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Spatiotemporal habitat use of large African herbivores across a conservation border

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Abstract

The rapid expansion of human populations in East Africa increases human-wildlife interactions, particularly along borders of protected areas (PAs). This development calls for a better understanding of how human-modified landscapes facilitate or exclude wildlife in savannas and whether these effects change through time. Here, we used camera traps to compare the distribution of 13 large herbivore species in Serengeti National Park with adjacent village lands used by livestock and people at both seasonal and diel cycle scales. The results show that body weight and feeding guild predict habitat use. Smaller sized grazers and mixed-feeders occurred more in village lands than larger herbivores. Across seasons, mixed-feeders and large browsers used edge areas year-round, while grazers were largely excluded during the dry season. At the diel cycle scale, wild herbivores' activity shifts towards the night in village lands compared to the protected area. A closer look revealed that wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) mainly used village lands from pre-dusk to midnight when pastoralists and their livestock were absent. Wildebeest and zebra activity in village lands peaked around dusk, which overlapped with peaks in predator activity. These results suggest that edge areas of PAs can provide valuable habitat to native herbivores. Intensive use of village lands by grazing herbivores during the wet season – particularly at night – suggests grazers benefit from high-quality grazing lawns and increased safety from predators during part of the year. Herbivores that (also) forage on browse can benefit year-round from both food availability and decreased predation risk. We further note that excluding nighttime observations in similar studies may underestimate the use of edge areas by wildlife. Understanding how edge areas fit into the risk-resource landscape will help identify the unique benefits of edge areas to wildlife and promote coexistence of people and wildlife around protected areas.

KEYWORDS

body size, camera trap, pastoralism, predation risk, predator–prey, rangelands, Serengeti

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1 | INTRODUCTION

People and wildlife have coexisted in East Africa for at least 500,000 years, but the continuation of this coexistence is increasingly being questioned (du Toit & Cumming, 1999; Lamprey & Reid, 2004; Veldhuis, Ritchie, et al., 2019). Native large herbivore populations once occurred abundantly all over this region (Western, 1989), but over the past decades, human and livestock population growth has increasingly fragmented and degraded pastoral rangelands, restricting wildlife to PAs (Ogutu et al., 2009). Edge areas of PAs are experiencing high immigration and land conversion rates, which squeezes wildlife even further inside core-PAs, threatening the ecological integrity of the last remaining habitats (Estes et al., 2012; Geldmann et al., 2019; Ogutu et al., 2012; Veldhuis, Ritchie, et al., 2019). Fencing, the hard separation of people and wildlife, is not yet accepted as a solution for the large PAs in East Africa (Hayward & Kerley, 2009, Ogutu et al., 2012, but see Packer et al., 2013), which urges rethinking of the management of these edge areas (DeFries et al., 2007).

The transition from transhumance pastoralism to a predominantly sedentary lifestyle has resulted in year-round high-intensity grazing by livestock in edge areas, which is altering landscapes through changes in vegetation species composition and vegetation structure (Western et al., 2009). Wildlife can still disperse into these human-dominated landscapes, yet we know little about the degree to which wildlife is attracted to or deterred from these edge areas across PA borders. The interaction between livestock and wildlife is often viewed as being competitive due to shared habitat and overlapping resources (Voeten & Prins, 1999), but in some contexts, livestock can facilitate wildlife and vice versa (Odadi et al., 2011). Competitive effects may arise when resources become limited during the dry season, but increased grazing pressure in the wet season may alternatively improve forage quality (Odadi et al., 2011). Grazing during the wet season removes dead standing biomass, which promotes the regrowth of high-quality forage (McNaughton et al., 1997). However, the benefit of improved quality may not outweigh reduced quantity (Voeten et al., 2010). Other positive effects may occur via redistribution of soil nutrients in pastoral lands through the use of temporary livestock corrals called "bomas", which increase spatial heterogeneity and local diversity of the vegetation (Augustine et al., 2011; Marshall et al., 2018). Pastoralists use bomas to protect their livestock overnight, resulting in the concentration of large quantities of dung and urine in small areas. Abandoned boma sites (often referred to as "glades") may persist for decades and attract native (lactating) large herbivores as they provide forage resources of high nutritional quality (Augustine et al., 2011; Reid, 2012).

Boma settlements in pastoral lands can also change the predation risk perceived by herbivores by repelling or attracting predators (Kolowski & Holekamp, 2006). Human activity and the presence of domestic dogs around bomas can markedly decrease attacks from lions (*Panthera leo*), leopards (*Panthera pardus*), and hyenas (*Crocuta crocuta*) on livestock from which wild herbivores may profit as well (Ogada et al., 2003). Animals are expected to weigh predation risk (fear) against gains (food and resources) (Laundré et al., 2001), where herbivore populations are regulated not only by direct predation but also by an "intimidation" or "perceived risk" effect (Creel & Christianson, 2008; Preisser et al., 2005). Edge areas may be perceived as safer by herbivores because reduced grass heights improve the ability to detect or escape from predators (Laundré et al., 2010; Riginos, 2015).

Human-modified edge areas may facilitate or exclude different species of large herbivores because they are differently regulated by resource quantity, resource quality, and predation (Hopcraft et al., 2010; Prins & Olff, 1998). Smaller herbivores have smaller gastrointestinal systems and higher energy expenditure per unit mass, so they must select highly nutritious food (Demment & van Soest, 1985). Larger herbivores can tolerate less nutritious food but require higher quantities (Wilmshurst et al., 2000). Body size also influences species' vulnerability to predation (Sinclair et al., 2003). Populations of smaller-sized species are relatively more regulated by predation because they are predated upon by many predators, while larger species are only predated upon by larger predators (Hopcraft et al., 2010; Olff et al., 2009). The largest megaherbivores (>1000 kg) are not predated upon at all since they are too big for any predator to handle (Owen-Smith, 1988). Therefore, small grazers may profit from nearby pastoral lands in edge areas following the increased food quality and reduced predation risk, while larger grazers are likely to be excluded due to a shortage of resources. These effects may be less straightforward for browsers. Due to a history of heavy grazing and resulting fire suppression, pastoral village lands in areas with sufficient rainfall have been subject to an increase in woody plant biomass (Reid et al., 2008). Resources for this feeding guild may thus be in surplus, especially for large species such as giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*) as they feed up high and thereby do not compete with browsing goats (*Capra hircus*).

Perceived predation risk is not a fixed spatial pattern and typically changes across much shorter timescales than forage quantity or quality. Large herbivores are expected to adaptively change their habitat selection across the diel cycle as local predation risk in specific habitats increases or decreases, for example, due to changes in the activity of predators (Kohl et al., 2018; Palmer et al., 2017; Veldhuis et al., 2020). Masai pastoralist activities in village lands add to this dynamic landscape of fear. Their daily activities may be perceived as a risk and exclude wildlife during specific periods, even though hunting for consumption is culturally unacceptable to Masai (Goldman, 2007). This exclusion may be amplified by thermal stress in larger bodied herbivores because disturbance by pastoralists prevents them from resting during the day's hottest hours (Owen-Smith & Goodall, 2014; Owen-Smith & Traill, 2017).

Spatial and temporal heterogeneity in the quality and quantity of food resources and security from predation in savanna landscapes hence play a major role in the distribution of native large herbivore assemblages. Here, we assess the spatiotemporal habitat use of African native large herbivores across the conservation border between the Serengeti National Park and the Loliondo communal pastoral village lands in Tanzania. Specifically, we asked (1) how do feeding guild and body size control relative activity of wild herbivores in pastoral village lands versus adjacent protected areas at the seasonal and diel cycle scale, and (2) how do diel activity patterns of wild herbivores compare to the diel activity patterns of both people (and their livestock) and predators?

