used to calculate associated production, measured in kcal.km^{-2}.yr^{-1}. We clumped wildlife species into two feeding guilds, defining them as either grazers (feeding predominantly on grass) which includes zebra and wildebeest, or browsers (feeding predominantly on herbs and shrubs) which includes Grant's gazelle, giraffe, and impala. Livestock browsers are sheep and goats, while livestock grazers are donkeys and cattle.

Estimates of production for livestock and wildlife across the two areas are displayed in Fig. 6. Total production in the grass bank (76,737 kcal km^{-2}.yr^{-1}) is higher than production in the livestock zone (61,971 kcal km^{-2}.yr^{-1}). Fig. 6 (a) splits production by guild, and then further still into species in Fig. 6 (b) across the two grazing areas.

In the grass bank 76.1% of production is associated with wildlife; dominated by zebra (43.0%), wildebeest (13.4%) and giraffe (12.9%); and the remaining 23.9% of production is livestock based, with cattle accounting for 15.2% of this. In the livestock zone production is dominated by livestock which comprises 59.6% of the total production, with it split at 26.1% shoats, 28.0% cattle and 5.5% donkeys. Wildlife
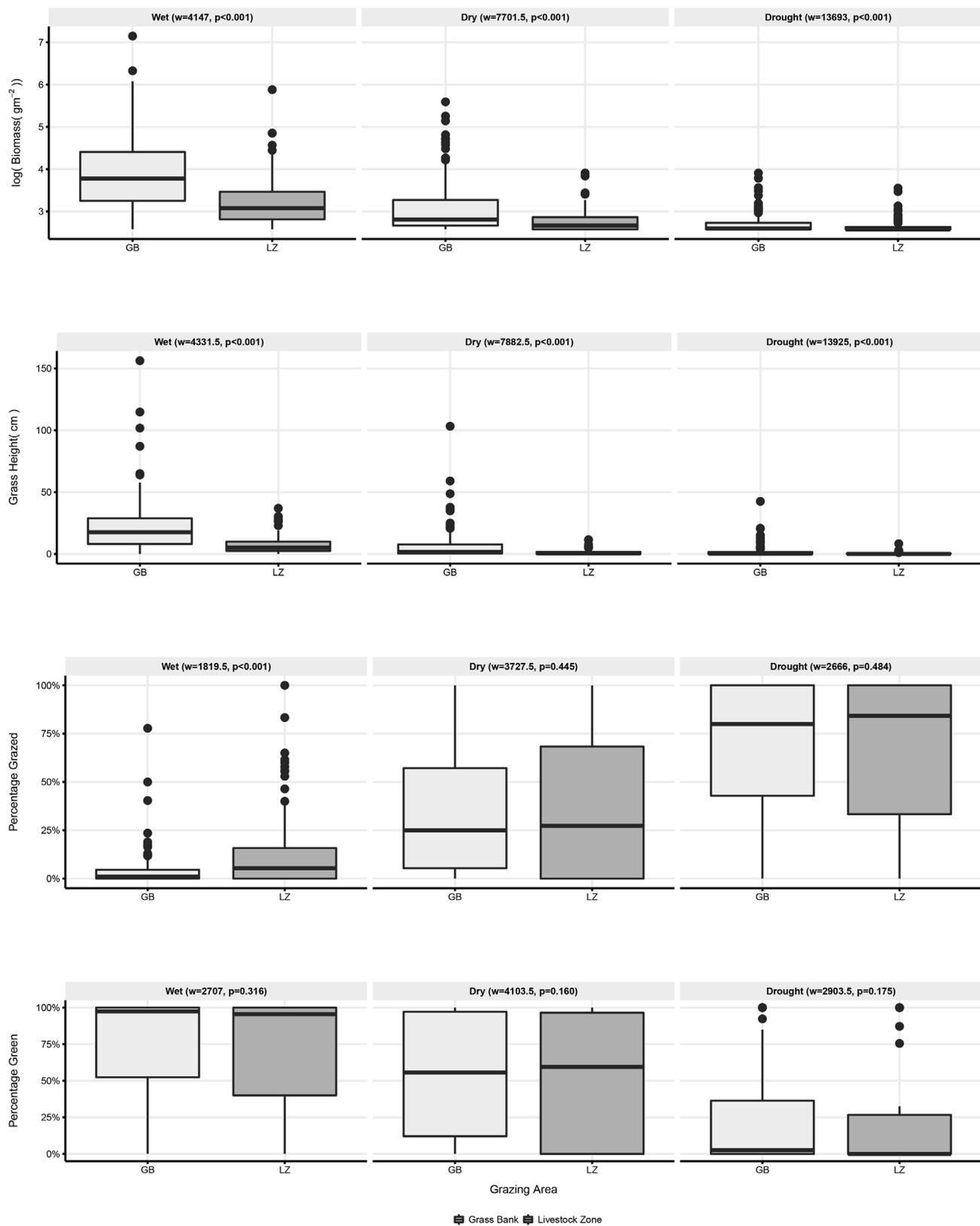
Fig. 2. Comparison of pasture characteristics between the two grazing areas, grass bank and livestock zone, across all three seasons. This includes the results of Mann-Whitney U-tests comparing the four pasture properties in each season and the associated p-values.
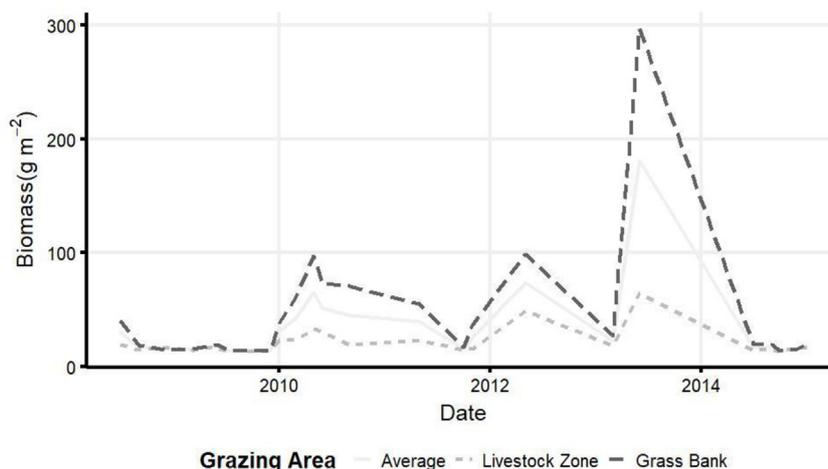
Fig. 3. Changes in mean monthly grass biomass ($g.m^{-2}$) over time within the grass bank and livestock zone.
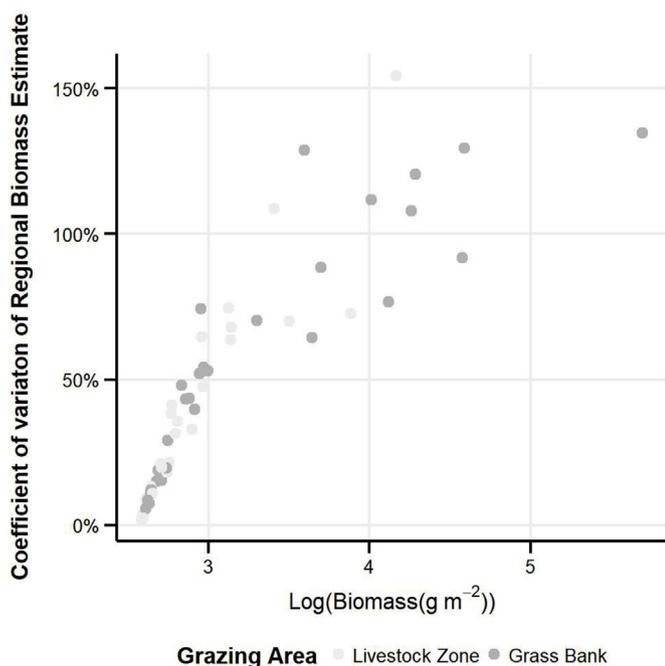

