Original Research Article

# Seasonal movements of wildlife and livestock in a heterogenous pastoral landscape: Implications for coexistence and community based conservation

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## ARTICLE INFO

## ABSTRACT

Rangelands across the world are home to millions of pastoral people and vast wildlife populations, which create a complex landscape for conservation. Community based conservation has been used to promote human-wildlife coexistence on pastoral lands, protecting wildlife outside of official protected areas. With the spread of community based conservation within the rangelands there is a need for more information on successful management practices. This study provides an example of this in the South Rift, Kenya, where seasonal movements of pastoralists aid coexistence. We used Density Surface Modelling (DSM), a novel tool for conservation managers in the rangelands, to predict wildlife and livestock abundance across the landscape and seasons. Wildlife grazers, zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*), follow expected metabolic patterns, feeding on short grass outside the conservation area in the wet season, before returning to the taller-lower quality grazing in the conservation areas during the drought. Browsing wildlife, impala (*Aepyceros melampus*) and Grant's gazelle (*Nanger granti*), move from open grassland and bushland areas into thicker, denser browse as the seasons progress towards the drought. Livestock, both shoats (*Ovis aries*, and *Capra aegagrus hircus*) and cattle (*Bos indicus*), are managed by community grazing committees, who enforce a grazing plan that creates spatial–temporal separation between wildlife and livestock. They exploit the high-quality grazing in the livestock area during the wet season while conserving pasture in the conservation area, which is utilized only as forage is depleted. This ensures that wildlife has access to a diverse resource base across all seasons and potentially reduces competition, allowing for a diverse and abundant wildlife community to coexist with livestock. This highlights the importance of the presence and maintenance of spatial and temporal heterogeneity of forage resources, through livestock management, for community based conservation. We encourage more community based conservation initiatives in pastoral landscapes to incorporate livestock management into planning.

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## 1. Introduction

Rangelands cover a vast area of the world's surface, support the livelihoods of thousands of pastoralists and contain some of the largest wildlife populations in the world (e.g. Mduma et al., 1999; Lund, 2007). This mixture of vast landscapes, large wildlife populations, and presence of pastoralists and their livestock creates a complex landscape for conservation. Historically, conservation in rangelands was focused on landscape preservation and fortress conservation of large wildlife populations (Adams, 2005), but since the 1970's, pastoralists communities have begun to be reintegrated into the conservation agenda, and community-based conservation initiatives have started to increase the space for wildlife, protect the livelihoods of indigenous pastoralists, and engage communities in participatory ecosystem management (Berkes, 2004; Western et al., 2015b).

Community conservation initiatives often create mixed-use landscapes containing both wildlife and livestock. This results in trade-offs of costs and benefits between wildlife and people, the balance of which can dictate the success of conservation interventions. Wildlife in conservancies can create substantial local revenue through wildlife-based tourism or wildlife utilization (Groom and Harris, 2008; Naidoo et al., 2016), but living with wildlife can have significant costs: predation of livestock (Zimmermann et al., 2010); complex disease interactions (Kock et al., 2009); and competition for grazing resources (Odadi et al., 2011). In particular, wildlife is viewed across many savannah rangelands as directly competing for forage resources with livestock, and often livestock is blamed for the large declines in wildlife seen in many community areas (e.g. Ogutu et al., 2016, 2011). Management decisions are often made based on this assumption, with livestock excluded for the benefit of wildlife. The tradeoff between the two is generally far more complex, and in some circumstances livestock can increase wildlife's access to forage resources (Butt and Turner, 2012; Odadi et al., 2011; Western, 1982). The dominance of livestock in communal lands means that finding solutions that reduce the negative aspects of the trade-off, and encourage coexistence between livestock and wildlife are an important goal for biodiversity conservation within the rangelands, and for reducing wide scale declines in wildlife numbers.

The situation is similar in the rangelands of Kenya, where pastoralists have used the rangelands for several thousand years (Williamson, 2000). While these rangelands are known for their large wildlife populations, livestock biomass generally considerably outweighs that of wildlife (Bourn and Blench, 1999). Until 50 years ago, wildlife and livestock coexisted at high densities over much of the Kenyan rangelands (Ogutu et al., 2016). Recently, country-wide declines in wildlife have highlighted the need for protection of wildlife outside of government protected areas and across the rangelands, which now contain 60% of Kenya's wildlife (Western et al., 2009b). In Kenya, wildlife conservancies, both private and community based, are one of the tools used to protect wildlife in these areas. The number of conservancies in Kenya has grown rapidly, from less than 5 in the early 1990's to over 140 in 2016 covering 30,000 km$^2$ (KWCA, 2016). Conservancies are now vital for the long term survival of wildlife both outside and inside protected areas (Dolrenry et al., 2014; Ihwagi et al., 2015; Mose et al., 2012; Western et al., 2015b). Many of these conservancies are community conservancies, involving multiple indigenous landowners, often pastoralists, whose predominant source of livelihood is livestock based.

Despite the importance of coexistence on community conserved lands, there are few examples of areas where both livestock and wildlife not only co-occur but also thrive. Most studies of wildlife populations in East Africa have focused on areas within, or bordering, government protected areas (e.g. Fryxell et al., 2005; Mose et al., 2013), with few studies solely focusing on community areas that have both wildlife and livestock present. We present work that was conducted in an unsubdivided, community conserved and managed ecosystem, which has relatively high densities of both wildlife and livestock (Russell et al., submitted). This area, the South Rift Valley, Kenya, is inhabited by indigenous Maasai pastoralists, who have a long history of coexistence with wildlife. Within many community and protected areas across East Africa seasonal wildlife movements have been drastically altered or stopped altogether (e.g Mose and Western, 2015), with this area as an exception to this rule. In this ecosystem, wildlife movements are not constrained by any physical barriers, such as settlement or fencing, and appear to respond to metabolic requirements, with wildlife grazers moving down a seasonal forage biomass gradient across the heterogeneous grazing areas (Russell et al., submitted). Similarly, livestock have access to spatially and temporally heterogeneous rangelands, with movements managed to maintain heterogeneity, with clearly designated seasonal grazing areas for livestock (Russell et al., submitted). This heterogeneity appears to allow spatial and temporal separation of resource use between wildlife and livestock, which could help reduce competition, provide late season forage, and potentially promote coexistence and high productivity of both groups (Ash et al., 2004; Fynn et al., 2016; Russell et al., submitted). In the early 2000's community conservation areas were set aside to protect wildlife, gain revenue from tourism, and protect the areas grass banks, which contain critical dry season forage for livestock.

