Received: 24 January 2023 | Revised: 18 October 2023 | Accepted: 19 October 2023

DOI: 10.1111/aje.13229

RESEARCH ARTICLE

African Journal of Ecology WILEY

Habitat selection by Grevy's zebra (*Equus grevyi*): Conservation implications

Joseph Nderitu Kirathe[1,2,3] | **John Maina Githaiga**[2] | **Robert Mutugi Chira**[2] | **Daniel I. Rubenstein**[3,4]

[1]School of Natural Resource, Tourism and Hospitality, Maasai Mara University, Narok, Kenya

[2]School of Biological Sciences, University of Nairobi, Nairobi, Kenya

[3]Mpala Research Centre, Nanyuki, Kenya

[4]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

Correspondence
Joseph Nderitu Kirathe, School of Natural Resource, Tourism and Hospitality, Maasai Mara University, 861-20500 Narok, Kenya.
Email: jkirathe@gmail.com

Funding information
Bremerhavener Gesellschaft für Investitionsförderung und Stadtentwicklung, Grant/Award Number: NSF IIS-CXT; National Science Foundation, USA

Abstract

Understanding the spatial dynamics of landscape use by free-ranging herbivores is essential for species management and conservation in its natural environment. We used Ivelv's selection index, binary logistic regression analyses and stepwise regression to understand how environmental factors shape habitat selection by the Grevy's zebra (*Equus greyvi*). We measured biotic, abiotic and human factors that may influence presence or absence of Grevy's zebra in Samburu-Laikipia landscape and showed: (1) during wet periods, percentage perennial grasses, livestock density and grass quality had the greatest effect on Grevy's zebra presence; but (2) during dry weather periods a different suite of factors determined their landscape distribution, namely, the percentage of tree and bush density, distance to water and overall grass abundance. In addition, different Grevy's zebra demographic and reproductive classes varied in their response to environmental selective forces, thus demonstrating flexibility in their patterns of habitat selection. While we recommend more detailed studies on how abiotic and biotic interact to shape habitat selection patterns, our findings underscored the need of maintaining both dry and wet season habitats to ensure essential grazing area refugia. Our findings show that 'soft' development with controlled livestock stocking rates within the landscape will enhance Grevy's zebra conservation.

KEYWORDS
grevy's zebra, habitat selection, landscape, logistic model

Résumé

La compréhension de la dynamique spatiale de l'utilisation du paysage par les herbivores en liberté est essentielle pour la gestion et la conservation des espèces dans leur environnement naturel. Nous avons utilisé l'indice de sélection d'Ivelv, des analyses de régression logistique binaire et des régressions pas à pas pour comprendre comment les facteurs environnementaux façonnent la sélection de l'habitat par le zèbre de Grévy (Equus grevyi). Nous avons mesuré les facteurs biotiques, abiotiques et humains susceptibles d'influencer la présence ou l'absence du zèbre de Grévy dans le paysage de Samburu-Laikipia et avons démontré que : (1) pendant les périodes humides, le pourcentage d'herbes vivaces, la densité du bétail et la qualité de l'herbe ont eu le plus grand effet sur la présence du zèbre de Grévy ; mais (2) pendant les périodes sèches, un ensemble différent de facteurs a déterminé leur répartition dans le paysage, notamment le pourcentage de densité d'arbres et de buissons, la distance par rapport à l'eau et l'abondance générale de l'herbe. En outre, les différentes classes démographiques et reproductives du zèbre de Grévy ont réagi différemment aux forces sélectives de l'environnement, démontrant ainsi la flexibilité de leurs schémas de sélection de l'habitat. Bien que nous recommandions des études plus détaillées sur la façon dont les facteurs abiotiques et biotiques interagissent pour façonner les schémas de sélection de l'habitat, nos résultats ont souligné la nécessité de maintenir les habitats de la saison sèche et de la saison humide pour garantir des refuges essentiels dans les zones de pâturage. Nos conclusions montrent qu'un développement « doux » avec des taux de charge du bétail contrôlés dans le paysage améliorera la conservation du zèbre de Grévy.

1 | INTRODUCTION

Habitat selection is central to understanding species ecology, movements, distribution and abundance within a given landscape (Moorcroft & Barnett, 2008; Northrup et al., 2022). Habitat selection is an essential animal behaviour whereby individuals actively choose habitat patches from among available patches that are important to them throughout different stages in their life-histories (Krebs, 2014; Stamps, 2009). Typically, habitats which are chosen enhance survival and reproduction (Bailey et al., 1996; Redfern et al., 2003; Stamps, 2009) thereby contributing to long-term fitness of a species. Since habitats are shaped by abiotic and biotic elements which change over time it is likely that a range of habitats will be used and that these will change as conditions change. In an effort to understand animal habitat selection decisions, scientists use many approaches to assess 'selectivity' depending on the study species as well as the types of data that are available (Manly et al., 2002; Strickland & McDonald, 2006). If one or more habitats are being used selectively, resource selection functions (RSFs) that assess both biotic and abiotic factors are normally employed to determine what habitat attributes characterises areas where animals are disproportionately observed (Boyce et al., 2016). Habitat selection can be determined directly from observation of where animals are sighted in relation to the abundance of different habitat types comprising the landscape. Why such habitats are chosen will depend on assessing the features of the habitats, especially the resource's they are utilising (Hirzel & Lay, 2008; Manly et al., 2002). When resource selection functions (RSFs) and related occupancy models are used cautiously, they provide a direct link to understanding populations movements, distribution and abundance (Boyce et al., 2016; Matthiopoulos et al., 2015), all features essential for species conservation.

Fostering conservation of large-bodied endangered species entails monitoring their habitat selection choices over time over large landscapes. Most large-bodied animals use a wide range of habitat containing a diverse array of resources (du Toit, 1995; Redfern et al., 2003) which are today being affected by changing climates and human land use patterns (Kirathe et al., 2021; Ogutu et al., 2016). The large-bodied Grevy's zebra (*Equus grevyi* Oustalet, 1882) listed as 'Endangered' on the IUCN Red List (Rubenstein et al., 2016), appear to be strongly affected by these challenges throughout its range. In order to design better conservation plans and management programs for Grevy's zebra and other endangered species, it is necessary to understand their patterns of habitat use as well as their degrees of habitat selectivity. By assessing the extent to which the habitats selected overlap with human land uses, it then becomes possible to identify the magnitude and type of conflict over resource use for development of actions to mitigate these conflicts.

The Grevy's zebra is a large grazing equid that historically ranged from central and northern Kenya into parts of Ethiopia (Bauer et al., 1994; Yalden et al., 1986). Since the mid-1970s, however, its range has shrunk immensely as has its population which has greatly declined from approximately 15,000 to under 2500 by the early 2000's. This represents a 75% population decline globally making it one of the most endangered mammals (IUCN, 2003; Rubenstein et al., 2016; Williams, 2002) in the world and has been placed on the CITES Appendix A since 1979. The Samburu-Laikipia landscape consists of arid and semi-arid grasslands (Pratt et al., 1966), providing habitats whose vegetation abundance and quality vary spatially and seasonally. The survival of Grevy's zebra in Samburu-Laikipa landscape will depend on their ability to select beneficial habitats that are now likely to be impacted by climate and human induced land use change.

Little is known about Grevy's zebra habitat selection on the expansive Samburu-Laikipia landscape. Sundaresan et al. (2007) showed that forage quantity and habitat openness affected areas chosen by Grevy's zebra depending on reproductive status in the Laikipia area. Mwangi et al. (2018) produced habitat distribution maps for Grevy's and plain zebra in Laikipia showing that at a coarse scale, they generally shared similar types of habitats, differing only slightly in their distribution. But differences in the water needs of these two zebra species are great, constraining plains zebras, which must drink daily, to remain closer to water than Grevy's zebras which only have to drink every 3–5 days (Gersick & Rubenstein, 2017; Rubenstein, 2010). We studied Grevy's zebra habitat selection on a fine scale across the Samburu-Laikipia landscape. The aim of the study was to determine what habitats they use in the landscape and whether they utilise them selectively. Then, using logistic regression (Allison, 2012; de Gabriel et al., 2021; Garshelis, 2000; Groom & Harris, 2009; Manly et al., 2002; Northrup et al., 2022; Sohl, 2014), we identified what habitat resources and features best accounted for the presence or absence of Grevy's zebra on each landscape parcel. Specifically, we set out to answer the following key questions; (1) Do Grevy's zebra select certain types of habitats over others? (2) If so, do the selected habitats change with weather season? (3) Are the patterns of habitat selection affected by different demographic class and reproductive state? And finally, (4) What landscape resource characteristics influence habitat choice? While focusing on questions above, we then predict how impending changes wrought by climate and human land use patterns are likely to impact the long-term survival and reproductive success of this endangered species and identify actions and policies that might mitigate these impacts to enhance their population sustainability.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted between November 2009 and January 2015 in Samburu-Laikipia landscape located between 36^0 15′-38^0 00′ E and 0^0 00′-1^0 00′N covering 15,634 square kilometres (Figure 1).

Across this landscape there is wide variation in seasonal rainfall which is largely affected by altitude and the fact that the landscape lies on the lee side of both the Aberdares mountain range and Mount Kenya. The southern region of our study receives on average about 500 mm, while sites in the north receive on average 250 mm annually (Jaetzold & Schmidt, 1983). The climate is hot during the day and cool at nights; mean annual temperature is 30°C (County Government of Laikipia, 2018; County Government of Samburu, 2018; SNR, 2003). The landscape is characterised by a mosaic of savannahs and bush-and wooded grasslands. often referred to as *Acacia*-grasslands and *Acacia-Commiphora* scrubs (Barkham & Rainy, 1976; Pratt et al., 1966) with large areas covered by *Acacia tortilis* grasslands containing perennial and annual grasses.