Fig. 4. Coefficient of variation of grazing area-specific biomass estimates from the two grazing areas (grass bank and livestock zone) compared to their log transformed biomass.

Table 1

Results of Kruskall Wallis Tests testing for differences in monthly grass biomass between sampling plots within each land use type, and for each season.

Season	Landuse	DF	H(2)	P - Value
Overall	Grass Bank	13	83.28	< 0.001
	Livestock Zone	10	82.69	< 0.001
Dry	Grass Bank	13	51.48	< 0.001
	Livestock Zone	10	51.71	< 0.001
Drought	Grass Bank	13	88.12	< 0.001
	Livestock Zone	10	58.66	< 0.001
Wet	Grass Bank	13	36.20	< 0.001
	Livestock Zone	10	37.87	< 0.001

production makes up the remaining 40.4% in this area, which is dominated by giraffe (15.9%) and zebra (12.6%).

4. Discussion

We have used long-term ecological data to distinguish the pasture characteristics and spatial distribution of wildlife and livestock in the livestock grazing zones used in the wet season and the grass banks used in the dry season under traditional grazing management by the Olkiramatian and Shompole Maasai people.

Grass biomass in the two group ranches is significantly correlated with rainfall over the preceding two months (p-value 0.003, $R^2 = 0.294$). Significant differences were, however, found between the seasonal grazing areas. The dry season grazing area used as a 'grass bank' and wildlife conservancy has consistently higher biomass and taller grass than that of the wet season grazing area, designated as the 'livestock zone'. The higher biomass corresponds to a rainfall gradient running from the Nguruman Escarpment edge in the western extremity of the group ranches to the dry central rift valley floor in the eastern portion of the group ranches.

The higher grass biomass in the dry season area is used by both livestock and wildlife grazers during the late dry season and in droughts. The grass bank is only grazed out during the longest dry periods. The seasonal uses by the Maasai are based on their grazing strategy of using the shorter milk-producing grasses of the livestock areas during the rains and the coarser grasses in the grass banks to tide their livestock through dry seasons (Butt et al., 2009; Western, 1982). The differential use is borne out by the greater grazing pressure in the livestock grazing area during the wet season and later depletion in the grass bank (Figs. 2 and 3).

In other East African systems differential use of shorter pastures in the wet season and taller pastures during the dry season has been shown to be an important factor in seasonal migrations of wildlife and pastoral livestock (Butt et al., 2009; Fynn et al., 2016; Mose et al., 2013). The shorter wet season pastures have a higher protein to fiber ratio and higher digestibility than the coarser dry season grasses (Fryxell et al., 2005; Mose et al., 2013). The seasonal movements allow herbivores to optimize the trade-off between forage quality and quantity by moving up the biomass gradient as the higher quality grasses are depleted (Bergman et al., 2001). Although grass biomass and quality may determine the main axis of seasonal movements as shown by Mose et al. (2013), and grass height is a key determinant of forage quality, other factors including growth form may contribute (Linstädter et al., 2014; Quiroga et al., 2010).

The results also show a mosaic of higher and lower biomass grasses in both the livestock zone and grass bank (Figs. 3 and 4). It is likely that

Table 2
Results from fitting models using Distance to the transect data for nine species with sufficient detection rates for analysis. Truncate distance is the distance of right truncation of the species detection data. Observations are the number of sightings used to fit the detection function, post-truncation. The key function fitted where either hazard-rate (HR) or half normal (HN). The adjustment terms were either cosine (COS) or hermite polynomial adjustments (HPO). Those species that used multiple-covariates distance sampling (MCDS) display which covariates were used in the detection function either: land use (LU) or season (SEA). The number of parameters used to fit each model is shown. Regional density estimates for each species are shown, along with their respective confidence intervals.

