

Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance

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Abstract. Resident white-bearded wildebeest (*Connochaetes taurinus*) have experienced widespread population declines across much of their range over the past few decades, the drivers of which are attributed to landscape changes. Despite the ecological significance of this decline, surprisingly little is known about the resource needs and habitat use of these animals. Using global positioning system data collected from 2010 to 2013, we assessed resource selection of wildebeest inhabiting three study areas in Kenya with varying degrees of natural and anthropogenic disturbance to identify potential behavioral mechanisms underlying potential landscape-driven declines. Wildebeest were observed to consistently avoid anthropogenic features and dense woody cover, irrespective of season, suggestive of avoidance of landscape features that would likely be associated with increased predation risk. Wildebeest also avoided primary roads, particularly across the Athi-Kaputiei Plains where human density and landscape alteration was greatest. The strongest response to normalized difference vegetation index was observed across the Amboseli Basin, the least productive and anthropogenically altered of our three study areas, leading to pronounced seasonal shifts in space use. Selection of natural and anthropogenic features was similar across the Mara and Athi-Kaputiei Plains, with the exception of the response to roads which likely relates to differences in road use. We also observed strong shifts in space use between day and night periods, particularly in relation to anthropogenic features and likely related to human circadian activity patterns. The observed variability in selection provides detailed information to how wildebeest react to local environmental factors across landscapes, and provides insight to how landscape fragmentation amplifies habitat loss for wildebeest by driving spatial avoidance, a likely mechanism contributing to population declines in this species. The quantified responses of wildebeest to landscape features can aid future conservation management efforts and planning to sustain imperiled wildebeest populations.

Key words: *Connochaetes taurinus*; global positioning system tracking; habitat use; Kenya; resource selection.

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INTRODUCTION

The loss and fragmentation of habitat is recognized as one of the leading causes of species loss and extinction worldwide (Dobson 1997). While

the effects of habitat loss are straightforward, fragmentation (i.e., the loss and isolation of habitat) related to anthropogenic disturbance can have indirect effects on wildlife populations that are more difficult to measure. Fragmentation,

for example, is known to impose restrictions on movement and force individuals into areas of poor habitat quality (Hobbs et al. 2008), potentially leading to lowered fitness (e.g., elk [*Cervus canadensis*]; Creel et al. 2009). Indirect fitness costs can also result from an increased exposure to risk, with fragmentation-enhanced predation pressure driving rapid population declines in woodland caribou (*Rangifer tarandus caribou*; Wittmer et al. 2005).

Increased recognition of the pressures imposed by fragmentation has stimulated study into the effects of these underlying landscape-level processes (e.g., Stabach et al. 2015), highlighting the importance of improved land-use planning initiatives to mitigate negative consequences. Characterizing the spatial requirements and habitat use patterns of species across landscapes that are becoming increasingly fragmented is a conservation priority. In dynamic environments, predicting the effects of habitat fragmentation can be difficult because animals often rely on spatially distinct habitat components (Mueller et al. 2008), the connectivity between which may be compromised directly or indirectly. Resource selection is expected to change seasonally between each of these habitat components (Boyce et al. 2002, Wiens et al. 2008). Comparing species responses across a gradient of anthropogenic impacts offers a powerful framework with which to investigate the response of animal populations to these changes.

Losses in connectivity between or reductions in the size of seasonal ranges of white-bearded wildebeest (*Connochaetes taurinus*) in East Africa have been shown to have pronounced effects on landscape carrying capacities (e.g., Mbaiwa and Mbaiwa 2006). Across the Mara Plains in Kenya, for example, resident wildebeest declined by 81% over a 20-yr time period (1977–1997), a result of wet season range restrictions stemming from increased human settlement along the region's western border (Ottichilo et al. 2001, Serneels and Lambin 2001, Ogutu et al. 2011). A similar result has been observed across the Athi-Kaputiei Plains, a neighboring ecosystem where resident populations declined 93% over a similar time period (1977–2011) due to rapid land-cover development and a severing of the populations seasonal habitat ranges (Reid et al. 2008, Ogutu et al. 2013, Stabach 2015). With agricultural and infrastructural development rapidly increasing across

many regions in Africa, many local wildlife populations are threatened with extinction. Despite the known threats from land-use change, no study has investigated the effect of human impacts on wildebeest resource selection. Such information is critical to understanding the response of wildebeest to increasing degrees of landscape change.

Resource selection functions (RSFs) are commonly used to examine species–habitat relationships (e.g., Hebblewhite and Merrill 2008, Matthiopoulos et al. 2011, Roever et al. 2012). Most often conducted in a logistic regression-based framework, RSFs evaluate the amount of habitat “used” by a species in relation to what is available (as defined by the investigator; Manly et al. 2002). If a resource is used in greater proportion to what is available, the resource is assumed to be selected by the individual. RSFs are ideally suited for studies using global positioning system (GPS) collars, especially in combination with remotely sensed data sources tracking resource dynamics. This approach is particularly useful for assessing the relative importance of different landscape features on space use.

We evaluated the resource selection of GPS-tracked resident white-bearded wildebeest across three study areas in Kenya, each with differing levels of natural and anthropogenic disturbance. We used a hierarchical approach to account for the lack of independence associated with repeatedly sampling individual movements. We fit separate models to wet and dry season periods and test the predictions that: (P1) wildebeest avoid areas with high levels of anthropogenic disturbance due to the inherent harassment and predation risk, and similar to the movement responses of migratory wildebeest and plains zebra (*Equus burchelli*) observed by Hopcraft et al. (2014) to these features; (P2) wildebeest take greater risks during dry season periods when conditions are poor, resulting in greater use of areas in close proximity to dense forage cover and human uses and which would be expected to be associated with increased predation risk (e.g., predator-sensitive foraging hypothesis [Sinclair and Arcese 1995]); and (P3) wildebeest select areas with greater primary productivity during dry season periods, maximizing energy intake (Wilmshurst et al. 1999). In addition, we inspect circadian changes in space use to test the prediction (P4) that wildebeest are attracted to local settlements at night

due to the extra predator security and resources that these areas provide (Reid 2012).