In the South Rift, it appears that seasonal changes in spatial abundance of wildlife and livestock is important for the high productivity of both wildlife and livestock, and their ability to coexist. Until recently, it was hard to document changes in animal spatial abundance. However a new technique, using density surface models (DSM), has led to novel methods for analyzing, modelling and predicting patterns of species abundance (Miller et al., 2013). This technique uses line transect methodology and distance sampling methodology (Buckland et al., 2001) combined with generalized additive models (GAMS; Wood, 2006), to use spatial variables to predict patterns of abundance across a landscape.

In this study, we used DSMs with the following aims. First, to document and visualize spatially the seasonal movement of wildlife and livestock in a community conserved landscape. Second, to understand the factors influencing changes in spatial abundance between seasons. Russell et al. (submitted) suggest that wildlife movements are not constrained and are in accordance with their metabolic requirements. Using DSMs, we incorporate several spatial covariates which allow for

inference of factors affecting seasonal abundance. Third, we aim to describe the seasonal and spatial covariance of livestock and wildlife, whose coexistence is partly attributed to seasonal variation in resource use (Russell et al., submitted). Finally, we wanted to produce spatially explicit and accurate estimates of wildlife and livestock numbers for the area. We then discuss the implications of these findings for other community conservation programs in mixed wildlife-livestock areas.

## 2. Methods

### 2.1. Study area

The study area is situated in southern Kenya, and has an altitude of 600–700 m and high temperatures ranging from 18 °C at night to 45 °C during the day. The area is semi-arid and rainfall is erratic and bimodal averaging 400–600 mm yr$^{-1}$ (Agnew, 2000). A perennial river, the Ewaso Ngiro bisects the area, providing an important source of water. The Ewaso Ngiro river creates the Shompole swamp, before ending up in Lake Natron. The area is inhabited by roughly 20,000 Maasai pastoralist and their livestock. The area has an intact community of large herbivores (except for black rhinoceros), 21 species of carnivore and a growing population of elephants (Ahlering et al., 2012; Schuette et al., 2013). The area is comprised of two group ranches, Shompole and Olkiramatian, roughly 62000 ha and 27000 ha respectively. Neither ranch has been subdivided or fully sedenterized, unlike many other areas of southern Kenya (Kimani and Pickard, 1998). Grazing committees from both group ranches manage livestock access to certain areas, with the conservancy (grass bank) rested during the wet seasons (Fig. 1), which can last up to 6 months. When grazing is permitted in the conservancy, as the dry season progresses, settlement is limited to an area that contains temporary settlements, called the 'buffer' zone. Livestock must then walk into the conservancy from the buffer zones to access grazing. The 'livestock rearing zone' is permanently settled and may be grazed year-round.

### 2.2. Transects

Sixteen line transects were sampled during the day and night at approximately six-week intervals between May 2008 and April 2011. In total, the combined transects length are 69.2 km, and were each sampled between 38 and 40 times (Fig. 1; Table S2).

Transects were driven using a four-wheel drive vehicle at 10 km/h. Night transects took place shortly after dark, from 19:30, and finished by midnight. Two observers sitting on the roof of the car scanned for animals. During night sampling, each observer used a spotlight to scan for sightings. Once sighted the vehicle was stopped and sighting information was recorded: species detected, number of animals in the cluster, to avoid pseudoreplication (Buckland, 2001); straight-line distance ($r_i$); and angle ($\theta_i$) to the center of the cluster. Perpendicular distance ($x_i$) from the transect can then be 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. A GPS position was taken for every sighting, so that detections could be assigned to individual segments during analysis.

### 2.3. Seasons

To compare changes in species abundances patterns with seasons, we allocated seasonal classifications to each month of data collection. We used the classification scheme followed by Russell et al. (submitted), which classified months based on regional grass biomass and greenness (Table S3). The three seasons show a decrease in regional grass biomass and greenness from wet to dry to drought.

### 2.4. Estimating patterns of spatial abundance

Our analysis focuses on six of the area's most common wildlife and livestock species: cattle (*Bos indicus*); and shoats (consisting of both sheep and goats due to the difficulty in distinguishing the two species in large mixed herds (*Ovis aries*; *Capra aegagrus hircus*). Wildlife species included: zebra (*Equus burchelli*); wildebeest (*Connochaetes taurinus*); Grant's gazelle (*Nanger granti*); and impala (*Aepyceros melampus*). Other species detected during the transects are listed in Table S1.

To estimate the spatial abundance across the study area we used the Density Surface Modelling (DSM) approach (Miller et al., 2013). This is a multi-step approach which first fits detection functions to the data (Buckland et al., 2001). Transects are then split into smaller segments and abundance is estimated using the detection function. Abundance is then modelled as a sum of smooth functions of spatial covariates using a generalized additive model (GAMs; Wood, 2006). This GAM can then be used to predict abundance over the larger study area. Analysis was conducted using R (R Development Core Team, 2008) using package *dsm* (Miller et al., 2015) and *Distance* (Miller et al., 2016).