Species	Truncate Distance (m)	Observations	Model	Parameters	Regional Density Estimate (Individuals /km² and 95% confidence intervals)
Shoats	500	634	HR	2	52.2 (41.87–65.06)
Grants	400	1190	HR	2	6.73 (5.86–7.72)
Zebra	500	772	HN + COS + LU + SEA	4	6.65 (5.37–8.23)
Cattle	500	194	HN + COS + LU + SEA	4	6.23 (4.35–8.92)
Wildebeest	600	607	HN + COS + LU + SEA	4	3.26 (2.54–4.17)
Impala	300	115	HN + HPOL + LU + SEA	4	1.47 (1.03–2.1)
Donkeys	500	189	HN	1	1.02 (1.35–1.79)
Ostrich	450	171	HN	1	0.44 (0.34–0.57)
Giraffe	500	265	HN + COS + SEA	3	0.95 (0.75–1.20)

the same quantity-quality gradient that could be driving seasonal movements between the two also determines grazing patterns within each. As seasonal differences in pasture biomass between grazing areas converge with heavy grazing, the small-scale variations will become increasingly important in driving the distribution of herbivores (Mose et al., 2013).

The Shompole and Olkiramatian ecosystem represents one of the few areas in East Africa where wildlife and livestock coexist and move unimpeded through the seasonal migrations. Here we demonstrate the presence of diverse and abundant wildlife populations that coexist with a productive livestock population within a community governed ecosystem. This is in contrast to other community managed rangelands of Kenya, where livestock populations continue to increasingly exceed that of wildlife, often to the detriment of wildlife populations (Ogutu et al., 2016).

Our wildlife and livestock density estimates present a static snapshot representing the long-term differences in species distributions across the two grazing areas in the ecosystem. While we don't explicitly estimate densities of these species across all area–season combinations, by understanding the seasonal pasture properties of the two grazing areas we can hypothesize how temporal and spatial changes in pasture have impacted the overall distribution of wildlife and livestock. We use
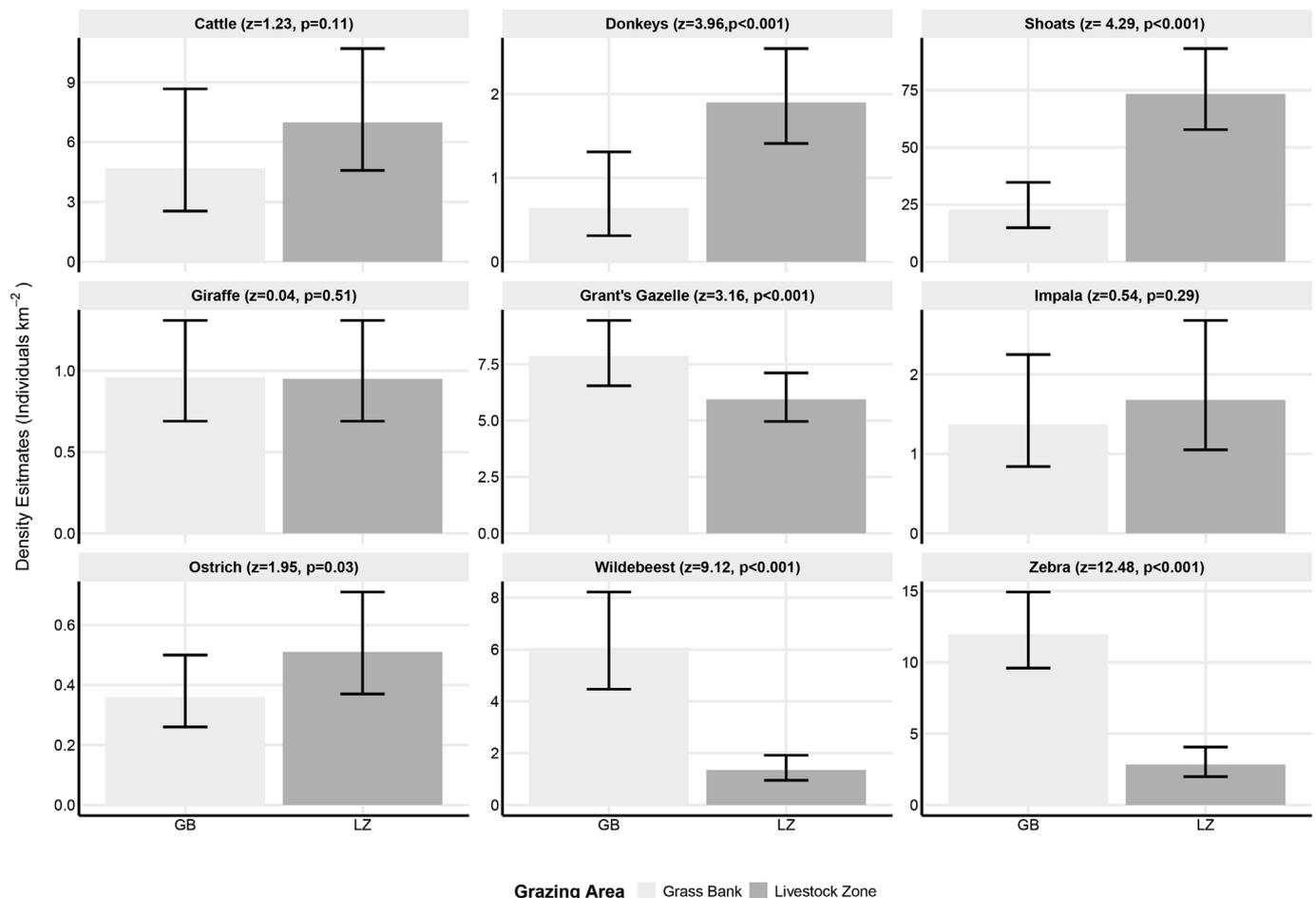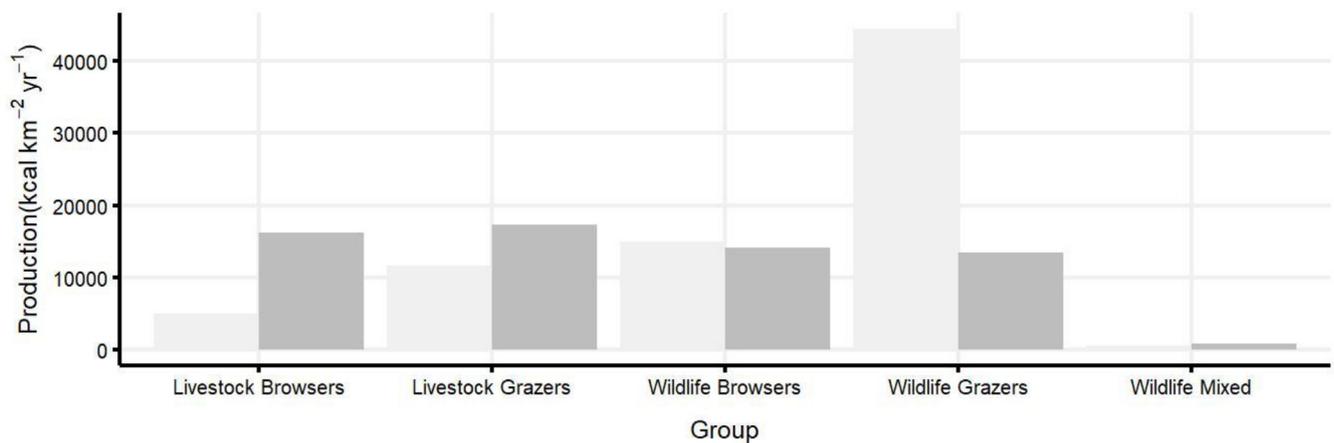