METHODOLOGY

Study area

The study area encompassed three landscapes in southern Kenya and northern Tanzania, broadly defined by the movements of resident wildebeest fitted with GPS collars over a three-year study period (2010–2013). We refer to these areas as the Amboseli Basin, Athi-Kaputiei Plains, and Mara (Fig. 1). Note, however, that these names denote study population units and not necessarily specific geographic regions. Amboseli Basin extends from 36°43' E, 2°17' S to 37°42' E, 2°57' S and includes Amboseli National Park. Average human population density, excluding the national park, is 14 people/km² (LandScan 2008). The Mara is the largest of the three study areas (26,000 km²), extending from 34°44' E, 1°4' S to 35°50' E, 2°58' S, covering portions of the Serengeti–Mara ecosystem and including the Maasai Mara National Reserve (MMNR) in Kenya and portions of Serengeti National Park (SNP) in Tanzania. Average human population density, exclusive of both national parks where settlement is prohibited, is 23 people/km² (LandScan 2008). Dense settlement and mechanized agriculture occur along the western boundary of the MMNR and the northwestern corner of SNP. The Athi-Kaputiei Plains (36°43' E, 1°18' S to 37°9' E, 1°55' S) is located directly south of Kenya's capital city, Nairobi, and is the most anthropogenically disturbed of the three study areas. Rapid development and growth have occurred across this region over the past few decades (Reid et al. 2008). Average human population density, exclusive of Nairobi National Park located at the northernmost section of this landscape, is 45 people/km² (LandScan 2008).

A pronounced southeast-to-northwest rainfall gradient exists across the region, with the majority of rainfall falling during two rainy seasons (broadly April–June and November–December). The Mara is the most productive of the three systems, receiving approximately 665 mm of rainfall annually (range: 350–1425 mm; Xie and Arkin 1997), and the Amboseli Basin the least productive (approximately 370 mm rainfall annually; range: 300–525 mm; Xie and Arkin 1997). Rainfall across the Athi-Kaputiei Plains is moderate in

comparison, averaging 475 mm annually (range: 415–570 mm; Xie and Arkin 1997). Each area is comprised of semiarid grassland, dominated by mixed Acacia and Commiphora woodlands.

Relocation (use) data

Thirty-six adult wildebeest (22 female and 14 male) were randomly selected from distinct groups and fitted with Lotek WildCell GPS collars (Lotek Wireless Incorporated, Newmarket, Ontario, Canada) between May and October 2010 (National Council for Science and Technology research permit no. NCST/RR1/12/1/MAS/39/4, Nairobi, Kenya). Nine animals were collared across the Amboseli Basin, 12 animals across the Athi-Kaputiei Plains, and 15 animals across the Mara. All collared individuals were adults, ranging in age (estimated from tooth wear) from 5 to 12 yr (Appendix S1). Mean pairwise distance between initial collaring locations was 12.7 km across the Amboseli Basin, 26.5 km across the Athi-Kaputiei Plains, and 21.8 km across the Mara. All aspects of animal handling were administered by Kenya Wildlife Service (Nairobi, Kenya) field veterinarians and approved by the International Animal Care and Use Committee (IACUC) at Colorado State University, Fort Collins, Colorado, USA (Approval No. 09-214A-02).

Collars were programmed to collect the location of animals 16 times per day, every hour from 06:00 to 18:00 and every three hours from 18:00 to 06:00 (local time). We removed two-dimensional data points with a dilution of precision (DOP) > 5.0 and three-dimensional points with a DOP > 10.0 to avoid using data that may have large spatial errors (Lewis et al. 2007). Data were rarified to a 3-h time interval. Mean fix success was 94.2% and ranged from 79.1% to 100.0%. The duration that wildebeest were collared ranged from 16 to 964 d (median = 538). A total of 139,634 fixes across the 36 individuals were collected, ranging from 119 to 7427 records of use per animal (Appendix S1).

Data were separated into dry and wet season periods and combined across years. Seasonal start/end dates were defined using MODIS normalized difference vegetation index (NDVI; MOD13Q1) data (Carroll et al. 2004) and the TIMESAT software package with a Savitzky–Golay function (Jonsson and Eklundh 2002, 2004). Transitional periods (i.e., ±10 d of seasonal start/end dates) were removed from analyses. Seasonal trends