The Samburu-Laikipia landscape is impacted by human activities that have resulted in a variety of land use types that we intensively monitored. These include: (1) commercial cattle ranches in Laikipia comprising Mpala and Oljogi ranches; (2) Community group ranches that included those in Samburu county like West gate conservancy, Sessia-Barsalinga, Ngaroni, Kalama; those in Isiolo county which included Oldonyiro and Kipsing area; Laikipia community group ranches which included Koinja, Tiamamut and Ilmotiok; and (3) Protected areas that included Samburu and Buffalo Springs National Reserves. Because these land use types were aligned along the cline of hundreds of kilometres, seasonal rainfall patterns and human activities varied and were temporally separated in the landscape.

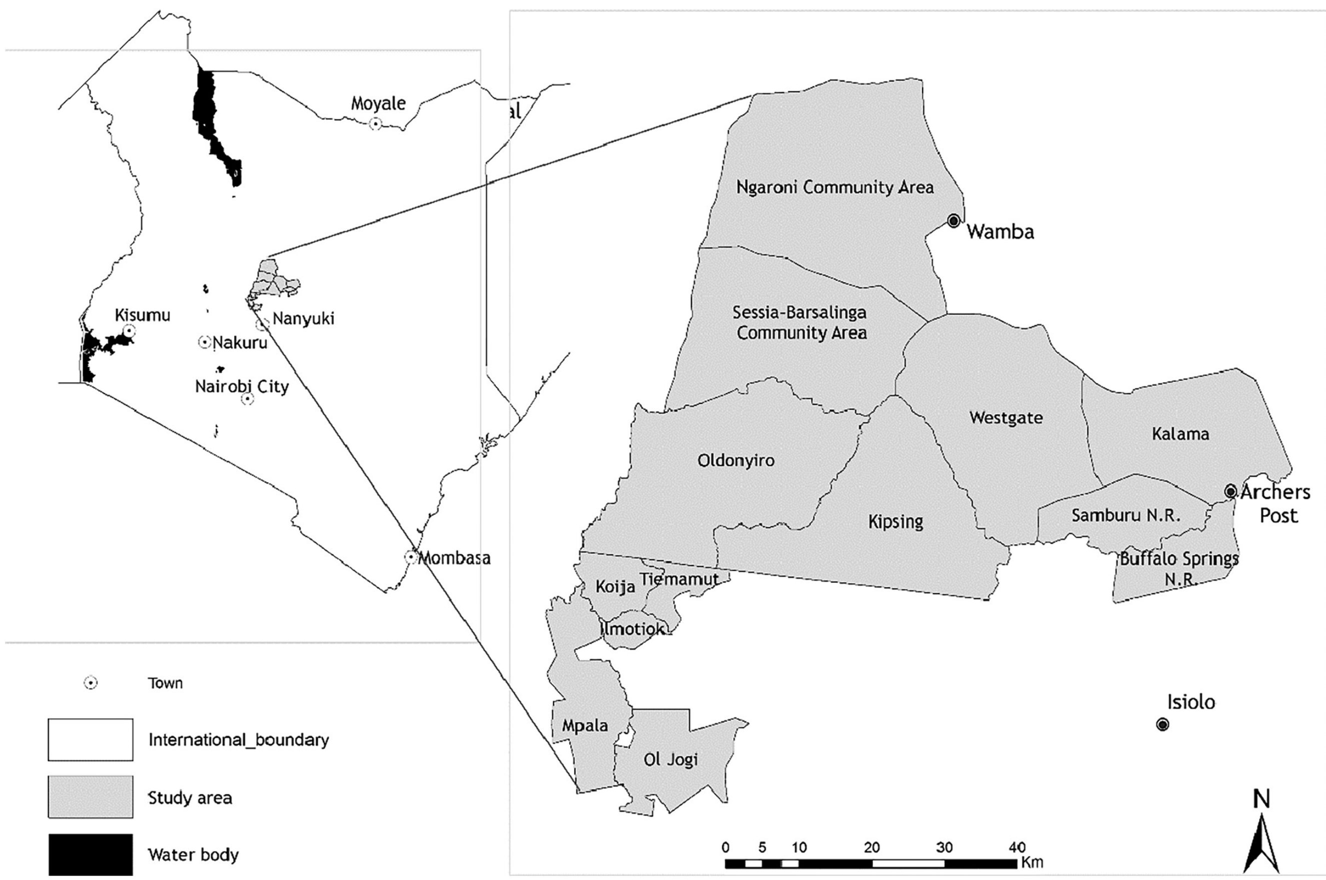

FIGURE 1 Kenya map showing the location of study area and study sites.

2.2 | Determination of Grevy's zebra, livestock and human settlement abundances

To evaluate the distribution and abundance of Grevy's zebras, human settlements (manyattas) and livestock, we delineated and travelled along, census routes to generate repeated replicate samples, each of which was treated as a long transect (Grimsdell, 1978; Norton-Griffiths, 1978, Figure 2). Estimates of zebra, livestock and human settlement numbers and densities were made using 'Distance Sampling' (Thomas et al., 2010) which involved driving slowly along the census routes which traversed a variety of landscapes and habitats conversing a total of 17,166 kilometres. At each sighting we recorded; (1) the GPS location on the route, (2) distances from the sighting point on the route and (3) the compass direction to the focal object in order to demarcate actual locations of zebras, manyattas and livestock on the landscape. Grevy's zebras were also visually characterised by demographic and reproductive classes. These classes included territorial males (TM), bachelor males (BM), non-lactating females (NLF), lactating females (LF) and recruits (infants and juveniles (2–3-year-olds). Since foals followed their mother, they were easy to separate from older sub-adults. For our analyses, though, all juveniles and foals were combined into one reproductive class called juveniles (J). Driving the transects from start to finish on any given day avoided double counting and ensuring that each census route was an independent event. GPS locations were superimposed onto the map of the study area using ARCMAP 10.4 from ARCGIS (ESRI, 1999–2015) to visualise distribution of focal objects and produce distributions or 'hot spots' of these objects for the entire study as well as across time periods.

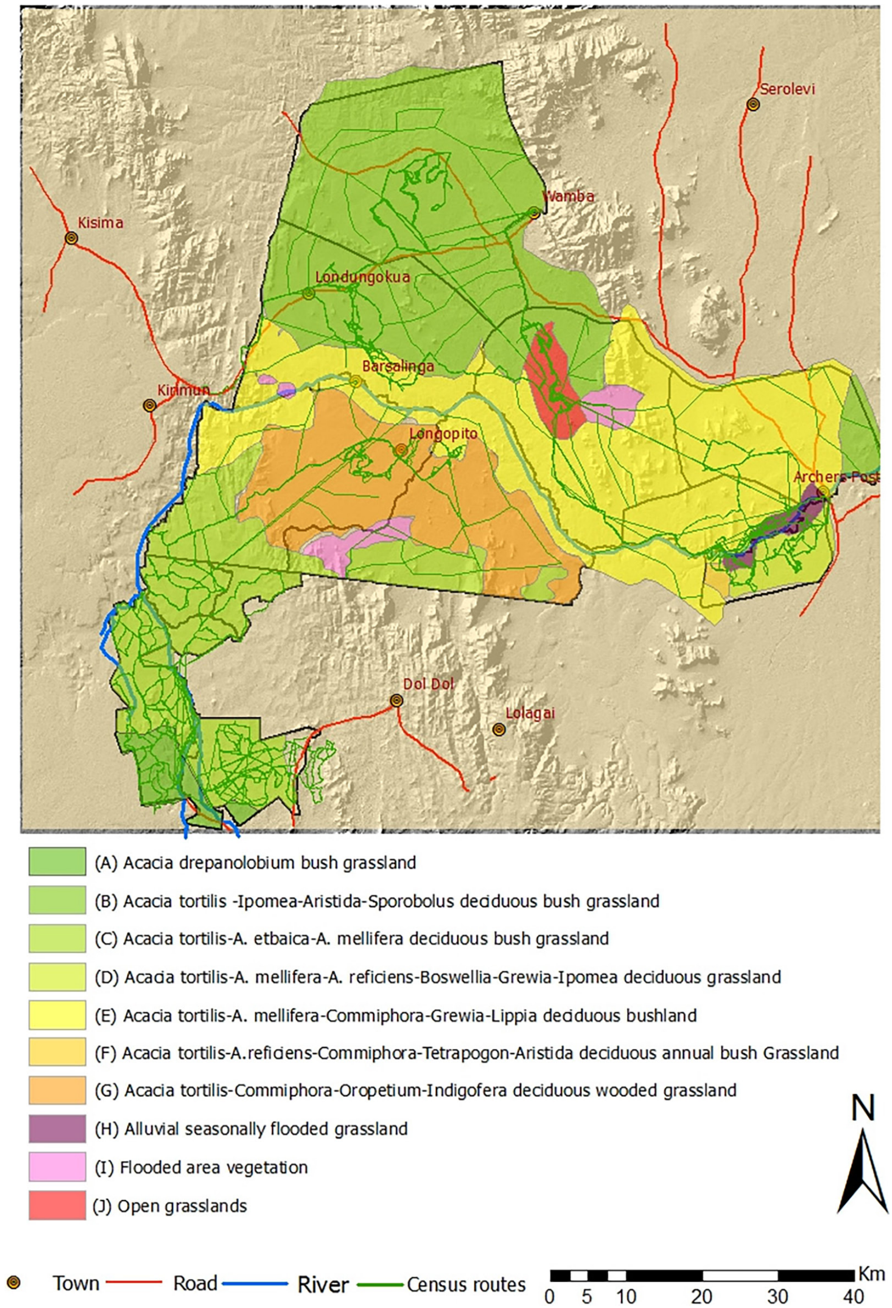

FIGURE 2 Habitats and census routes used for sighting Grevy's zebra in the Samburu-Laikipia landscape. NB: *Alphabets indicate different habitat codes.*

2.3 | Vegetation surveys

A multivariate approach adopted from Hutchinson (1957); Asim and Zafar (2021) was used to identify habitats and characterise the resource they contained. Along the census routes, 1 km grids were established using ARCGIS. 1902 grids where Grevy's zebra were present were selected randomly to ensure that the distribution of vegetation type used was unbiased. In addition, 1461 randomly chosen grids where no Grevy's zebras sighted were also selected randomly for comparison. For every randomly chosen grid cell, whether or not Grevy's zebra were present, a 100 m transect was walked from the centre of the chosen grid in order to assess tree and herbaceous cover (forbs and grasses). By choosing new grids and transects monthly, spatial variation of vegetation cover and type across time was ensured.

