

Habitat use by a large herbivore guild in a fenced South African protected area

Elena Mariotti^{1*} (ID)[§], Francesca Parrini¹ (ID), Cornelius J. Louw² (ID) & Jason P. Marshal¹ (ID)

¹Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein, Johannesburg, 2000 South Africa

²Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Hatfield, 0028 South Africa

Received 21 November 2019. To authors for revision 20 February 2020. Accepted 23 April 2020

In fenced protected areas with limited opportunities to disperse, resources and constraints vary in space and time, affecting herbivore behaviour. The distribution, availability and quality of resources, burnt areas, and potential inter-specific competition all play a role in sustaining populations of large sympatric African herbivores. We investigated the role of resources, constraints and interspecific relationships on habitat use by three ruminants – black and blue wildebeest (*Connochaetes gnou*, *C. taurinus*) and red hartebeest (*Alcelaphus buselaphus*), and a non-ruminant, plains zebra (*Equus quagga*), across seasons and in different landscape types in a South African reserve. Black wildebeest, blue wildebeest and red hartebeest preferred the open grassland landscape, with homogeneous vegetation, while zebra favoured the wooded grassland landscape, with more heterogeneous vegetation. Burnt areas and vegetation greenness were important for all species, while elevation represented a constraint for black wildebeest only. The presence/absence of other species was important in shaping landscape use for black and blue wildebeest, and this suggests the possibility of competition. Our findings confirm the importance of heterogeneity and, in particular, the important role of a planned burning regime in maintaining such heterogeneity to sustain multi-species herbivore assemblages in small fenced nature reserves, where competition might arise between species using similar resources.

Keywords: large herbivore habitat use, competition in a small fenced reserve, heterogeneity, NDVI, red hartebeest, zebra, black wildebeest, blue wildebeest.

INTRODUCTION

Landscape use and distribution of large mammalian herbivores are primarily driven by availability of resources and presence of constraints. Resources are usually related to forage characteristics, while constraints can limit the use of otherwise favourable environments (Bailey *et al.*, 1996; Redfern, Grant, Biggs & Getz, 2003). Currently, the majority of wild large herbivores in South Africa are found in fenced protected areas, meaning that available resources are limited in space and time (Hayward & Kerley, 2009). Because vegetation, herbivory and their interaction contribute to shaping the environment (Bailey *et al.*, 1996; Bergman, Fryxell, Gates & Fortin, 2001), it is crucial to understand herbivore landscape use and distribution in relation to resources and constraints to implement effective management strategies of

enclosed areas (Senft *et al.*, 1987; Bailey *et al.*, 1996). Grass quality and distribution are important characteristics defining the availability of forage resources for herbivores (Owen-Smith, 2004; Cromsigt, van Rensburg, Etienne & Olf, 2009). Indeed, heterogeneity in forage distribution explained 57% of variance of mule deer (*Odocoileus hemionus*) home range use in California (Kie, Bowyer, Nicholson, Boroski & Loft, 2002), and affected herd size and home range of African buffalos (*Syncerus caffer*) in the Kruger National Park (Winnie, Cross & Getz, 2008). In addition, a heterogeneous landscape has the advantage of offering many potential ecological niches, thus potentially sustaining a higher biodiversity (Owen-Smith, 2004; Cromsigt, Prins & Olf, 2009) than a homogeneous landscape (Owen-Smith, 1996; Harrington *et al.*, 1999).

Grass quality and distribution vary across seasons due to changes in temperature and rainfall patterns (Owen-Smith, 2002) and ultimately influence herbivore distribution. Grass quality declines

*To whom correspondence should be addressed.
E-mail: elenamariotti8@gmail.com



to low levels during the dry season, when most of the grasses are high in fibre and low in protein (Illius & O'Connor, 2000; Owen-Smith, 2002). To cope with the dry season, grazers can increase the use of key resources such as recently burnt areas (Moe, Wegge & Kapela, 1990; Parrini & Owen-Smith, 2010), or widen their diet selection and move to areas that were previously avoided (Casebeer & Koss, 1970; Owen-Smith, 1994). Burnt areas not only offer a layer of new high-quality grasses (Gureja & Owen-Smith, 2002; Archibald & Bond, 2004), but the use of these areas also increases herbivore diet quality, especially during the dry season (Parrini & Owen-Smith, 2010). Grass quality also varies with elevation. When it rains, water tends to move towards bottomlands and accumulate. Therefore, grass is more abundant and retains its greenness for longer in bottomlands compared to uplands, and herbivores tend to prefer these low-lying areas, especially in the dry season (Bell, 1971; Wilms-hurst, Fryxell, Farm, Sinclair & Henschel, 1999).