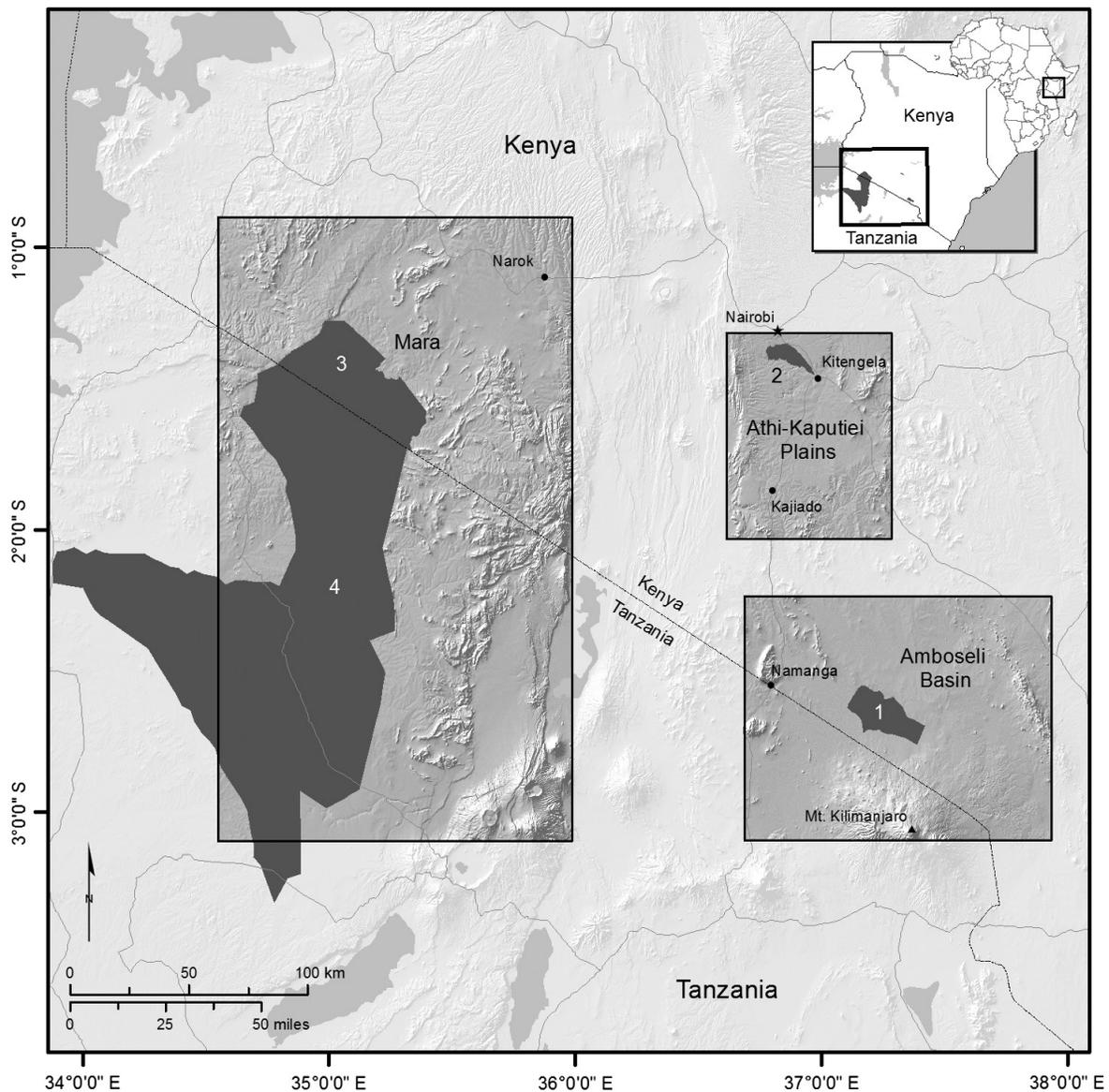


Fig. 1. Study areas (labeled) and protected areas, (1) Amboseli National Park; (2) Nairobi National Park; (3) Maasai Mara National Reserve; (4) Serengeti National Park, across southern Kenya and northern Tanzania. Main roads are displayed in light gray. Large rectangles represent general areas where resource selection was assessed, based on wildebeest global positioning system data.

across each study area are displayed in Stabach (2015). The total number of locations used for each time period was 41,330 among 35 individuals for the dry season (Amboseli Basin: 15,018 locations, $n = 9$; Athi-Kaputiei Plains: 12,215 locations, $n = 12$; Mara: 14,097 locations, $n = 14$) and 66,461 among 36 individuals for the wet season (Amboseli Basin: 8813 locations, $n = 9$; Athi-Kaputiei Plains: 27,150

locations, $n = 12$; Mara: 30,498 locations, $n = 15$). The difference in the number of locations collected across study area/season relates to the length of seasonal periods (i.e., dry season periods are longer/more consistent across the Amboseli Basin [Stabach 2015]) and the length of time in which individual collars collected data. Relocation data were further separated within each season into

day (06:00–17:59) and nighttime (18:00–05:59) temporal periods. Data were projected to Albers Equal Area projection, WGS84 datum.

Habitat covariates

Wildebeest are variable grazers (Gagnon and Chew 2000), preferring grass shoots <3 cm in height to maximize energy intake (Wilmshurst et al. 1999), and are restricted to areas with available surface water (Talbot and Talbot 1963). The distribution of wildebeest is also limited to open areas, based more on an aversion to woody habitats that may conceal predators than by geographic relief (Georgiadis 1995). To assess resource selection across study areas, we amassed eight data layers (Appendix S2) in a geographic information system based on the known or suspected space use of the species. We included only those variables that could be constructed across all three study areas to facilitate population-level comparisons. An additional analysis was conducted on the Athi-Kaputiei Plains study area, due to additional fine-scale data being available (described below).

To assess vegetation quality, we extracted (1) the 16-d mean NDVI value at the time and location of each wildebeest observation (i.e., each “use” location) and (2) the difference between the current mean NDVI value and the previous NDVI value ($\Delta\text{NDVI}_t = \text{NDVI}_t - \text{NDVI}_{t-1}$). NDVI is known to be strongly correlated with a location’s vegetation productivity/greenness (Tucker 1979, Goward and Prince 1995) and has been shown to be an important parameter in models predicting animal movement (Pettorelli et al. 2005), including wildebeest (Boone et al. 2006, Hopcraft et al. 2014). Vegetation quantity (biomass) is also thought to strongly influence wildebeest space use, with wildebeest preferring the short grass plains while avoiding wooded areas (high biomass) due to the reduced digestible material (Wilmshurst et al. 1999) and inherent predation risk (Hopcraft et al. 2005, 2014). We used the topographic wetness index (TWI; Sørensen et al. 2006) as a proxy for biomass, as this metric simultaneously accounts for the total water catchment area and the slope of a cell. Cells with high TWI values tend to be concave areas with large catchment areas, holding more water than low TWI values and leading to increased biomass (Hopcraft et al. 2014).

To capture the response of wildebeest to measures of anthropogenic disturbance, we digitized

roads and visible structures from available satellite imagery (ESRI 2011, GoogleEarth 2013). To maintain consistency across each study area, we created a vector grid and digitized all features at a scale of 1:7000. We separated roads into two distinct categories (primary, secondary) based on attributes associated with the satellite imagery (ESRI 2011) and reflective of the road type. Distances to primary (tarmac/main roads) and secondary (dirt/all other roads) roads were calculated across each study area at a resolution of 50 m.

Wildebeest are also known to be particularly sensitive to anthropogenic fragmentation (e.g., Kahurananga and Silkiluwasha 1997). Although difficult to quantify across dryland grasslands, we calculated the distance to 86,565 digitized structures across the three study areas weighted by the estimated human population density (LandScan 2008) as a corollary to anthropogenic habitat fragmentation. Termed “Anthropogenic Footprint” and adopted from Hopcraft et al. (2014), densely populated areas have the highest values while areas furthest from small or sparsely populated villages have the lowest values. This method allowed us to incorporate small-scale disturbances that would have otherwise been missed due to the coarse resolution of the population data set (1 km²). Additional details of this data layer are provided in Appendix S3.

Landscape features such as dense woodland, embankments, or river confluences are known to form natural traps for wildebeest (Hopcraft et al. 2005, Balme et al. 2007). To capture these features, we edited rivers digitized by the World Research Institute (WRI 2007) using the same grid scale and procedure described above. We ignored small or ephemeral rivers, visible in the satellite imagery, but not included in the WRI data set. Across the Amboseli Basin, perennial swamps within the national park were also digitized and incorporated as features within this layer. We assumed that water was abundantly available during the wet season and that the distance to permanent rivers and swamps captured water sources that wildebeest relied on during the dry season. Woody vegetation, defined as shrubs, woodland, or trees with >40% cover, was selected from the Africover Global Land Cover data set (FAO 2014). Distances to each feature were calculated at a resolution of 50 m.

Two additional layers, the distance to human created water use points (i.e., dams) and fence

boundaries, were available only for the Athi-Kaputiei Plains and incorporated into an additional/separate model for this study area. These layers, digitized by staff at the International Livestock Research Institute (ILRI; Nairobi, Kenya) from 2004 to 2010 (Reid et al. 2008), describe fine-scale factors that were expected (positively and negatively, respectively) to effect the distribution of wildebeest across the region. We restricted the study area boundary to the extent of these data layers for models specific to this region. All predictor variables for every used and available location (described below) were extracted using tools from the raster package (Hijmans and van Etten 2012) in the R statistical package (R Development Core Team 2013). All geospatial analyses were completed using the Spatial Analyst extension in ArcGIS 10.1 (ESRI 2012). No variables were observed to be highly correlated (Pearson's $r > |0.6|$).