To assess herbaceous layer abundance and quality, ten sampling points, ten meters apart along the 100 m transect were sampled following McNaughton's (1979) procedure. At each point on the transect, a 1 meter pin frame containing 10 pins was used to count all grass or forb parts touching the pin while identifying them to genus or species where possible. Each pin contact was later used to compute metrics that categorised phenological attributes of the grasses and forbs as proportions or percentages. This produced the following measurements for characterising resource features of each plot and transect; proportion or percentage of leaves, stems, green plant parts (greenness) or brown, grass seeds and grass cover (McNaughton, 1979). Grass height was measured to the nearest cm using a meter rule.

$$\% \text{ / proportion vegetation characteristic} = \frac{\text{number of pin hits of the attribute}}{\text{total pin hits in a transect}} \times 100$$

Using Shannon-Weaver index (H = −*pi*lnp*i*) where pi represents the proportion occurrence of a species.

To obtain herbaceous standing crop biomass, four quadrants of 0.5 m^2 for both grass and forbs were established (Cornelissen et al., 2003; DÖrgeloh, 1997; Schwinning & Weiner, 1998). Quadrants were placed systematically at points 0, 25, 50 and 75 m along the 100 m transect. All above ground herbaceous vegetation was cut, oven-dried at 60°C until no further weight loss occurred and final weights recorded.

We counted all woody tree and shrub plant individuals within five meters on both sides of the transect and computed density for each transect. Canopy cover was measured using line intercept method along the 100 m transect. Here using a tape measure, we determined length on the ground covered by tree or shrub to generate percentage canopy cover. Tree height was determined from an extension pole marked at 1 cm intervals.

2.4 | Other environmental factors

All permanent water points were known and were mapped using a Garmin GPS. All GPS locations of Grevy's zebra individuals or groups and water points were entered into ARCGIS (ESRI, 1999–2015) and shortest linear distance to permanent rivers, luggas or temporary (ephemeral) water computed. Percent Hill slope was extracted by overlaying Grevy's zebra locations and random points on digital elevation model (DEM) maps (accurate to 90 m) using ARCMAP 10.4 from ARCGIS. Normalised difference vegetation index (NDVI) satellite imagery obtained from the US National Oceanic and Atmospheric Administration (NOAA) were acquired (NASA-EO, 2009–2015; Appendix B). These were used to obtain monthly mean NDVI values as a measure of vegetation productivity and greenness (Bernt & Hans, 2014; Tucker & Sellers, 1986). NDVI values vary from −1 to 1 with high values indicating greener and more photosynthetic production.

2.5 | Determination of habitats and habitat availability

Surveys were conducted on 10 plants communities identified on the Samburu-Laikipia landscape in Figure 2. To calculate habitat availability, the study area map was superimposed on the vegetation map (Di Gregorio & Latham, 2000; Herlocker, 1992, 1993) and using ARCMAP 10.4 from ARCGIS, area of each vegetation type calculated. Percent availability was calculated as the area of a vegetation type divided by total study area multiplied by 100. Since vegetation area remained constant during the study period, habitat availability was the same over the study period.

2.6 | Habitat selection index

Habitat selection was calculated using a method described by Aebischer et al. (1993). We calculated selection ratios as percent habitat use divided by percent habitat available. Number of Grevy's zebra sighted in a habitat were also used to determine Ivelv's electivity index, E (Ivlev, 1961). Ivelv's index is independent of the relative abundance of each habitat available to the animals (Jacobs, 1974; Kauhala & Auttila, 2010; Lechowicz, 1982) presenting an additional and often a more robust selection metric.

Ivlev's electivity index is calculated according to the formula: $Ei = (ri - Pi)/(ri + Pi)$, where *ri* is the proportion of relative habitat use by the zebras and *Pi* the proportion of relative habitat potentially available. E values varies from −1 (total avoidance) to +1 (exclusive selection) on a habitat while values close to zero indicate non selective.

2.7 | Data analysis

Environmental and anthropogenic factors that could influence Grevy's zebra habitat selection were determined for each habitat. Since many of the herbaceous layer variables (grass and forbs) co-varied, we used principal component analysis to identify independent composite variables of the suite of original variables characterising zebra use. This effectively reduced a multi-dimension suite of traits into two important independent variables; (1) the first one termed 'PCA1'and labelled as 'Grass Abundance' a combination of percentage grass cover, grass height and herbaceous layer biomass. and (2) the second termed 'PCA2'- 'Grass Quality' a combination of proportion grass leaves, grass diversity and proportion green grass. In addition, percent annual grasses, percent perennial grasses, tree/bush density, percentage tree/bush cover, percentage hill slope, distance to nearest water, manyatta density and livestock density were added as factors that influenced Grevy's zebra habitat selection.

JMP PRO 12 Statistic program from SAS was used for all the analysis (SAS Institute Inc., 2020–2021). Data in proportions or percentages were ARCSINE transformed and checked for normality before a parametric test was applied and results back transformed in presentation of graphs or statistics.

Habitat and environmental variables were tested to determine whether they influenced Grevy's zebra presence or absence. Binary logistic regression was applied to estimate the impact of each habitat variable on the presence or absence of Grevy's zebra (DÖrgeloh, 2006; Groom & Harris, 2009). Selected variables were entered into a series of models where Akaike's Information Criterion (AIC, Akaike, 1974) scores for each possible model resulted and the one with lowest value, separated by 2 units from the other lowest value was chosen as the best. Further, odds ratios of habitat variable contributing to selection of the model were compared against each other, respectively, and −log likelihood estimates determined.

In an effort to weigh and determine the importance of each habitat variables to Grevy's zebra, demographic and reproductive classes, stepwise regression analysis was applied as a data reduction technique. Here, predictor variables were trained to enter a model at a probability of $p<0.001$ and leave at probability above $p>0.05$ considering the lowest AIC.

3 | RESULTS

3.1 | The seasonal distribution of Grevy's zebra in samburu-laikipia landscape

Overall, the distribution of Grevy's zebra on the Samburu-Laikipia landscape differed significantly from the distribution of randomly chosen points ($\chi^2_9=1505.57$, $p<0.001$). Similarly, non-random distributions were also observed during dry seasons (variance/mean ratio = 4.62; $\chi^2_9=926.43$, $p<0.001$) and wet seasons (variance/mean ratio = 19.19; $\chi^2_9=578.33$, $p<0.001$; Fowler et al., 1998). These patterns indicate that the distribution of Grevy's zebra is patchy, irrespective of season. (Figure 3).

3.2 | Grevy's zebra seasonal habitat selection

Grevy's zebras disproportionately favoured some habitats over others and selected habitats changed seasonally (Table 1).

We observed that common and wide-ranging habitats like *Acacia tortilis-A. reficiens-Commiphora-Tetrapogon-Aristida* deciduous annual bush grassland and Acacia *tortilis-Ipomea-Aristida-Sporobolus* deciduous bush grassland which comprised 40% and 18% of the study area, respectively, were not selected or used disproportionately by Grevy's zebras. Small and rare habitats such as alluvial seasonally flooded grassland, flooded area vegetation and open grasslands approximately 1% in the study area were used disproportionately relative to their abundance. And since the habitats that were disproportionately selected varied seasonally, Grevy's zebra appear not to favour any one suite of habitats year round or between years (Duun's all pair test, $p<0.05$). For example, Grevy's zebras were seen in some habitats approximately 70% of the time during dry seasons, but only 30% of the time during wet seasons (Table 1 and Figure 4).

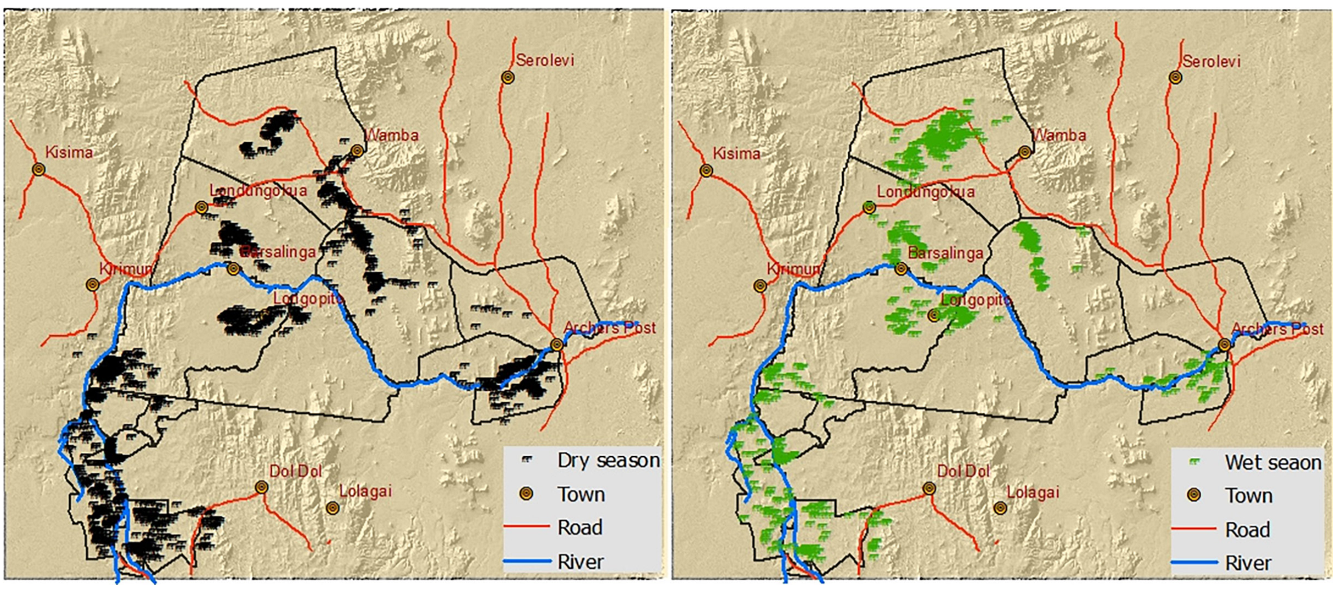

FIGURE 3 Distribution of Grevy's zebra sightings in Samburu-Likipia landscape during dry and wet season in the period between 2009–2015.