2 | METHODS AND MATERIALS

2.1 | Study area and design

The study was conducted in the Greater Serengeti-Mara ecosystem (GSME) in East Africa, one of the world's largest remaining PA complexes and home to abundant and diverse wildlife. The GSME includes the Serengeti National Park (SNP) in Tanzania and the Masai Mara National Reserve in Kenya, with human activities restricted in both PAs. They are bordered by multiple land management types, such as game reserves allowing hunting, wildlife management areas allowing livestock, conservancies promoting tourism benefits on leased private lands, game-controlled areas, and regular village lands. We performed our camera trapping study in the North-eastern corner of the Tanzanian side of the GSME, where the SNP borders the Loliondo Game Controlled Area (LGCA) (Figure 1). The LGCA is mainly inhabited by Masai, whose economic mainstay is livestock keeping through herded, free-ranging grazing (pastoralism). Communally used grazing lands in Ololosokwan are grazed and browsed year-round by cattle (*Bos taurus*), sheep (*Ovis aries*), and goats. Mean annual precipitation is approximately 1000 mm. Rainfall is highly variable in the entire region but generally peaks during the short rainy season from November to December and during the long rainy season from March to May, while the peak of the

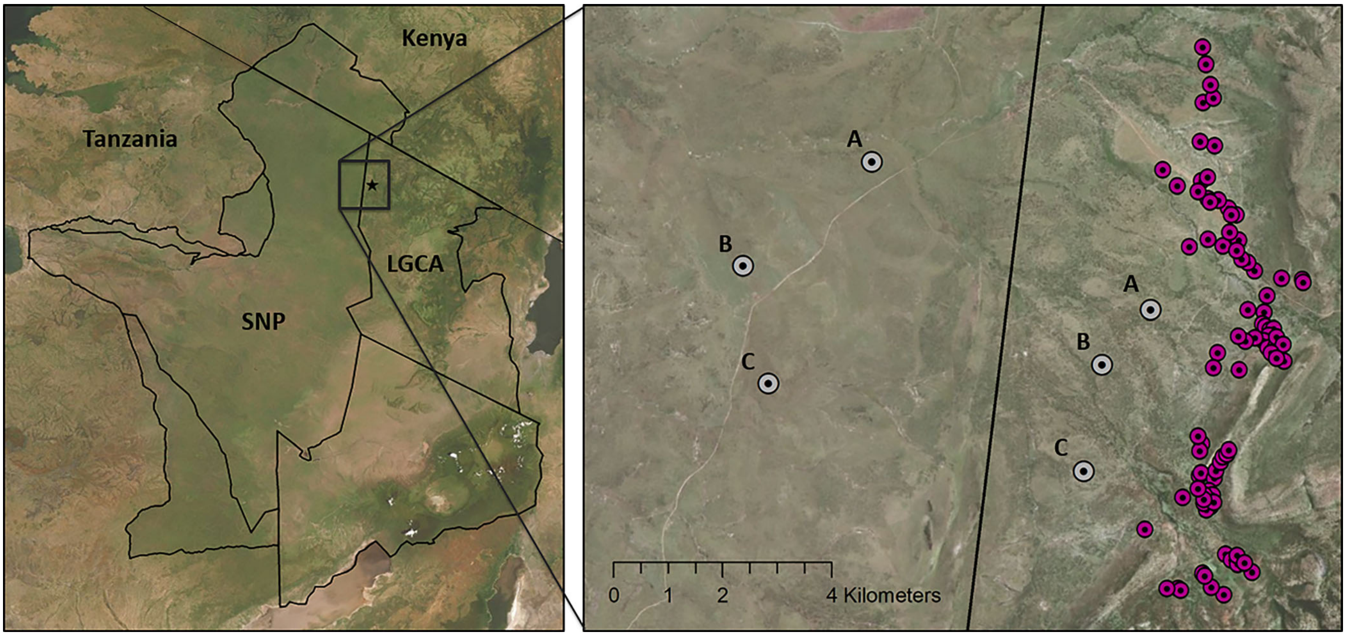

FIGURE 1 Map showing the location of the study area within the greater Serengeti-Mara ecosystems (left panel) and the study design showing the location of blocks (a-c) in Serengeti National Park (SNP) and adjacent communal village lands of Ololosokwan within Loliondo game controlled area (LGCA) (right panel). Sites in the village lands are solely used for livestock husbandry and are situated between the park boundary and Masai bomas (purple dots)

dry season falls in July–September when it generally does not rain at all (Mahony et al., 2021). The landscape is characterized by gently rolling granitic pediplains (Jager, 1982), and the vegetation can be classified as savanna woodlands. The area is frequented by a diverse suite of large resident herbivores and migratory wildebeest, zebra, and Thomson's gazelle (*Eudorcas thomsonii*).

We deployed 12 camera traps in the PA and adjacent Ololosokwan communal grazing lands. Study sites ($N = 6$) were located between two to five kilometers away from the park boundary on both sides. The sites in the village lands are located in the center of the main grazing lands, rather than between active bomas, while the sites in the PA are located further away from the park boundary to ensure there are no edge effects (Figure 1). All sites are on the same landform and geology (as indicated by geomorphology and dominant tree species) in the PA and the village land. Sites followed a block design (A-C), where each of the three sites within the PA is paired with a site in the village lands (Figure 1). Each of the six sites consisted of two plots, each with one camera trap. Each plot was placed approximately halfway the catenae gradient (for definition and history of the concept, see Borden et al., 2020) to control for potentially elevated predation risk in drainages due to reduced overview of the surroundings. In order to limit the influence of confounding factors within the blocks, we placed the two plots relatively close to each other (~500 meters) compared to the distance between blocks. While a greater distance would decrease the potential double-counting of individual animals within a block, this was typically the maximum distance at which two plots could be placed at the same sloping area, at the same catenae position, and with a similar density of woody plants.

2.2 | Data collection and processing

At each plot, we fitted one camera trap (Bushnell Trophy Cam, model 119,736) to collect motion-triggered images within timeframes of 3 weeks during the end of the wet season (28th of May – 17th of June) and the dry season (8th of August–28th of August) of 2016. Cameras were attached on single standing trees at 2.5 meters from the ground and with a viewing angle set so that approximately 20% sky was visible in each frame. Because our study focuses on large mammalian herbivores (Thomson's gazelle to elephants) rather than the small to medium-sized vertebrates like hare, we could deviate from the standard practice of installing cameras at ~50 cm height (Swanson et al. 2015). Instead, we ensured a wide view of the entire plot, allowing full-body images of our focal species, even in taller grass. The camera trapping period encompassed 504 trap days (21 days * 2 seasons * 12 cameras), resulting in 88,463 images. To ensure that the detection area during the daytime matches the detection area during the night, animals were only counted up to 15 meters away from the camera (marked with a stone in the field) as the camera's infrared light only illuminates up to this distance. To minimize double-counting of individuals that remained within the camera's field of view for prolonged periods, we used 10-min time slots in which we used the image within each sequence with the most individuals for scoring. This ensures statistical independence of measurements as individual animals are unlikely to stay in the same place (in front of cameras) longer than 4–5 min in these systems (Palmer et al., 2017).

2.3 | Body size and feeding guild

Information on the bodyweight of wild herbivores present in the study area was derived from Maloiy et al. (1982), Smith et al. (2003), and Hopcraft et al. (2015), where body weights estimated on the East-African population were favored in case of multiple reports, and sexes were averaged. Information on feeding guilds was extracted from Hofmann and Stewart (1972) (Table S1).