Fig. 5. Results from post-stratification by land use of the transect data following model fitting. Density estimates and their associated confidence intervals are shown for each species in each grazing area. Difference in densities between grazing areas is tested using a z statistic and the p-values from these tests are shown.
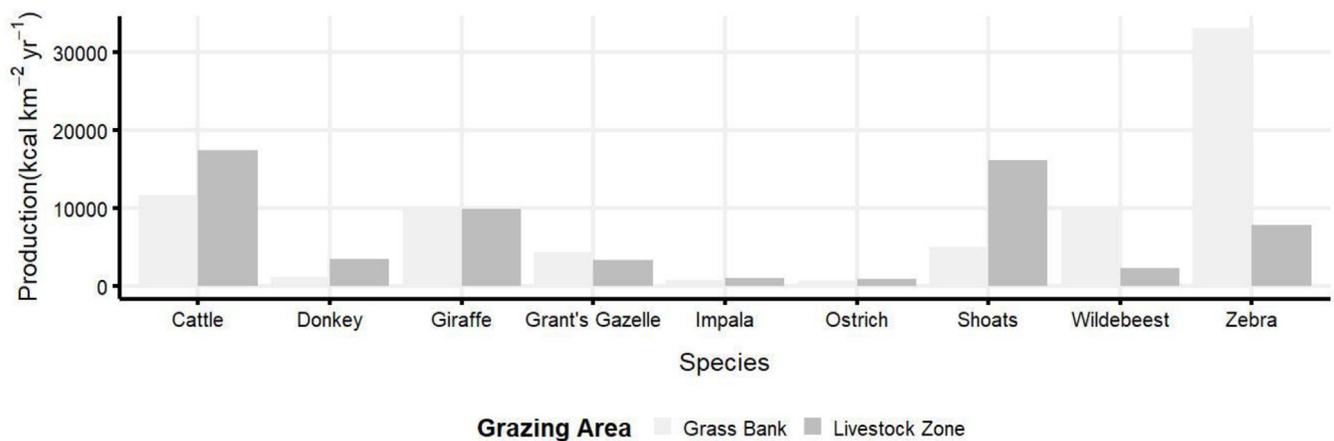
Fig. 6. Mean production (kcal.km^{-2}.yr^{-1}) of wildlife and livestock across the study period, separated by grazing area. a) Wildlife species have been separated into guilds representing their metabolic and feeding requirements. Wildlife grazers are represented by zebra and wildebeest. Wildlife browsers are represented by impala, Grant's gazelle and giraffe. Mixed feeders are represented by ostriches. Livestock browsers are sheep and goats, while livestock grazers are donkeys and cattle. b) Production across grazing area at the individual species level.

production in addition to densities because when comparing species, it normalizes for differences in metabolic rate. Production figures illustrate the relative importance of cattle compared to sheep and goats despite their numerical abundance, the dominance of livestock over wildlife, and grazing wildlife species over browsers (Fig. 6).

The variability in livestock and wildlife distribution between the two areas corresponds to the trade-off between quality and quantity of grazing resources as the dry season progresses. Differences in gut morphology, diet, and body size dictate the trade-off and variations in species according to feeding allometry theory (Fynn et al., 2016; Illius and Gordon, 1992; Mose et al., 2013; Redfern et al., 2003). Sheep and goats are found at higher densities within the livestock rearing zone, unlike cattle, which over the course of the study were evenly distributed between the two grazing areas. Shoats, which have a lower energy requirement than cattle, can stay longer in the livestock zone. Herders consider this area the primary livestock rearing zone because of the higher quality grasses, and the dry season area as the grass bank for late season grazing. Within the livestock rearing zone, short, green, nutritious grass is available during the wet and dry seasons (Fig. 2).

