

ESTIMATING WILDLIFE AND LIVESTOCK INTENSITY: INDICATIONS OF COMPETITION IN AN EAST AFRICAN PROTECTED AREA

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I. INTRODUCTION

Research on the nature of wildlife-livestock interactions in East Africa has focused primarily on the level of competition that exists between wild and domestic ungulate species. Habitat and dietary overlap are historically the most commonly cited mechanisms of competition; however, various authors have proffered mutually exclusive explanations of these mechanisms whereby both overlap and lack of overlap (displacement) are used as evidence of competition (Butt and Turner 2012). These conflicting results reduce the utility of the concept of competition when seeking to explain wildlife-livestock interactions. Recent research suggests that habitat and dietary overlap are insufficient to prove competition, and that in real-world situations it is more likely external factors such as drought and habitat loss that have a greater impact on the fitness of these species (Butt and Turner 2012; Homewood et al 2001; Thompson and Homewood 2004; Serneels, Said, and Lambin 2001).

As livestock and wildlife both require large, contiguous rangeland habitats, pastoralism is considered more compatible with wildlife conservation than other land use patterns that fragment the landscape (Homewood and Brockington 1999; Homewood et al 2001; Western 1975). This is supported by research that finds integrated livestock-wildlife systems in East Africa are more productive than either livestock or wildlife systems alone (Western 1989; du Toit and Cumming 1999; Reid et al. 2002). Undergrazing of remote pastures can allow unpalatable plants to invade and decrease the overall diversity of vegetation available, as grazing animals are an important vector for the dispersal of annual grass seeds (Niamir-Fuller 1999; Woldu and Saleem 2000). However, most national and private protected areas exclude pastoralists from key resource areas in an attempt to preserve declining wildlife populations. Estimates place losses as high as 80% since the mid-1970s - both within and around protected areas (Homewood et al. 2001).

This discrepancy between policy and practice highlights the need for more research that explores interspecific grazing patterns, to inform relevant and accurate policy decisions regarding the integration of wildlife and livestock grazing areas in East Africa. The literature indicates that competition is primarily due to the exploitation of a shared, limited resource by one species (Butt

and Turner 2012; Odadi et al. 2011; Prins 2000). The sporadic rainfall patterns and soil properties of these arid and semi-arid rangelands affect the viability and spatial distribution of grazing grounds for both livestock and wildlife, yet the geographies of these species remain largely unexplored at fine spatial and temporal scales. This study aims to advance our understanding of when and where livestock and wildlife might be compatible.

Specifically, I describe the clustering patterns of wildlife and livestock, using my understanding of the system to help explain those patterns. I also demonstrate through point pattern analysis the effect of the spatial density of livestock on the presence of wildlife, which is commonly believed to be deleterious by wildlife resource managers in East Africa.

II. METHODOLOGY

Study Site

The Olare Motorogi Conservancy (OMC) (Figure 1) was chosen as a case study to examine the interactions of wildlife and livestock in an East African protected area. The OMC shares a border with the Maasai Mara National Reserve in southwestern Kenya. This region contains some of the highest densities of wildlife in Africa (Waithaka 2004), and the annual wildebeest migration in late summer draws large numbers of tourists to the MMNR (Butt 2011). It is also representative of the broader trends in pastoralist relationships with PA due to the large number of pastoralists in the area (Butt 2011). Rainfall is bi-modal, with a long dry season occurring between June and September, short rains between October and December, and long rains between February and May (Lamprey and Reid 2004).

Data Collection

Data collection was carried out in two phases. The first phase involved the fieldwork collection of spatial and demographic data for twenty-six species, six of which are used in this analysis (Table 1). The second phase (post-fieldwork) included collecting and processing geospatial data. ArcMap 10.0 (2010) and ERDAS Imagine (2010) computer software was used in the data processing.

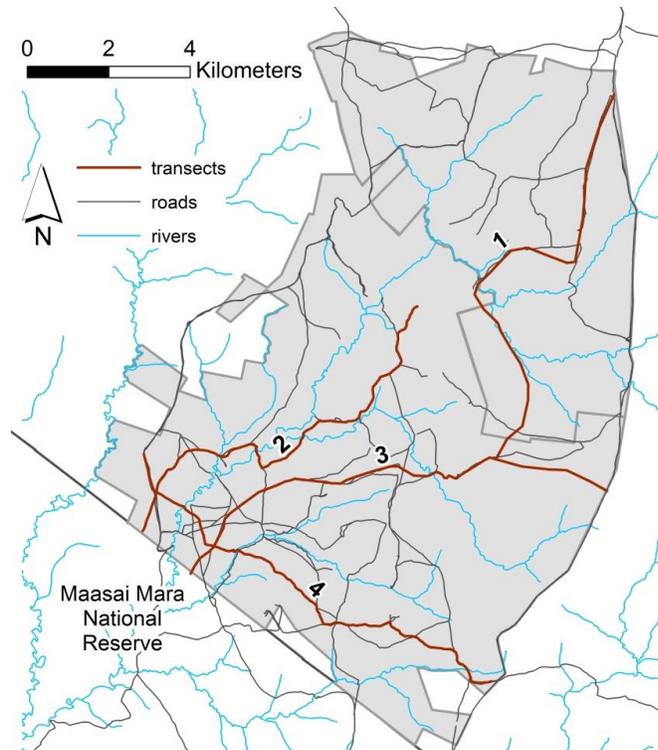


Figure 1. Olare Motorogi Conservancy with roads, rivers, and study transects labeled.

Species Recorded	Number Sightings		Total Counts	
	1	2	1	2
domestic cattle (<i>Bos primigenius</i>)	26	52	982	4,053
domestic sheep and goats (<i>Ovis aries</i> and <i>Capra aegagrus hircus</i>)	29	49	3,878	10,871
Thomson's gazelle (<i>Gazella rufifrons thomsoni</i>)	687	617	7,463	6,503
impala (<i>Aepyceros melampus</i>)	311	289	2,969	3,870
wildebeest (<i>Connochaetes taurinus albojubatus</i>)	445	440	20,217	13,333
Burchell's zebra (<i>Equus quagga boebei</i>)	175	193	4,035	2,208

Fieldwork

This study used four transects, each between 10.3 to 12.0 km long, chosen in collaboration with the OMC manager in order to maximize coverage of the conservancy (136.5 km²) while restricting movement to the most commonly traveled roads for tourist game drives (another aim of the study) (Figure 1). Each transect was run twice daily on a weekly basis, over the course of nine weeks (June 4 – August 6 2013), resulting in eighteen data collection sessions for each transect. Data on wildlife and livestock included vehicle GPS points, time of encounter, bearing, distance to animal, and counts. Bearing and distance were used to calculate a new X and Y field for each species seen at the GPS points, resulting in a map of actual species locations that fell within a 200m buffer of the transects. Four wild ungulate species are chosen for this analysis due to their high populations and theorized role of competition with either cattle (*Bos primigenius*) or shoats (sheep and goats - *Ovis aries* and *Capra aegagrus hircus*). These species are Thomson's gazelle (*Gazella rufifrons Thomsoni*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus albojubatus*), and zebra (*Equus quagga boehmi*). Presence points were aggregated across the field season to assess differences in morning (1) and afternoon (2) distributions of species (Table1).