2.4 | Data analysis

The dataset to assess the spatiotemporal distribution of different wild herbivore species across land use and season consisted of the sum of all counts of individuals scored at each plot per season. These counts of photographic rates should be interpreted as an index of activity as these rates can increase because more individuals use a particular site or use that site more often (Sollmann, 2018). The response variable thus represents the activity of a particular species within 3-week intervals. Only species that occurred in both village lands and protected areas and had at least five scorings within one land use (regardless of season) were included in the analysis. Initially, generalized linear mixed models (GLMM) assuming a negative binomial distribution and a logarithmic link function were fitted using the *lme4* package in the R coding environment (Bates et al., 2007). *Land use*, *season*, and their interaction were used as fixed terms and *block* was used as a random term. However, between-block variability was insufficient (estimated variance = 0) to include random effects for all but one species, the hyena. Therefore, generalized linear models (GLM) using the MASS package (Ripley et al., 2013) were fitted instead for the other species. We opted for a negative binomial distribution because of overdispersion and a quadratic relationship between the mean and variance (Ver hoef & Boveng, 2007). To examine the role of body weight and feeding guild in seasonal habitat choice of herbivore species across the conservation border, we calculated the log response ratio for each block as follows:

$$\text{Response ratio} = Log\frac{N_{VL}+0.01}{N_{PA}+0.01} \tag{1}$$

Where N_{VL} represents the number of individuals of a specific species in the village lands, N_{PA} represents the number of individuals of the same species in the protected area. A constant with a value of 0.01 is added to enable zero values to be used in the calculation of the response ratio. Positive response ratio values signify a preference for village lands for a given species, while negative values mean preference for protected areas. The mean log response ratios across the blocks for each species were analyzed using ANCOVA. The dataset thus included a log response ratio value for each species for each season (fixed factor) and information on that species feeding guild (fixed factor) and body weight (covariate). Body-weight was log-transformed to meet the assumptions of a normal distribution of residuals. Interaction terms between all predictor combinations were tested. Models were evaluated based on AIC scores, where the least-complex but the still-sufficient fitting model was selected when ΔAIC was lower than two (Burnham & Anderson, 2004). Because this analysis also includes less common species with less than five individual recordings within one land use, weights based on the number of blocks (1–3) in which a species occurred were used in the fitting process.

The effect of land use, body weight, and feeding guild on diel habitat choice was analyzed in a similar way to seasonal habitat choice. Captures between sunrise (06:45) and the start of civil twilight (18.45) were classified as “daytime” while captures between 18.45–06.45 were classified as “nighttime”. Due to relatively low captures during the dry season, we did not include the effect of season in this analysis. Additionally, we wanted to examine whether body weight and feeding-guild determine nighttime use. Here, we used the log response ratio between day (06:45–18:45) and night (18:45–06:45) captures for each species that occurred in both land uses to examine whether nighttime use changes with *land use* (fixed factor), *feeding-guild* (fixed factor), and *body weight* (covariate). In this analysis, positive response ratio values signify a preference for daytime activity for a given species, while negative response ratio values indicate a preference for nighttime activity.

We obtained sufficient data over the study period for wildebeest and zebra to perform a more detailed analysis for these species and assess whether their activity was higher in village lands at specific times of the day. To this purpose, we used the counts of animals captured by cameras at each site, each day and each hour of the day. This part of the study focused on the wet season, as these two species made only limited use of village lands during the dry season. A similar analysis during the dry season would require more data (more trap days). The counts of animals captured by cameras at each site, each day, and each hour of the day contained many zeros. We, therefore, used specialized statistical models to accommodate data with excess zeros (Martin et al., 2005). Here, we assume that the zero counts in the data set are a mixture of structural zeros and random zeros. For example, browsers that prefer woodlands, such as giraffe, will likely avoid more open grassy areas leading to structural zeros instead of random zeros. However, not all woodlands can be continuously used by giraffes, resulting in random zeros in the dataset. Because the non-zero counts were overdispersed (having a greater variance than expected based on the assumed distribution), we fitted zero-inflated GLMs assuming a negative binomial distribution (ZINB) with a logarithmic link function for the count portion of the data and a logit link function for the zero portion of the data using the *GlmmTMB* package (Magnusson et al., 2017). Site within block was added as a random effect, and we accounted for within-site temporal autocorrelation by including an AR1 covariance structure for the temporal covariance between observations from hour to hour within sites. Due to the cyclic nature of diel data, the candidate models included periodic components, represented by pairs of sine and cosine functions over the day with a fundamental period of 24 h and one to three harmonics of 12-, 8-, and 6-h periodicity to modulate the signal (Nelson, 1979). The model was specified as:

$$\begin{aligned}\log(\text{count}(x)) = \alpha_0 + \left(\alpha_1\cos\frac{2\pi x}{24}+\beta_1\sin\frac{2\pi x}{24}\right)\\ +\left(\alpha_j\cos\frac{h_j 2\pi x}{24}+\beta_j\sin\frac{h_j 2\pi x}{24}\right)\end{aligned} \tag{2}$$

With x representing the hour of the day and h representing the j_{th} harmonic, where a full model would comprise all three harmonics. The periodic components were first included in the zero portion of the model, then in the count portion, and lastly in both the zero and count portions. A null model (intercept-only for both the count and the zero portion) was also considered, which assumed that activity was constant across the diel cycle. Models were evaluated based on AIC scores, where the least-complex but the still-sufficient fitting model was selected when ΔAIC was lower than 2 (Burnham & Anderson, 2004). Land use was