Shoats can continue grazing in these low biomass areas during periods of resource scarcity. Cattle move up the biomass gradient and into the grass bank sooner in order to sustain their higher energy intake. These decisions on livestock movement are governed by the community grazing committees, who regulate settlements and access to the grass bank for all types of livestock.

The prevalence of wildlife grazers within the grass bank is attributed to several factors. Grazers are pushed sooner onto the poorer, higher biomass pastures by the high density of livestock in the livestock zones, and so faster along the quality-quantity gradients and into the grass bank. Livestock, especially cattle, are controlled by herders who can target areas of higher forage quality and quantity (Butt, 2010) and so displace wildlife (Western, 1997). This enables cattle to remain within the livestock zone longer than the wildlife grazers. Wildlife browsing species have lower densities than wildlife grazers overall and are spread more evenly between wet and dry seasons, reflecting the more even distribution of browse species and lack of water constraints (Redfern et al., 2003).

Further work within this system will focus on determining the

factors driving wildlife and livestock movements through the eco-system.

5. Implications

Despite the predominance of livestock, the Shompole-Olkiramatian area still maintains a rich diversity and abundance of wildlife. We attribute the coexistence to the continuance of the traditional seasonal movements between wet and dry season ranges and ability of wildlife to maneuver freely among the domestic herds along the pasture gradient (Groom and Western, 2013). The maintenance of heterogeneous grazing resources has been shown theoretically to support larger populations of livestock and wildlife during times of resource scarcity (Ash et al., 2004; Illius and O'Connor, 1999; Illius and O'Connor, 2000; Müller et al., 2007). The Shompole-Olkiramatian ecosystem showed considerable resilience during the 2009 drought compared to neighboring Amboseli, where losses in both livestock and wildlife were far higher (Table A.3, Western, 2009). Where the seasonal movements breakdown with land subdivision and human population sedentarisation, wildlife populations decline due to the lack of maneuverability and decline in pasture seasonality (Groom and Western, 2013). Sedenterisation and subdivision, which have become widespread in the East African rangelands (Homewood et al., 2009), pose a growing threat to wildlife abundance (Western et al., 2009a) due to range degradation (Boone, 2005; Western et al., 2015) and increased frequency of droughts (du Toit and Cumming, 1999; Western et al., 2015).

This study shows that despite large livestock populations, the seasonal migrations and mobility practiced by traditional Maasai pastoralism can sustain a diverse and productive wildlife community. Land use and settlement planning aimed at keeping lands open to allow livestock and wildlife to move freely and optimize digestible energy in response to seasonal and local pasture heterogeneity is important for sustaining herbivore productivity and the coexistence of wildlife and livestock.

Appendices

Table A.1

Sampling Date	Grass Biomass (g/m^2)	Percentage Green	Season
01/07/2008	32.65	6.05%	Dry
01/09/2008	16.77	4.20%	Drought
01/10/2008	17.19	44.83%	Dry
01/12/2008	14.98	23.28%	Drought
01/01/2009	15.24	39.54%	Drought
01/03/2009	14.58	21.33%	Drought
01/05/2009	17.06	86.47%	Dry
01/06/2009	17.75	90.45%	Dry
01/07/2009	14.79	19.23%	Drought
01/09/2009	13.90	6.78%	Drought
01/10/2009	13.51	1.20%	Drought
01/11/2009	13.70	15.22%	Drought
01/12/2009	13.85	72.08%	Drought
01/01/2010	32.17	91.42%	Wet
01/03/2010	46.56	98.03%	Wet
01/05/2010	55.71	98.92%	Wet
01/06/2010	52.35	27.09%	Wet
01/09/2010	51.48	14.41%	Dry
01/05/2011	41.68	77.75%	Wet
01/10/2011	15.93	38.99%	Drought
01/11/2011	26.66	95.25%	Dry
01/02/2012	36.73	35.64%	Wet
01/05/2012	74.46	97.05%	Wet
01/10/2012	32.22	16.26%	Dry
01/03/2013	23.61	60.68%	Dry
01/06/2013	169.06	31.04%	Wet
01/10/2013	62.22	8.75%	Dry
01/01/2014	28.02	42.45%	Dry
01/07/2014	16.73	21.18%	Drought
01/09/2014	17.27	41.67%	Dry
01/10/2014	14.21	30.25%	Drought
01/12/2014	16.03	48.15%	Drought
01/01/2015	19.13	42.07%	Dry

Table A.2
Detections before truncation

Species	Total Detections
Baboon	1
Bat Eared Fox	9
Black Backed Jackal	2
Cape Buffalo	5
Cattle	192
Cheetah	3
Dik Dik	16
Donkey	182
Egyptian mongoose	1
Eland	29
Elephant	1
Genet	11
Gerenuk	52
Golden jackal	1
Giraffe	258
Grant's gazelle	1189
Cape Hare	116
Impala	120
Kori bustard	210
Lesser Kudu	2
Lion	2
Oryx	10
Ostrich	174
shoats	619
Warthog	17
Wild cat	1
Wild dog	1
Wildebeest	590
Waterbuck	5
Zebra	818

Table A.3
Results from post-stratification by year of the transect data following model fitting. Expected cluster size E(S) is shown for each species in each year, as are local density estimates and their associated confidence intervals.