Geospatial Data Collection and Processing

A 2011 digital elevation model (DEM) was downloaded from ASTER, and imported into ArcMap to generate the 'slope' and 'elevation' variables used in the analysis. NDVI data from 2009 at 250m resolution were downloaded from MODIS and averaged over the course of the dry season (which dominated our fieldwork) using ERDAS Imagine. Future iterations of this analysis will incorporate 2013 NDVI products, which are currently being processed.

Data Exploration

Visual Assessment

It is readily apparent from the point patterns that there is a tendency towards clustering for all species (Figure 2). It is also apparent that both livestock species were encountered less frequently than their wildlife counterparts. This is likely attributable to a number of factors, primarily the implementation of a "grazing ban" within the OMC during peak tourist season, which significantly limits the number of livestock allowed in to graze while also restricting their spatial distribution. There are also sampling biases in the fieldwork, which did not sample during midday or at night time

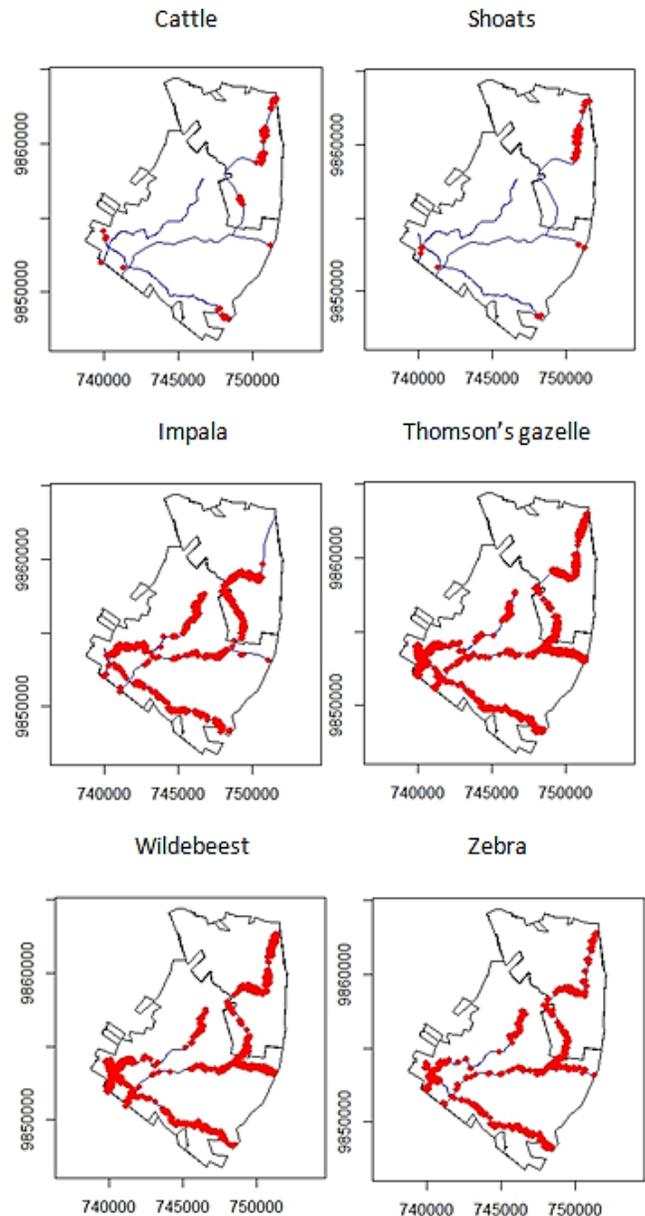


Figure 2. Plots of observed species presence locations, aggregated and representing both morning and afternoon across the entire fieldwork season

(common grazing times for livestock), and which only sampled roads that are heavily traveled by tourists (far from the allowed grazing zones). There is a dominant trend for livestock presence points to be located nearest the Maasai bomas (homesteads) in the northeast corner of the OMC.

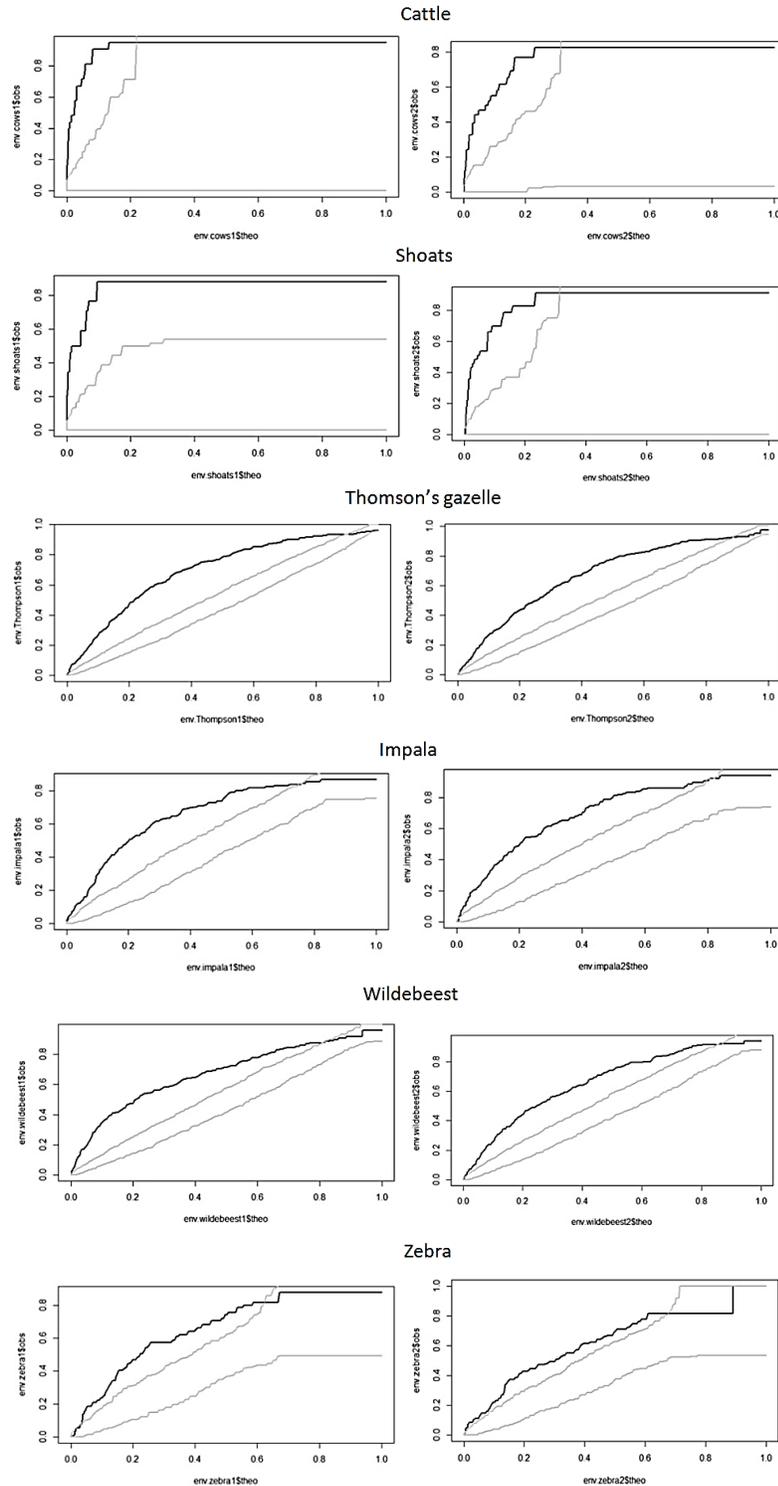


Figure 3. Black lines indicate G observed (y axis) and G theoretical (x axis), with 95% CI in grey. The left column represents the morning patterns and the right column represents the afternoon.