TABLE 1 Broad scale habitat selection of Grevy's zebra in Samburu-Laikipia landscape.

		Dry season						Wet season					
Habitat Type	Hab[†]	Obs[‡]	Exp[§]	χ^{2}[¶]	*p*	*E*	*Sp*[#]	*Obs*[‡]	*Exp*[§]	χ^{2}[¶]	*p*	*E*	*Sp*[#]
A	2.16	164	236.95	22.46	<0.05	0.19	+	460	387.05	13.73	>0.05	0.45	+
B	10.38	914	1031.34	13.35	<0.001	0.21	+	1802	1684.88	8.17	<0.05	0.35	+
C	2.34	301	190.24	64.48	<0.001	0.38	+	200	310.76	39.47	<0.001	−0.04	
D	4.77	692	435.93	150.42	<0.001	0.43	+	456	712.07	92.09	<0.001	0.01	
E	43.96	1749	2224.82	101.76	<0.001	−0.19	–	4110	3634.18	62.30	<0.001	0.004	
F	14.72	568	276.82	306.28	<0.001	−0.20	–	161	452.20	187.50	<0.001	−0.81	–
G	18.11	85	53.16	2.63	>0.05	−0.85	–	75	85.84	1.61	>0.05	−0.93	–
H	0.99	210	118.47	70.71	<0.001	0.57	++	102	193.53	43.30	<0.001	0.05	
I	0.8	209	90.40	155.71	<0.001	0.63	++	29	147.63	95.32	<0.001	−0.45	–
J	1.18	309	522.89	87.50	<0.001	0.50	++	1068	854.10	58.56	<0.001	0.76	++

Note: habitats type codes (in alphabet) stands for those outlined in Figure 2 and Table 2.

p Is the Significance level and E is Ivelv's electivity index; While Symbols.

[†]Habitat availability as a percentage of the whole study area.

[‡]Observed frequency occurring in the habitat type.

[§]Expected observations.

[¶]Chi-square test.

[#]Selection and avoidance denoted by ++ (highly selected), + (selected) and – (highly avoided), − avoided, respectively, or blank for non-selection.

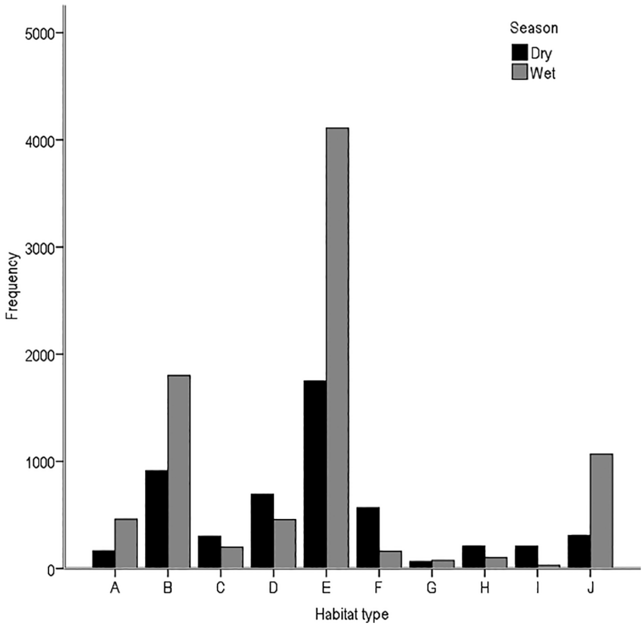

FIGURE 4 Frequencies of Grevy's zebra sightings in different habitats of Samburu-Laikipia landscape in dry and wet season. NB: *Habitats codes/type as outlined in* Figure 2 and Table 2.

Ivlev's electivity indexes show that during dry seasons, Grevy's zebra strongly selected alluvial seasonally flooded grasslands, flooded area vegetation and open grasslands. Other disproportionately selected habitats were *Acacia drepanolobium* bush grassland, *Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grassland, *Acacia tortilis-A. mellifera-A. reficiens-Boswellia-Grewia-Ipomea* deciduous grassland *and Acacia tortilis-A. mellifera-Commiphora-Grewia-Lippia* deciduous bushland. In wet seasons, however, Grevy's zebras used fewer habitats disproportionately, only favouring open grasslands as well as only two of the Acacia bushed habitats, namely *Acacia drepanolobium* bush grasslands *and Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grasslands. They disproportionally avoided flooded area vegetation as well as the other Acacia dominated habitats (Table 1).

Different Grevy's zebra demographic and reproductive classes showed variations in habitat selection in both dry and wet seasons (Table 2). Territorial males strongly selected flooded area vegetation and open grasslands habitats in both dry ($\chi^2_9 = 60.85$, $p < 0.001$) and wet seasons ($\chi^2_9 = 51.22$, $p < 0.001$). Bachelor males disproportionately selected *Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grassland, *Acacia tortilis-A. mellifera-A. reficiens-Boswellia-Grewia-Ipomea* deciduous grasslands, alluvial seasonally flooded grasslands, flooded area vegetation and open grasslands during dry seasons ($\chi^2_9 = 300.13$, $p < 0.001$). In wet seasons, however, different Acacia dominated landscapes, namely *Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grassland as well as open grasslands ($\chi^2_9 = 179.46$, $p < 0.001$) were favoured.

Non-lactating females disproportionately selected *Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grassland, *Acacia tortilis-A. mellifera-A reficiens-Boswellia-Grewia-Ipomea* deciduous grasslands, alluvial seasonally flooded grasslands, flooded area vegetation and open grasslands in both dry season ($\chi^2_9 = 304.13$, $p < 0.001$). In wet season, non-lactating females also favoured, *Acacia drepanolobium* bush lands, but avoided this habitat in the dry season. And while they favoured *Acacia tortilis-Commiphora-Ropetium-Indigofera* deciduous wooded grasslands in the dry season, they avoided them in the wet season ($\chi^2_9 = 227.05$, $p < 0.001$).

Lactating females highly selected *Acacia tortilis-A. mellifera-Commiphora-Grewia-Lippia* deciduous bushland, flooded area vegetation

TABLE 2 Habitat selection by different Grevy's zebra reproductive groups in Samburu-Laikipia landscape.

		Dry season					Wet season				
		Demographic/reproductive class					Demographic/reproductive class				
Habitat code	Habitat type	TM	BM	NLF	LF	J	TM	BM	NLF	LF	J
A	*Acacia drepanolobium* bush grassland		–		–	–	+	+	+	–	+
B	*Acacia tortilis-A. etbaica-A. mellifera* deciduous bush grassland	+	++	++	+	+	+	++	++	+	+
C	*Acacia tortilis-A. mellifera-A. reficiens-Boswellia-Grewia-Ipomea* deciduous grassland	+	++	++	+	++	–	+	++	–	+
D	*Acacia tortilis-A mellifera-Commiphora-Grewia-Lippia* deciduous bushland	+	+	++	++	+	–	_-	+	+	
E	*Acacia tortilis-A. reficiens-Commiphora-Tetrapogon-Aristida* deciduous annual bush Grassland			+	–	–	–	+	+	–	+
F	*Acacia tortilis-Commiphora-Oropetium-Indigofera* deciduous wooded grassland		–	+	–	–	–	–	–	–	–
G	*Acacia tortilis-Ipomea-Aristida-Sporobolus* deciduous bush grassland	–	__	–	–	–	–	–	–	–	–
H	Alluvial seasonally flooded grassland	+	++	++	+	++	–	+	+		–
I	Flooded area vegetation	++	++	++	++	–	++	+	++	++	–
J	Open grasslands	++	++	++	++	++	++	++	++	++	++

Note: Significant selection and avoidance denoted by ++ (highly selected), + (selected) and – (highly avoided), − avoided, respectively, or blank for non-selection.

Abbreviations: BM, bachelor males; J, Juveniles; LF, Lactating females; NLF, non-lactating females; TM, territorial males.

and open grasslands in both seasons ($\chi^2_9 = 59.36$, $p < 0.001$), while in the wet season, they avoided alluvial seasonally flooded areas which they preferred in the dry season ($\chi^2_9 = 45.95$, $p < 0.001$). Juveniles also selected *Acacia tortilis-A. mellifera-A. reficiens-Boswellia-Grewia-Ipomea* deciduous grassland, alluvial seasonally flooded grasslands and open grasslands habitats in both seasons, but the ones preferred differed by season ($\chi^2_9 = 157.08$, $p < 0.001$). Overall, *Acacia tortilis -Ipomea-Aristida-Sporobolus* deciduous bush grassland, *Acacia tortilis-Commiphora-Oropetium-Indigofera* deciduous wooded grassland and *Acacia tortilis-A. reficiens-Commiphora-Tetrapogon-Aristida* deciduous annual bush Grassland were disproportionately avoided by most demographic classes of Grevy's zebra in both wet and dry seasons. Flooded area vegetation, alluvial seasonally flooded grassland habitats in wet season were generally disproportionately avoided as well.