|	2008				2009				2010			
	E(S)	Density	Low 95%	High 95%	E(S)	Density	Low 95%	High 95%	E(S)	Density	Low 95%	High 95%
Shoats	80.48	48.34	31.11	75.12	60.14	47.29	33.73	66.30	63.08	58.97	40.76	85.33
Cattle	20.93	5.68	3.18	10.15	13.36	1.05	0.45	2.44	44.07	15.00	8.89	25.29
Donkeys	4.93	1.06	0.61	1.84	6.15	1.32	0.84	2.08	5.83	1.79	1.17	2.75
Livestock totals		**55.09**	**37.28**	**81.41**		**49.66**	**36.00**	**68.51**		**75.76**	**55.85**	**102.77**
Zebra	8.74	6.70	4.67	9.62	6.51	3.89	2.56	5.90	8.55	9.43	6.74	13.20
Wildebeest	5.46	5.12	3.40	7.69	8.58	2.12	1.25	3.58	4.87	3.21	2.27	4.53
Grant's	3.83	7.60	6.13	9.41	3.58	6.33	5.11	7.85	4.78	6.00	4.69	7.67
Impala	5.55	1.23	0.64	2.34	6.92	1.27	0.66	2.44	6.57	2.21	1.31	3.72
Ostrich	1.92	0.32	0.22	0.47	3.22	0.50	0.35	0.72	2.65	0.36	0.23	0.56
Giraffe	2.77	1.04	0.72	1.49	3.19	0.84	0.60	1.18	3.62	1.03	0.62	1.71
Wildlife totals		**22.00**	**18.60**	**26.02**		**14.95**	**12.60**	**17.75**		**22.23**	**18.68**	**26.46**
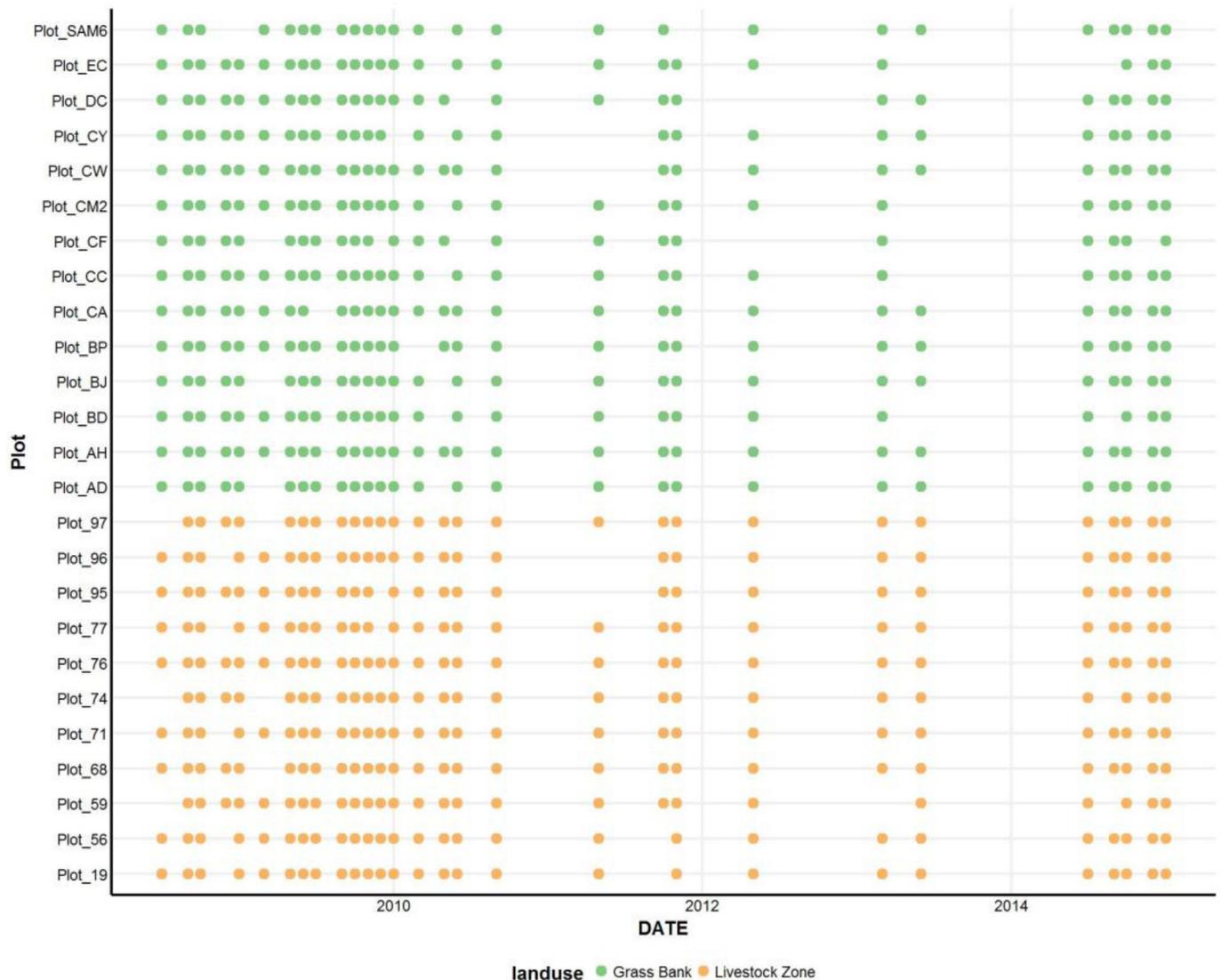
Fig. A 1. Distribution of sampling effort at each plot across the study period.

References

Agnew, A.D.Q., Mwendia, C.M., Oloo, G.O., Roderick, S., Stevenson, P., 2000. Landscape monitoring of semi-arid rangelands in the Kenyan rift valley. Afr. J. Ecol. 38, 277–285. http://dx.doi.org/10.1046/j.1365-2028.2000.00224.x.