Complete Spatial Randomness

Point pattern analysis begins with a test for Complete Spatial Randomness (CSR) amongst the data points, which demonstrates whether an event has equal probability of occurring at any location in the study area. CSR also assume that all points are occurring independently of one another. I used the G-function to test the point pattern of each species for CSR, both in the morning and in the afternoon. The G function measures the distance from an arbitrary point to its nearest neighbor, testing whether those randomly chosen points have a neighbor within a specified distance.

The observed value of G can then be compared to the theoretical G function, which assumes a random distribution of points. When G observed is larger than the theoretical G, the point pattern is exhibiting clustering. All point patterns exhibited clustering in this analysis, for all species and all times of day, which is not unexpected in a highly heterogeneous environment.

To test that the results of the G function are accurate within a 95% confidence interval (CI), envelopes were created using 200 Monte Carlo simulations of a CSR point pattern within the study area. All observed G functions in this study fell outside the 95% CI demonstrated by the envelopes, indicating there is significant clustering in the system.

Analysis

In order to assess the impact that livestock presence is having on wildlife presence, I first modeled the livestock intensity non-parametrically over the sampled area (a 200m buffer of the transects), for each livestock species, morning and afternoon. I then used this output, along with NDVI and elevation, to parametrically model the wildlife intensity for each species, morning and afternoon. The significance of the livestock predictor variable is then evaluated as a measure of interspecific competition. All analysis was done in R (v.3.0.2, 2013) using the “spatstat” and “splancs” packages.

Estimating Livestock Intensity

A first description of the point pattern begins with estimating the spatial density (intensity) of the observed data pattern (Bivand et al. 2013). Here I assume an Inhomogeneous Poisson Process (IPP) for the data, which maintains independence of events while allowing for intensity to vary spatially according to the environmental conditions of the study area (Bivand et al. 2013).

In R, I used the quartic kernel function to estimate the intensity of each species of livestock first independently, and then aggregated, for morning and afternoon patterns. I applied a border correction to account for missing observations outside of my sampled area; the buffered transects create a polygon window with a large perimeter, and thus border corrections become an important consideration for this analysis. A 20km grid with 100m cells was defined over which to apply the kernel smoothing, and it too was bounded by the buffered transect polygon.

The selection of an appropriate bandwidth for this analysis was determined by finding the optimal mean squared error (mse) that was also supported by my understanding of the system. Using the mse, and a visual comparison of the resulting intensity maps, I determined a bandwidth of 1500m (1.5km). This is based on the fact that livestock herds can occupy large areas at any moment due to natural dispersion patterns, and their grazing movements can easily cover 1.5km in a matter of hours (the length of one sampling session).

Estimating Wildlife Intensity

I then used a parametric trend of three covariates (elevation, NDVI, and a livestock intensity variable) to estimate the intensity of the four wildlife species for both morning and afternoon point patterns. A stochastic point process model was fit by a Poisson process following a log-linear form, which can be expressed as

$$\text{logit}(\lambda_i) = \alpha_{(i)} + \beta_1 * \text{Livestock}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

where the intensity (λ) is modeled using a logit link, α represents the intercept, and β_* represents the regression coefficients for the independent variables. β_* were estimated by maximizing the likelihood of the point process, and a border correction was applied. Each livestock variable (cattle, shoats, and livestock combined) was used for each wildlife species in order to examine the individual and combined effects of these species.

III. RESULTS AND DISCUSSION

Livestock Intensity

Though difficult to see at this scale (Figure 4, Appendix A), one of the most obvious patterns that emerges from the livestock intensity grids is the expansion of livestock range in the afternoon as compared to the morning. In morning patterns intensity is focused entirely around the bomas in the

northeast corner of the OMC. Afternoon patterns have a lower level intensity emerging in the outer regions of the transects, which are known to correspond with large grassland habitat.

Wildlife Intensity

Coefficients of the covariates (β_i) are considered significant if the 95% Confidence Interval (CI) does not include 0. An evaluation of the relationship and significance of the variables for each species, for each time slot, provides a more nuanced understanding of the species distribution patterns across the OMC. Plots of intensity and SE are found in Appendix B. All model results (intercept, estimates, standard error (SE), and CI) are included in Appendix C.

Thomson's gazelle

All livestock and NDVI parameters were significant in the estimation of Thomson's gazelle intensity for both times of day. Livestock estimates were positive, and NDVI estimates were negative. Afternoon patterns of Thomson's gazelle have higher intensity than morning patterns (Figure 5). The highest estimates of intensity (and also the highest SE) are in the eastern central grasslands.

Impala

All livestock variables in the morning patterns were significant in the estimation of impala intensity. Elevation was also a significant variable in both livestock aggregated models, and for all afternoon patterns. NDVI was significant for all afternoon patterns. All livestock variables were positive, whether or not they were significant. All elevation estimates were also positive. NDVI estimates were uniformly positive for this species, which is unique for this analysis as all other species demonstrated a negative relationship with NDVI.

Patterns of impala intensity, though significantly related to livestock intensity for the morning hours, do not mimic the livestock intensity patterns (Figure 4, Appendix A) – though the SE for those models does (Figure 6). Lower intensities (green here) overlap with the large grassland areas, indicating that vegetation type might be a better estimator of impala intensity. Afternoon patterns of impala intensity are higher in areas of thicker vegetation cover, which in this environment corresponds to scrub or acacia forest. This is supported by the finding of a positive relationship with NDVI, as forest will have higher NDVI values than grasslands. In practice, impala are also generally found on steeper slopes than many other species, so the significance of elevation in estimating intensity is sound.

In general, impala intensity estimates range from $5e^{-6}$ to $4e^{-5}$, which is much smaller than estimates of intensity for wildebeest ($1e^{-5}$ to $5e^{-5}$) and Thomson's gazelle ($2e^{-5}$ to $1e^{-4}$). However, the 95% CI for these estimates all still overlap and so cannot be considered significantly different from each other.

Wildebeest

Wildebeest showed a similar pattern in variable significance and relationship as did Thomson's gazelle, with all livestock and NDVI variables significant for both time slots. Again, all livestock estimates were positive and all NDVI estimates were negative, indicating wildebeest and livestock tend to share the same spaces and that those spaces tend to be located in grassland vegetation types. Morning and afternoon wildebeest intensities show very similar patterns, with only a slight increase in intensity for the afternoon (Figure 7). All models show very small SE.