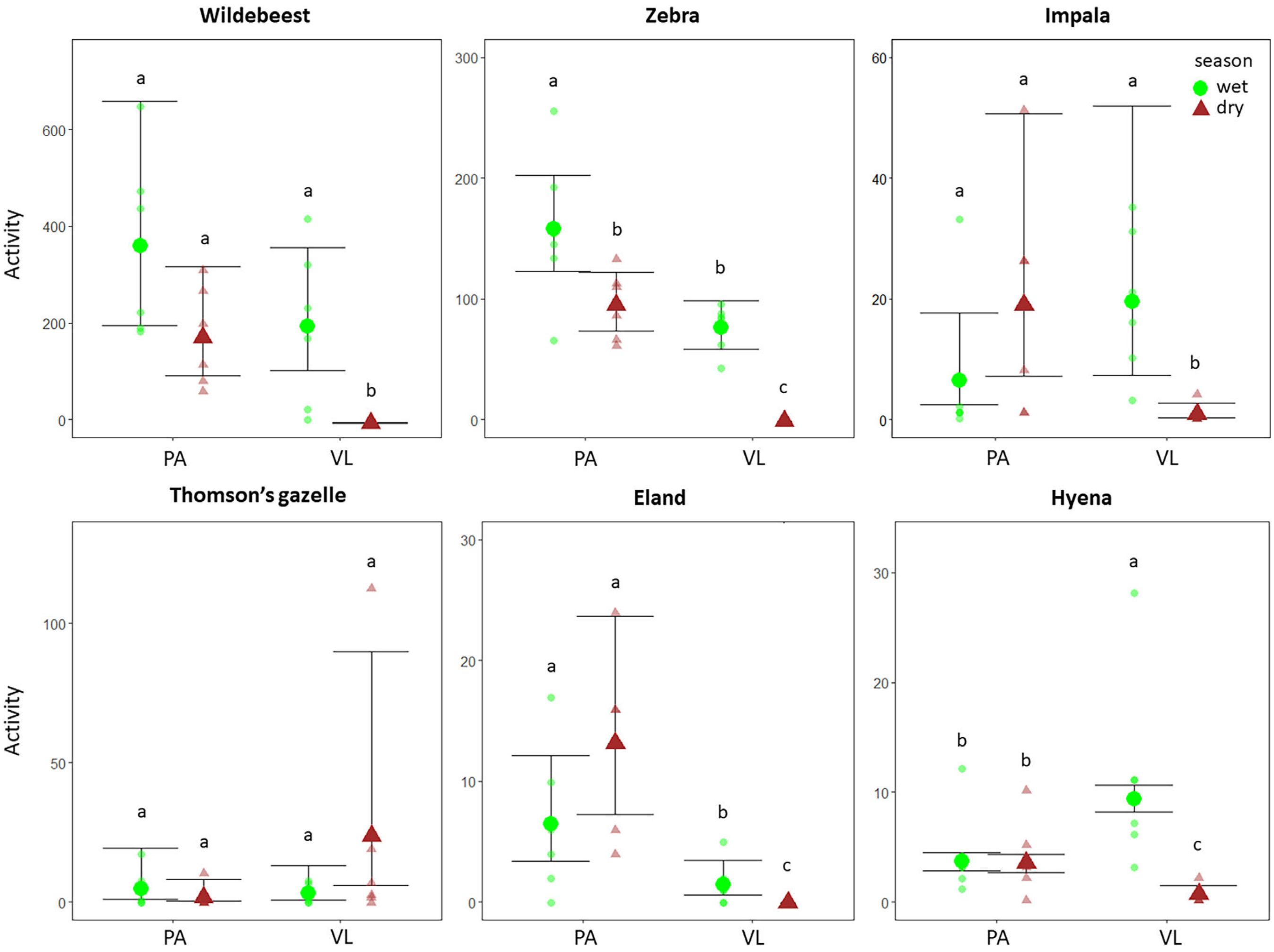

FIGURE 2 The effect of land use (PA, protected area; VL, village lands) and season on the activity of six large mammal species. Activity represents the total counts (or photographic rate) of individuals within 3-week intervals. Large symbols represent the predicted mean, while small symbols show the actual counts for each plot. Error bars represent 95% confidence intervals. Groups marked with similar letters were not different ($\alpha > 0.05$). For zebra and eland, likelihood ratio tests were used to test differences between groups

included as a fixed factor, and interaction terms between periodic components and land use were tested. We also modeled hyena activity (the only predator species scored during the study period) and livestock activity over the diel cycle. Activity models for livestock were limited to village lands as no livestock incursions into protected areas were recorded during the study period. All analyses were performed in the statistical environment R, version (3.6.1) (R Development Core Team 2019).

3 | RESULTS

3.1 | Seasonal habitat choice

Considering all species with more than one occurrence during the study period, a total number of 7333 animals were scored, representing 14 species (Table S2). Hyena was the only predator species observed, with a total number of 119 records. Out of the 13 wild herbivores, we found that wildebeest, zebra, impala (*Aepyceros melampus*), Thomson's gazelle, eland (*Tragelaphus oryx*), topi (*Damaliscus lunatus*), hartebeest (*Alcelaphus buselaphus)*, Grant's gazelle (*Nanger granti*), and elephant occurred both in protected areas and in adjacent village lands. Giraffe only occurred in the village lands while dik-dik (*Madoqua kirkii*), duiker (*Sylvicapra grimmia*) and buffalo (*Syncerus caffer*) were only observed in the protected area during both seasons.

The activity of wildebeest, zebra, impala, eland, and hyena was low in village lands during the dry season but increased during the wet season (Figure 2, Table 1). In contrast, the activity of Thomson's gazelle seemed to increase during the dry season compared to the wet season in village lands (GLM, Land use x Season effect, $X^2 = 3.975$, $df = 1$, $p = 0.046$). In the wet season, the activity of wildebeest,

TABLE 1 Generalized linear (mixed) model estimates for each study species analyzing the effect of land use, season, and their interaction on activity. The estimated variance between blocks was 0.352 for hyenas. For other species, between-block variability was insufficient to include random effects in models (estimated variance = 0)

	Intercept		**Land-use**		**Season**		**Land use × season**	
Species	**Estimates**	**z**	**Estimates**	**z**	**Estimates**	**z**	**Estimates**	**z**
Wildebeest	**5.905 ± 0.305**	19.356	−0.605 ± 0.432	−1.402	−0.723 ± 0.432	−1.673	**−4.982 ± 0.789**	−6.314
Zebra	**5.069 ± 0.126**	40.286	**−0.721 ± 0.181**	−3.982	**−0.506 ± 0.180**	−2.815	*	
Impala	**1.846 ± 0.520**	3.549	1.116 ± 0.724	1.543	1.090 ± 0.724	1.506	**−4.457 ± 1.127**	−3.954
Thomson's gazelle	**1.764 ± 0.695**	2.537	−0.420 ± 0.991	−0.424	−0.916 ± 1.004	−0.912	**2.887 ± 1.403**	2.058
Eland	**1.872 ± 0.321**	5.833	**−1.466 ± 0.540**	2.716	0.706 ± 0.439	1.607	*	
Hyena	**1.260 ± 0.425**	2.968	**0.967 ± 0.305**	3.169	−0.041 ± 0.347	−0.117	**2.770 ± 0.652**	−4.250

Note: Estimates are presented as the estimate ± standard error, with significant predictors highlighted in bold ($\alpha < .05$). For the categorical predictor ‘land use’, PA is the reference group. For the categorical predictor ‘season’, the wet season is the reference group. *Parameter estimates became infinite because of zero-only observations within a combination of land use and season (representing a mean of zero).

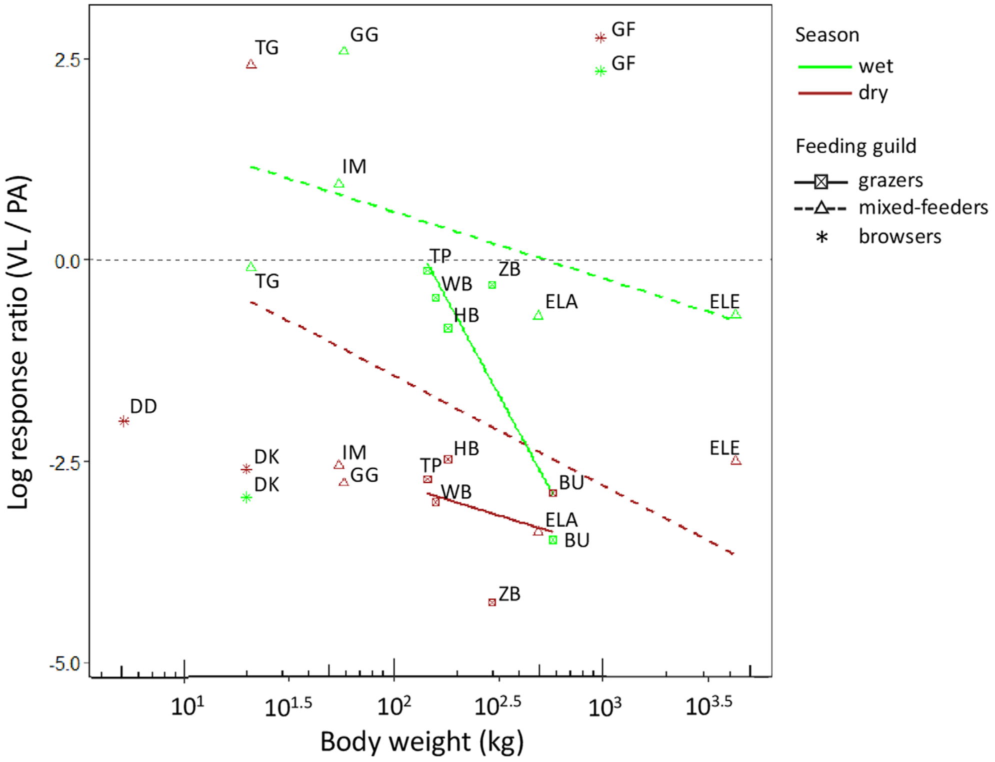

FIGURE 3 The effect of body weight on the relative occurrence of large herbivore species in village lands as given by the log response ratio. A negative ratio indicates a preference for the protected area, while a positive ratio indicates a preference for the village lands. The figure shows the mean log response ratio for three guilds, grazers (squares), mixed-feeders (triangles), and browsers (asterisks) in the wet season (green symbols) and dry season (brown symbols). Lines represent the conditional means for the grazer (solid lines) and mixed-feeder (dashed lines) guilds in the wet and dry season. Browsers species were not included in the model to prevent overfitting due to low number of species, but the mean log response ratio is shown in the figure. Full species names for the codes: BU, buffalo; DD, Dik dik; DK, gray duiker; ELA, eland; ELE, elephant; GF, giraffe; GG, Grant's gazelle; IM, impala; HB, hartebeest; TP, topi; WB,wildebeest; ZB, zebra

impala, and Thomson's gazelle was similar between village lands and the protected area, while the activity of the larger-bodied zebra and eland was significantly lower in village lands (Figure 2). Lastly, the activity of hyenas was higher in village lands compared to the protected area during the wet season (Figure 2).