3.3 | Factors influencing Grevy's zebra presence or absence

All habitat variables recorded in the field were tested to determine whether they influenced Grevy's zebra presence or absence. Table 3 shows that of the two composite principal components. PCA1 ('Grass Abundance') was significantly correlated with Grevy's zebra numbers in the dry season ($r^2 = 0.20$, $p < 0.001$, $n = 1045$) while PCA2 ('Grass Quality') was significantly correlated with Grevy's number in wet season ($r^2 = 0.10$, $p < 0.001$, $n = 997$).

Two other habitat variables were also correlated with the number of Grevy's zebra using particular habitats: the percentage annual and perennial grasses (Table 4 and Appendix A).

TABLE 3 Principal components (rotated verimax) of grass characteristics in Samburu – Laikipia landscape study sites for both dry and wet weather season.

	Dry season		Wet season	
Grass characteristic	PCA1	PCA2	PCA1	PCA2
% Grass cover	**0.46**	0.04	**0.53**	0.04
Grass leaves	0.16	**0.54**	−0.26	**0.32**
Green grass	0.29	**0.45**	0.06	**0.53**
Grass seeds	0.10	**−0.31**	0.12	0.12
Grass diversity	0.16	**0.37**	0.10	**0.50**
Grass height	**0.38**	−0.28	**0.48**	−0.21
Grass biomass	**0.42**	−0.12	**0.41**	0.26
Variance	2.96	1.80	2.26	1.79
% Variation	29.60	18.00	22.59	17.90
% Cumulative variation	29.60	47.60	22.59	40.49
Pearson correlation with Grevy's zebra	$r^2 = 0.20$, $p < 0.001$, $n = 1489$	Ns	Ns	$r^2 = 0.16$, $p < 0.001$, $n = 1513$

Note: Values in bold indicates grass charateristics that contributed significantly to a composite principal component.

Table 4 shows also that the combination of variables comprising the habitats chosen by Grevy's zebras varied seasonally. In both seasons, Grevy's zebras chose habitats where grass quality was high, with abundant perennial grasses, low percentage tree cover, and where the terrain was not steep. Only in the dry season did they favour habitats close to water, where grass was abundant and livestock density was high with low manyatta density. In the wet

TABLE 4 Group statistics for continuous habitat variables in dry and wet season in areas where Grevy's zebra were present or absent in Samburu-Laikipia landscape.

		Dry season		Wet season	
Habitat variable	Grevy's zebra	Mean ± SE	Sign. p.	Mean ± S	Sign. p
% Annual grass	Absent	21.57 ± 0.44	0.02*	25.32 ± 0.62	0.11
	Present	20.16 ± 0.47		24.10 ± 0.43	
% Perennial grass	Absent	47.69 ± 0.78	<0.001***	55.50 ± 0.72	0.02*
	Present	54.63 ± 0.77		57.44 ± 0.52	
% tree/bush cover	Absent	7.56 ± 0.15	<0.001***	7.93 ± 0.15	<0.001***
	Present	6.62 ± 0.11		7.27 ± 0.13	
Tree/bush density	Absent	178.35 ± 4.43	<0.001***	181.96 ± 6.62	0.17
	Present	151.21 ± 4.13		193.80 ± 5.40	
Distance to water	Absent	1371.00 ± 55.01	0.03*	3513.98 ± 134.99	<0.001***
	Present	1127.44 ± 47.61		2942.88 ± 81.21	
Manyatta density	Absent	2792.76 ± 138.93	0.76	3392.90 ± 167.74	<0.01**
	Present	2734.19 ± 128.33		2774.53 ± 106.95	
Livestock density	Absent	1852.92 ± 196.70	0.15	651.86 ± 118.47	<0.01**
	Present	2211.85 ± 154.77		1021.77 ± 101.79	
% Hill slope	Absent	15.72 ± 0.93	0.001***	10.63 ± 0.70	0.01**
	Present	11.73 ± 0.51		8.37 ± 0.46	
NDVI	Absent	0.31 ± 0.00	<0.001***	0.29 ± 0.01	<0.001***
	Present	0.33 ± 0.00		0.24 ± 0.00	
Grass abundance	Absent	−0.06 ± 0.05	0.21	−0.13 ± 0.06	0.01**
	Present	0.03 ± 0.05		0.05 ± 0.05	
Grass quality	Absent	−0.42 ± 0.05	<0.001***	−0.10 ± 0.04	0.02*
	Present	0.22 ± 0.04		0.14 ± 0.04	

Note: Differences were tested using two tailed *t*-test and significant probability indicated with asterisk where $p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

season, distance to water was also significantly correlated with habitat use, but then the converse was found; Grevy's zebras were found in habitats farther from water but with high livestock density than were random points. Differences in the other factors did not differ among habitats they frequented and those they did not.

3.4 | The logistic regression model

This model supports the presence-absence results. The dry season logistic model was highly significant ($\chi^2 = 128.97$, $p < 0.001$; Nagelkerke $R^2 = 0.36$ Nagelkerke, 1991) and was positively dependent on percent perennial grasses, grass abundance, distance to water, tree and bush density (Wald χ^2 test Table 5).

In the wet season, the logistic regression model was also significant ($\chi^2 = 216.83$, $p < 0.0001$; Nagelkerke $R^2 = 0.42$, Nagelkerke, 1991). Percent perennial grasses, livestock density and grass quality were strong predictors of Grevy's zebra presence (Table 6). Equally, NDVI values which indicate habitat quality was very important factor where Grevy's zebra were present. Again, distance to water mattered but during the wet season the coefficient was negative showing the ability of individuals to roam away from water was important. Bushy habitats were also avoided, presumably because dense foliage makes detecting predators and staying connected to conspecifics difficult.

3.5 | Grevy's zebra habitat selection prediction models

Stepwise regression models helped identify the habitat features associated with habitat selection by different reproductive classes of Grevy's zebras. Table 7 shows the variables that contributed significantly to the models that characterised the habitats favoured by the different reproductive classes.

The models illustrated that overall, Grevy's zebras selected habitats characterised by abundant grass cover, especially cover by annual grasses, high tree cover and closeness to water during the dry season. In the wet season, distance to water no longer mattered, but associations with livestock did. With respect to specific demographic classes, non-lactating females generally followed the overall species pattern of habitat choice, but favoured habitats with high quality vegetation in the dry season. Lactating females, however, strongly preferred high quality habitats in the

TABLE 5 Result of binary logistic regression model predictors ($n=1489$) used to investigate dry weather season habitat variables affecting Grevy's zebra presence in Samburu-Laikipia landscape.

Independent variable	$\beta \pm$ SE	Wald χ^2	Sign. *p*	Lower 95%	Upper 95%	Exp (B)
Intercept	2.300±0.530	18.86	<0.001***	1.262	3.334	
% Annual grass	0.003±0.006	0.17	0.67	−0.0098	0.0151	0.9973
% Perennial grass	0.011±0.005	4.72	0.02*	0.0011	0.0218	0.9885
% Tree/bush cover	−0.095±0.024	16.07	<0.00***	−0.1419	−0.0487	1.1000
Tree/bush density	0.003±0.001	29.06	<0.001***	0.0021	0.0045	0.9967
Distance to water	0.000±0.000	12.89	0.001***	−0.0001	−0.0004	1.0001
Manyatta density	−0.000±0.000	0.33	0.56	−0.0001	0.0003.	1.0000
Livestock density	0.000±0.000	0.65	0.41	0.00003	0.0001	0.9999
% Hill slope	−0.022±0.004	23.79	<0.001***	−0.0307	−0.0131	1.0221
NDVI	−0.454±0.091	13.75	0.001***	−0.528	0.1628	0.6347
Grass abundance	0.370±0.005	11.64	<0.001***	−0.0959	0.1363	0.97910
Grass quality	0.047±0.005	0.77	0.3806	−0.0584	0.1530	0.9538

*$p<0.05$, **$p<0.01$, ***$p<0.001$, Nagelkerke $R^2=0.36$.

TABLE 6 Result of binary logistic regression model predictors ($n=1513$) used to investigate wet weather season habitat variables affecting Grevy's zebra presence in Samburu-Laikipia landscape.

Independent variable	$\beta \pm$ SE	Wald χ^2	Sign. *p*	Lower 95%	Upper 95%	Exp (B)
Intercept	−0.908±0.460	3.80	0.0512	−1.8209	0.0045	
% Annual grass	−0.009±0.005	2.32	0.1279	−0.0208	0.0026	1.0092
% Perennial grass	0.025±0.004	38.52	<0.001***	0.0168	0.0323	0.9757
% Tree/bush cover	−0.102±0.023	19.84	<0.001***	−0.1471	−0.0572	1.1075
Tree/bush density	−0.001±0.001	1.85	0.1742	−0.0025	0.0005	1.0010
Distance to water	−0.0001±0.000	7.67	<0.001***	0.0000	0.0002	0.9998
Manyatta density	−0.0001±0.000	34.87	<0.001***	−0.0002	−0.0001	1.0001
Livestock density	0.000±0.000	8.46	0.01**	--0.0000	0.0000	1.0000
% Hill lope	−0.017±0.004	18.92	<0.001***	−0.0254	−0.0096	1.0177
NDVI	0.510±0.018	18.06	<0.001***	0.27134	0.7357	0.0065
Grass abundance	0.130±0.06	0.20	0.659	0.1538	0.09735	1.0287
Grass quality	0.320±0.06	24.81	<0.001***	0.1943	0.4465	0.7258

*$p<0.05$, **$p<0.01$, ***$p<0.001$, Nagelkerke $R^2=0.42$.

wet season, presumably because at that time they are nursing rapidly growing young foals. Both territorial and bachelor males also generally followed the overall species pattern in the wet season, but showed preferences for habitats with high percentages of perennial grasses during the dry season. More than any other demographic class, juveniles showed similar patterns of habitat use in dry and wet seasons. Access to both abundant and high quality forage, use of bushy habitats and closeness to water characterised their habitat preferences, presumably because their rapid growth is energetically demanding. Such strong demographic specificities in habitat preferences, some of which cut across weather seasons whereas other are season specific, underscore why the Grevy's zebra exhibit a fission-fusion society where individuals join and leave groups frequently (Rubenstein, 1986) to avoid intraspecific competition for resources.