Zebra

Estimates of zebra intensity proved more complex than for other species; while the parameters followed similar relationships to the response as with Thomson's gazelle and wildebeest, only the NDVI estimates for the morning patterns were significant. Morning patterns of zebra intensity are

most similar to those exhibited by Thomson's gazelle, though it is worth noting that the maximum zebra intensity estimate is only as large as the minimum Thomson's intensity estimate ($2e^{-5}$).

IV. CONCLUSIONS

Research on wildlife and livestock interactions has tended to focus on the level of competition between wild and domestic ungulate species, with habitat and dietary overlap often the only mechanisms cited for this complex relationship. These studies are hindered by a lack of fine spatial and temporal data on interspecific grazing patterns, which is what this study aimed to provide for one private conservancy in southwestern Kenya. What this study finds is that wildebeest and Thomson's gazelle are more likely to be found in the same areas that livestock frequent for grazing. However, the estimation of competition as solely a function of spatial overlap is far too simplistic given the complexities of this system. Undoubtedly there are more significant variables influencing both livestock and wildlife intensities across this study area, which were not included in this analysis.

In an environment such as this, with highly heterogeneous resource distributions, it is unsurprising that all species showed a tendency to cluster, as evidenced by the G function plots above. However, the relative patterns of intensity for wildlife species did have some interesting differences. Perhaps most important is the similarity in pattern between Thomson's gazelle and zebra intensity in the morning hours. These species show very similar patterns of intensity (at different magnitudes), and yet zebra do not have a significant relationship with livestock intensity and gazelle do. This would indicate to me that NDVI is a much stronger indicator of these species' density distributions than is the influence of livestock.

Another important result of this analysis is the tendency for impala to avoid areas that other species gravitate towards, as evidenced by their intensity patterns and the overall positive relationship with NDVI when all other species were negatively correlated. Higher NDVI values are associated with more dense vegetation, such as scrub and acacia forest. The inclusion of a vegetation type variable in this analysis could result in a better estimation of impala intensity. Impala also demonstrated the only significant relationship to elevation amongst all the species in this analysis, further supporting my initial impression that this species does not follow the same grazing patterns as the others.

It is undeniably difficult to quantify competition, particularly amongst highly mobile species, yet their ability to make choices about their location does indicate that these species have the potential to co-exist (Ritchie 2002). More detailed analyses have used specific forage preferences to add further nuance to our understandings of competition when the species are exhibiting overlapping spatial patterns. While these studies have largely focused on highly controlled experiments and not real-world observation, they would still advance this analysis by allowing us to make inferences about how species are interacting when they are found in the same area. Further research into these findings would likely aid my interpretation of these results.

Finally, this analysis has stopped short of testing the second-order properties of these point patterns, which could be used to advance our understanding of the strength and type of interactions between points. The inhomogeneous K function is the next step in this analysis, as it will help describe the size of scope of the clustering and determine where residual clustering is occurring. Optimizing the models by removing insignificant variables, and introducing new ones, will further explain the variability in this complex and fascinating system.

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Appendix A: Livestock Intensity

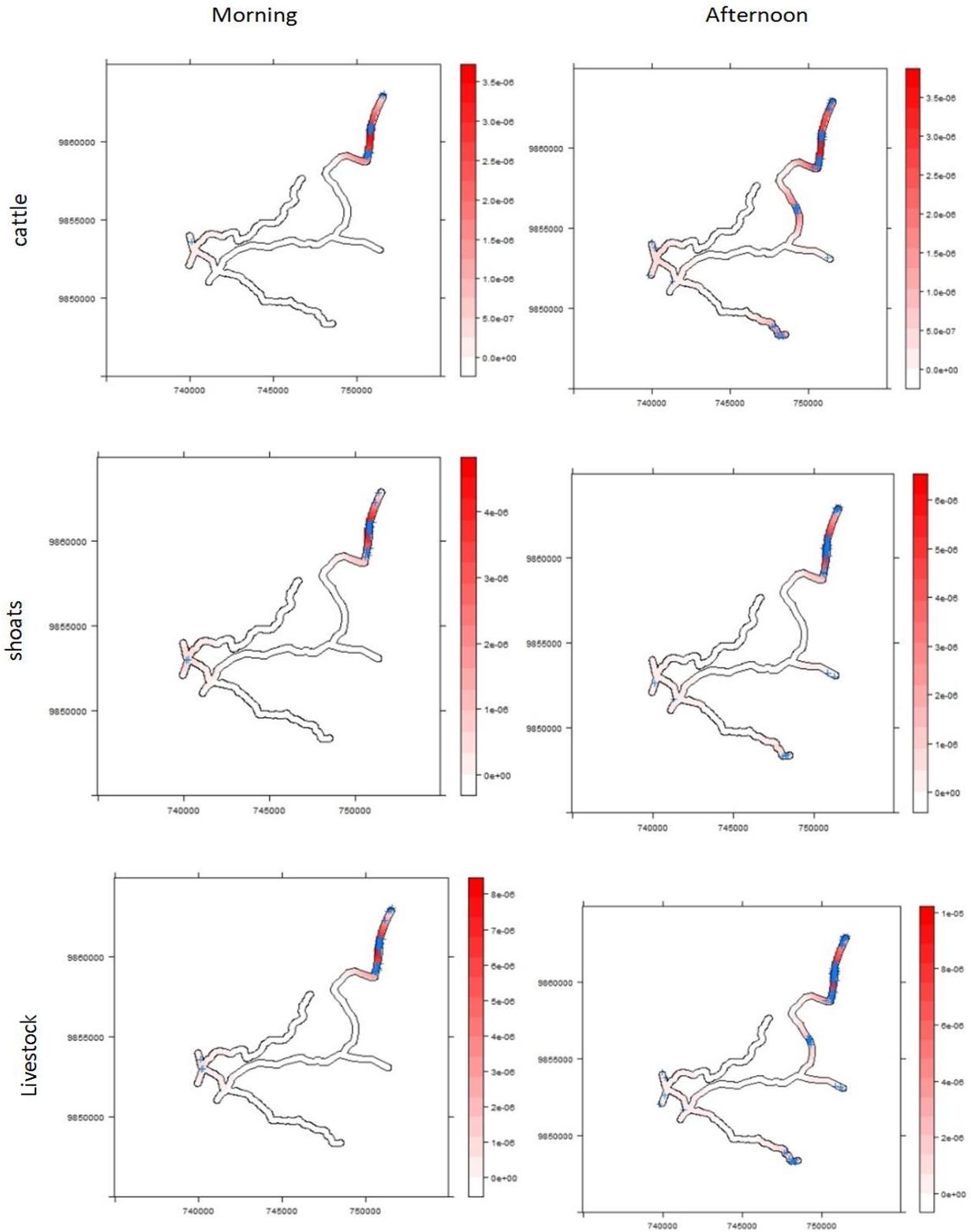


Figure 4. Estimated Intensity for livestock in the morning and afternoon, using a quartic kernel function with a bandwidth of 1500m and a border correction. Blue dots indicate presence points for the species.