#### 2.4.1. Detection function
Seasonal detection functions were fitted for each species, except cattle (see below). Data was right truncated for all species at 500 m to maximize model fit (Buckland et al., 2001). Candidate models included the half-normal key with cosine adjustments or hermite polynomial adjustments, and hazard-rate key with simple polynomial adjustments (Thomas et al., 2010). The series adjustment terms were selected sequentially using the Akaike information criterion (AIC). Transects
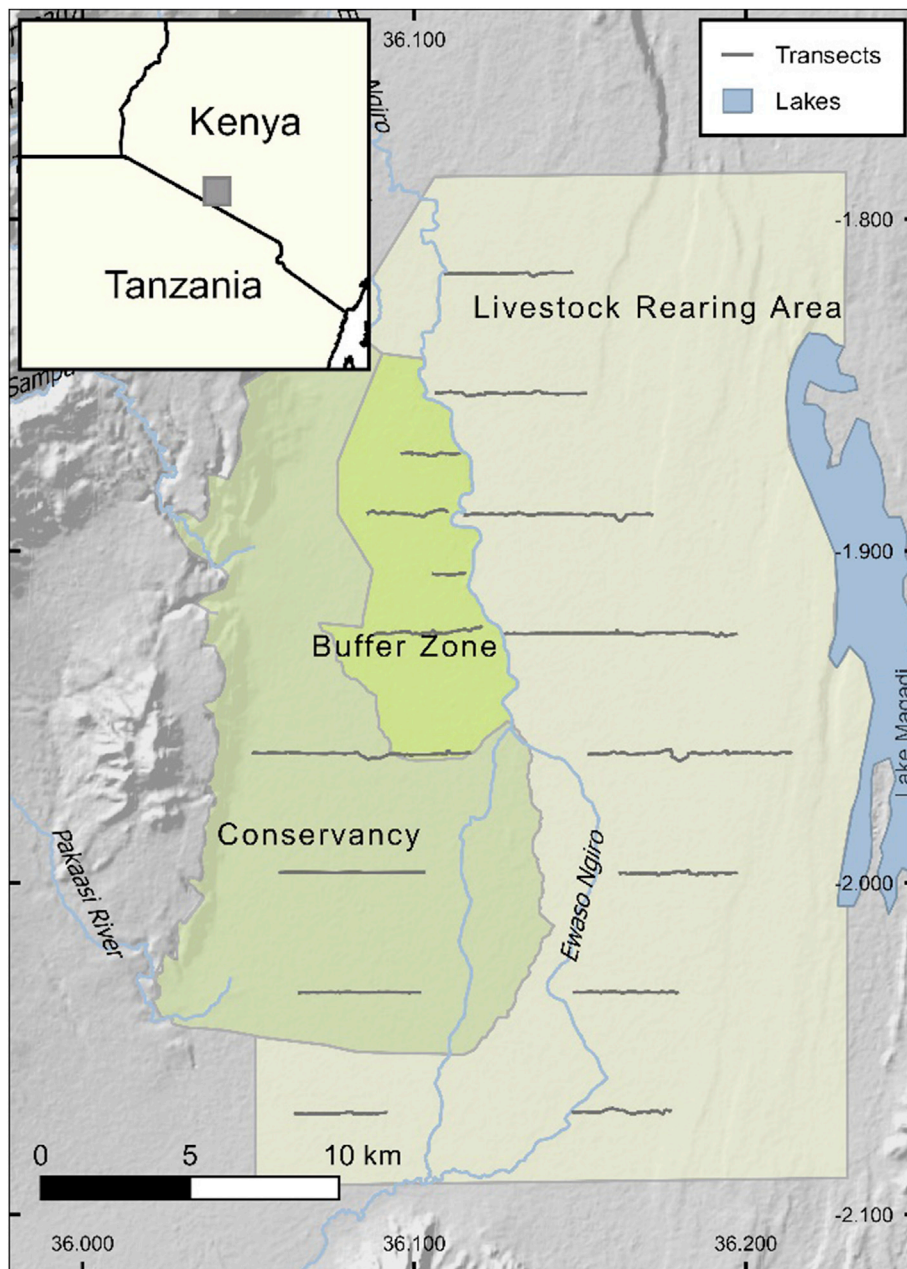
**Fig. 1.** The study area within the South Rift, Kenya. Three different landuse zones are marked: Conservancy, a seasonally grazed grass bank, with no permanent settlement allowed; Buffer Zone, area of seasonal settlement; and Livestock Rearing Area, the main wet season grazing area. The Ewaso Nyiro is the main North–South river, and splits forming the Shompole Swamp. The inset shows the location of the study site within Kenya (grey box).

were sampled both at day (Between 06:30 and 18:30) and night (after 19:30). To account for the variation in detection distance between day and night, multiple covariate distance sampling was also used (MCDS) for wildlife species, with day or night as a two-level covariate. This accounts for changes in detection functions based on the sampling covariates, which increases model precision (Marques et al., 2007; Thomas et al., 2010). Two MDCS models were tested: half-normal key, and hazard rate key. This produced five candidate models for each wildlife species − three CDS and two MCDS models. Livestock species were not sampled during the night, as they are protected in fenced enclosures to prevent predation.

Low number of detections (<60) of cattle during the drought meant that a global detection function was fitted to all the cattle observation data, covering all seasons (Buckland et al., 2001). To account for potential changes in detection across seasons, MCDS analysis using season as a covariate was also performed for cattle.

The model fit for all species was examined by visual observation of histograms, quantile–quantile plots, and using the statistical tests provided: $\chi^2$ 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 (Buckland et al., 2015).

### 2.4.2. GAM fitting

Each transect was divided into smaller segments each 1 km long and wide (78 total), which is equal to sum of the truncation distance on either side of the transect (Miller et al., 2013). The length of some segments at the end of transects was shorter than this, but the width was always 1 km. Each observation was assigned to a segment and season, and the effort per segment per season was calculated. Abundance per segment was then calculated for each species and season using the distance sampling estimates:

$$\widehat{N_j} = \sum_{r=1}^{R_j} \frac{S_{jr}}{\widehat{p}(Z_{rj})}.$$

where $R_j$ is the number observations in segment j and $S_{jr}$ is the size of the r$^{\text{th}}$ cluster in segment j. The probability of detection is a function of the object level covariates $\widehat{p}(Z_{rj})$.

The following model is then fitted for each season–species combination. With $A_j$ representing the area of the segment,

$$\mathrm{E}\left(\widehat{N_j}\right) = A_j \exp\left[\beta_0 + \sum_k f_k\left(z_{jk}\right)\right],$$

The distribution of $\widehat{N_j}$ can be modelled as an overdispersed Poisson, negative binomial or Tweedie distribution, where the $f_k's$ are smooth functions of the covariates and $\beta_0$ is an intercept term.

Several factors are known to influence the distribution of both livestock and wildlife: water availability; forage quality; forage quantity; predation risk; and human disturbance (Holdo et al., 2009; Mose et al., 2013; Redfern et al., 2003; Schuette et al., 2016; Turner and Hiernaux, 2002). While the influence of these factors on each species will vary depending on the species feeding guild, gut morphology, water dependence, predation susceptibility, and allometric scaling laws (Fryxell et al., 2005; Illius and Gordon, 1992; Smit, 2011). The following covariates were used in the modelling process (Table 1 and Fig. S1) and were prepared using QGIS (QGIS Development Team, 2015): Normalized Difference Vegetation Index (NDVI); Normalized Difference Vegetation Index coefficient of variation (NDVI - CV); Distance to Boma (Settlement); and Distance to Water. The preparation of the variables and their justification for inclusion is outlined in Table 1. Other variables were considered but either lacked the spatial resolution required or showed collinearity with other variables.