Availability data

The most common method for characterizing third/fourth-order selection (Johnson 1980) entails generating a random sample of points to characterize availability within a buffer around each used location (Northrup et al. 2013). We employed a modified version of this method, using the maximum distance displaced over a 3-h period (the resolution of our data set) for each individual and season as the radius around each "use" point in which to generate availability. Following Northrup et al. (2013), we performed sensitivity analyses to determine the appropriate number of random points to sample per each "use" point, using one randomly selected animal across each study area. We randomly drew a number of points ranging from 1 to 100 (1, 3, 5, 10, 20, 30, 50, 100) per "use" point and fit RSFs using logistic regression to each of these sample sizes. We repeated this process 100 times and calculated the expectation of the coefficient estimates and the 95% simulation envelopes. In doing so, we determined a sample of 50 availability points per "use" point provided stable coefficient estimates. Resulting sensitivity plots, with R code to conduct the analysis, are provided in Data S1.

Resource selection models

Important considerations in a RSF analysis include accounting for statistical independence between data points and appropriately

evaluating availability, both of which can effect coefficient estimates and statistical inference (Gillies et al. 2006, Northrup et al. 2013). We modeled resource selection for each study population and season using generalized linear mixed-effects logistic regression. Wildebeest "use" locations (1) were compared to "availability" locations (0) for each individual i , taking the form:

$$w(x_i) = \exp(\beta + \beta_1 x_{1i} + \dots + \beta_n x_{ni} + \gamma_i) \quad (1)$$

where $w(x_i)$ is the RSF, β_n is the coefficient for the n th predictor variable x_n , and γ is the random intercept for animal i (Manly et al. 2002, Gillies et al. 2006). Incorporating random effects into the model structure has been shown to better account for inherent differences between individuals and allows for the inclusion of unbalanced sampling designs (Gillies et al. 2006). We standardized $([x - \bar{x}]/\sigma_x)$ all predictor variables for every used and available location to facilitate cross-seasonal and cross-study area comparisons. Quadratic terms were included on all distance parameters to test for nonlinear relationships.

Seven a priori candidate models (Table 1) were created and ranked using Akaike's information criterion (AIC; Burnham and Anderson 2002). Model fit of each top-ranked model (study area/season) was evaluated using Spearman rank correlations between area-adjusted frequencies using presence-only validation predictions and RSF bins (Boyce et al. 2002), for which we randomly selected 20% of the presence-only data from each study area/season for validation. NDVI and Δ NDVI were not included in validation as values changed temporarily.

Additional models, separated into day and night periods and (for the Athi-Kaputiei Plains) inclusive of the parameters "Distance to water use points" and the "Distance to fences," were fit using the same methodology described above. All statistical analyses were conducted in R (R Development Core Team 2013) using the lme4 package (Bates et al. 2014).

RESULTS

Dry season models

The full model was the top-ranked model across all study areas (model 7; Table 2), indicating inclusion of all parameters in study area models was important in predicting wildebeest

Table 1. Candidate models considered to assess habitat selection by wildebeest across three study areas in southern Kenya.

Model	Structure	K
1. Null		2
2. Vegetation	NDVI + Δ NDVI + TWI	5
3. Predation	Distance to Woody Vegetation + (Distance to Woody Vegetation) ² + Distance to Rivers + (Distance to Rivers) ²	8
4. Human disturbance	Anthropogenic Footprint + Distance to Primary Road + (Distance to Primary Road) ² + Distance to Secondary Road + (Distance to Secondary Road) ²	7
5. Vegetation and human risk	NDVI + Δ NDVI + TWI + Anthropogenic Footprint	6
6. Vegetation and predation risk	NDVI + Δ NDVI + TWI + Distance to Woody Vegetation + (Distance to Woody Vegetation) ² + Distance to Rivers + (Distance to Rivers) ²	9
7. Full	NDVI + Δ NDVI + TWI + Distance to Woody Vegetation + (Distance to Woody Vegetation) ² + Distance to Rivers + (Distance to Rivers) ² + Anthropogenic Footprint + Distance to Primary Road + (Distance to Primary Road) ² + Distance to Secondary Road + (Distance to Secondary Road) ²	14

Notes: NDVI is normalized difference vegetation index. TWI is the topographic wetness index. Parameters are defined in the text. K is the number of fixed and random parameters included in the model.

resource selection. Cross-validation results highlight data for the Mara population strongly fit the prediction, with weaker results for the Athi-Kaputiei Plains and Amboseli Basin (Table 2). A list of model selection results, ranked by AIC, is provided in Appendix S4.

Wildebeest consistently selected areas further from anthropogenic features and of an intermediate distance (i.e., depicted by a hump-shaped response curve) to dense woody vegetation across study areas (Table 3, Fig. 2). The effect of distance from anthropogenic features was strongest across the Athi-Kaputiei Plains where levels of anthropogenic disturbance and alteration are highest. Responses to other parameters, namely distance to rivers and the distance to roads (primary and secondary), were less consistent across study areas, with the relative probability of selection declining in relation to rivers at intermediate distances across the Amboseli Basin but increasing strongly across the Athi-Kaputiei Plains and Mara (Table 3, Fig. 3). Similar responses were observed for roads, especially in relation to primary roads.

Wildebeest selection did not differ across the range of vegetation parameters (NDVI, Δ NDVI, and TWI) in the Athi-Kaputiei Plains (Table 3). Across the Amboseli Basin, wildebeest selection increased as NDVI increased. The opposite was observed in the Mara. Effect sizes, however, were generally small for these parameters (Table 3). Response curves for each parameter, inclusive of bootstrapped 95% confidence intervals, are provided in Appendix S5.

Wet season models

In wet season periods, the top-ranked models remained the same as those observed in the dry season (Table 2). Cross-validation results indicated strong predictive performance for the Athi-Kaputiei Plains and the Mara (Table 2). The spatial avoidance of anthropogenic features and woody vegetation was apparent during the wet season, similar to that found in dry season models, although effect sizes increased appreciably across the Amboseli Basin for both variables and decreased across the Athi-Kaputiei Plains in relation to woody vegetation. Effect sizes for these two variables remained relatively consistent across the Mara (Table 3, Fig. 2).

Table 2. Top-ranking models across three study areas in Kenya using Akaike information criteria.

Study area	Top model	<i>w</i>	<i>r_s</i>
Dry season			
Amboseli Basin	7. Full	1.0	0.39
Athi-Kaputiei Plains	7. Full	1.0	0.48
Mara	7. Full	1.0	0.96**
Wet season			
Amboseli Basin	7. Full	1.0	0.43
Athi-Kaputiei Plains	7. Full	1.0	0.94*
Mara	7. Full	1.0	0.94*

Notes: Results are provided for models across dry and wet season periods. Model weight (*w*) and Spearman rank correlation coefficient (*r_s*) are provided. Model structure is provided in Table 1.