Appendix B: Wildlife Intensity

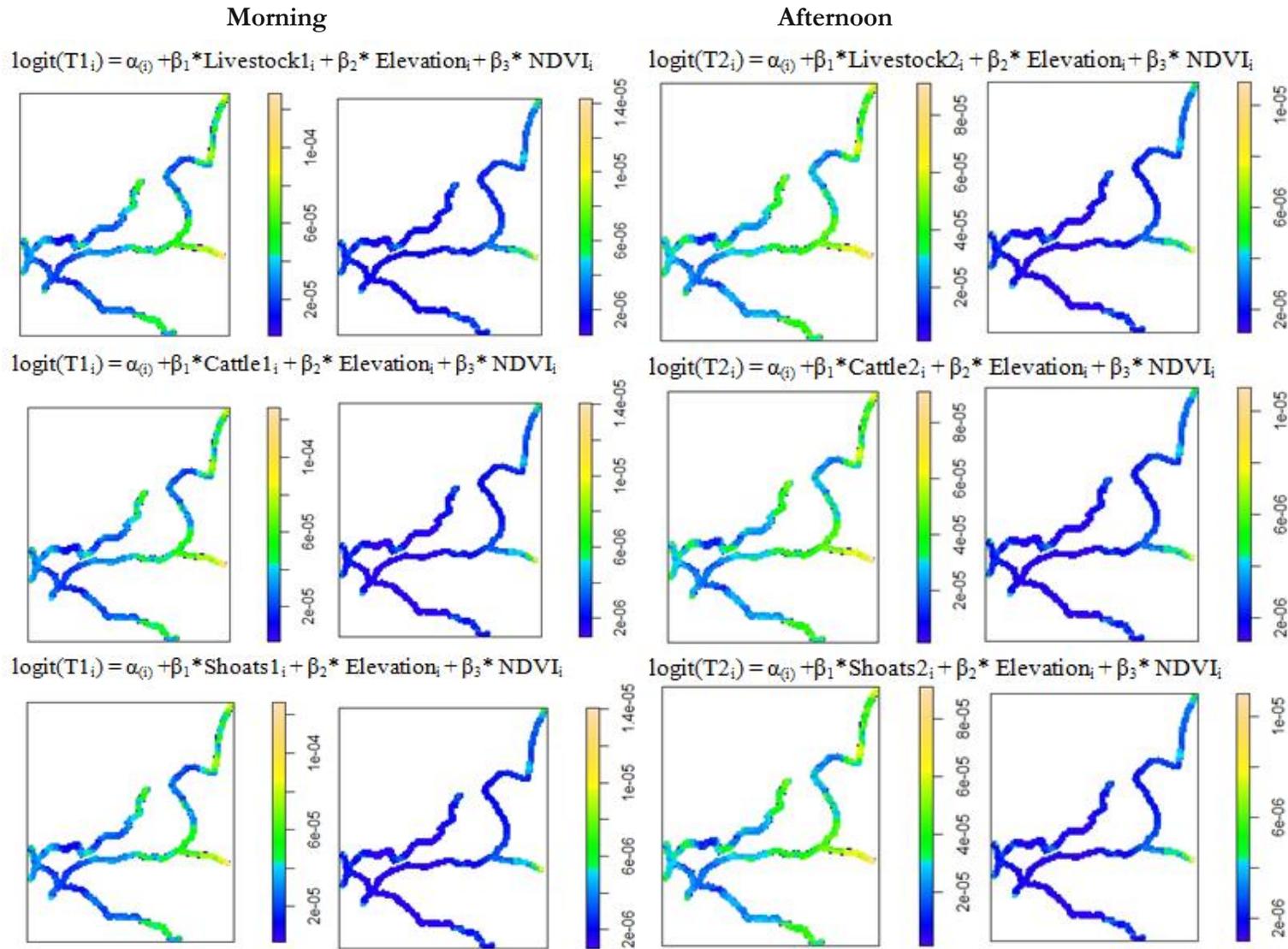


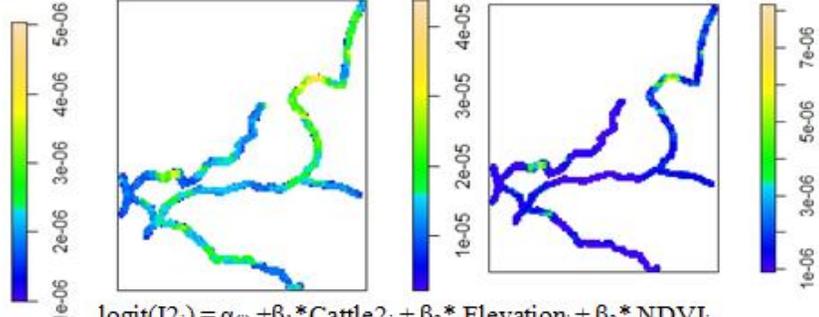
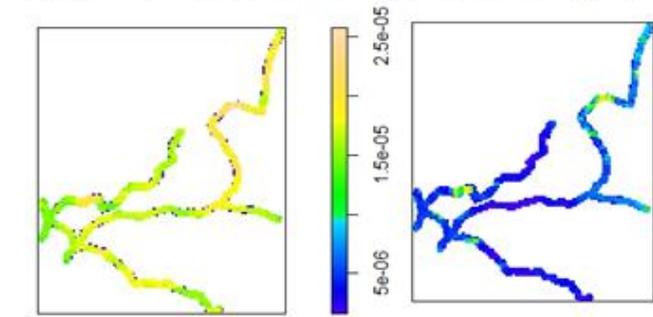
Figure 5. Fitted trend (left column) and standard error (right column) for point process models of Thomson's gazelle intensity, separated according to morning and afternoon point patterns. Yellow indicates higher values and blue indicates lower values. Model forms are printed above the results for reference.

Morning

Afternoon

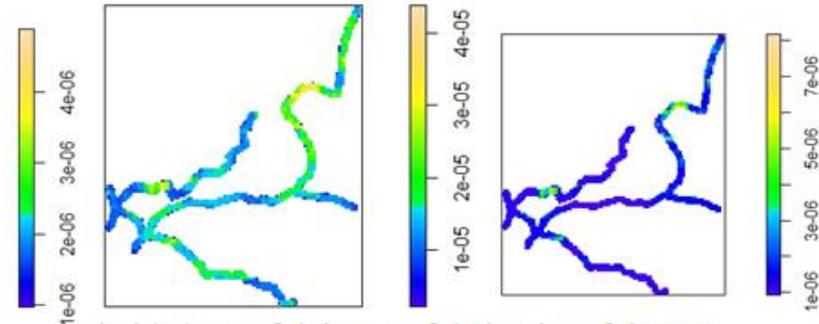
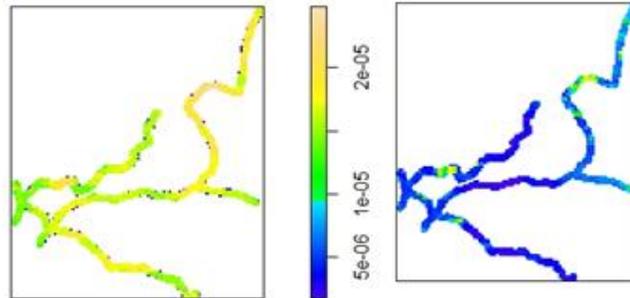
$$\text{logit}(I1_i) = \alpha_{(i)} + \beta_1 * \text{Livestock}1_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

$$\text{logit}(I2_i) = \alpha_{(i)} + \beta_1 * \text{Livestock}2_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(I1_i) = \alpha_{(i)} + \beta_1 * \text{Cattle}1_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

$$\text{logit}(I2_i) = \alpha_{(i)} + \beta_1 * \text{Cattle}2_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(I1_i) = \alpha_{(i)} + \beta_1 * \text{Shoats}1_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

$$\text{logit}(I2_i) = \alpha_{(i)} + \beta_1 * \text{Shoats}2_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