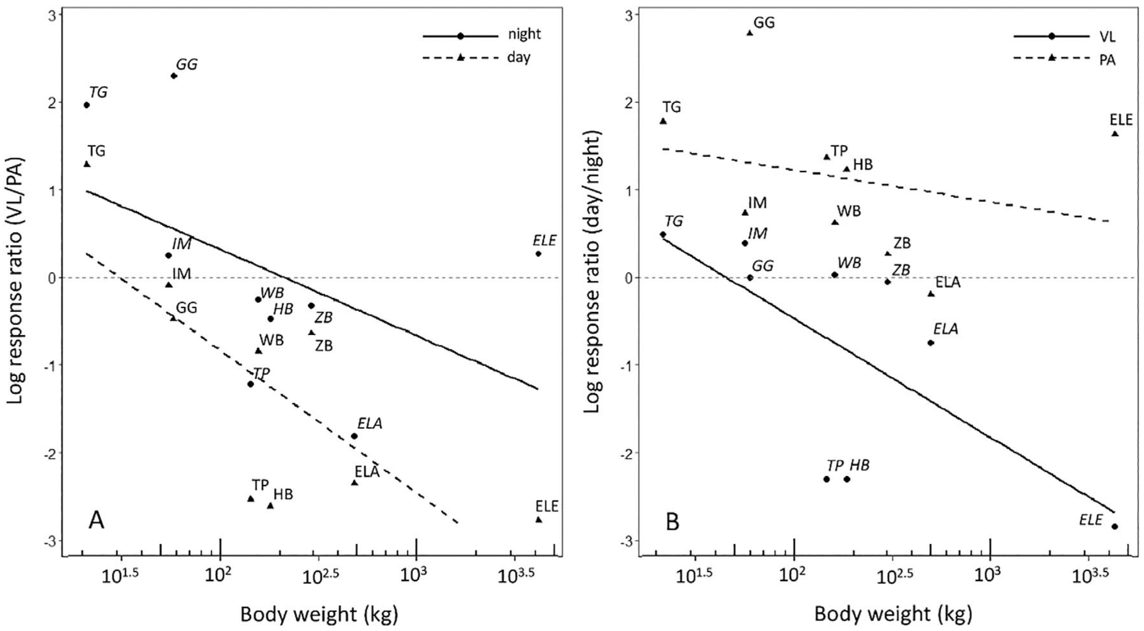

FIGURE 4 The effect of time of the day (daytime or nighttime) on the relative occurrence of large herbivore species with different bodyweights in village lands versus protected areas (a). A negative ratio indicates a preference for the protected area, while a positive ratio indicates a preference for the village lands. Figure a shows the conditional mean for nighttime activity (solid line) and daytime activity (dashed line). Panel B shows the effect of land use and bodyweight on the relative occurrence during the daytime versus the nighttime. A negative ratio indicates a preference for nighttime activity, while a positive ratio indicates a preference for daytime activity. The figure shows the conditional mean for the village lands (VL, solid line) and protected area (PA, dashed line). Full species names for the codes: ELA, eland; ELE, elephant; GG, Grant's gazelle; IM, impala; HB, hartebeest; TP, topi; WB, wildebeest; ZB, zebra

3.2 | The role of body weight and feeding guild

Only three browser species were observed in the study, so we excluded this feeding guild from the models to avoid low statistical power. Relative occurrence in village lands, expressed by the log response ratio, was best predicted by a model that included main effects of the covariate bodyweight ($p = .019$), the factor season ($p = .004$), and a non-significant effect of the factor feeding guild ($p = .068$, Figure 3; $F_{3,16} = 7.40$, adj. $R^2 = .50$, $p = .003$). The log response ratio was higher overall during the wet season, meaning that wild herbivores mostly use village lands during the wet season (Figure 3). Bodyweight had a negative effect on the log response ratio while species belonging to the grazers guild tended to have a lower log response ratio than mixed feeders (Figure 3), meaning that smaller species and mixed-feeders made relatively more use of village lands than larger species and grazers (Figure 3).

3.3 | Habitat choice over the diel cycle

The relative activity of wild herbivores in village lands increased during nighttime, as signified by the higher log response ratios during the night ($p = 0.028$) (Figure 4a). Log response ratios increased for every single species (Figure 4a). For two small-sized species (impala and Grant's gazelle) and the largest species (elephant), the log response ratio was negative during the daytime (more individuals active in the park) but turned positive during the nighttime (more individuals active in village lands). Similarly to the analysis on seasonal habitat choice, there was a negative effect of body size on the log response ratio ($p = .003$) ($F_{2,15} = 9.00$, adj. $R^2 = .48$, $p = .003$). Log response ratios of day to nighttime activity were higher than 0 for all species in the protected area, except for eland, meaning that herbivores are mostly active during the daytime in the park (Figure 4b). Relative daytime activity decreased significantly in village lands compared to protected area ($p = .005$) (Figure 4b), with some species (elephant, topi, and hartebeest) only occurring in village lands at night. Furthermore, nighttime activity appeared to increase with, although this effect is non-significant ($p = .059$) ($F_{2,15} = 7.49$, adj. $R^2 = .43$, $p = .006$).

A closer look at the activity of wildebeest and zebra over the entire diel cycle shows that activity was not equally distributed over the day, as indicated by the significant periodic components in the best models (Table S3). In addition, multiple interactions between periodic components and land use were included in the best models, implying that diel cycle activity patterns are different