P* < 0.05; *P* < 0.01.

Table 3. Parameter estimates of the top-ranked Akaike information criteria model for each study area across dry and wet season periods.

Parameter	Amboseli Basin	Athi-Kaputiei Plains	Mara
Dry season			
Anthropogenic footprint	-0.15 (0.02)	-0.42 (0.02)	-0.80 (0.03)
NDVI	0.26 (0.02)	-0.04 (0.02)	-0.32 (0.02)
Δ NDVI	-0.05 (0.02)	-0.03 (0.01)	-0.12 (0.01)
TWI	-0.14 (0.01)	-0.13 (0.01)	0.03 (0.01)
Distance to woody vegetation	0.63 (0.04)	0.85 (0.05)	0.68 (0.05)
(Distance to woody vegetation) ²	-0.50 (0.04)	-0.71 (0.05)	-0.98 (0.05)
Distance to rivers	-0.20 (0.02)	0.40 (0.07)	0.50 (0.06)
(Distance to rivers) ²	-0.08 (0.01)	-2.78 (0.22)	-1.57 (0.17)
Distance to primary road	-0.13 (0.03)	1.49 (0.06)	0.17 (0.04)
(Distance to primary road) ²	0.18 (0.03)	-2.35 (0.09)	-0.17 (0.04)
Distance to secondary road	-0.73 (0.03)	-1.33 (0.11)	-0.74 (0.03)
(Distance to secondary road) ²	0.41 (0.02)	-0.29 (0.40)	0.59 (0.03)
Wet season			
Anthropogenic footprint	-0.43 (0.03)	-0.47 (0.01)	-0.47 (0.02)
NDVI	-0.28 (0.02)	-0.19 (0.01)	-0.11 (0.01)
Δ NDVI	-0.25 (0.02)	-0.08 (0.01)	-0.11 (0.01)
TWI	-0.03 (0.01)	-0.18 (0.01)	0.02 (0.01)
Distance to woody vegetation	0.99 (0.05)	0.23 (0.04)	0.61 (0.03)
(Distance to woody vegetation) ²	-0.92 (0.05)	-0.42 (0.03)	-0.65 (0.03)
Distance to rivers	0.47 (0.03)	2.48 (0.06)	0.19 (0.02)
(Distance to rivers) ²	-0.47 (0.03)	-9.59 (0.21)	-0.28 (0.05)
Distance to primary road	-0.52 (0.04)	1.60 (0.04)	0.02 (0.01)†
(Distance to primary road) ²	0.50 (0.03)	-2.05 (0.06)	-0.00 (0.01)†
Distance to secondary road	0.32 (0.03)	-1.13 (0.07)	-0.52 (0.02)
(Distance to secondary road) ²	0.28 (0.02)	-1.74 (0.26)	0.41 (0.02)

Notes: Standard errors are provided in parentheses. See text for parameter descriptions. All model parameters were standardized to facilitate study area comparisons.

† Coefficient estimates with confidence intervals that cross zero. Distances measured in kilometers.

A shift in space use was observed in relation to the distance to rivers and primary roads between dry and wet season periods across the Amboseli Basin, with wildebeest selection increasing at intermediate distances to rivers and declining as distance increased. Higher probability of selection was observed across all distances from primary roads. Selection across the Athi-Kaputiei Plains and Mara was similar to dry season results for these parameters (Table 3, Fig. 3), although the relative probability of selection increased at longer distances across the Mara.

Similar trends to dry season periods were observed across the Athi-Kaputiei Plains and the Mara regarding the parameters NDVI, Δ NDVI, and TWI. Across the Amboseli Basin, we observed a shift in the response of wildebeest to NDVI, with the relative probability of selection being highest at low NDVI values and decreasing as NDVI increased during the wet season. The relative probability of selection also decreased

as Δ NDVI increased (Table 3). See Appendix S5 for response curves with confidence intervals for each parameter.

Day/night models

Wildebeest space use remained generally consistent between day and night periods, shifting in relation to anthropogenic features across each study area and in relation to NDVI across the Amboseli Basin (Fig. 4; Appendix S6). During daytime periods, wildebeest continued to select areas further from anthropogenic features. During nighttime periods, however, we observed a shift in space use, with wildebeest selecting areas in closer proximity to anthropogenic features. These results were strongest across the Amboseli Basin and the Athi-Kaputiei Plains and consistent across seasonal periods. Parameter estimates and response curves, separated between dry and wet season periods, are provided in Appendix S6.

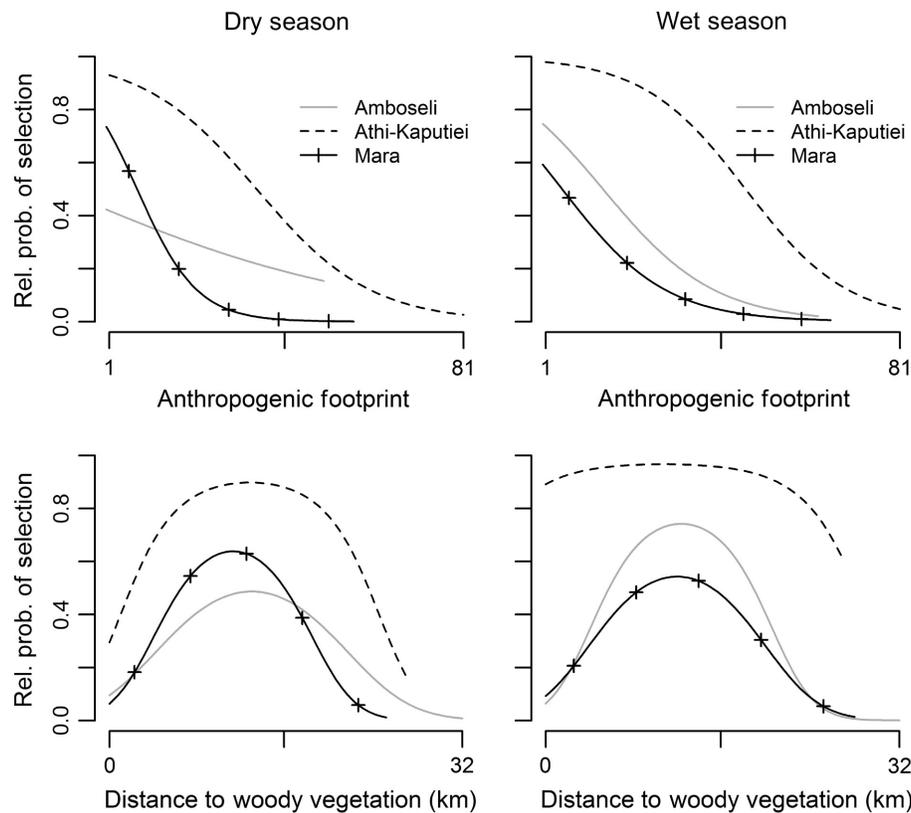


Fig. 2. Relative probability of selection for the parameters Anthropogenic Footprint and Distance to Woody Vegetation. Parameters are defined in the text. Dry and wet season response curves are displayed only across the range of values observed within each study area.