4 | DISCUSSION

Ecological theory predicts that animals using spatially localised resources, especially those inhabiting arid and semi-arid landscape, must be able to locate and use key resources that meet their specific needs. Most important are forage and water in addition to areas that attenuate predation risks (Groom & Harris, 2009). Large herbivore distributions, abundances and movements at landscape levels are often influenced by spatial and temporal distributions of context dependent key resources (Matthiopoulos et al., 2020; Ritchie et al., 2009; Rondinini et al., 2005) which if disproportionately used relative to their abundance will result in habitat selectivity. Grevy's zebras selected a wide range of habitats in dry season including those with high tree/bush density, waterlogged during wet season, heavily used by livestock and close to water.

TABLE 7 Slope coefficients (β) for different habitat variables used in stepwise regression models to predict habitat selection for Grevy's zebra and different reproductive groups in Samburu-Laikipia landscape.

	Dry season						Wet season					
Variable	Total	TM	BM	NLF	LF	J	Total	TM	BM	NLF	LF	J
Intercept	6.29***	−6.03**	15.27***	4.98**	2.12*	4.08**	29.44***	6.26***	−0.37*	16.64***	0.79*	7.08***
% Annual grass	53.40*	16.01*				40.01*						
% Perennial grass		11.49*	−13.25*									
% tree/bush cover	74.13*								42.00*	−0.06*		
Tree /bush density				0.02*	0.02*	0.01***	−0.02		−0.06*			0.01*
Distance to water	0.01*	0.001*		0.002*		0./001*						0.001*
Manyatta density			0.01**	0.02*						0.03*	0.01*	
Livestock density							1.08***	0.08**	0.21**	1.37***		
% Hill slope												
NDVI												
Grass abundance	19.14***	1.83*	2.40*	2,96*		1.87**	28.06*		7.42**	28.57***		1.86*
Grass quality			2.25*	4.94**		1.74**					4.06***	1.74*
Model ANOVA	$F_{7,149}=5.64$***	$F_{10,93}=4.62$***	$F_{10,61}=4.44$*	$F_{9,101}=1.98$*	$F_{9,98}=1.76$	$F_{10,69}=1.84$	$F_{7,151}=5.31$***	$F_{10,70}=17.37$***	$F_{10,45}=1.97$	$F_{9,50}=3.63$***	$F_{10,55}=4.37$**	$F_{10,557}=4.43$**
Model r^2	0.40	0.36	0.47	0.21	0.24	0.23	0.27	0.36	0.32	0.38	0.39	0.32

Note: Two tailed *t*-test was used to establish the importance of each habitat variable and significance indicated with asterisk *$p<0.05$, **$p<0.01$, ***$p<0.001$.

Abbreviations: Blank, Not significant in the model; BM, Bachelor males; J, Juveniles; LF, Lactating females; NLF, Non-lactating females; TM, Territorial males.

In wet seasons, few habitats were disproportionately selected specifically those characterised by open grasslands of high quality as depicted by high NDVI and percentage greenness. Here, livestock were abundant suggesting that Grevy's zebras prefer short green grazing lawns on moist soils where livestock can stimulate regrowth of highly digestible and nutritious vegetation. Habitats that were densely wooded or waterlogged during wet periods would appear to be avoided during rainy periods presumably because of both poor predator visibility and escapability. Such seasonal variability shows that Grevy's zebras do not favour one habitat type year round. Needs and risks change and Grevy's zebras respond by changing their use of particular habitats. Because changes in climate and land use will continue to alter the availability and patterning of these habitats, scientists and policy makers need to understand how seasonal and demographic dynamics interact if Grevy's zebras and other this endangered species are to be brought back from the edge.

Grevy's zebra demographic and reproductive classes showed difference in habitats they used. These differences likely resulted from differences in physiological demands, nutrients requirement and survival strategies. For example, non-lactating females and bachelor males showed similar habitat selection patterns, perhaps because they both have similarly high energic demands. For non-lactating female's energy is required for recovering from their last reproductive episode, or if already pregnant, for supporting a developing foetus. For bachelor males, energy is required for rapid growth so that they have enough stamina to seize and maintain good territories that attract females to enhance their reproductive success. Or, bachelor males may simply be seeking habitats that receptive females, often those no longer lactating, but reproductively cycling frequently so that they can steal mating when they are apart from territorial males (Sundaresan et al. (2007).

Lactating females and juveniles both preferred habitats with high quality resource and that were near to water in both seasons. While both have high energetic demands, their need for water is also high. Territorial males showed some small differences in the attributes of the habitat selected during dry and wet weather seasons. Given that both lactating and non-lactating females shift habitats seasonally, males may simply be shifting the habitats they defend, anticipating the arrival of shifting females (Rubenstein, 2010).

Our study also shows that different nutritional features in vegetation likely under pin seasonal changes in habitat use by various Grevy's zebra demographic and reproductive classes. For a hindgut fermentor like the Grevy's zebra which can subsist on low quality vegetation if necessary (Hack et al., 2002; Mandlate Jr et al., 2019; Redfern et al., 2003; Sinclair, 1985), grass abundance is important in determining habitat selection in both dry and wet seasons. During wet seasons, however, we observed that they often were found in areas of high grass quality. Seeking area containing patches of high quality vegetation may be driven by the need to replenish energy and nutrients after long dry periods. Livestock grazing and transformations of the landscape may be attracting Grevy's zebras to emerging grazing lawns. But when this vegetation becomes too short to crop after the rains cease, Grevy's zebras depart these areas, returning to areas of high grass abundance.

In dry season, Grevy's zebra also selected areas with high tree / bush density and those grassy areas that were waterlogged during the rainy season. Tree thorns could protect grass under their canopies from being grazed by bulk feeding grazers like cattle, while high tree numbers or density could increase shading and alter soil moisture levels, especially if *Acacia tortilis* is present since their roots acts as water pumps (Ludwig et al., 2003, 2004; Treydte et al., 2009). This will enable grass to senesce slowly, thus creating grass banks that Grevy's zebra could access. Although trees during the wet season may hide predators, during the dry season leaf drop will increase visibility enabling zebras to more easily detect and flee from predators (Sundaresan et al., 2007). While waterlogged habitats during the rainy season are difficult to navigate and escape from attacking predators, during the dry season predation risk reduces and their ability to retain soil moisture will enhance grass growth.

Remaining close to water was very important to Grevy's zebras in the dry weather season, unlike in the wet season. This could have been due to many ephemeral water points during wet season unlike in dry season which releases most individuals to range widely in search of forage. In dry season, however, youngsters and territorial males seeking to mate with females as they come and go from water tend to remain near water where they are likely to suffer higher levels of parasitic nematode infection (Tombak & Rubenstein, 2023). Since most Grevy's zebra only need to drink every 3–5 days (Rubenstein, 2010; Williams, 2002), they can avoid these habitats as confirmed by this study.

The type of flexibility in habitat and resources use shown in this study is very important for Grevy's zebra survival in this type of landscapes. First, it ensures the use of high quality resources during wet seasons thus avoiding direct interspecific competition with numerically more abundant livestock. Secondly, context dependent changes in the needs of different reproductive and demographic classes of Grevy's zebras also reduces intraspecific competition both within and between different seasons. Thus in order to sustain, and even increase, the numbers of this endangered species, it is essential that access is maintained to an array of habitats which themselves change with the seasons. Since changing climate and landscapes induced by people are likely to reduce the abundance and access to essential habitats, understanding which habitats are disproportionately used or avoided will be necessary to shape policies for sustaining populations of this endangered highly social species whose associations change frequently.

ACKNOWLEDGEMENTS

We highly appreciate the assistance from Princeton University who provided financial support, analysis software's and field logistics. Prof. Dan Rubenstein did marvellous job in providing field advice and making sure funds were available for this study from Princeton University (Grant no. NSF IIS-CXT). In the field, assistance from Nicolas and Rikapo is highly appreciated. Mpala Ranch and Research Centre provided a working bench and we are grateful. We highly acknowledge Samburu community, Laikipia community, Samburu National Reserve and Buffalo Springs National Reserve for allowing us to conduct the research on their land.

CONFLICT OF INTEREST STATEMENT

No conflict of interest.

DATA AVAILABILITY STATEMENT

The data presented here was purely collected from the field by ourselves. In the event that the data is requested, I will humbly make it available on request.

ORCID

Joseph Nderitu Kirathe https://orcid.org/0000-0001-9305-3686
Daniel I. Rubenstein https://orcid.org/0000-0002-3747-9946

REFERENCES

Aebischer, J. N., Robertson, A. P., & Kenward, E. R. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, *74*, 1313–1325. https://doi.org/10.2307/1940062

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.

Allison, P. D. (2012). *Logistic regression using SAS®: Theory and applications* (Second ed.). SAS Institute INC.