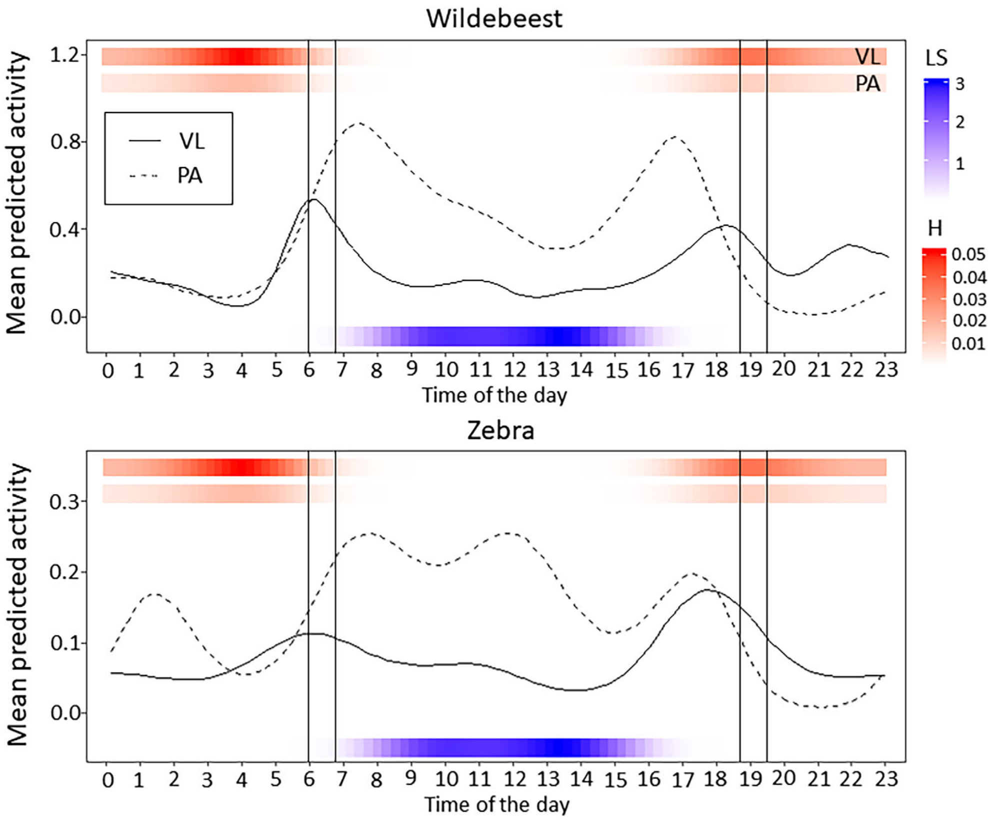

FIGURE 5 Mean predicted activity for village lands and adjacent protected areas for wildebeest (upper panel) and zebra (bottom panel) over the diel cycle. Blue color gradients represent the mean predicted activity of livestock (LS) in village lands, and red color gradients represent the mean predicted activity of hyenas (H) in village lands (VL, upper bar) and protected areas (PA, bottom bar). Vertical lines represent dawn (start of nautical twilight–Sunrise) and dusk (sunset–End of nautical twilight)

across protected areas and village lands (Table S3). Activity over the diel cycle follows broadly the same pattern for wildebeest and zebra (Figure 5). The mean predicted activity was higher in protected areas than in village lands during the daytime (Figure 5). During dusk, activity decreased more sharply in protected areas than in village lands and mean activity was higher in village lands until midnight. After midnight, zebra activity showed a peak between 01:00 and 02:00 in protected areas, while activity remained more constant in village lands. Wildebeest activity remained low after midnight in both protected area and village lands until the hour before dawn. The livestock activity model revealed that Masai started to use the village lands between 07:00 and 08.00 in the morning and returned to their bomas around 15:00 and 16:00. These times coincide with respectively the decrease and increase of wildebeest and zebra activity in village lands (Figure 5). The best model for hyena activity over the diel cycle revealed a peak in activity between 04:00 and 05:00 and a smaller peak at 20:00. The best model did not include interactions between periodic components and land use, implying that patterns over the diel cycle are comparable in village lands and protected areas (Table S3). Land use was a significant predictor in the best model describing hyena activity, with overall higher activity in village lands (Table S3, Figure 5). The stronger predicted peak in hyena activity in the early morning coincided with the strongest depression in predicted wildebeest activity, but not for zebra (Figure 4).

4 | DISCUSSION

We found that the edges of a protected area hosted a diverse assemblage of wildlife. Bodyweight and feeding guild were found to be important traits determining village grazing lands' relative suitability across two temporal scales (seasons and the diel cycle) for different herbivore species. Smaller sized herbivores occurred more in village lands than larger herbivores, but only for grazers and mixed-feeders (Figure 3). Furthermore, while mixed-feeders and large browsers may use edge areas year-round, grazers appear to be largely excluded from village lands during the dry season. Finally, we showed that wild herbivores' activity shifts towards the night in village lands compared to the protected area (Figures 4 and 5). This result implies that the use of edge areas by wildlife may easily be underestimated when excluding nighttime observations (as is the case in many surveys executed from vehicles or airplanes).

4.1 | The role of body weight and feeding guild in seasonal habitat choice

The role of body weight in predicting the occurrence of wild herbivores in village lands versus the protected area was expected to be due to a combined difference in forage quality and predation risks. However, our findings show that hyena activity was highest in the village lands during the wet season (Figure 2). Therefore, positive effects in terms of safety from predation may be more related to an increase in visibility, allowing wild herbivores to spot predators in time due to the shorter grass. The increase in activity of hyenas in village lands in the wet season may explain why Thomson's gazelle showed lower activity in the wet season than the dry season (Figure 2). This would imply a form of "apparent competition" (Holt & Bonsall, 2017), where the increase of multiple prey species (impala, wildebeest, and zebra) in village lands negatively impacts a fourth (and the smallest) prey species (Thomson's gazelle). The occurrence of Thomson's gazelle was found to be higher in pastoral ranches year-round by Bhola et al. (2012), which can be explained by sharper contrasts in the risk-resource landscape in the Mara reserve versus surrounding ranches. While the herbaceous layer is short and hence of higher quality in the village grazing lands of Ololosokwan, high tree density may still allow for successful hunting by hyenas due to better stalking opportunities, a phenomenon observed for lions (Hopcraft et al., 2005). As habitat choice is expected to be the outcome of animals weighing predations risks (costs) to gains (resources) (Bakker et al., 2005; Creel & Christianson, 2008; Preisser et al., 2005), costs for the smallest species may be higher during the wet season in these village lands.

The change in activity between seasons for Thomson's gazelle can also be explained by feeding strategy. Herbaceous plants generally senesce rapidly at the onset of the dry season, while many savanna trees can maintain productivity weeks into the dry season by extracting water from deeper soil layers (Scholes & Archer, 1997). Mixed feeders tend to switch guilds on a seasonal basis, where they show a preference for fresh grass in the wet season, while browse is a fall-back option in the dry season (du Toit, 2003; Jarman, 1979). While access to high-quality graze during the wet season in village lands may be limited due to predation risk constraints, Thomson's gazelle have ample browse opportunities and safety during the dry season in the village lands. The switch in mixed-feeders' diet also explains the overall higher log response ratios for mixed feeders compared to grazers (Figure 3). The use of village lands is restricted to the wet season for grazers because resources are generally too low in the dry season, while mixed feeders can use village lands year-round. However, this explanation does not fit the seasonal habitat choices of eland as they were not scored in the village lands in the dry season. Despite its large bodyweight, eland was repeatedly observed in village lands during the wet season. Bhola et al. (2012) found an increased eland occurrence on pastoral ranches in the wet season as well, which they explained by a potentially higher density of (by eland) favored nutritious forbs (Watson & Owen-Smith, 2000).

While the generalization on the role of body size and feeding guild provides a useful framework, it is important to note that there are exceptions that can be explained by individual species' specific ecology. For example, all species used in our analysis are more or less social/gregarious, with implications for strategies to escape from predation. While the low number of browser species in this study prohibited us from including dik-dik and gray duiker in the analysis, the fact that they were only captured in the National Park contrasts with the general patterns of body weight found for more abundant species. While gregarious species find safety in numbers (dilution effect, mutual warnings) (Lehtonen & Jaatinen, 2016), dik-dik and duiker live respectively in pairs or solitary and tend to avoid predation by crypsis (Jarman, 1974). Predator avoidance by crypsis may be less effective in village lands where herbaceous vegetation is short, and hiding places for these elusive animals are scarce.

4.2 | Activity of wildlife across the diel cycle

Besides the strong seasonal effect, our results show that wild herbivores also change habitat selection across the diel cycle (Figure 4). Wild herbivores were relatively more active during the nighttime in village lands compared to protected areas (Figure 4a), which can be explained by the daily activities of Masai pastoralists (livestock herding, traveling by motorcycles) as this leads to disturbance and could be perceived as a risk by wild herbivores (Frid & Dill, 2002). Alternatively, the relative increase in nighttime activity may be caused by safety from predators in the village lands compared to the protected area. Wild herbivores are expected to continuously balance trade-offs in fitness between gains in resources, predation risk, as well as thermal constraints (Bakker et al., 2005; Veldhuis, Kihwele, et al., 2019). This trade-off may explain why we overall found a trend of increased nighttime activity with bodyweight (Figure 4b). On hot days, large-bodied herbivores face the risk of thermal stress and have to trade-off resource gains with thermoregulation (Mason et al., 2017). Switching foraging activities to cooler times of the day is not that simple because of nocturnal predation risk. Especially, intermediate-sized herbivores (100 – 550 kg) appear to have a relatively tight time window for foraging activity as their body size makes them both vulnerable to predation and thermal stress (Hopcraft et al., 2010; Veldhuis et al., 2020). Edge areas may thus be important in alleviating the simultaneous pressures on this group of intermediate-sized herbivores by providing nearby safe habitat, thereby relaxing the nocturnal predation constraint.