Herbivores select resources based on their morphology, digestive system and energy requirements which are species-specific. Ruminants select high-quality grass more consistently than non-ruminants, due to the different digestion mechanism, which allows non-ruminants to sustain themselves with high quantities of low-quality grass (Owaga, 1975). Because of the broader dietary tolerance, indeed non-ruminants can use a larger variety of resources; they also tend to have a wider distribution than ruminants, and are considered to be more generalist (Du Toit & Cumming, 1999). Among ruminants, some species such as black and blue wildebeest (*Connochaetes gnou*, *C. taurinus*) are classified as short-grass specialists (Bothma, Van Rooyen & Du Toit, 2002). Though these two species are morphologically very similar, black wildebeest are described as grassland specialist and are endemic to southern Africa, while blue wildebeest can use a wider variety of habitats and are widespread in Africa (Codron & Brink, 2007). Red hartebeest (*Alcelaphus buselaphus*) have a narrow muzzle that allows them to feed selectively on nutrient-rich forage in high-biomass areas (Janis & Ehrhardt, 1988). Non-ruminants such as zebra (*Equus quagga*) are less selective but are known to have a preference for medium-to-tall grass (Arsenault & Owen-Smith, 2008; Hamunye, 2017).

Interactions between different species, such as

competition and facilitation, affect mammalian distribution (Kröger & Rogers, 2005; Odadi, Jain, Wieren, Prins & Rubenstein, 2011). When sympatric species use similar resources, one species might partition its resource use or move to a different area to relieve competition (Day & Young, 2004), having thus a more dispersed pattern than by chance (Sinclair, 1985). In contrast, facilitation might occur when grazing by one species increases the quality of forage available to another species through the stimulation of grass regrowth (Arsenault & Owen-Smith, 2002), thus these species generally use the same areas but at different times, creating a grazing succession (Sinclair, 1985; Arsenault & Owen-Smith, 2002).

To investigate possible factors shaping herbivore resource use at landscape scale, we investigated the role of vegetation greenness, heterogeneity, elevation, fire and distance from potential competing species on the distribution and habitat use of three ruminants (black and blue wildebeest, and red hartebeest) and one non-ruminant (plains zebra), and how this varied with season and between two landscape types, a homogeneous low-lying open grassland, and a more heterogeneous mountainous grassland interspersed with trees. We expected ruminants to select for areas of highest greenness and heterogeneity, and therefore to have a narrower distribution compared to non-ruminants. The non-ruminant zebra was expected to be generalist and thus to not show much selection (Du Toit & Cumming, 1999). In addition, we expected black and blue wildebeest to also be positively associated with burnt areas and low elevations, as previously observed in the same protected area (Helm, 2007). Because of their similar morphology and grass preferences, we expected the two species of wildebeest to avoid potential competition for resources by separating themselves from each other more than expected by chance. A similar pattern of avoidance was expected for red hartebeest and zebra, which both prefer medium to tall grasses (Janis & Ehrhardt, 1988; Arsenault & Owen-Smith, 2002).

MATERIALS AND METHODS

Study area

The study area is Telperion and Ezemvelo Nature Reserves, a 13 000 ha protected area that is situated on the edge of the central inland plateau of the northern part of South Africa (25°38'S, 29°03'E) (Coetzee, 2012) (Fig. 1). The Wilge