Athi-Kaputiei Plains submodel

Models inclusive of the parameters “Distance to Water Use Points” and “Distance to Fences” were more highly ranked (based on AIC) than models that did not contain these parameters (Appendix S7). In addition to parameters already discussed, selection for water use points increased in the dry season, with avoidance of areas directly adjacent to water use points in the wet season. Wildebeest were observed to rarely select areas greater than 6 km from identified water use points in either season (Fig. 5). Observed selection was greatest for areas within 1 km of fences during the wet season, although this relationship was nonlinear with reduced selection at the shortest distances. The range in which wildebeest demonstrated selection for water points and fences was reduced in dry season compared to wet season periods, suggesting tighter aggregation to these resources/parameters during these periods

(Fig. 5). Coefficient estimates for each parameter are provided in Appendix S7.

DISCUSSION

Over the past half century, resident wildebeest have experienced widespread and precipitous declines across much of their range in east Africa (Ottichilo et al. 2001, Reid et al. 2008, Ogutu et al. 2011, 2013). Central to these declines is the pervasive loss and fragmentation of available habitat (Serneels and Lambin 2001), factors that are likely to continue as human populations rise and expand into formerly open or contiguous rangeland. By comparing resource selection across a gradient of anthropogenic disturbance and vegetation productivity, we provide an improved empirical understanding of the response of wildebeest to these factors. Wildebeest are the dominant grazers across grassland savannas in

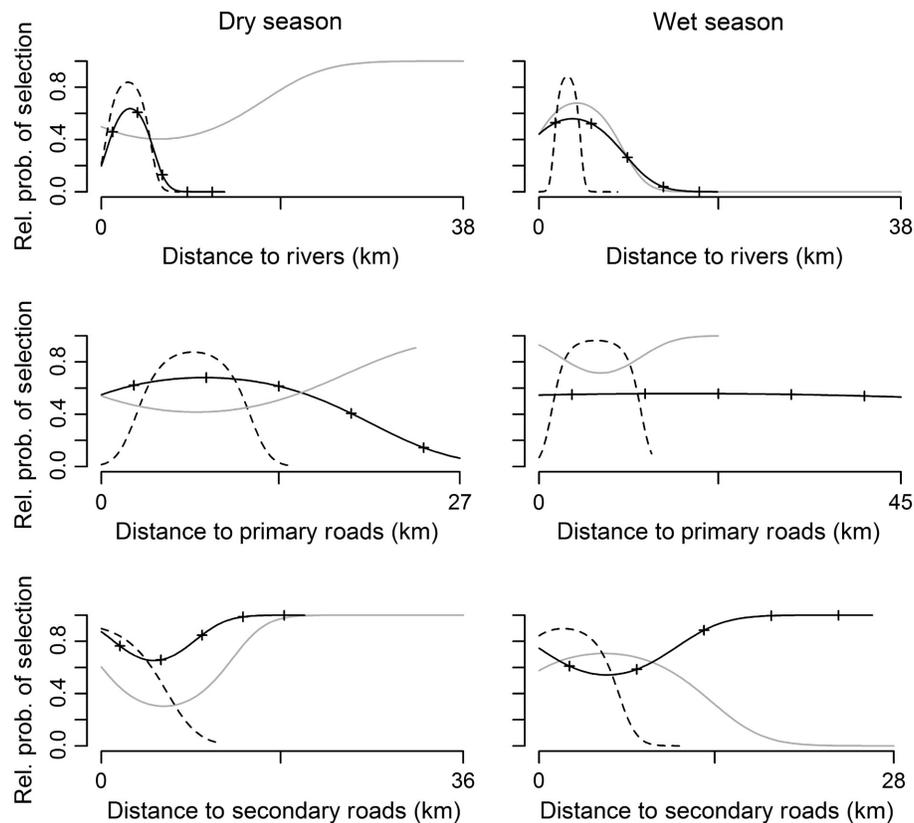


Fig. 3. Relative probability of selection for the parameters distance to rivers and distances to primary/secondary roads. Dry and wet season response curves are displayed only across the range of values observed within each study area (Amboseli Basin [gray line], Athi-Kaputiei Plains [dashed black line], Mara [crossed black line]).

eastern and southern Africa and are known to affect nearly every aspect of the ecosystem, including biodiversity, grassland-tree dynamics, wildfire intensity, food web structure, and the local economy (Sinclair 2003, Holdo et al. 2009, 2011b, Hopcraft et al. 2014). Thus, although our statistical inference is based solely on a single species, the loss or severe reduction in wildebeest would be expected to have widespread and long-lasting ecosystem consequences, providing valuable information to conservationists and land-use planners across the region, especially as it relates to losses in space use related to proposed road construction and development.

Scale is recognized as a fundamental consideration in RSF analyses (Boyce 2006). We analyzed selection at an intermediate scale of inference, due to the acknowledged large area requirements of the species (Estes 2014). Availability was drawn

within the maximum distance traveled in a three-hour time interval and analyzed across the animal's entire home range. Other authors (e.g., Kie et al. 2002) have drawn availability from buffers that are even larger than the estimated home range of animals to adequately characterize landscape heterogeneity. To capture finer-scale details of forage selection and potentially provide additional insight, methods incorporating an animal's movement process (i.e., step lengths, turning angles) could be used to generate availability, analyzing results in a step selection or conditional logistic regression framework (Compton et al. 2002, Fortin et al. 2005, Forester et al. 2009, Duchesne et al. 2010, Thurfjell et al. 2014). These analyses have the added benefit of including increased biologic realism beyond the spatial point process analysis that we conducted, but are known to be difficult to implement and have the potential to