Ash, A., Gross, J., Smith, M.S., 2004. Scale, heterogeneity and secondary production in tropical rangelands. Afr. J. Range Forage Sci. 21, 137–145. http://dx.doi.org/10.2989/10220110409485846.

Bekure, S., International Livestock Centre for Africa, 1991. Maasai herding: an analysis of the livestock production system of Maasai pastoralists in eastern Kajiado District, Kenya. In: ILCA Syst. Study xviii, pp. 154.

Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing? J. Anim. Ecol. 70, 289–300. http://dx.doi.org/10.1046/j.1365-2656.2001.00496.x.

Bhola, N., Ogutu, J.O., Piepho, H.P., Said, M.Y., Reid, R.S., Hobbs, N.T., Olff, H., 2012. Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. Biodivers. Conserv. 21, 1509–1530. http://dx.doi.org/10.1007/s10531-012-0261-y.

Boone, 2005. Quantifying changes in vegetation in shrinking grazing areas in Africa. Conserv. Soc. 3, 150.

Bourn, D., Blench, R., 1999. Can Livestock and Wildlife Co-exist?: an Interdisciplinary Approach, vol. 280.

Buckland, J.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 1993. Distance sampling: estimating abundance of biological population. Urapman Hell 446.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. New York, USA. https://doi.org/10.1007/s00531-004-0408-5.

Butt, B., 2010. Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. J. Arid Environ. 74, 403–413. http://dx.doi.org/10.1016/j.jaridenv.2009.09.025.

Butt, B., Shortridge, A., MGA, W.A., 2009. Pastoral herd management, drought coping strategies, and cattle mobility in southern Kenya. Ann. Assoc. Am. Geogr. 99, 309–334. http://dx.doi.org/10.1080/00045600802685895.

Butt, B., Turner, M.D., 2012. Clarifying competition: the case of wildlife and pastoral livestock in East Africa. Pastor. Res. Policy Pract 2, 9. http://dx.doi.org/10.1186/2041-7136-2-9.

Cole, M.M.M., 1982. The influence of soils, geomorphology and geology on the distribution of plant communities in savanna ecosystems. Ecol. Trop. savannas 42, 145–174. http://dx.doi.org/10.1007/978-3-642-68786-0_8.

Coughenour, M.B., Coppock, D.L., Ellis, J.E., 1990. Herbaceous forage variability in an arid pastoral region of Kenya: importance of topographic and rainfall gradients. J. Arid Environ. 19, 147–159.

Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E., Hutton, J.M., 2010. Large mammal population declines in Africa's protected areas. Biol. Conserv. 143, 2221–2228. http://dx.doi.org/10.1016/j.biocon.2010.06.007.

Du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. Biodivers. Conserv. 8, 1643–1661. http://dx.doi.org/10.1023/A:1008959721342.

Estes, R.D., Atwood, J.L., Estes, A.B., 2006. Downward trends in Ngorongoro Crater ungulate populations 1986-2005: conservation concerns and the need for ecological research. Biol. Conserv. 131, 106–120. http://dx.doi.org/10.1016/j.biocon.2006.02.009.

Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R.E., Haydon, D.T., Holt, R.D., Abrams, P.A.,

2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecol. Lett. 8, 328–335. http://dx.doi.org/10.1111/j.1461-0248.2005.00727.x.

Fynn, R.W.S., Augustine, D.J., Peel, M.J.S., de Garine-Wichatitsky, M., 2016. REVIEW: strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife-livestock coexistence. J. Appl. Ecol. http://dx.doi.org/10.1111/1365-2664.12591.

Glew, L., 2012. Evaluating the Effectiveness of Community-based Conservation in Northern Kenya. Unpubl. Proj. Rep. .

Groom, R.J., Western, D., 2013. Impact of land subdivision and sedentarization on wildlife in Kenya's southern rangelands. Rangel. Ecol. Manag. 67, 1–9. http://dx.doi.org/10.2111/REM-D-11-00021.1.

Hobbs, N.T., Galvin, K.A., Stokes, C.J., Lackett, J.M., Ash, A.J., Boone, R.B., Reid, R.S., Thornton, P.K., 2008. Fragmentation of rangelands: implications for humans, animals, and landscapes. Glob. Environ. Chang 18, 776–785. http://dx.doi.org/10.1016/j.gloenvcha.2008.07.011.

Homewood, K., Kristjanson, P., Trench, P. (Eds.), 2009. Staying Maasai? Livelihoods, Conservation and Development in East African Rangelands. Springer Science + Business Media, New York, USA.

Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434. http://dx.doi.org/10.1007/BF00317422.

Illius, A.W., O'Connor, T.G., 2000. Resource heterogenity and ungulate population dynamics. Oikos 89, 283–294. http://dx.doi.org/10.1034/j.1600-0706.2000.890209.x.

Illius, A.W., O'Connor, T.G., 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. Ecol. Appl. 9, 798–813. http://dx.doi.org/10.1890/1051-0761(1999)009[0798:OTRONC]2.0.CO;2.

Jensen, C.L., 1982. The Pin-frame and Photometer Methods for Estimating Plant Biomass.

Kimani, K., Pickard, J., 1998. Recent ranch trends and implications of group and fragmentation in Kajiado District, Kenya. Geogr. J. 164, 202–213. http://dx.doi.org/10.2307/3060370.

Linstädter, A., Schellberg, J., Brüser, K., García, C.A.M., Oomen, R.J., Du Preez, C.C., Ruppert, J.C., Ewert, F., 2014. Are there consistent grazing indicators in drylands? Testing plant functional types of various complexity in South Africa's grassland and savanna biomes. PLoS One 9. http://dx.doi.org/10.1371/journal.pone.0104672.