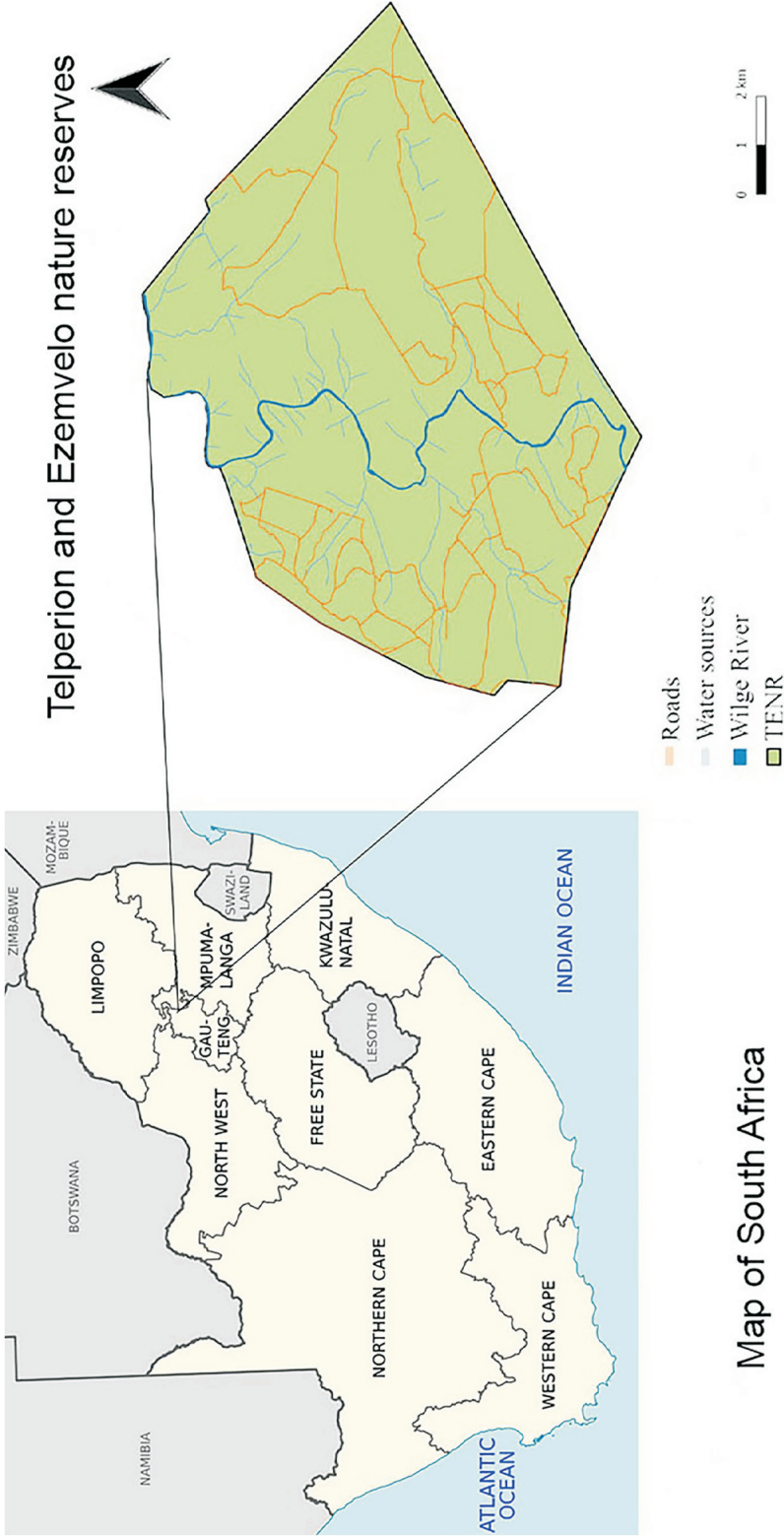


Fig. 1. Telperion and Ezemvelo Nature Reserves, located on the border of Gauteng and Mpumalanga, South Africa.

River, the largest water source, divides the study area into the ‘open grassland landscape’ (Ezemvelo Nature Reserve and Bohlokwa) and the ‘wooded grassland landscape’ (Telperion Nature Reserve). The open grassland landscape is a homogeneous, low-lying and mostly flat area, only disrupted by wetlands along the rivers. The wooded grassland landscape is a heterogeneous, undulating area with scattered wooded zones and several rocky hills (Helm, 2007) (Fig. 2). The wet season ranges from November to March (mean rainfall 462 ± 6 mm) and the dry season spreads from April to October (mean rainfall 163 ± 10 mm) (Swanepoel & Bredenkamp, 2007). The study was conducted during a period of below-average rainfall: 104 ± 2 mm for the wet season (November 2017–March 2018), 52 ± 2 mm for dry season (April–October 2018) and a total of 443 ± 53 mm in 2017 (Ezemvelo Nature Reserve, unpubl. data). In addition, in August 2017 a large area of the open

grassland landscape was burnt as part of the regular management of this part of the reserve, which consists of block burns on a yearly rotational basis. This large area was considered as ‘burnt’ for the whole study period, as previous studies have shown a preference for burnt areas well within the second year after a fire (Parrini & Owen-Smith, 2010). The wooded grassland landscape presented fire breaks along roads, but no large burnt areas. Plant communities of the study area form a mosaic of woodlands and grasslands (Swanepoel & Bredenkamp, 2007). The most common grass species are *Elionurus muticus*, *Eragrostis curvula* and *Setaria sphacelata*, while *Themeda triandra* and *Eragrostis gummiflua* are also common (Swanepoel & Bredenkamp, 2007). The area has over 20 herbivores species, including blesbuck (*Damaliscus pygargus phillipsi*), eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*) and the