The geographic coordinates (in meters) were used as a bivariate covariate in this model, which often produces better fitting models, because it can account for changes in abundance not captured by the other covariates (Miller et al., 2013).

**Table 1**
Spatial variables used during the model selection and prediction process.

| Variable | Source | Processing | Justification |
|---|---|---|---|
| Normalized Difference Vegetation Index (NDVI) | MODIS 250 m 16 Day composites. https://lpdaac.usgs.gov/ | Images which fell in the survey months were used to create average NDVI for each seasonal period. Dry months 13 images; drought months 17 images; and wet months 8 images. | NDVI is related to grass greenness and biomass (Western et al., 2015a). Grass greenness is indicative of grass quality (Mose et al., 2013) |
| Normalized Difference Vegetation Index coefficient of variation (NDVI - CV) | MODIS 250 m 16 Day composites. https://lpdaac.usgs.gov/ | Coefficient of variation (CV) of all images across the period (69) was calculated. | Larger CVs indicate productive grasslands, while lower CVs indicate stable patches of woodland and bushland.(Harihar et al., 2014). |
| Distance to Boma (Settlement) | Field data collection | Data collected on settlement patterns between 2008 and 2015. We calculated Euclidean distances to settlement for the drought and dry, and wet months. | Both wildlife and livestock abundance are influenced by settlement. (Butt, 2010; Turner and Hiernaux, 2002) |
| Distance to Water | Field data collection | Calculated from two different layers. First, major rivers were mapped using Google Earth. Second, distance to both artificial and natural water resources was collected across several seasons. We then calculated Euclidean distances from water across the study area for the drought and dry, and wet months. | Distance from water has been shown to influence both livestock and wildlife abundance (Western, 1982) |

Smooth terms for the variables in Table 1 were modelled using thin plate regression splines (Wood, 2003). Smoothing parameter selection was performed via Restricted Maximum Likelihood (REML; Wood, 2011). Most species showed large edge effects due to the east to west gradient in livestock and wildlife abundances, Duchon splines were used for the smoothers of the geographic coordinates to alleviate this problem (Miller et al., 2013). The univariate smooths of all covariates and the bivariate smooth of geographic location were included in a base model. Before covariate selection, for each GAM, the residual plots of overdispersed Poisson, negative binomial and Tweedie distribution were compared and the best fitting model was selected. Covariate selection then proceeded using p-values to select significant smooth terms (Wood, 2006).

### 2.4.3. Prediction

After GAM fitting, we predicted abundance across the study area (602.88 km$^2$) on a grid of 3768, 0.16 km$^2$ cells, bounded by the impassable Nguruman Escarpment to the west; and Lake Magadi to the east. The rest of the boundary was limited to being a maximum of 4 km from the edge of the transects, and two areas near dense human settlement were removed. Variance estimates used a Bayesian interpretation of the GAM, and combined GAM variance with the detection function variance using the delta method (Wood, 2006).

## 3. Results

### 3.1. Detection functions results

In total, 41 species were detected on line transects. Five of our focal species had sufficient detections to fit seasonal detection functions for each seasons (Buckland et al., 2001). Cattle did not have sufficient detections to fit seasonal detection functions, so we used all detections to fit the model. All wildlife species used MCDS models, with the day−night variable incorporated into the detection function. All detection functions fitted the data well, with coefficient of variations between 3% and 11% (Fig. S2). Cattle used a global half normal detection function without covariates.

### 3.2. Density surface model

The DSMs are shown in Tables 2 and 3. Most DSMs used the Tweedie distribution which was deemed to fit the data best after observations of residual plots, although both the negative binomial and quassi-poisson distribution were used. The univariate smooth terms for each DSM are displayed in Fig. 3, and the predicted abundances are displayed in Fig. 2. Deviance explained from the models varied from 15% to 88%, while the coefficient of variation for the population estimates varied from 13% to 70%. Coefficient of variation plots for abundance estimates are show in Fig. S4, 5&6.

### 3.2.1. Grazers

The two wildlife grazers, wildebeest and zebra, show changes in spatial abundance across the seasons. In the wet season zebra and wildebeest are found at higher abundances at intermediate levels of NDVI (Table 2; Fig. 2), and are dispersed across the ecosystem. Wildebeest distribution during the dry season peaks at intermediate NDVI (Table 2; Fig. 2), while zebra abundance was unrelated to NDVI and was highest in the grass bank (Fig. 2; Table 2). In the drought, concentration of both species increased, and only the bivariate smooth was significant (Table 2).

### 3.2.2. Browsers

The two-browser species, Grant's gazelle and impala, also show changes in spatial abundance across the seasons. Across all seasons, Grant's show a tight relationship with NDVI (Fig. 2; Table 2), and are spread widely across the ecosystem. In the wet season, impala are dispersed across the landscape and abundance is related closely to NDVI -CV (Fig. 2; Table 2). During dry months impala abundance is highest in areas of intermediate NDVI − CV and higher NDVI (Fig. 2; Table 2), which are areas of thicker bushland. During the drought, the strongest predictor of impala abundance is distance to water (Table 2).

### 3.2.3. Livestock

During the wet season, livestock abundance for both shoats and cattle is predicted only using the spatial term, with highest abundance to the east of the river, in the livestock rearing zone. During the dry season shoats' abundance is patchy and close to settlements (Table 3 Fig. 3), and during drought the highest abundance is closest to water, and in areas of lowest NDVI-CV (Table 3, Figs. 2 and 3). In the dry, cattle are found at highest abundance in low NDVI areas, close to water (Table 3, Figs. 2 and 3), and move to the west of the river during the drought (Fig. 2).

## 4. Discussion

Density surface models of abundance have been used to display the changes in spatial abundance across three seasons, as defined by pasture conditions, for several key species in a community conserved rangeland in southern Kenyan. The results suggest that there are broad scale seasonal changes in wildlife and livestock distribution across the ecosystem, with both groups expanding out of the conservation areas during the wet season, and retreating towards them during dry and drought months.