Asim, F. H., & Zafar, I. (2021). Multivariate analysis of the vegetation composition and community structure of Kok (Arai Valley, district swat). *Journal of Global Ecology and Environment*, *13*(3), 25–37.

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, *49*, 386–400.

Barkham, J. P., & Rainy, M. E. (1976). The vegetation of the Samburu-Isiolo game reserve. *African Journal of Wildlife Research*, *14*, 297–329.

Bauer, I. E., McMorrow, J., & Yalden, D. W. (1994). The historic ranges of three equid species in North-East Africa: A quantitative comparison of environmental tolerances. *Journal of Biogeography*, *21*, 169–182.

Bernt, J., & Hans, T. (2014). The relationship between phytomass, NDVI and vegetation communities on Svalbard. *International Journal of Applied Earth Observation and Geoinformation*, *27*(Part A), 20–30.

Boyce, M. S., Solberg, E. J., Johnson, C. J., Merrill, E. H., Nielsen, S. E., & van Moorter, B. (2016). Can habitat selection predict abundance? *Journal of Animal Ecology*, *2016*(85), 11–20. https://doi.org/10.1111/1365-2656.12359

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380. https://doi.org/10.1071/BT02124

County Government of Laikipia. (2018). *Laikipia county integrated development plan 2018–2022* (p. 217). County Government of Laikipia, Kenya.

County Government of Samburu. (2018). *Samburu county integrated development plan 2018–2022* (p. 399). County Government of Samburu, Kenya.

de Gabriel, M. H., Alexandros, A. K., Konstantinos, G., Lambros, K. J., & Beecham, G. P. (2021). Habitat use and selection patterns inform habitat conservation priorities of an endangered large carnivore in southern Europe. *Endangered Species Research*, *44*, 203–215. https://doi.org/10.3354/esr01105

Di Gregorio, A., & Latham, J. (2000). Land use, land cover and soil sciences. *Africover land cover classification and mapping project* (Vol. *1*, p. 2000). FAO.

DÖrgeloh, W. G. (1997). Estimating sample size for a small-quadrat method of botanical survey for application in mixed bushveld. *African Journal of Range and Forage Science*, *14*, 87–89.

DÖrgeloh, W. G. (2006). Habitat suitability for tsessebe Damaliscus lunatus lunatus. *African Journal of Ecology*, *44*, 329–336.

du Toit, T. J. (1995). Determinants of the composition and distribution of wildlife communities in southern Africa. *Ambio*, *24*(1), 2–6. http://www.jstor.org/stable/4314277

ESRI. (1999–2015). *ArcGIS for Desktop*. ESRI INC.

Fowler, J., Cohen, L., & Jarvis, P. (1998). *Practical statistics for field biology* (2nd ed.). John Wiley & Sons.

Garshelis, D. L. (2000). Delusions in habitat evaluation: Measuring use, selection, and importance. In L. Boitani & T. K. Fuller (Eds.), *Research techniques in animal ecology: Controversies and consequences* (pp. 110–164). Columbia University Press.

Gersick, A. S., & Rubenstein, D. I. (2017). Physiology modulates social flexibility and collective behaviour in equids and other large ungulates. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *372*(1727), 20160241.

Grimsdell, J. J. R. (1978). *Ecological monitoring, handbook No. 4*. African Wildlife Foundation.

Groom, R., & Harris, S. (2009). Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment. *African Journal of Ecology*, *48*, 159–168.

Hack, M. A., East, R., & Rubenstein, D. I. (2002). Status and action plan for the plains zebra (*Equus burchellii*). In P. D. Moehlman (Ed.), *Zebras, asses and horses* (pp. 43–60). IUCN.

Herlocker, D.J. (1992). Vegetation types. In S. Shaabani, M. Walsh, D. J. Herlocker, D. Walther (Eds.), *Samburu District, range management handbook of Kenya*, (Vol. *II*(2):pp. 19–26). Republic of Kenya, Ministry of Livestock Development.

Herlocker, D.J. (1993). Vegetation types. In S. Shaabani, M. Walsh, D. J. Herlocker, D. Walther (Eds.), *Isiolo District, range management handbook of Kenya*, (Vol. *II*(5):pp. 21–57). Republic of Kenya, Ministry of Livestock Development.

Hirzel, A. H., & Lay, G. L. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, *45*, 1372–1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, *22*, 415–427.

IUCN. (2003). *IUCN red list of threatened species*. IUCN.

Ivlev, V. S. (1961). *Experimental ecology of the feeding of fishes*. Yale University Press.

Jacobs, J. (1974). Quantitative measurement of food selection: A modification of the forage ratio and Ivlev's electivity index. *Oecologia (Berl.)*, *14*, 413–417.

Jaetzold, R., & Schmidt, H. (1983). *Farm management handbook of Kenya: Central Kenya* (Vol. *II/B*). Ministry of Agriculture.

Kauhala, K., & Auttila, M. (2010). Estimating habitat selection of badgers-a test between different methods. *Folia Zoologica*, *59*(1), 16–25.

Kirathe, J. N., Githaiga, J. M., Chira, R. M., & Rubenstein, I. D. (2021). Land use influence on distribution and abundance of herbivores in Samburu-Laikipia, Kenya. *Journal Of Sustainability, Environment and Peace*, *4*(1), 21–29. http://www.jsep.uonbi.ac.ke

Krebs, C. J. (2014). *Ecology: The experimental analysis of distribution and abundance* (6th ed., 656). Pearson Education LTD.

Lechowicz, J. M. (1982). The sampling characteristics of electivity indices. *Oecologia*, *52*(1), 22–30.

Ludwig, F.,·Dawson, T. E., Kroon, H., Berendse, F. & Prins, H. H. T. (2003). Hydraulic lift in Acacia tortilis trees on an East African savanna. *Oecologia*, *134*, 293–300.

Ludwig, F., Kroon, H., Berendse, F., & Prins, H. H. T. (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, *170*, 93–105.
Mandlate, L. C., Jr., Cuamba, E. D. L., & Rodrigues, F. H. G. (2019). Postrelease monitoring habitat selection by reintroduced burchell's zebra and blue wildebeest in southern Mozambique. *Ecology and Evolution*, *9*, 6458–6467. https://doi.org/10.1002/ece3.5221
Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical design and analysis for field studies* (2nd ed.). Kluwer Academic Publishers.
Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H. L., Morales, J. M., Daniel, T., & Haydon, D. T. (2015). Establishing the link between habitat selection and animal population dynamics. *Ecological Monographs*, *85*(3), 413–436.
Matthiopoulos, J., Fieberg, J. R., & Aarts, G. (2020). *Species habitat associations: Spatial data, predictive models, and ecological insights*. University of Minnesota Libraries Publishing, Retrieved from the University of Minnesota Digital Conservancy. https://hdl.handle.net/11299/217469
McNaughton, S. J. (1979). Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. *The American Naturalist*, *113*, 691–703.
Moorcroft, P. R., & Barnett, A. (2008). Mechanistic home range models and resource selection analysis: A reconciliation and unification. *Ecology*, *89*, 1112–1119.
Mwangi, T. S., Waithaka, H., & Boitt, M. (2018). Ecological niche modeling of zebra species within Laikipia County, Kenya. *Journal of Geoscience and Environment Protection*, *6*, 264–276. https://doi.org/10.4236/gep.2018.64016
Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, *78*(3), 691–692. https://doi.org/10.1093/biomet/78.3.691
NASA-EO. (2009–2015). NASA-Earth Observatory (NASA-EO); Measuring vegetation (NDVI & EVI). https://earthobservatory.nasa.gov/Features/MeasuringVegetation/measuring_vegetation_2.php
Northrup, J. M., Vander Wal, E. M., Bonar, J., Fieberg, M. P., Laforge, M., Leclerc, C. M., Prokopenko, C. M., & Gerber, B. D. (2022). Conceptual and methodological advances in habitat-selection modeling: Guidelines for ecology and evolution. *Ecological Applications*, *32*(1), e02470. https://doi.org/10.1002/eap.2470
Norton-Griffiths, M. (1978). *Counting animals. Handbook No.1* (2nd ed.). African Wildlife Foundation.
Ogutu, J. O., Piepho, H. P., Said, M. Y., Ojwang, G. O., Njino, L. W., Kifugo, S. C., & Wargute, P. P. (2016). Extreme Willife declines and concurrent increase in livestock numbers in Kenya. *What Are the Causes? PLoSONE11*(9), e0163249. https://doi.org/10.1371/journal.pone.0163249
Oustalet, E. (1882). Une nouvelle espece de Zebre. Le Zebre de Grevy (*Equus grevyi*). *La Nature, Paris*, *10*(470), 12–14.
Pratt, D. J., Greenway, P. J., & Gwynne, M. D. (1966). A classification of East African rangeland, with an appendix on terminology. *Journal of Applied Ecology*, *3*, 369–382.
Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, *84*, 2092–2107.
Ritchie, E. G., Martin, J. K., Kroc Johnson, C. N., & Fox, B. J. (2009). Separating the influences of environment and species interactions on patterns of distribution and abundance: Competition between large herbivores. *Journal of Animal Ecology*, *78*, 724–731. https://doi.org/10.1111/j.1365-2656.2008.01520.x
Rondinini, C., Stuart, S., & Boitani, L. (2005). Habitat suitability models and the shortfall in conservation planning for african vertebrates. *Conservation Biology*, *19*, 1488–1497.
Rubenstein, D. I. (1986). Ecology and sociality in horses and zebras. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological aspects of social evolution* (pp. 282–302). princeton university press.
Rubenstein, D. I. (2010). Ecology, social behavior, and conservation in zebras. In R. Macedo (Ed.), *Advances in the study behavior: Behavioral ecology of tropical animals* (Vol. *42*, pp. 231–258). Elsevier Press.
Rubenstein, D. I., Low Mackey, B., Davidson, Z. D., Kebede, F., & King, S. R. B. (2016). Equus grevyi. *The IUCN Red List of Threatened Species*, *2016*. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T7950A89624491.en
SAS Institute Inc. (2020–2021). *Discovering JMP 13®*. SAS Institute Inc.
Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, *113*, 447–455.
Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? *Journal of Applied Ecology*, *54*, 899–918.
SNR. (2003). Samburu National Reserve Draft Management Plan, 2003–2008. Unpublished report.
Sohl, T. L. (2014). The relative impacts of climate and land-use change on conterminous United States bird species from 2001 to 2075. *PLoS One*, *9*, e112251.
Stamps, J. (2009). Habitat selection. In L. A. Simon (Ed.), *The Princeton guide to ecology* (pp. 38–44). Princeton University Press.
Strickland, M. D., & McDonald, L. L. (2006). Introduction to the special section on resource selection. *Journal of Wildlife Management*, *70*(2), 321–323. https://doi.org/10.2193/0022-541X(2006)70[321:ITTSSO]2.0.CO;2
Sundaresan, R. S., Ilya, R., Fischhoff, R. I., Hartung, M. H., Akilong, P., & Rubenstein, I. R. (2007). Habitat choice of Grevy's zebras (*Equus grevyi*) in Laikipia, Kenya. *African Journal of Ecology*, *46*, 359–364.
Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., & Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *2010*(47), 5–14. https://doi.org/10.1111/j.1365-2664.2009.01737.x
Tombak, K. J., & Rubenstein, D. I. (2023). How equids cope with macroparasites. In H. H. T. Prins, & I. J. Gordon (Eds.), *The Equids. Fascinating life sciences* (pp. 299–322). Springer. https://doi.org/10.1007/978-3-031-27144-1_11
Treydte, A. C., Grant, C. C., & Jeltsch, F. (2009). Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. *Biodiversity and Conservation*, *18*, 3989–4002.
Tucker, C. J., & Sellers, P. J. (1986). Satellite remote sensing of primary production. *International Journal of Remote Sensing*, *7*(11), 1395–1416.
Williams, S. D. (2002). Status and action plan for Grevy's zebra (*Equus grevyi*). In P. D. Williams (Ed.), *Zebras, asses and horses* (pp. 11–27). IUCN.
Yalden, D. W., Largen, M. J., & Kock, D. (1986). Catalogue of the mammals of ethiopia 6: perissodactyla, proboscidea, hyracoidea, lagomorpha, tubulidentata, sirenia and cetacea. *Monitore zoologico Italiano/Italian Journal of Zoology, N.S Supplement*, *4*, 31–103.