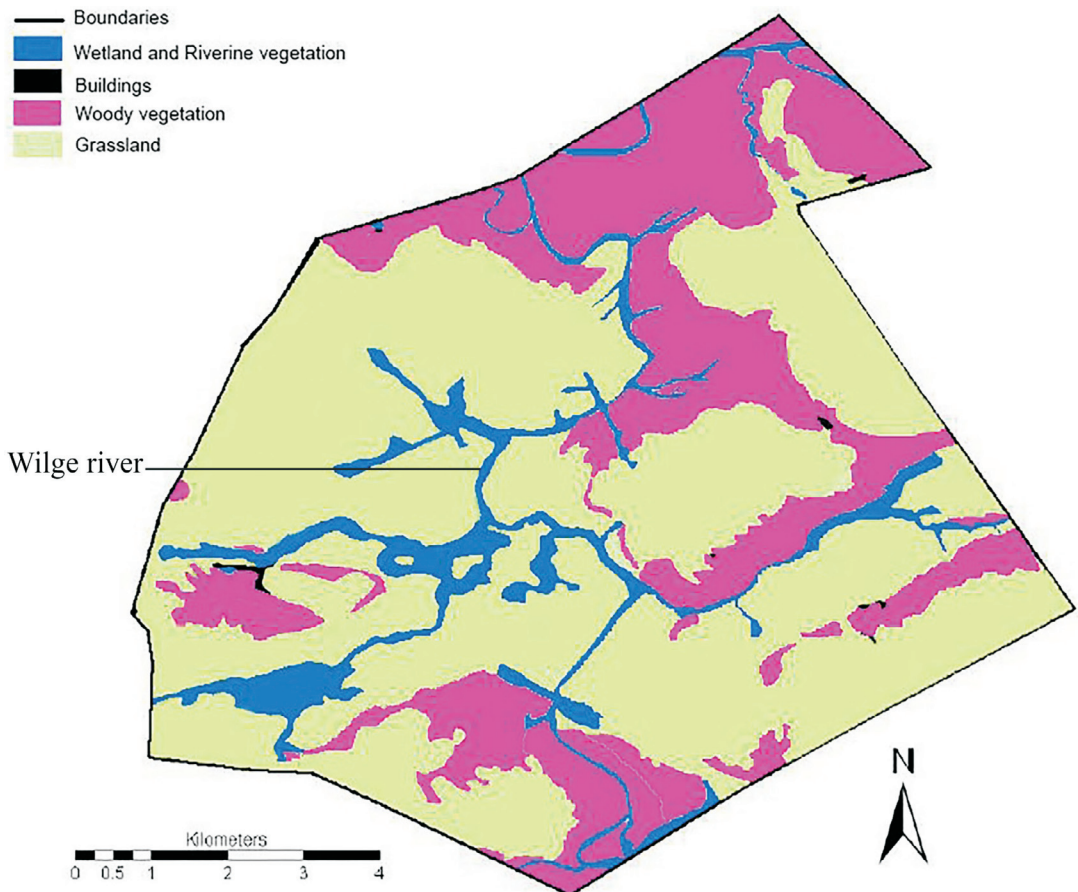


Fig. 2. Vegetation map of Telperion and Ezemvelo Nature Reserves, South Africa. Figure adapted from Helm (2007).

focal species black and blue wildebeest, red hartebeest and plains zebra. Some small carnivores, such as aardwolf (*Proteles cristata*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) are also present and leopards (*Panthera pardus*) have been observed in the study area. Observations suggest that there is movement of large mammals between the two landscapes of the study area.

Data collection

We collected data over one year, from September 2017 to August 2018, visiting the study area once per season for a period of 3 weeks each. The seasons were identified from rainfall and normalized difference vegetation index (NDVI, a proxy for vegetation quality and primary productivity) patterns: late-dry season (October 2017), wet season (February 2018), early-dry season (May 2018) and mid-dry season (August 2018).

During each data collection we drove every available road in the study area twice, following a pre-determined route, searching for the focal species during peak grazing times, *i.e.* in the early morning and late afternoon (Gureja & Owen-Smith, 2002). Each time a foraging individual or group of the study species was encountered, we recorded the species, as well as the season and the landscape type, open grassland or wooded grassland. We also recorded our GPS position (Montana 600 GPS Garmin), the distance (Leica Rangemaster 1600B 7.0X rangefinder) and the angle (military compass) between us and the sighting to later triangulate the locations of the focal species. Testing the triangulation method in the field, we calculated a precision of about 20 m. Herds of single species were considered as one sighting and data were collected for the most central foraging individual.

We used QGIS 2.18 (2016) to model habitat components for the study species. We used a shapefile to identify the burnt area in the open grassland landscape (Ezemvelo Nature Reserve, unpubl. data). We downloaded an elevation raster covering the whole study area with a resolution of 7.5 arc-seconds from the Global Multi-resolution Terrain Elevation Data 2010 database (<https://www.usgs.gov>) and four NDVI rasters, one per season, from the Moderate Resolution Imaging Spectroradiometer (MODIS) database (<https://lpdaac.usgs.gov>). It is common to use MODIS NDVI in animal movement studies at landscape scales as a proxy for vegetation quality and

primary productivity as it gives a measure of photosynthetic activity, which is positively correlated to vegetation quality (McNaughton, 1985; Pettorelli *et al.*, 2005; Winnie *et al.*, 2008). MODIS images represent 16-day composite images with a 250 m spatial resolution. We used one MODIS NDVI image for each three-week period of data collection, the only image falling within the three weeks of data collection or the last one. We created four heterogeneity rasters, one per season, with a spatial resolution of 250 m, by computing the average difference in absolute values between the NDVI value of each pixel and the NDVI values of the eight pixels surrounding it. Open grasslands and thick wooded areas had the lowest heterogeneity values, while transitional zones between grassland, woodland, burnt area and rivers had the highest heterogeneity values.

All the GPS sightings were imported into QGIS 2.18 (2016). We created a buffer of 500 m along all the accessible roads to delineate areas visible from the vehicle. Then, we generated ten random locations for each observed animal location within the visibility buffer. To each observed and random location we assigned a landscape type attribute, ('open grassland' or 'wooded grassland'), an elevation, an NDVI value, a heterogeneity value and a burnt status attribute ('burnt' if on the burnt area, 'unburnt' if not). To analyse relationships between the species, we calculated the distance from each observed and random location to the closest observed individual of a different study species.

Data analysis

The data analysis was conducted in R version 3.5.1 (R Development Core Team, 2018), by fitting 22 generalized linear models (GLM) with a binomial error distribution. The response variable was 'used' *versus* 'random' location. We tested seven independent and not correlated factors, three categorical (landscape type, burnt status and season) and four continuous (NDVI, heterogeneity, elevation and distance from the closest individual of other species). The effect of season and landscape type was also included in interaction with NDVI and heterogeneity.

To make them comparable, we scaled all the continuous variables to have a mean of zero and a standard deviation of 1 (Burnham & Anderson, 2002). Model selection was conducted through the 'AICcmodavg package' (Mazerolle & Mazerolle, 2017) applying the Akaike's information criterion

corrected for small sample bias (AICc) (Anderson, 2008). When multiple models had similar AICc values ($\Delta AICc \leq 2$), we took the one with the lowest AICc value and that accounted for significant variables only, *i.e.* the most parsimonious one (Tack & Fedy, 2015; Stommel, Hofer & East, 2016). From the selected model, we calculated the predicted logit and associated 95% confidence intervals for both categorical and continuous variables.