**Table 2**

—Showing all wildlife DSMs. For each DSM, the detection model selected (hn — half-normal, hz — hazard-rate, dn — day/night covariate in an MCDS analysis), the coefficient of variation of the detection model, and the number of detections are shown. The significant smooth terms, with the estimated degrees of freedom are also presented, along with the significance of the relationship. ***p < 0.001, * *p < 0.01, *p < 0.05,.p < 0.1. Landscape abundance with standard errors are presented.

| | Burchell's Zebra | | | Wildebeest | | | Grant's Gazelle | | | Impala | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Wet | Dry | Drought | Wet | Dry | Drought | Wet | Dry | Drought | Wet | Dry | Drought |
| Detection Model | hn.dn | hr.dn | hn.dn | hn.dn | hr.dn | hn.dn | hn.dn | hr.dn | hr.dn | hn.dn | hr.dn | hn.dn |
| Detection CV | 5% | 4% | 6% | 7% | 4% | 11% | 4% | 3% | 3% | 9% | 10% | 10% |
| Observations | 277 | 414 | 250 | 170 | 415 | 126 | 297 | 712 | 912 | 74 | 109 | 78 |
| Response | Tweedie (p = 1.476) | Tweedie (p = 1.476) | Tweedie (p = 1.482) | Tweedie (p = 1.425) | Tweedie (p = 1.553) | Negative Binomial (0.182) | Tweedie (p = 1.494) | quasipoisson | Tweedie (p = 1.448) | Tweedie (p = 1.402) | quasipoisson | Tweedie (p = 1.409) |
| s(x,y) | 9.11*** | 12.94*** | 15.93*** | 13.44*** | 6.50*** | 14.26*** | 0.41 | 2.61** | 0.78 | 2.16. | 11.35*** | 2.34. |
| s(NDVI) | 2.58 ** | | | 2.68*** | 2.27* | | 2.42*** | 2.96*** | 2.79*** | | 4.43*** | |
| s(NDVI-CV) | | | | | | | | | | 2.53** | 2.31*** | |
| s(Distance to Water) | | | | | 0.80* | | | | | | | 1.06*** |
| s(Distance to Boma) | | | | | | | | | | | | |
| Deviance explained (%) | 49% | 74% | 74% | 61% | 48% | 74% | 20% | 42% | 37% | 23% | 88% | 56% |
| GAM CV | 18% | 12% | 22% | 24% | 19% | 69% | 16% | 29% | 40% | 23% | 45% | 33% |
| Total CV | 19% | 13% | 23% | 25% | 19% | 70% | 16% | 29% | 40% | 25% | 46% | 35% |
| Abundance ± SE | 4748 ± 859 | 4943 ± 604 | 2097 ± 461 | 1408 ± 340 | 1917 ± 366 | 1186 ± 822 | 2978 ± 465 | 3900 ± 1126 | 4394 ± 1752 | 1935 ± 451 | 861 ± 389 | 815 ± 273 |

**Table 3**

Showing all livestock DSMs. For each DSM, the detection model selected (hn − half-normal, hz − hazard-rate, dn − day/night covariate in an MCDS analysis, global − a global pooled detection function, which was fitted to cattle data only after inspecting the fit of a MCDS model for season), the coefficient of variation of the detection model, and the number of detections are shown. The significant smooth terms, with the estimated degrees of freedom are also presented, along with the significance of the relationship. \*\*\*p < 0.001, \* \*p < 0.01, \*p < 0.05, . p < 0.1. GAM coefficient of variation, and total DSM variation are presented. Landscape abundance with standard errors are presented.

| | Shoats | | | Cattle | | |
|---|---|---|---|---|---|---|
| Season | Wet | Dry | Drought | Wet | Dry | Drought |
| Detection Model | hr | hr | hn | hn.global | hn.global | hn.global |
| Detection CV | 11% | 8% | 10% | 7% | 7% | 7% |
| Observations | 114 | 267 | 243 | 54 | 104 | 29 |
| Response | Tweedie(p = 1.315) | Tweedie(p = 1.348) | quasipoisson | Tweedie(p = 1.503) | Tweedie(p = 1.436) | Tweedie(p = 1.621) |
| s(x,y) | 9.94\*\*\* | 7.54\*\*\* | 3.92\*\*\* | 8.14\*\*\* | 3.92\*\*\* | 3.07\* |
| s(NDVI) | | | | | 1.00\* | |
| s(NDVI-CV) | | | 0.86\* | | | |
| s(Distance to Water) | | | 0.99\*\* | | 0.92\*\* | |
| s(Distance to Boma) | | 0.96\*\* | | | | |
| Deviance explained (%) | 61% | 43% | 42% | 41% | 15% | 21% |
| GAM CV | 30% | 17% | 14% | 40% | 22% | 44% |
| Total CV | 32% | 18% | 17% | 41% | 23% | 44% |
| Abundance ± SE | 34567 ± 10351 | 30751 ± 5139 | 26420 ± 3598 | 7783 ± 3129 | 4243 ± 927 | 831 ± 362 |

## 4.1. Abundance estimates

This is the first attempt to produce spatially explicit abundance estimates for wildlife and livestock within the South Rift, and as demonstrated from previous work (Table S4), livestock and wildlife densities are high within this area. Although this technique has been widely used to estimate populations of marine mammals (e.g. Mannocci et al., 2015) and seabirds (e.g Winiarski et al., 2014) this new technique has not been used widely for terrestrial fauna (Harihar et al., 2014). Unlike most surveys of large ungulates in African savannahs this technique accounts for detection probability of the species of interest, and uses a spatially explicit model to estimate abundance in relation to environmental variables (e.g Ogutu et al., 2016; Western et al., 2009a). In addition, this process also creates a fine -scale surface of population abundance across a landscape at the resolution of the spatial covariates. With an increase in attention on wildlife and ecological monitoring within the East African rangelands, and particularly within community conserved areas, this could prove a useful tool for abundance estimates for wildlife managers and communities. In addition, spatial abundance data is required to make better conservation decisions for wildlife, and as proved by our example DSMs can provide simple accurate information for conservation managers on wildlife abundance, displayed through easy-to-interpret maps and graphics.

## 4.2. Seasonal changes in species abundances

The DSMs produced show clear seasonal variation in spatial abundance for all species in the study area. Season has been defined by available pasture biomass and greenness, with decreasing available biomass and greenness from wet to dry to drought (Russell et al., submitted). Grass greenness is positively correlated with quality (van Beest et al., 2010). So, low biomass, high quality grasses are available in the wet season. As regional biomass decreases into the drought, the only remaining areas of grazing are high biomass, low quality areas (Russell et al., submitted).