More detailed activity models for wildebeest and zebra over the diel cycle revealed that the use of village lands versus protected areas continuously changed over the course of the day (Table S3, Figure 5). While the mean activity over the entire day is lower in village lands for both species, mean activity was predicted to be higher in village lands from the hour preceding dusk until midnight for both species (Figure 5). Time allocation to different activities such as foraging or resting may indicate how animals make the trade-off between resource gains, predation risk, and thermal stress over the diel cycle (Bunnell & Harestad, 1990; Owen-Smith, 1998). Owen-Smith and Goodall (2014) found depressions in activity (resting) during midday and pre-dawn for buffalo and zebra. At the same time, activity (both foraging and traveling) peaked during the early morning and late afternoon (Owen-Smith & Goodall, 2014). These schedules largely overlap with our activity models and may, therefore, reflect the same activities (Figure 5). The lower activity of wildebeest and zebra in village lands compared to protected areas during the daytime may be explained by the presence of Masai and livestock, while peaks in the late afternoon may reflect the onset of grazing activities.

After the peak in the late afternoon, the drop in activity is more apparent for both wildebeest and zebra in the PA (Figure 5). Concurrently, the activity peak is predicted to be slightly later in village lands than in the PA (Figure 5). The drop coincides with the increasing activity of hyenas in both village lands and the protected area. Combined, these patterns may point towards rewards in the form of relief from predation risk in village lands. Risk allocation theory predicts that animals should invest time in intense feeding efforts during pulses of safety (Lima & Bednekoff, 1999). In this case, the higher visibility in village lands may allow wildebeest to allocate time to foraging, explaining the higher activity in the hours up until midnight (Figure 5).

Hyenas showed a second (higher) peak in activity during pre-dawn, which coincides with the lowest predicted activity of both wildebeest and zebra in both land uses. It may, however, be too simple to view the low activity of wildebeest and zebra as being the direct consequence of a higher hyena activity (Figure 4). A sleeping period alternatively explains the pre-dawn depression in activity (Owen-Smith & Goodall, 2014). A short sleeping/resting period has been recorded for several species around this time, including greater kudu (Owen-Smith, 1998) and impala (Jarman & Jarman, 1973). While it may seem counterintuitive that wild herbivores choose to sleep during a time with high predator activity and low ambient temperatures, the net effect on fitness may be positive as the rest period clears the rumen space right before prime foraging hours in the morning (Owen-Smith, 1988). This explains why the depression is more pronounced in wildebeest (ruminant) than in zebra (hindgut fermenters). Higher food intake requirements of hindgut fermenters may explain why zebra activity showed two more peaks during midday and between 01:00 and 02:00 during the night (Janis, 1976). Zebras have to consume more food to meet their nutritional demands and a nightly feeding session during a temporary depression in hyena activity would be in line with risk allocation theory (Lima & Bednekoff, 1999).

In this study, we showed that body size and feeding guild are key traits in predicting large African herbivores' habitat choice across a soft-edge conservation border. Persistent high-intensity grazing by livestock in edge areas has resulted in, and maintains, short swards of high-quality forage, which likely favored small-sized herbivores requiring nutritious grasses while excluding larger bodied herbivores requiring bulk forage. Furthermore, long-term fire suppression (> 15 years) in the pastoral village lands of Ololosokwan gave rise to a cohort of predominantly single-stemmed *Vachellia gerrardii* trees that offer forage to mixed-feeders and browsers without reducing visibility. These human-induced landscape changes may have promoted wildlife occurrence, especially during the most dangerous times of the day, when the activity of predators is highest, and human activity is lowest. This study confirms that edge areas that are used for livestock grazing alone can be compatible with wildlife conservation in edge areas. Compatibility in other edge areas around the GSME or other protected areas in East Africa may depend on land use and other characteristics such as tree cover. The novel insight that wild herbivores use edge areas at specific times of the day furthers our understanding of the unique benefits of edge areas to conservation and could aid in future management opportunities for the continued coexistence of people and wildlife.

AUTHOR CONTRIBUTIONS

Inger K. de Jonge, Han Olff, and Michiel P. Veldhuis conceived the ideas and designed methodology; Inger K. de Jonge and Remo Wormmeester collected the data; Inger K. de Jonge and Remo Wormmeester analyzed the data; Inger K. de Jonge led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

To the best of our knowledge, none of the above-suggested persons have any conflict of interest, financial or otherwise.

DATA AVAILABILITY STATEMENT

The data associated with this manuscript will be published in a repository of the University of Groningen and will be issued searchable DOIs cited in the manuscript.

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REFERENCES

Augustine, D. J., Veblen, K. E., Goheen, J. R., Riginos, C., & Young, T. P. (2011). Pathways for positive cattle–wildlife interactions in semiarid rangelands. *Smithsonian Research online*, *632*, 55–71.

Bakker, E. S., Reiffers, R. C., Olff, H., & Gleichman, J. M. (2005). Experimental manipulation of predation risk and food quality: Effect on grazing behaviour in a central-place foraging herbivore. *Oecologia*, *146*, 157–167.

Bates, D., Sarkar, D., Bates, M. D., & Matrix, L. (2007). The lme4 package. R package version, *2*(1), 74.

Bhola, N., Ogutu, J. O., Piepho, H.-P., Said, M. Y., Reid, R. S., Hobbs, N. T., & Olff, H. (2012). Comparative changes in density and demography of large herbivores in the Masai Mara reserve and its surrounding human-dominated pastoral ranches in Kenya. *Biodiversity and Conservation*, *21*, 1509–1530.

Borden, R. W., Baillie, I. C., & Hallett, S. H. (2020). The east African contribution to the formalisation of the soil catena concept. *Catena*, *185*, 104291.

Bunnell, F. L., & Harestad, A. S. (1990). Activity budgets and body weight in mammals. How sloppy can mammals be? *Current mammalogy*, *2*, 245–305.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*, 261–304.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, *23*, 194–201.

DeFries, R., Hansen, A., Turner, B. L., Reid, R., & Liu, J. (2007). Land use change around protected areas: Management to balance human needs and ecological function. *Ecological Applications*, *17*, 1031–1038.

Demment, M. W., & van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*, 641–672.

du Toit, J. T. (2003). Large herbivores and savanna heterogeneity. In *The Kruger experience: Ecology and management of savanna heterogeneity* (pp. 292–309). Island Press.

du Toit, J. T., & Cumming, D. H. M. (1999). Functional significance of ungulate diversity in\rAfrican savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, *8*, 1643–1661.

Estes, A. B., Kuemmerle, T., Kushnir, H., Radeloff, V. C., & Shugart, H. H. (2012). Land-cover change and human population trends in the greater Serengeti ecosystem from 1984-2003. *Biological Conservation*, *147*, 255–263.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*, 11.

Geldmann, J., Manica, A., Burgess, N. D., Coad, L., & Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proceedings of the National Academy of Sciences*, *116*, 23209–23215.

Goldman, M. (2007). Tracking wildebeest, locating knowledge: Maasai and conservation biology understandings of wildebeest behavior in northern Tanzania. *Environment and Planning D: Society and Space*, *25*, 307–331.