RESULTS

We totalled 719 sightings during the study period, 92 in the late-dry season, 228 in the wet season, 205 in the early-dry season and 194 during the mid-dry season. Sightings amounted to 141 for black wildebeest, 253 for blue wildebeest, 52 for red hartebeest and 273 for zebra. For all

species, the most parsimonious model included burnt status, distance to other species, NDVI (as an interaction with landscape type for red hartebeest), and heterogeneity (as an interaction with landscape type for blue wildebeest) (Table 1). Zebra and black wildebeest had landscape type as a standalone factor, and the best model for black wildebeest also included elevation (Table 1).

Black wildebeest

Compared to the other species, black wildebeest used the smallest portion of the study area, being concentrated in the burnt area of the open grassland region (Fig. 3). Indeed, black wildebeest favoured burnt areas more than unburnt areas (log-odds = 1.26 ± 0.74) (Fig. 4) and they avoided the wooded grassland landscape (log-odds =

Table 1. AICc model results of the three best predictive models for each species probability of presence, at Telperion and Ezemvelo Nature Reserves, South Africa, 2018.

#	Models	<i>k</i>	AICc	$\Delta AICc$	w_i
Black wildebeest (<i>n</i> = 1551)					
<i>m1</i>	Status + NDVI + heterogeneity+ distance from other species + elevation + vegetation type	9	672.38	0	0.97
<i>m13</i>	NDVI + heterogeneity + distance from other species + status + vegetation type	4	681.21	8.84	0.01
<i>m15</i>	Status + NDVI + distance from other species + heterogeneity* vegetation type	3	682.23	9.85	0.01
Blue wildebeest (<i>n</i> = 2783)					
<i>m15</i>	Status + NDVI + distance from other species + heterogeneity* vegetation type	3	1519.92	0	0.89
<i>m14</i>	Status + heterogeneity + distance from other species + NDVI* vegetation type	11	1524.17	4.25	0.11
<i>m13</i>	NDVI + heterogeneity + distance from other species + status + vegetation type	4	1529.81	9.89	0.01
Red hartebeest (<i>n</i> = 572)					
<i>m14b</i>	Status + heterogeneity + distance from competitor + NDVI* vegetation type	4	291.6	0	0.51
<i>m15b</i>	Status + NDVI + distance from competitor + heterogeneity* vegetation type	2	293.94	2.34	0.16
<i>m7b</i>	Distance from competitor + elevation + vegetation type	7	294.81	3.21	0.1
Zebra (<i>n</i> = 3003)					
<i>m13</i>	NDVI + heterogeneity + distance from other species + status + vegetation type	4	1702.37	0	0.39
<i>m1</i>	Status + NDVI + heterogeneity+ distance from other species + elevation + vegetation type	9	1703.4	1.03	0.23
<i>m14</i>	Status + heterogeneity + distance from other species + NDVI* vegetation type	11	1703.51	1.14	0.22

= Model identification number; *n* = no. observation; *k* = number of parameter in the model; AICc = Akaike's information criterion corrected for small-sample bias; $\Delta AICc$ = difference between model AICc and that of the lowest model; w_i = model probability (Akaike weight); * = interaction; NDVI = normalized difference vegetation index; Status: unburnt or burnt.