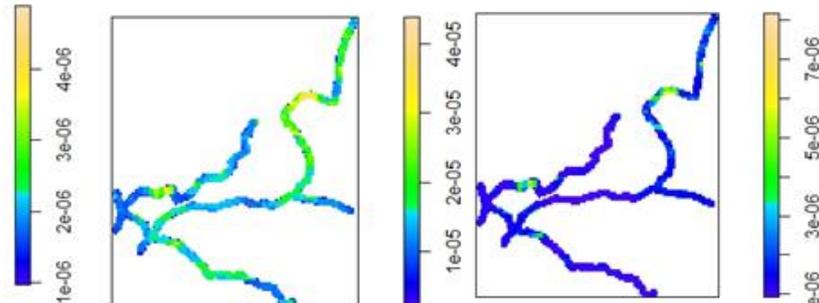
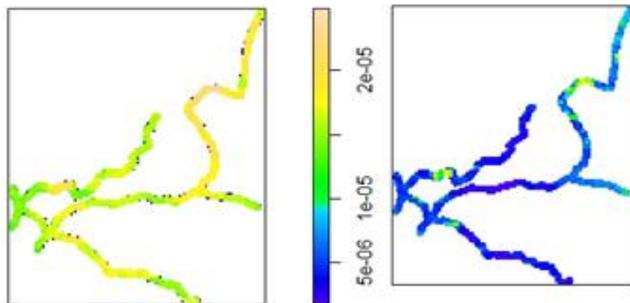
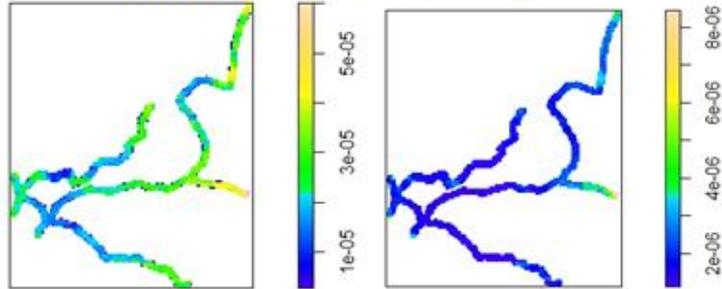


Figure 6. Fitted trend (left column) and standard error (right column) for point process models of impala intensity, separated according to morning and afternoon point patterns. Yellow indicates higher values and blue indicates lower values. Model forms are printed above the results for reference.

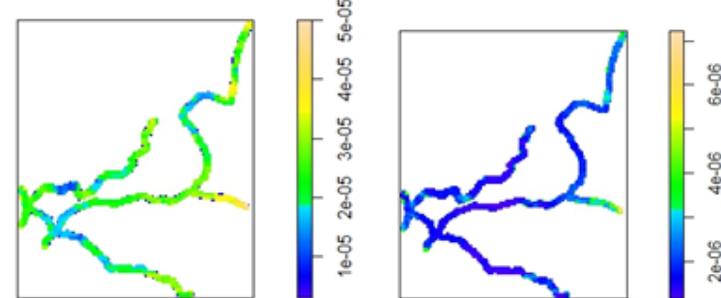
Morning

Afternoon

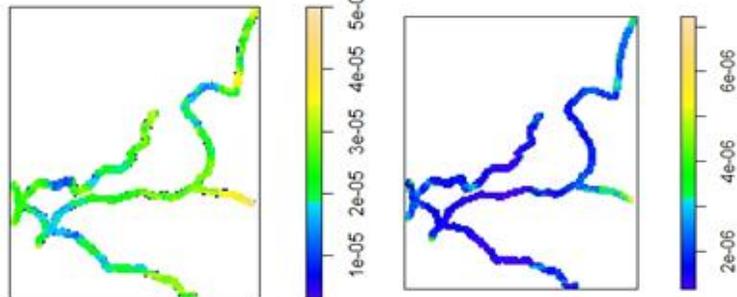
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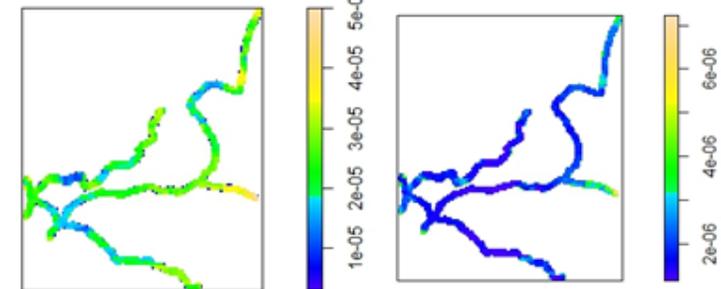
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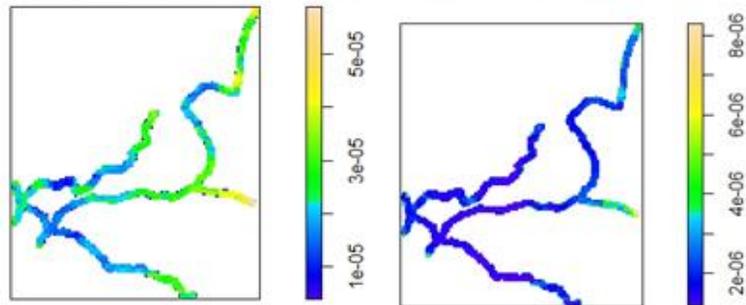
$$\text{logit}(W1_i) = \alpha_{(i)} + \beta_1 * \text{Cattle1}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(W2_i) = \alpha_{(i)} + \beta_1 * \text{Cattle2}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(W1_i) = \alpha_i + \beta_1 * \text{Shoats1}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(W2_i) = \alpha_{(i)} + \beta_1 * \text{Shoats2}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

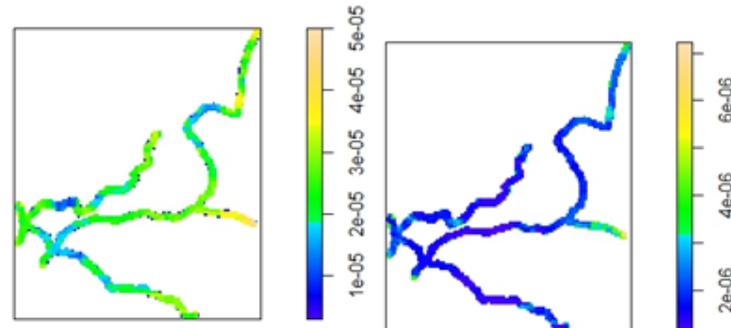
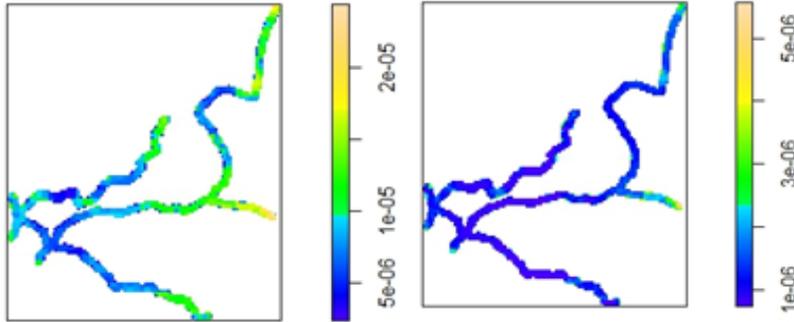


Figure 7. Fitted trend (left column) and standard error (right column) for point process models of wildebeest intensity, separated according to morning and afternoon point patterns. Yellow indicates higher values and blue indicates lower values. Model forms are printed above the results for reference.