### 4.2.1. Grazers

In this area movement is driven by the heterogeneity of pasture quality and quantity, with the conservation area having consistently higher grass biomass and height across all seasons, acting as dry season grass bank for livestock (Russell et al., submitted). When there is a large amount of green biomass, as found in the wet season, NDVI is largely accurate in predicting the available grass biomass (Western et al., 2015a,b). During the wet season, high abundance of both grazing species at intermediate NDVI suggest that they are utilizing areas of intermediate grass biomass, closer to human settlement. Wildlife grazers will select for these lower biomass, green areas of pasture because it is often of higher quality (Mose et al., 2013; van Beest et al., 2010), with higher crude protein content in these more intensively grazed areas (Anderson et al., 2010). In addition, these short grassland areas have reduced predation risk, due to greater predator visibility (Hopcraft et al., 2012).

As regional grass biomass decreases, into the dry season, wildebeest and zebra both concentrate (Fig. 2), but have different patterns of spatial abundance. Wildebeest target greener, low biomass areas outside of the grass bank, while zebra are found within the grass bank. The differences in areas utilized is explained primarily by differences in gut morphology. Zebra, a larger, non-ruminating grazer, can graze on lower quality grazing than wildebeest, but must obtain a higher daily food intake to be able to match their metabolic requirements (Bell, 1971; Illius and Gordon, 1992). Zebra tend to utilize taller, higher biomass pasture, while wildebeest utilize the shorter greener pasture, which is of higher quality but closer to settlement (Russell et al., submitted). This matches other research in East Africa, indicating that wildebeest movements are more influenced by grass greenness and quality than grass biomass (Holdo et al., 2009; Mose et al., 2013). In addition, the higher susceptibility of wildebeest to predation than zebra, although small, could encourage wildebeest to graze in these areas of
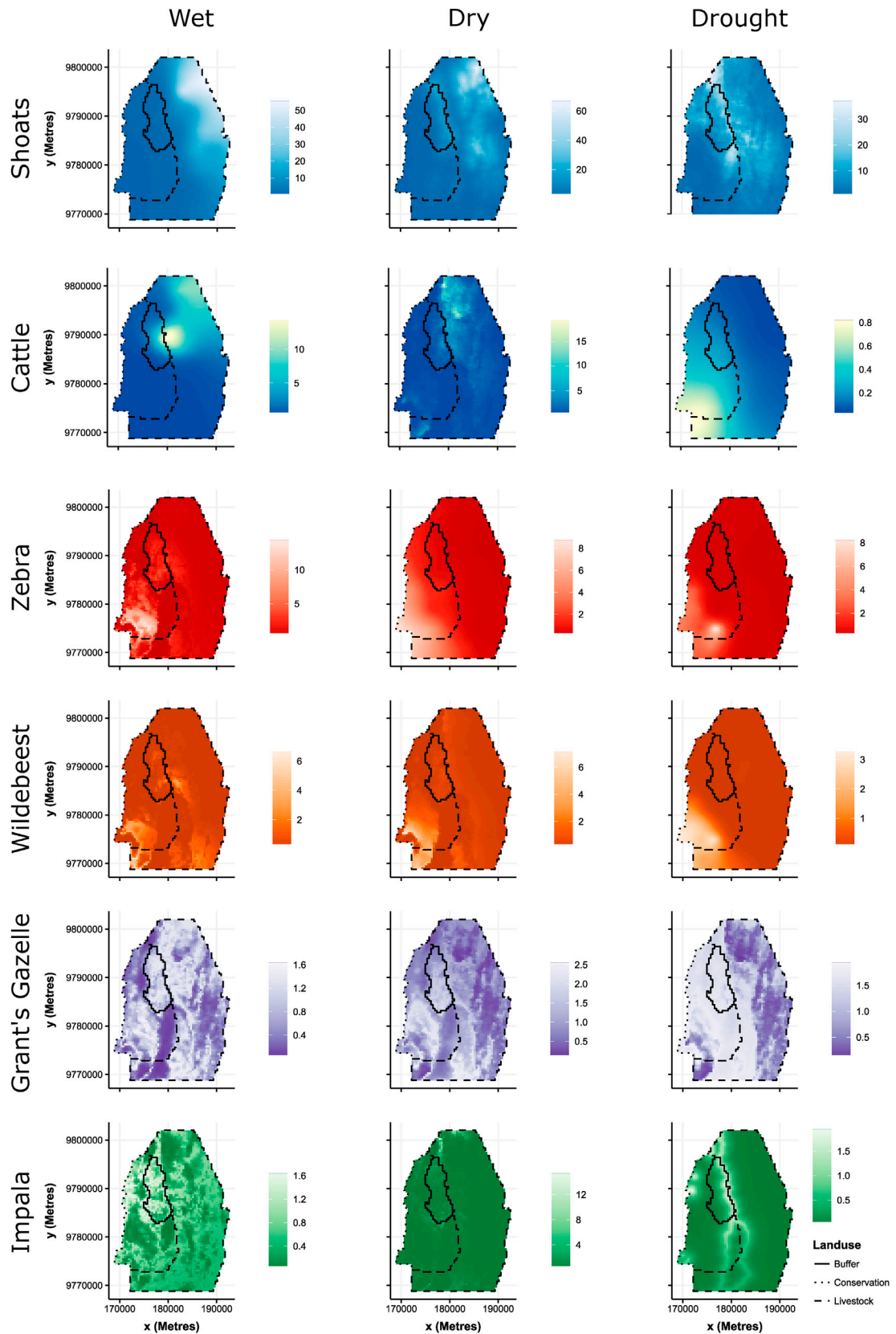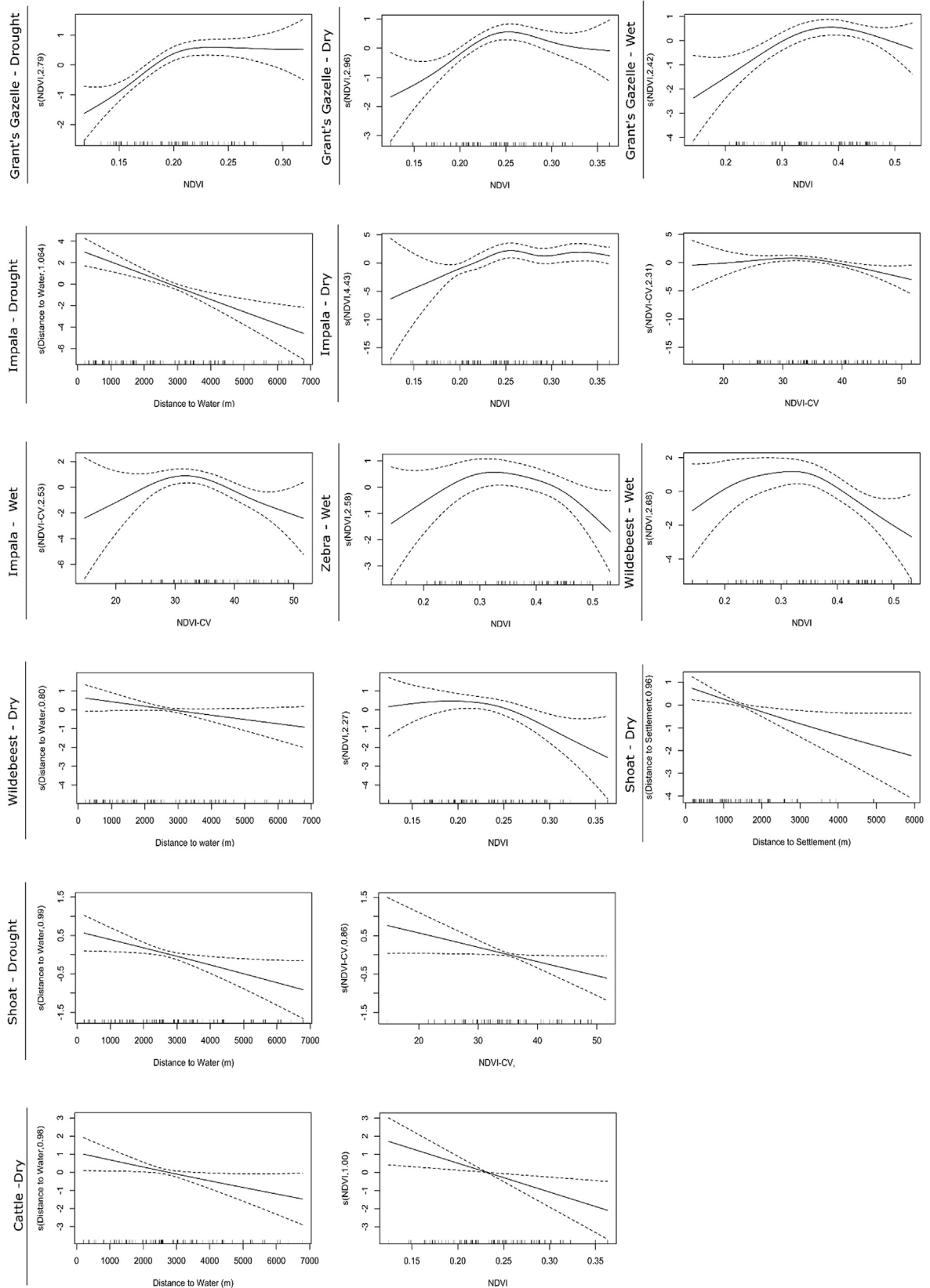
**Fig. 2.** Abundance estimates for all species during all months predicted across a 0.16 km² grid.