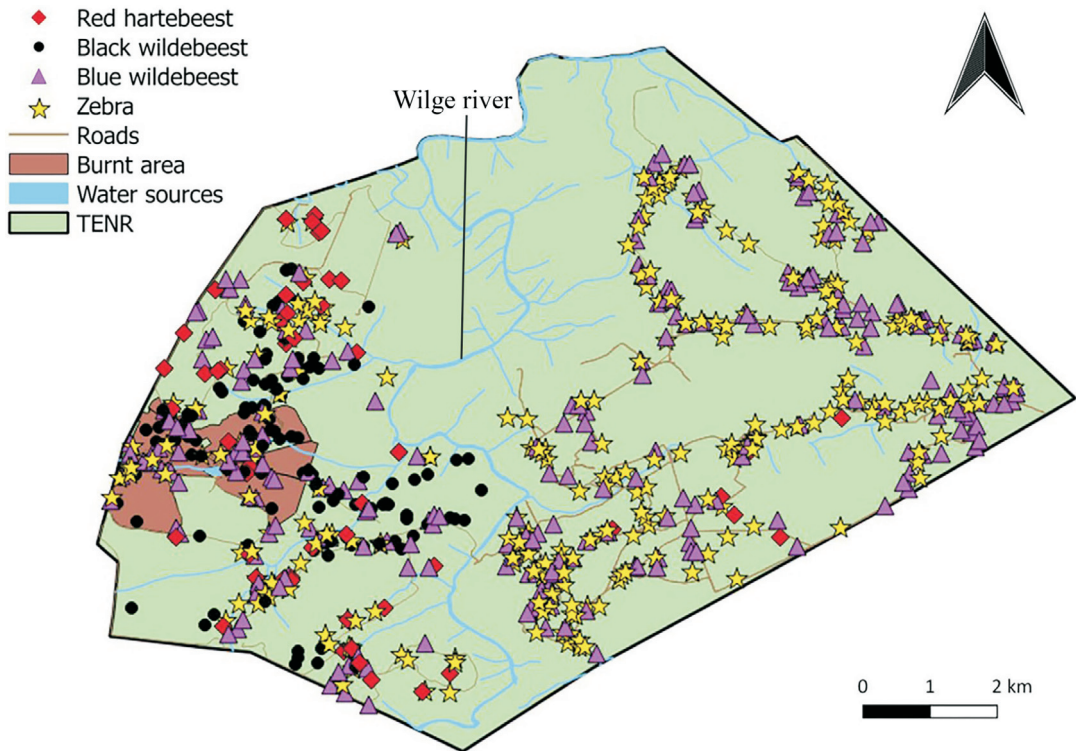


Fig. 3. All the sightings collected between September 2017 and August 2018 at Telperion and Ezemvelo Nature Reserves, South Africa.

-4.24 ± 2) (Fig. 5). In addition, they were preferentially found in low-lying areas (Fig. 6) and closer than expected to all the other study species (Fig. 7). Although NDVI and heterogeneity were part of the best model, their effect on landscape selection by black wildebeest was extremely low (Table 2).

Blue wildebeest

Blue wildebeest used both landscape types, having thus a wide distribution, although they were seen more often in the open grassland landscape than in the wooded grassland ($\log\text{-odds} = -0.40 \pm 0.31$) (Fig. 4). In addition, blue wildebeest favoured burnt areas over unburnt ones ($\log\text{-odds} = 1.03 \pm 0.50$) (Fig. 5). The probability of finding blue wildebeest increased with the presence of zebra and the absence of black wildebeest, while the presence of red hartebeest only slightly increased the probability of sighting a blue wildebeest (Fig. 7). Blue wildebeest preferred areas having a higher heterogeneity value than what was available when in the open grassland landscape, while preferring areas with a lower heterogeneity values

than what was available when in the wooded grassland landscape (Fig. 6). The best model also contained NDVI, but it did not have a significant effect on landscape selection by blue wildebeest (Table 2).

Red hartebeest

Red hartebeest distribution was mainly based in the open grassland landscape and appeared to be slightly wider than that of black wildebeest, as red hartebeest were not concentrated in the burnt area (Fig. 3). Indeed, red hartebeest used both unburnt and burnt areas, slightly preferring the first over the latter ($\log\text{-odds} = -0.90 \pm 1.11$) (Fig. 4). In addition, red hartebeest selected the open grassland landscape more than the wooded grassland ($\log\text{-odds} = -3.25 \pm 1.41$) (Fig. 5). They favoured areas with higher NDVI than what was available when in the open grassland landscape, and areas with lower NDVI compared to what was available when in the wooded grassland landscape (Fig. 6). There was a negative relationship between distance from zebra and the probability of sighting a red hartebeest, as red hartebeest used