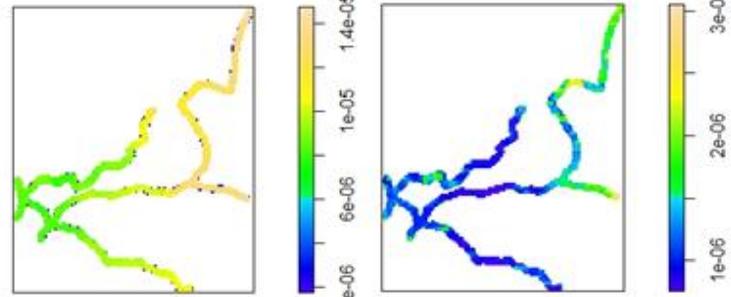
Morning

Afternoon

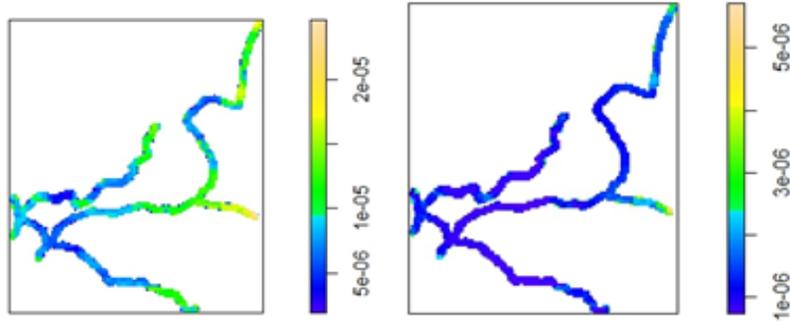
$$\text{logit}(Z1_i) = \alpha_{(i)} + \beta_1 * \text{Livestock1}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



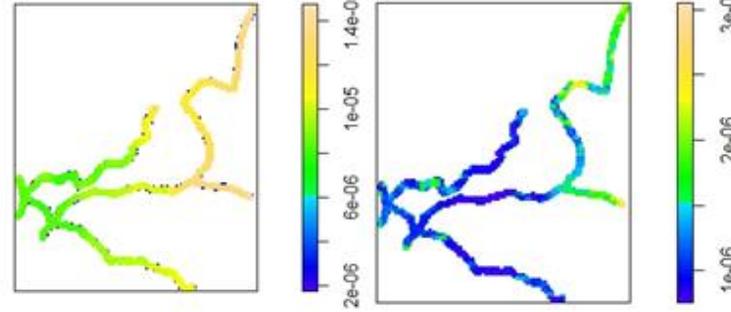
$$\text{logit}(Z2_i) = \alpha_{(i)} + \beta_1 * \text{Livestock2}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



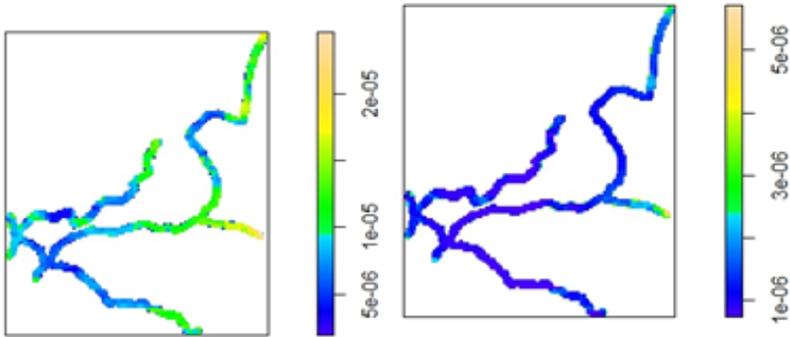
$$\text{logit}(Z1_i) = \alpha_{(i)} + \beta_1 * \text{Cattle1}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(Z2_i) = \alpha_{(i)} + \beta_1 * \text{Cattle2}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(Z1_i) = \alpha_{(i)} + \beta_1 * \text{Shoats1}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$



$$\text{logit}(Z2_i) = \alpha_{(i)} + \beta_1 * \text{Shoats2}_i + \beta_2 * \text{Elevation}_i + \beta_3 * \text{NDVI}_i$$

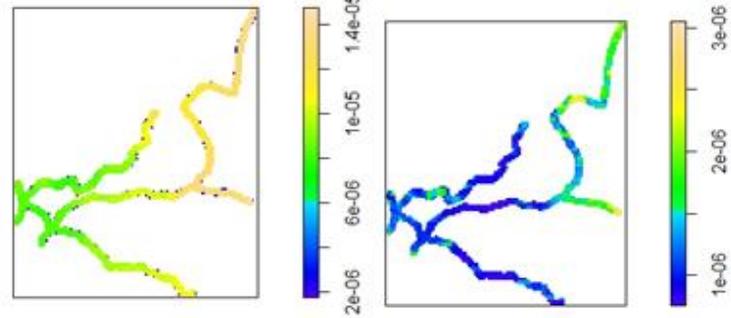


Figure 8. Fitted trend (left column) and standard error (right column) for point process models of zebra intensity, separated according to morning and afternoon point patterns. Yellow indicates higher values and blue indicates lower values. Model forms are printed above the results for reference.