How to cite this article: Kirathe, J. N., Githaiga, J. M., Chira, R. M., & Rubenstein, D. I. (2024). Habitat selection by Grevy's zebra (*Equus grevyi*): Conservation implications. *African Journal of Ecology*, *62*, e13229. https://doi.org/10.1111/aje.13229

APPENDIX A

Pearson correlational matrixes for Grevy's zebra numbers and habitat variables over both dry and wet season of Samburu-Laikipia landscape.

Correlational variables		Dry weather			Wet weather		
Variable	*By*	r^2	Count	Sign. *p*.	r^2	Count	Sign. *p*.
Manyatta density	*Tree & bush density*	−0.16	1489	<0.0001*	−0.14	1513	<0.0001*
Manyatta density	*Near water*	0.43	1489	<0.0001*	0.34	1513	<0.0001*
Livestock density	*Grevy's number*	−0.01	1489	0.6468	0.09	1513	0.0003*
Livestock density	*% Annual grass*	−0.40	1489	<0.0001*	−0.44	1513	<0.0001*
Livestock density	*% Perennial grass*	0.28	1489	<0.0001*	0.46	1513	<0.0001*
Livestock density	*% Tree & bush cover*	−0.03	1489	0.2779	0.09	1513	0.0006*
Livestock density	*Tree & bush density*	−0.01	1489	0.7519	−0.01	1513	0.7922
Livestock density	*Near water*	−0.32	1489	<0.0001*	−0.38	1513	<0.0001*
Livestock density	*Manyatta density*	0.01	1489	0.6244	−0.02	1513	0.3925
% Hill slope	*Grevy's number*	−0.003	1489	0.9111	−0.06	1513	0.0151*
% Hill slope	*% Annual grass*	−0.22	1489	<0.0001*	−0.24	1513	<0.0001*
% Hill slope	*% Perennial grass*	0.19	1489	<0.0001*	0.30	1513	<0.0001*
% Hill slope	*% Tree & bush cover*	0.08	1489	0.0016*	0.06	1513	0.0193*
% Hill slope	*Tree & bush density*	0.13	1489	<0.0001*	0.25	1513	<0.0001*
% Hill slope	*Near water*	−0.33	1489	<0.0001*	−0.44	1513	<0.0001*
% Hill slope	*Manyatta density*	0.05	1489	0.0678	−0.08	1513	0.0013*
% Hill slope	*Livestock density*	0.40	1489	<0.0001*	0.51	1513	<0.0001*
NDVI	*Grevy's number*	−0.03	1489	0.2965	0.03	1513	0.2003
NDVI	*%annual grass*	−0.07	1489	0.0170*	−0.32	1513	<0.0001*
NDVI	*% Perennial grass*	0.06	1489	0.0250*	0.42	1513	<0.0001*
NDVI	*% Tree & bush cover*	0.03	1489	0.2914	0.01	1513	0.6657
NDVI	*Tree & bush density*	0.04	1489	0.1075	0.005	1513	0.8382
NDVI	*Near water*	−0.08	1489	0.0022*	−0.21	1513	<0.0001*
NDVI	*Manyatta density*	0.04	1489	0.1696	0.29	1513	<0.0001*
NDVI	*Livestock density*	0.09	1489	0.0005*	0.37	1513	<0.0001*
NDVI	*% Hill slope*	0.07	1489	0.0118*	0.25	1513	<0.0001*
Grass abundance	*Grevy's number*	0.17	1489	<0.0001*	−0.01	1513	0.6321
Grass abundance	*% Annual grasses*	−0.43	1489	<0.0001*	−0.55	1513	<0.0001*
Grass abundance	*% Perennial grasses*	0.36	1489	<0.0001*	0.59	1513	<0.0001*
Grass abundance	*% Tree & bush cover*	0.03	1489	0.2433	−0.09	1513	0.0007*
Grass abundance	*Tree & bush density*	0.20	1489	<0.0001*	0.01	1513	0.6714
Grass abundance	*Near water*	−0.10	1489	0.0001*	−0.29	1513	<0.0001*
Grass abundance	*Manyatta density*	0.28	1489	<0.0001*	0.33	1513	<0.0001*
Grass abundance	*Livestock density*	0.54	1489	<0.0001*	0.44	1513	<0.0001*
Grass abundance	*% Hill slope*	0.31	1489	<0.0001*	0.37	1513	<0.0001*
Grass abundance	*NDVI*	0.07	1489	0.0086*	0.41	1513	<0.0001*
Grass quality	*Grevy's number*	0.03	1489	0.1812	0.14	1513	<0.0001*
Grass quality	*% Annual grasses*	0.13	1489	<0.0001*	0.02	1513	0.4916
Grass quality	*% Perennial grasses*	0.02	1489	0.5587	0.22	1513	<0.0001*
Grass quality	*% Tree & bush cover*	0.08	1489	0.0029*	−0.09	1513	0.0005*
Grass quality	*Tree & bush density*	0.20	1489	<0.0001*	−0.23	1513	<0.0001*
Grass quality	*Near water*	0.07	1489	0.0063*	0.07	1513	0.0105*

(Continues)

APPENDIX A (Continued)

Correlational variables		Dry weather			Wet weather		
Variable	*By*	r^2	Count	Sign. *p*.	r^2	Count	Sign. *p*.
Grass quality	*Manyatta density*	−0.05	1489	0.0787	0.14	1513	<0.0001*
Grass quality	*Livestock density*	−0.09	1489	0.0006*	0.29	1513	<0.0001*
Grass quality	*% Hill slope*	−0.15	1489	<0.0001*	0.02	1513	0.3659
Grass quality	*NDVI*	0.0	1489	0.0005*	0.40	1513	<0.0001*
Grass quality	*Grass abundance*	0.00	1489	0.9974	0.01	1513	0.6784
% Annual grass	*Grevy's number*	−0.23	1489	<0.0001*	0.36	1513	<0.0001*
% Annual grass	% Perennial grass	−0.67	1489	<0.0001*	−0.47	1513	<0.0001*
% Annual grass	*% Tree & bush cover*	−0.05	1489	0.0706	0.12	1513	<0.0001*
% Annual grass	*Tree & bush density*	−0.06	1489	0.030*	0.15	1513	<0.0001*
% Annual grass	Near_water	0.20	1489	<0.0001*	0.19	1513	<0.0001*
% Annual grass	Manyatta density	−0.11	1489	<0.0001*	−0.36	1513	<0.0001*
% Perennial grass	*Grevy's number*	0,18	1489	<0.0001*	0.39	1513	<0.0001*
% Perennial grass	*% Tree & bush cover*	−0.09	1489	0.0005*	0.16	1513	<0.0001*
% Perennial grass	*Tree & bush density*	−0.11	1489	<0.0001*	0.18	1513	<0.0001*
% Perennial grass	Near_water	−0.17	1489	<0.0001*	−0.27	1513	<0.0001*
% Perennial grass	Manyatta density	0.22	1489	<0.0001*	0.28	1513	<0.0001*

APPENDIX B

Example of NDVI maps used to extract mean NDVI in Samburu- Laikipia landscape in dry and wet season.