Hayward, M. W., & Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation*, *142*, 1–13.

Hofmann, R. R., & Stewart, D. R. M. (1972). Grazer or browser: A classification based on the stomach-structure and feeding habits of east African ruminants. *Mammalia*, *36*, 226–240.

Holt, R. D., & Bonsall, M. B. (2017). Apparent competition. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 447–471.

Hopcraft, J. G. C., Holdo, R. M., Mwangomo, E., Mduma, S. A. R., Thirgood, S. J., Borner, M., Fryxell, J. M., Olff, H., & Sinclair, A. R. E. (2015). Why are wildebeest the most abundant herbivore in the Serengeti ecosystem. In *Serengeti IV: sustaining biodiversity in a coupled human-natural system* (pp. 35–71). University of Chicago Press.

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution*, *25*, 119–128.

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*, 559–566.

Jager, T. (1982). *Soils of the Serengeti woodlands, Tanzania*. Pudoc.

Janis, C. (1976). The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution*, *30*, 757–774.

Jarman, P. (1974). The social organization of antelope in relation to their ecology. *Behaviour*, *48*, 215–267.

Jarman, P. J. (1979). In A. R. E. Sinclair & N. Norton-Griffiths (Eds.), *Feeding strategy and the pattern of resource partitioning in ungulates. In 'Serengeti: dynamics of an ecosystem'* (pp. 130–163). University of Chicago Press.

Jarman, P. J., & Jarman, M. V. (1973). Social behaviour, population structure and reproductive potential in impala. *African Journal of Ecology*, *11*, 329–338.

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W., & MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, *88*, 638–652.

Kolowski, J. M., & Holekamp, K. E. (2006). Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*, *128*, 529–541.

Lamprey, R. H., & Reid, R. S. (2004). Expansion of human settlement in Kenya's Maasai Mara: What future for pastoralism and wildlife? *Journal of Biogeography*, *31*, 997–1032.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*, 1401–1409.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, *3*, 1–7.

Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: The dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*, 449–458.

Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, *153*, 649–659.

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. 2017. Package 'glmmTMB.' R Package Version 0.2. 0.

Mahony, J., Dyer, E., & Washington, R. (2021). The precipitation patterns and atmospheric dynamics of the Serengeti National Park. *International Journal of Climatology*, *41*, E2051–E2072.

Maloiy, G. M. O., Clemens, E. T., & Kamau, J. M. Z. (1982). Aspects of digestion and in vitro rumen fermentation rate in six species of east African wild ruminants. *Journal of Zoology*, *197*, 345–353.

Marshall, F., Reid, R. E. B., Goldstein, S., Storozum, M., Wreschnig, A., Hu, L., Kiura, P., Shahack-Gross, R., & Ambrose, S. H. (2018). Ancient herders enriched and restructured African grasslands. *Nature*, *561*, 387–390.

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A. J., & Possingham, H. P. (2005). Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecology Letters*, *8*, 1235–1246.

Mason, T. H., Brivio, F., Stephens, P. A., Apollonio, M., & Grignolio, S. (2017). The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. *Behavioral Ecology*, *28*(3), 908–918.

McNaughton, S. J., Banyikwa, F. F., & McNaughton, M. M. (1997). Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*, *278*, 1798–1800.

Nelson, W. (1979). Methods for cosinor-rhythmometry. *Chronobiologia*, *6*, 305–323.

Odadi, W. O., Karachi, M. K., Abdulrazak, S. A., & Young, T. P. (2011). African wild ungulates compete with or facilitate cattle depending on season. *Science*, *333*, 1753–1755.

Ogada, M. O., Woodroffe, R., Oguge, N. O., & Frank, L. G. (2003). Limiting depredation by African carnivores: The role of livestock husbandry. *Conservation Biology*, *17*, 1521–1530.

Ogutu, J. O., Owen-Smith, N., Piepho, H. P., Kuloba, B., & Edebe, J. (2012). Dynamics of ungulates in relation to climatic and land use changes in an insularized African savanna ecosystem. *Biodiversity and Conservation*, *21*, 1033–1053.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara-Serengeti ungulates in relation to land use changes. *Journal of Zoology*, *278*, 1–14.

Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society B*, *364*, 1755–1779.

Owen-Smith, N. (1998). How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (Tragelaphus strepsiceros). *Journal of Zoology*, *246*, 183–192.

Owen-Smith, N., & Goodall, V. (2014). Coping with savanna seasonality: Comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *Journal of Zoology*, *293*, 181–191.

Owen-Smith, N., & Traill, L. W. (2017). Space use patterns of a large mammalian herbivore distinguished by activity state: Fear versus food? *Journal of Zoology*, *303*, 281–290.

Owen-Smith, R. N. (1988). *Megaherbivores: The influence of very large body size on ecology*. Cambridge university press.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., Zander, K. K., Swanson, A., MacNulty, D., & Balme, G. (2013). Conserving large carnivores: dollars and fence. *Ecology Letters*, *16*, 635–641.

Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., & Packer, C. (2017). A 'dynamic' landscape of fear: Prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology Letters*, *20*, 1364–1373.

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*, 501–509.

Prins, H. H. T., & Olff, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In D. M. Newbery, H. H. T. Prins, & N. D. Brown (Eds.), *BES Symp.: Dynamics of tropical communities* (pp. 449–490). Blackwells Scientific.

Reid, R. S. (2012). *Savannas of our birth: people, wildlife, and change in East Africa*. Univ of California Press.

Reid, R. S., Galvin, K. A., & Kruska, R. S. (2008). *Global significance of extensive grazing lands and pastoral societies: An introduction* (pp. 1–24). Fragmentation in semi-arid and arid landscapes. Springer.

Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, *84*, 124–133.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass'. Cran r, *538*, 113–120.

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, *28*, 517–544.

Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature*, *425*, 288–290.

Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., & Haskell, J. P. (2003). Body mass of late quaternary mammals: ecological archives E084-094. *Ecology*, *84*, 3403.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, *56*, 740–749.

Swanson, A., Kosmala, M., Lintott, C., Simpson, R., Smith, A., & Packer, C. (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific data*, *2*(1), 1–14.

Veldhuis, M. P., Hofmeester, T. R., Balme, G., Druce, D. J., Pitman, R. T., & Cromsigt, J. P. (2020). Predation risk constrains herbivores' adaptive capacity to warming. *Nature Ecology & Evolution*, *4*(8), 1069–1074.

Veldhuis, M. P., Kihwele, E. S., Cromsigt, J. P. G. M., Ogutu, J. O., Hopcraft, J. G. C., Owen-Smith, N., & Olff, H. (2019). Large herbivore assemblages in a changing climate: Incorporating water dependence and thermoregulation. *Ecology Letters*, *22*, 1536–1546.

Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., Mwakilema, W., Ojwang, G. O., Parr, C. L., Probert, J., Wargute, P. W., Grant Hopcraft, J. C., & Olff, H. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science*, *363*, 1424–1428.

Ver Hoef, J. M., & Boveng, P. L. (2007). Quasi-Poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology*, *88*(11), 2766–2772.

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, *120*, 287–294.

Voeten, M. M., Van De Vijver, C. A. D. M., Olff, H., & Van Langevelde, F. (2010). Possible causes of decreasing migratory ungulate populations in an east African savannah after restrictions in their seasonal movements. *African Journal of Ecology*, *48*, 169–179.

Watson, L. H., & Owen-Smith, N. (2000). Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, *38*, 130–137.

Western, D. 1989. Conservation without parks: Wildlife in the rural landscape. Conservation for the Twenty-first Century: 158–165.

Western, D., Groom, R., & Worden, J. (2009). The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. *Biological Conservation*, *142*, 2538–2546.

Wilmshurst, J. F., Fryxell, J. M., & Bergman, C. M. (2000). The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*, 345–349.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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