Appendix C: Model Results

		Wildebeest				Zebra				
Morning	Wbeest1	Estimate	S.E.	CI95.lo	CI95.hi	zebra1	Estimate	S.E.	CI95.lo	CI95.hi
	(Intercept)	-6.5129	2.8319	-12.0634	-0.9624	(Intercept)	-5.4849	4.5129	-14.3299	3.3602
	live1***	1.6124	0.4111	0.8066	2.4182	live1	0.7640	0.4538	-0.1254	1.6534
	elev	-0.0005	0.0012	-0.0029	0.0019	elev	-0.0010	0.0020	-0.0049	0.0030
	ndvi***	-0.0012	0.0002	-0.0016	-0.0007	ndvi***	-0.0012	0.0004	-0.0019	-0.0005
	wbeest2	Estimate	S.E.	CI95.lo	CI95.hi	zebra2	Estimate	S.E.	CI95.lo	CI95.hi
(Intercept)	-5.9069	2.8434	-11.4798	-0.3340	(Intercept)	-5.6688	4.5235	-14.5348	3.1971	
cow1**	1.1891	0.4501	0.3069	2.0713	cow1	0.9581	0.5825	-0.1836	2.0998	
elev	-0.0006	0.0012	-0.0030	0.0018	elev	-0.0009	0.0020	-0.0048	0.0030	
ndvi***	-0.0012	0.0002	-0.0016	-0.0007	ndvi***	-0.0013	0.0004	-0.0020	-0.0006	
Afternoon	wbeest5	Estimate	S.E.	CI95.lo	CI95.hi	zebra5	Estimate	S.E.	CI95.lo	CI95.hi
	(Intercept)	-5.9069	2.8434	-11.4798	-0.3340	(Intercept)	-5.6688	4.5235	-14.5348	3.1971
	shoat1**	1.1891	0.4501	0.3069	2.0713	shoat1	0.9581	0.5825	-0.1836	2.0998
	elev	-0.0006	0.0012	-0.0030	0.0018	elev	-0.0009	0.0020	-0.0048	0.0030
	ndvi***	-0.0012	0.0002	-0.0016	-0.0007	ndvi***	-0.0013	0.0004	-0.0020	-0.0006
	wbeest3	Estimate	S.E.	CI95.lo	CI95.hi	zebra3	Estimate	S.E.	CI95.lo	CI95.hi
(Intercept)	-4.6416	2.9017	-10.3289	1.0458	(Intercept)	-17.3282	4.1939	-25.5481	-9.1083	
cow2***	1.5680	0.5796	0.4321	2.7040	cow2	1.5115	1.0031	-0.4546	3.4776	
elev	-0.0019	0.0013	-0.0043	0.0006	elev	0.0029	0.0018	-0.0007	0.0065	
ndvi***	-0.0011	0.0002	-0.0015	-0.0006	ndvi	-0.0001	0.0003	-0.0007	0.0005	
Afternoon	wbeest4	Estimate	S.E.	CI95.lo	CI95.hi	zebra4	Estimate	S.E.	CI95.lo	CI95.hi
	(Intercept)	-4.6416	2.9017	-10.3289	1.0458	(Intercept)	-17.3282	4.1939	-25.5481	-9.1083
	live2**	1.5680	0.5796	0.4321	2.7040	live2	1.5115	1.0031	-0.4546	3.4776
	elev	-0.0019	0.0013	-0.0043	0.0006	elev	0.0029	0.0018	-0.0007	0.0065
ndvi***	-0.0011	0.0002	-0.0015	-0.0006	ndvi	-0.0001	0.0003	-0.0007	0.0005	
Afternoon	wbeest6	Estimate	S.E.	CI95.lo	CI95.hi	zebra6	Estimate	S.E.	CI95.lo	CI95.hi
	(Intercept)	-4.6416	2.9017	-10.3289	1.0458	(Intercept)	-17.3282	4.1939	-25.5481	-9.1083
	shoat2**	1.5680	0.5796	0.4321	2.7040	shoat2	1.5115	1.0031	-0.4546	3.4776
	elev	-0.0019	0.0013	-0.0043	0.0006	elev	0.0029	0.0018	-0.0007	0.0065
ndvi***	-0.0011	0.0002	-0.0015	-0.0006	ndvi	-0.0001	0.0003	-0.0007	0.0005	

Figure 9. Model results for wildebeest and zebra, separated for morning and afternoon patterns. Parameter estimates that are in bold are considered statistically significant within a 95% CI. Asterisks denote the level of significance, *=.05, **=.01, ***=.001.

Thomson's gazelle

Impala

		Estimate	S.E.	CI95.lo	CI95.hi
Morning	T1				
	(Intercept)	-5.6596	2.4105	-10.3842	-0.9350
	live1***	3.0426	0.7082	1.6546	4.4306
	elev	-0.0005	0.0010	-0.0025	0.0015
	ndvi***	-0.0016	0.0002	-0.0020	-0.0012
	T5				
	(Intercept)	-4.7786	2.4144	-9.5107	-0.0465
	cowr1***	2.4349	0.7083	1.0467	3.8232
	elev	-0.0006	0.0010	-0.0026	0.0013
	ndvi***	-0.0016	0.0002	-0.0020	-0.0012
	T2				
	(Intercept)	-4.7786	2.4144	-9.5107	-0.0465
shoat1***	2.4349	0.7083	1.0467	3.8232	
elev	-0.0006	0.0010	-0.0026	0.0013	
ndvi***	-0.0016	0.0002	-0.0020	-0.0012	
T3					
(Intercept)	-6.4029	2.5157	-11.3336	-1.4722	
shoat2***	2.3833	0.7084	0.9948	3.7718	
elev	-0.0005	0.0011	-0.0026	0.0016	
ndvi***	-0.0013	0.0002	-0.0017	-0.0009	
T4					
(Intercept)	-6.4029	2.5157	-11.3336	-1.4722	
live2***	2.3833	0.7084	0.9948	3.7718	
elev	-0.0005	0.0011	-0.0026	0.0016	
ndvi***	-0.0013	0.0002	-0.0017	-0.0009	
T6					
(Intercept)	-6.4029	2.5157	-11.3336	-1.4722	
cowr2***	2.3833	0.7084	0.9948	3.7718	
elev	-0.0005	0.0011	-0.0026	0.0016	
ndvi***	-0.0013	0.0002	-0.0017	-0.0009	
Afternoon	I1				
	(Intercept)	-19.7224	3.1939	-25.9824	-13.4624
	live**	2.1869	0.7095	0.7964	3.5774
	elev *	0.0028	0.0014	0.0001	0.0055
	ndvi	0.0005	0.0003	0.0000	0.0010
	I5				
	(Intercept)	-19.5606	3.2785	-25.9863	-13.1350
	cowr1 *	2.1214	1.0019	0.1577	4.0851
	elev	0.0027	0.0014	0.0000	0.0055
	ndvi	0.0005	0.0003	0.0000	0.0009
	I2				
	(Intercept)	-19.5606	3.2785	-25.9863	-13.1350
shoat1*	2.1214	1.0019	0.1577	4.0851	
elev	0.0027	0.0014	0.0000	0.0055	
ndvi	0.0005	0.0003	0.0000	0.0009	
I3					
(Intercept)	-29.6476	3.2234	-35.9654	-23.3297	
shoat2	1.3603	0.7100	-0.0313	2.7519	
elev***	0.0071	0.0014	0.0043	0.0098	
ndvi***	0.0013	0.0003	0.0008	0.0018	
I4					
(Intercept)	-29.6476	3.2234	-35.9654	-23.3297	
live2	1.3603	0.7100	-0.0313	2.7519	
elev***	0.0071	0.0014	0.0043	0.0098	
ndvi ***	0.0013	0.0003	0.0008	0.0018	
I6					
(Intercept)	-29.6476	3.2234	-35.9654	-23.3297	
cow2	1.3603	0.7100	-0.0313	2.7519	
elev***	0.0071	0.0014	0.0043	0.0098	
ndvi***	0.0013	0.0003	0.0008	0.0018	

Figure 10. Model results for Thomson's gazelle and impala, separated for morning and afternoon patterns. Parameter estimates that are in bold are considered statistically significant within a 95% CI. Asterisks denote the level of significance, *=.05, **=.01, ***=.001.