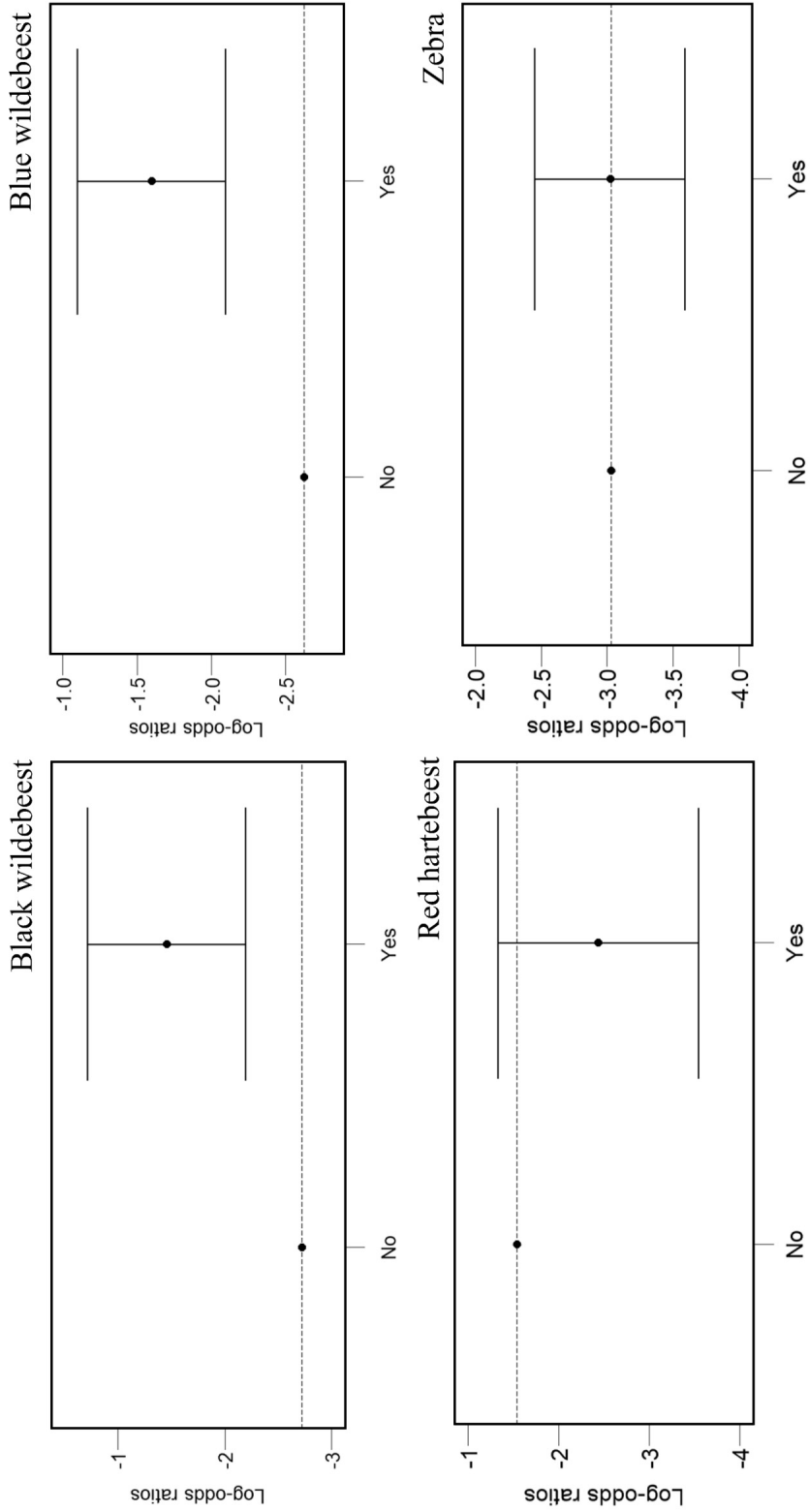


Fig. 4. Predicted estimates ($\pm 95\%$ confidence interval) for landscape selection by black wildebeest, blue wildebeest, red hartebeest and zebra for burnt area ('No' and 'Yes') at Telperion and Ezemvelo Nature Reserves, South Africa, 2018. The dashed line indicates the reference level: 'No'.