**Fig. 3.** Generalized additive model response curves (solid lines) with 95% confidence intervals (dashed lines) presented for each of the covariates (except location) used in the final fitted models.

greater visibility (Sinclair et al., 2003), although previous work in this system suggests predation risk does not have a strong effect on the broad scale distribution of grazers (Schuette et al., 2016).

In periods of extremely low regional grass biomass (drought), both wildebeest and zebra are tightly concentrated in areas with the highest remaining biomass: seasonal swamps and high biomass grassland within the grass bank (conservation area; Fig. 2). They are reliant on poor quality grazing during times of regional biomass deficit to simply meet their minimal metabolic requirements, despite the potential increased risk of predation within the conservation areas (Schuette et al., 2016).

### 4.2.2. Browsers

Impala and Grant's gazelle's are mixed feeders with their diet split between browse and graze (Mcnaughton and Georgiadis, 1986). During the wet season, Grant's are present in intermediate biomass area, avoiding areas of thick bush and forest (Fig. 2), but as regional grass biomass decreases the predicted abundance indicates movement of Grant's into denser thickets with areas of higher browse and graze biomass (Fig. 2). This ability to mix feed and utilize browse is highlighted by the constant spread of Grant's across the ecosystem, unlike the grazing species they do not contract into areas of high pasture biomass.

Impala are widely spread during the wet season (Fig. 2), and utilise both bushland and grassland, which have a mix of short pasture and fresh browse. As grass quality decreases they shift into areas of thicker bushland. In dry months, and continuing into the drought, impalas shift to thick vegetation for a browse based diet, and closer to bodies of water (Fig. 2; Augustine and Mcnaughton, 2004).

### 4.2.3. Livestock

During the wet season, livestock moves into the livestock rearing zones, outside the conservation area, under direction of the grazing committees, which dictate patterns of settlement and grazing areas. Herders themselves are targeting areas of short nutritious grasses, which in this case are spatially distinct from areas utilized by wildlife (Western, 1982, Fig. 2). As biomass decreases, areas of cattle utilization are allowed to spread across the landscape, targeting areas of remaining high-quality grazing (Fig. 2). In the drought, cattle move into the conservancy to utilize the only remaining pasture (Russell et al., submitted). During this period, cattle populations across the landscape were low (831 ± 362), as many herders grazed their cattle outside of the ecosystem during prolonged droughts. It must be noted that most of the cattle DSMs explained only a small amount of the deviance (15%–41%). Spatial variables alone do not account for the variability in foraging strategies of cattle herds, which are decided by individual herd owners and grazing committees, with areas exploited for a variety of reasons not necessarily captured with the simple spatial variables (Butt, 2010).

Like cattle, the movement of the shoats into the livestock rearing areas is evident, with herders targeting areas of new grass growth during the wet season (Fig. 2). Shoats then begin to spread over the ecosystem in the dry season, until the drought, where shoats abundance is highest in thicker areas of bush and tree cover − with high browse availability (Fig. 2). This represents a shift in diet through the seasons, with herders targeting pasture during the wet season, but with a shift towards browse based diets during the drought.