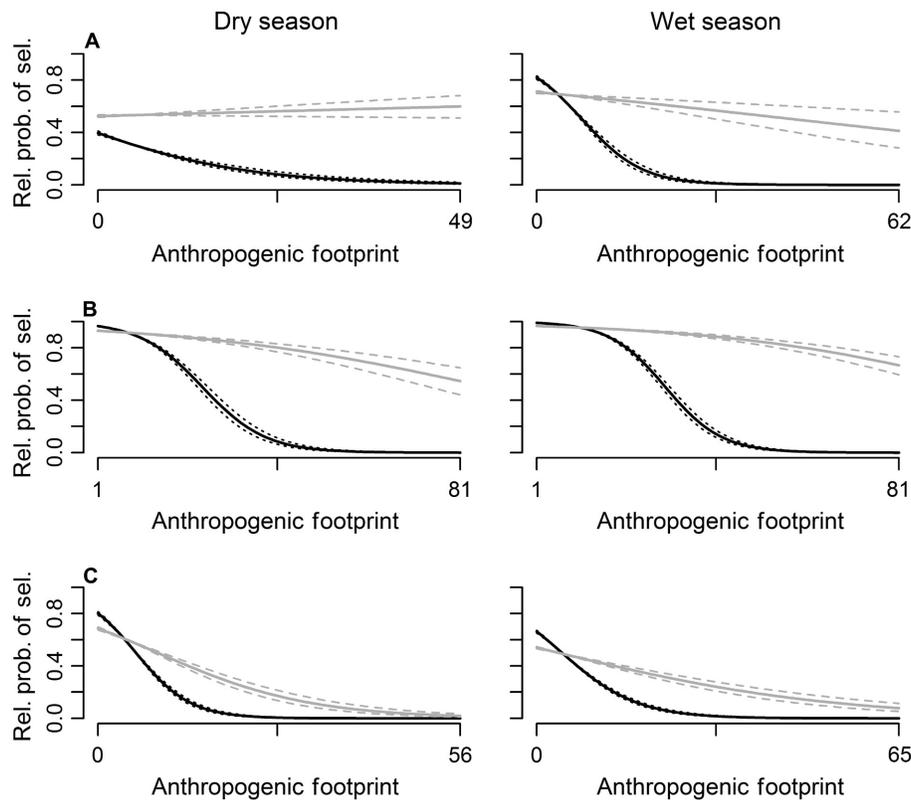


Fig. 4. Relative probability of selection for the parameter “Anthropogenic Footprint.” Day (black lines) and nighttime (gray lines) model responses are displayed across (A) the Amboseli Basin, (B) the Athi-Kaputiei Plains, and (C) the Mara. Dry and wet season response curves are displayed only across the range of values observed within each study area. 95% confidence intervals (dotted and dashed lines, respectively) are provided for reference.

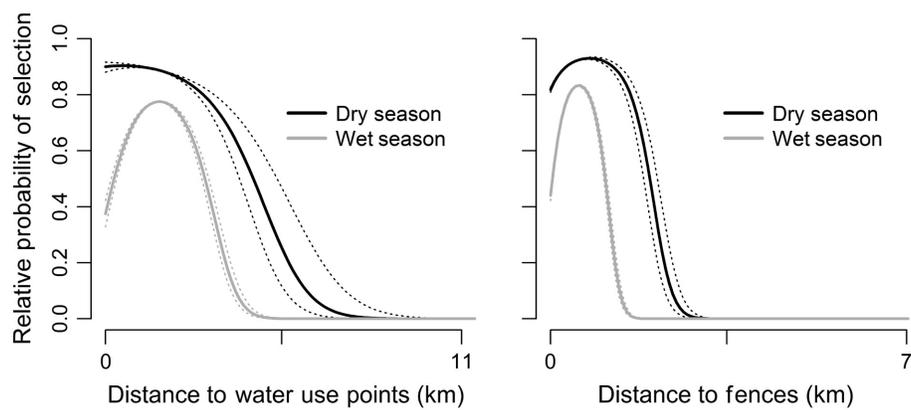


Fig. 5. Relative probability of selection for the parameters distance to water use points and distance to fences across the Athi-Kaputiei Plains study area. Dry and wet season response curves are displayed.

bias results based on the fix collection schedule chosen (Fieberg et al. 2010, Thurfjell et al. 2014). These analyses could limit the strength of statistical inference, but would be unlikely to change the general patterns we observed.

Human factors structuring space use

Human disturbances have been observed to disrupt herbivore movements in other species, altering step lengths and turning angles (Dobson et al. 2010, Hopcraft et al. 2014), and leading to declines in genetic diversity from population isolation (Epps et al. 2005, Jackson and Fahrig 2011). Stabach et al. (2015) surmised that human disturbance is likely to alter wildebeest space use, even if quantified stress levels were not elevated across heavily disturbed areas. Our results provide empirical support for this expectation (P1), with strong negative effects related to habitat selection as human disturbance increased. This effect was most clearly observed across the Athi-Kaputiei Plains, where levels of disturbance were highest among our study areas. Response curves related to this parameter also declined much more sharply across the Mara and Amboseli Basin, perhaps indicating greater sensitivity to anthropogenic disturbance than was observed across the Athi-Kaputiei Plains.

The effect of primary roads provides empirical support related to the expected response of wildebeest to current and/or future road building, an issue that has received considerable attention across the region (Dobson et al. 2010, Holdo et al. 2011a). Current plans exist to build a bypass road around Nairobi and along the southern boundary of Nairobi National Park, further limiting connectivity between the park and the larger dispersal area, and likely leading to indirect threats on mortality that are most often undervalued in infrastructure development programs (Dobson et al. 2010).

Importantly, we separated roads into two distinct categories (primary and secondary) based on attributes associated with the satellite imagery (ESRI 2011), but not necessarily reflective of traffic volume. That is, the primary road extending from Kenya's capital city (Nairobi) has considerably more traffic across the adjacent Athi-Kaputiei Plains than it does across the more distant Amboseli Basin (i.e., a distance decay function). As such, our results related to primary

roads (i.e., a repulsive effect at short distances) are likely more reliable across the Athi-Kaputiei Plains than the Amboseli Basin or Mara where traffic volumes are lower, but represent a scenario to be avoided if wildebeest are to move freely across these ecosystems. Line transects conducted at 500-m intervals and perpendicular to the primary road connecting Kitengela with Kajiado across the Athi-Kaputiei Plains (Fig. 1) support this result, as wildebeest were never observed (direct sighting, print, or scat) within 500 m of this linear feature during field surveys conducted in 2011 and 2013 (J. Stabach, *unpublished data*). While further research to provide empirical results on traffic volumes is necessary, our results indicate that the indirect negative effects of roads extend beyond the actual road footprint and lead to additional habitat loss that is otherwise unaccounted for (Bolger et al. 2008).