Marques, T.A., Thomas, L., Fancy, S.G., Buckland, S.T., 2007. Improving estimates of bird density using multiple- covariate distance sampling. Auk 124, 1229. http://dx.doi.org/10.1642/0004-8038(2007)124[1229:IEOBDU]2.0.CO;2.

McAllister, R.R.J., Gordon, I.J., Janssen, M.A., Abel, N., 2006. Pastoralists' responses to variation of rangeland resources in time and space. Ecol. Appl. 16, 572–583. http://dx.doi.org/10.1890/1051-0761(2006)016[0572:PRTVOR]2.0.CO;2.

McNaughton, S.J., 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol. Monogr. 53, 291–320. http://dx.doi.org/10.2307/1942533.

MEWNR, 2015. Kenya Biodiversity Atlas* Ministry of Environment Natural Resources and Regional Development Authorities.

Mose, V.N., Nguyen-Huu, T., Western, D., Auger, P., Nyandwi, C., 2013. Modelling the dynamics of migrations for large herbivore populations in the Amboseli National Park, Kenya. Ecol. Modell 254, 43–49. http://dx.doi.org/10.1016/j.ecolmodel.2013.01.016.

Müller, B., Linstädter, A., Frank, K., Bollig, M., Wissel, C., 2007. Learning from local knowledge: modeling the pastoral-nomadic range management of the Himba, Namibia. Ecol. Appl. 17, 1857–1875. http://dx.doi.org/10.1890/06-1193.1.

Mwangi, E., Ostrom, E., 2009. Top-down solutions: looking up from East Africa's rangelands. Environment 9157, 37–41. http://dx.doi.org/10.3200/ENVT.51.1.34-45.

Mwangi, E.M., Western, D., 1998. Fluctuations in food supply in an insularized and heavily grazed savanna ecosystem in Kenya. Afr. J. Ecol. 36, 207–212. http://dx.doi.org/

org/10.1046/j.1365-2028.1998.00121.x.

Niamir-Fuller, M., 1999. Prelims - managing mobility in african rangelands. Manag. Mobil. African Rangelands i–xiv. http://dx.doi.org/10.3362/9781780442761.000.

Ogutu, J.O., Piepho, H.-P., Said, M.Y., Ojwang, G.O., Njino, L.W., Kifugo, S.C., Wargute, P.W., 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? PLoS One 11http://dx.doi.org/10.1371/journal.pone.0163249. e0163249.

Quiroga, R.E., Golluscio, R.A., Blanco, L.J., Fernández, R.J., 2010. Aridity and grazing as convergent selective forces: an experiment with an Arid Chaco bunchgrass. Ecol. Appl. 20, 1876–1889. http://dx.doi.org/10.1890/09-0641.1.

R Development Core Team, R., 2008. R: a Language and Environment for Statistical Computing. R Found. Stat. Comput. http://dx.doi.org/10.1007/978-3-540-74686-7.

Redfern, J.V., Grant, R., Biggs, H., Getz, W.M., 2003. Surface-water constraints on herbivore foraging in the kruger national park, South Africa. Ecology 84, 2092–2107. http://dx.doi.org/10.1890/01-0625.

Schuette, P., Creel, S., Christianson, D., 2013. Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. Biol. Conserv. 157, 148–154. http://dx.doi.org/10.1016/j.biocon.2012.09.011.

Strum, S.C., Stirling, G., Mutunga, S.K., 2015. The perfect storm: land use change promotes Opuntia stricta's invasion of pastoral rangelands in Kenya. J. Arid Environ. 118, 37–47. http://dx.doi.org/10.1016/j.jaridenv.2015.02.015.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. 47, 5–14. http://dx.doi.org/10.1111/j.1365-2664.2009.01737.x.

Turner, M.D., Hiernaux, P., 2002. The use of herders' accounts to map livestock activities across agropastoral landscapes in semi-arid Africa. Landsc. Ecol. 17, 367–385. http://dx.doi.org/10.1023/A:1021238208019.

Western, D., 2009. Drought in the Amboseli Ecosytem [WWW Document]. URL. http://www.amboseliconservation.org/drought-in-the-amboseli-ecosystem.html (accessed 10.26.16).

Western, D., 1997. In the Dust of Kilimanjaro. Island Press.

Western, D., 1983. Production, reproduction and size in mammals. Oecologia 59, 269–271. http://dx.doi.org/10.1007/BF00378847.

Western, D., 1982. The environment and ecology of pastoralists in arid savannas. Dev. Change 13, 183–211. http://dx.doi.org/10.1111/j.1467-7660.1982.tb00117.x.

Western, D., 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. East African Wildl. J. 13, 265–286. http://dx.doi.org/10.1111/j.1365-2028.1975.tb00139.x.

Western, D., Finch, V., 1986. Cattle and pastoralism: survival and production in arid lands. Hum. Ecol. 14, 77–94. http://dx.doi.org/10.1007/BF00889211.

Western, D., Groom, R., Worden, J., 2009a. The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. Biol. Conserv. 142, 2538–2546. http://dx.doi.org/10.1016/j.biocon.2009.05.025.

Western, D., Mose, V.N., Worden, J., Maitumo, D., 2015. Predicting extreme droughts in savannah Africa: a comparison of proxy and direct measures in detecting biomass fluctuations, trends and their causes. PLoS One 10, 1–18. http://dx.doi.org/10.1371/journal.pone.0136516.

Western, D., Russell, S., Cuthil, I., 2009b. The status of wildlife in protected areas compared to non-protected areas of Kenya. PLoS One 4. http://dx.doi.org/10.1371/journal.pone.0006140.

Western, D., Russell, S., Mutu, K., 2006. The status of wildlife in Kenya's protected and non protected areas. In: First Stakeholders Symposium of the Wildlife Policy and Legislation Review.

Williamson, K., 2000. The Origins and Development of African Livestock.