### 4.3. Coexistence

Unlike much of the Kenyan rangelands, this area has high forage and habitat heterogeneity with different grazing resources available through the seasons (Russell et al., submitted). In other areas subdivision, sedenterisation, compression, and
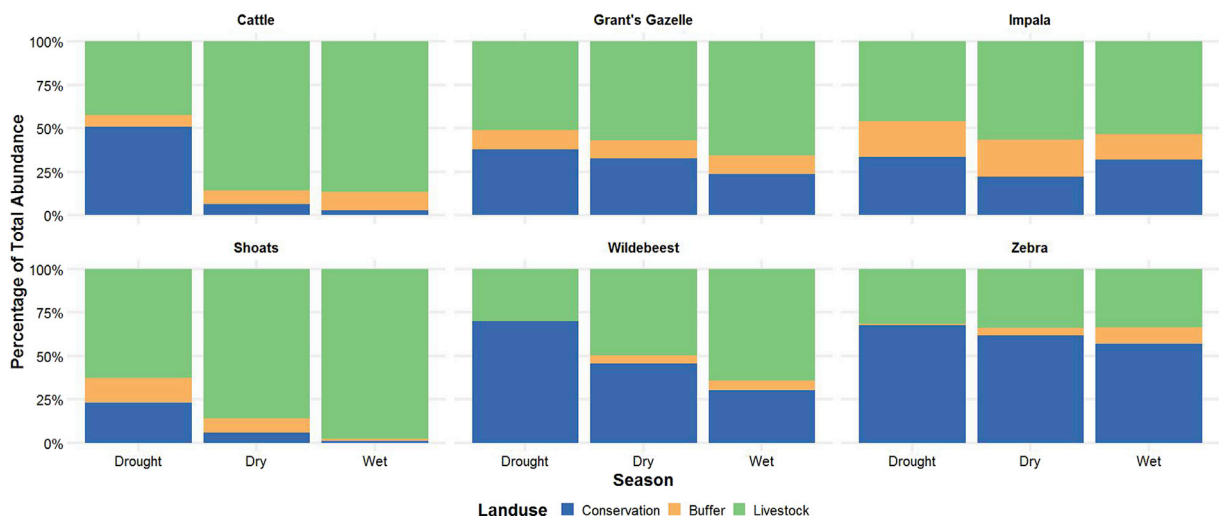


**Fig. 4.** Percentage of total predicted abundance for each DSM within the different land-use areas.

land conversion have negatively impacted grazing resources, and subsequently have negatively impacted both wildlife and livestock (Groom and Western, 2013; Hobbs et al., 2008; Western et al., 2009a). Even in the remaining intact community areas, rangelands have become highly degraded and have suffered losses in productivity (Glew, 2010). Whether subdivided or not, the loss of traditional grazing management has become widespread, and with it the loss of spatial and temporal variations in forage quality and quantity. Within this study area the two communities tightly manage grazing patterns to maximize energy gains for livestock. By removing livestock from the conservation areas during the wet season (Fig. 2), they benefit from the utilization of nutritious grasses in the livestock rearing zone and preserve forage within the conservation area which acts as a grass bank during the drought (Russell et al., submitted). This is important for survival of livestock, and theoretically allows for much higher stocking rates than a homogenous system (Ash et al., 2004; Illius and O'Connor, 2000). Although these management decisions are made with livestock in mind, these decisions maintain a heterogenous landscape which ensures that wildlife can follow their natural metabolic gradients through the varied resource base, and maintain large populations (Fynn et al., 2016; Illius and O'Connor, 2000: Fig 6). Wildlife grazers, in particular, benefit from the preservation of grass within the conservation area, which sustains a large percentage of the zebra and wildebeest populations during the dry and drought seasons (Fig. 4). In addition, many of the wildlife species also target areas of short high-quality grass during the wet season, which has been created near settlements (Russell et al., submitted), pulling them out from the conservation areas (Fig. 4). While we focus on the impact of management on just four wild herbivore species, other studies have also linked this semi-nomadic management in this ecosystem to coexistence with large carnivores (Schuette et al., 2016, 2013) and elephants (Ahlering et al., 2012).

While many studies attribute increased livestock numbers with a decline in wildlife (Ogutu et al., 2016), planned management of the rangelands can ensure that competition is minimized. Competition between wild and domestic herbivores is generally the largest at times of resource scarcity, but facilitation can occur during the wet season (Odadi et al., 2011). In this system, during the wet and dry seasons, competition between livestock and wildlife, especially grazers, is potentially minimized through pastoralists exploitation of the heterogonous landscape, with spatial management of livestock targeting areas of short nutritious grasses within the livestock rearing zone, resulting in areas of distinct use compared to wild herbivores (Fig. 2). This spatial management of livestock may also facilitate coexistence with wild herbivores by providing them access to areas of short nutritious grasses, on the edge of the livestock rearing zone and buffer during wet months. However, in the drought, space utilization is similar especially for wildlife grazers and cattle, which suggest that during this time there may be increased competition (Odadi et al., 2011). Yet even during these periods of incredibly low resource availability, small scale heterogeneity in the resource base could allow for small scale spatial separation between species of similar diets (Russell et al., submitted; Fig. 2), which could facilitate a reduction in competition. During this period coexistence between wildlife and livestock may also be facilitated by the diurnal corralling of livestock, allowing for wildlife to access key resources such as water and forage overnight, despite the influence of human settlement. Although competition may appear to be minimized, changes in stocking densities, management practices, or longer periods of resource scarcity could potentially increase competition across all seasons (Bhola et al., 2012; Fynn et al., 2016). Future adaptive management will be critical to promoting longer term coexistence between wild herbivores and livestock.

In Kenya, conservation outside of government protected areas has long been focused on incentives from tourism funded community based conservancies (Western et al., 2015b). A complementary mechanism, displayed by our example here, is the maintenance of good grazing management, and forage resource heterogeneity, both temporally and spatially, as a tool for both livestock production and subsequently indirect conservation of wildlife. Community based conservation initiatives which plan around the principles of livestock and grazing management, to maintain and exploit resource heterogeneity, could facilitate wildlife-livestock coexistence by providing critical resource space for wildlife (Fynn et al., 2016).

### 4.4. Conclusions

We advocate for more conservation planning initiatives in pastoral lands, including community conservation areas, to be focused around livestock grazing and production systems, which should encourage the maintenance of open rangelands with heterogonous resource distribution, without the demand for financial returns for wildlife protection (Berkes, 2004). This planning needs to occur at multiple scales. Planning just within a conservation area may be effective, but during periods of regional biomass deficits, heterogeneity of rangelands outside of conservancies, across divisional and international boundaries becomes important for not only livestock, but also wildlife.

## 5. Author contributions statement

SR, PT, and DW conceived the ideas and designed methodology; SR collected the data; PT analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.gecco.2017.08.006.

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