Seasonal predation risks

We expected space use to change in relation to woody vegetation between seasons (P2), with wildebeest taking additional risks and being located in closer proximity to woodlands during dry season periods (i.e., predator-sensitive foraging hypothesis [Sinclair and Arcese 1995]). Instead, wildebeest space use relative to woodlands was generally consistent across seasonal periods, with space use declining at short distances in the Amboseli Basin and the Mara and consistent with observations by Georgiadis (1995) related to increased predation risk. Patterns across the Athi-Kaputiei Plains differed, however, with space use remaining high at short distances to woodlands. This anomaly disappeared in models inclusive of water use points and fences across this region, with the relative probability of use declining at short distances, indicating an interactive effect between one (or both) of these parameters. As such, wildebeest likely use areas typically associated with predation risk due to attraction to water or range restrictions caused by fences. Hopcraft et al. (2014) did not find a shift in movement between seasonal periods related to woody cover or other predator traps (e.g., river drainages). These data, however, were based on Serengeti migratory wildebeest, which are most often observed in groups of 10–3000 individuals (Hopcraft et al. 2014). Resident wildebeest congregate in much smaller

groups, never observed to exceed 200 individuals. Thus, these differences likely relate to stronger risk aversion associated with smaller groups.

Space use relative to water sources (rivers and swamps) was generally consistent within seasonal periods, except across the Amboseli Basin where wildebeest were observed to avoid areas in close proximity to water sources during the dry season. The response curve across this study area/season highlights spatial shifts in the species' distribution between seasonal periods that are known to occur (Western 1975). Across the Amboseli Basin, rivers are devoid of water during dry season periods, accounting for why we observed reduced selection at short distances during this time period. During dry seasons, wildebeest across this region are restricted to swamps within the national park boundary and other perennial water sources to access available surface water, and likely face increased predation risk in doing so. The increased selection at the largest range of distances measured likely indicates that there are additional water sources across the landscape, not included in our digitized water source layer, that are utilized by wildebeest in the dry season. Thus, our results related to our second prediction (P2) are inconclusive, with wildebeest taking greater risks in the dry season related to the distance to rivers but no change in selection related to dense woody cover.

Response to changes in vegetation productivity

Boone et al. (2006) and Hopcraft et al. (2014) identified and empirically showed NDVI to be a major driver related to the movements of Serengeti wildebeest. We observed only minor effects related to NDVI and Δ NDVI (lack of support for P3), with the strongest response to these variables observed across the Amboseli Basin, the driest of our study areas. Boone et al. (2006), however, used NDVI data derived from the SPOT Earth Observation System, which has an improved temporal resolution (10 d) to the data we incorporated (16 d). We also rarified our "use" data to a three-hour time interval, linking all data points within a 16-day time period to the same NDVI value. Incorporating daily NDVI data would offer the possibility of more appropriately linking our data with satellite-based measures of vegetation productivity. These data would have inherent problems related to clouds,

but could be analyzed in a conditional logistic framework (Compton et al. 2002, Boyce 2006, Duchesne et al. 2010) to potentially identify fine-scale patterns that were missed. Even more interesting would be to interact NDVI with other variables amassed in our analysis, such as the distance to woody vegetation or anthropogenic footprint, to identify how resource selection changes in relation to changes in productivity, potentially identifying functional responses in selection (Myrsetrud and Ims 1998).

Changes in circadian space use

Results of day and nighttime models supported research hypotheses, with space use increasing in close proximity to anthropogenic features during nighttime periods (P4). Reid (2012) observed these shifts in the Mara and hypothesized that settlements likely provide protection from nighttime predators and increased vegetation quality as a result of nutrient inputs from livestock. During daytime periods, wildebeest are pushed away from settlements by pastoralists to keep their livestock separated from wildlife, especially wildebeest, and minimize disease transmission. Bovine malignant catarrhal fever, for instance, is passed from mother to offspring and is deadly to cattle (Mushi and Rurangirwa 1981, Baxter et al. 2014). We commonly observed this phenomenon across the Athi-Kaputiei Plains (by pastoralists and their dogs), a system in which livestock now outnumber wildlife approximately 4:1 (Reid et al. 2008).

In wet season periods, the relative probability of selection peaks (0.83 relative probability of selection) at 580 m from fence boundaries, meaning that wildebeest do not take the additional risk of being located in the immediate vicinity of fences to meet energy requirements (as observed during the dry season), most likely due to greater resource availability during this season. Fences, however, are also unlikely to act as a repulsive force to wildebeest by themselves. Instead and more likely (importantly) is that it is the combination of fencing and the density of human settlement (i.e., anthropogenic footprint) that leads to decreased space use.

Response to fine-scale habitat variables

We created additional models for the Athi-Kaputiei Plains, inclusive of fine-scale data that

were unavailable across the Amboseli Basin or the Mara. These data, the distance to fences and water use points, proved to be important in predicting wildebeest space use and improved the fit of modeled results. Results of the distance to water use points provided support for expected outcomes, with wildebeest selecting areas that were in close proximity to this important resource, most especially during dry season periods. These water use points provide a valuable resource for livestock across the region and are likely avoided by wildebeest if other sources of water are available. Less dependence on these water use points during wet season periods is supported by the decline in use at short distances. In addition, our results show that wildebeest across this region rarely move to areas > 6 km from water use points, a distance easily dispersed by a wildebeest over a 24-h period (Stabach 2015).

Results observed related to the distance to fence boundaries, however, were contrary to expected outcomes. Wildebeest space use peaked at intermediate distance during both seasonal periods and remained high at short distance during the dry season. It is possible that settlements and resulting fences are built in areas that maximize livestock survival and production (i.e., areas that have the best resources, especially in dry season periods). Wildebeest could be keying in on the same factors that make these areas attractive as settlement locations, taking additional risk by moving to areas in close proximity to fences in dry season periods to meet resource demands.

CONCLUSIONS

Our results highlight a strong negative effect related to anthropogenic risk (P1), indicating a shift in space use of wildebeest toward areas with low levels of disturbance, regardless of season. Wildebeest also showed avoidance of primary roads across the Athi-Kaputiei Plains, providing empirical support to the expected effect of roads on the space use of extant populations. Results related to predictions P2 and P3, however, were inconclusive. Wildebeest space use increased in close proximity to rivers and water use points in dry season periods, representative of a potential functional response between seasonal periods to this valuable resource, while no change was observed in the distance to areas

of dense woody cover during seasonal periods. Weak parameter responses were observed in relation to NDVI, with a shift in space use observed across the Amboseli Basin, the driest of our study areas. No change in relative selection probability was observed in relation to NDVI or Δ NDVI across the Athi-Kaputiei Plains or Mara. We did, however, observe a shift in space use between different temporal periods (P4), with wildebeest space use increasing in relation to anthropogenic features during nighttime periods. Taken together, these results related to predation risks and potential limiting factors provide detailed information on the space use of resident wildebeest, a species that has experienced widespread declines over the past few decades, and offer insight into the likely response of wildebeest to future environmental changes by comparing resource selection across a gradient of vegetation and anthropogenic disturbance.

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