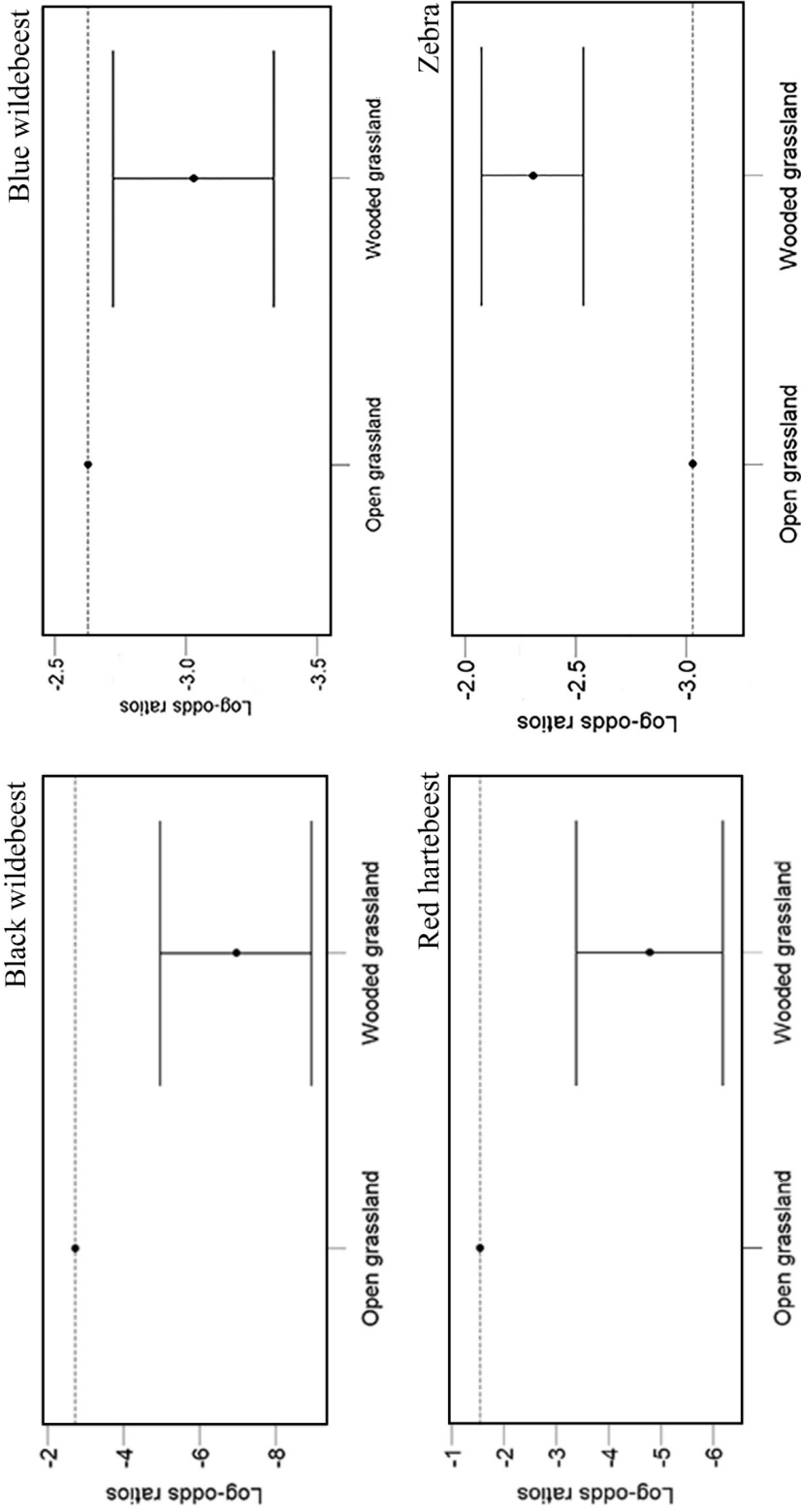


Fig. 5. Predicted estimates ($\pm 95\%$ confidence interval) for landscape selection by black wildebeest, blue wildebeest, red hartebeest and zebra for the study area vegetation type landscape ('Open grassland' and 'Wooded grassland') at Teiperion and Ezemvelo Nature Reserves, South Africa, 2018. The dashed line indicates the reference level: 'Open grassland'.

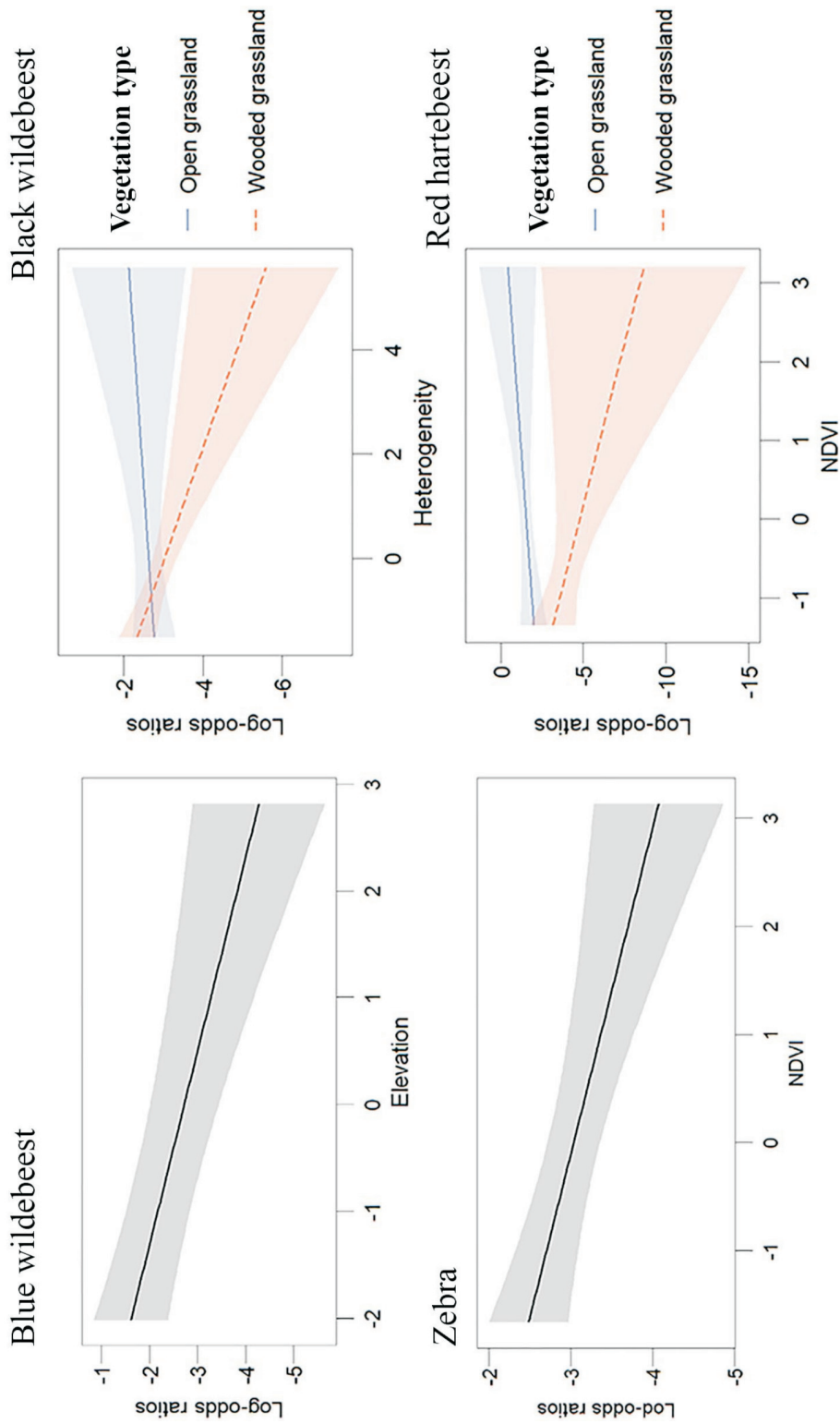


Fig. 6. Predicted estimates ($\pm 95\%$ confidence interval) for landscape selection by black wildebeest, blue wildebeest, red hartebeest and zebra for the study area continuous variables: NDVI, heterogeneity and elevation at Telperion and Ezemvelo Nature Reserves, South Africa, 2018. On the right-hand side are shown the interactions between vegetation type and heterogeneity and NDVI, respectively.

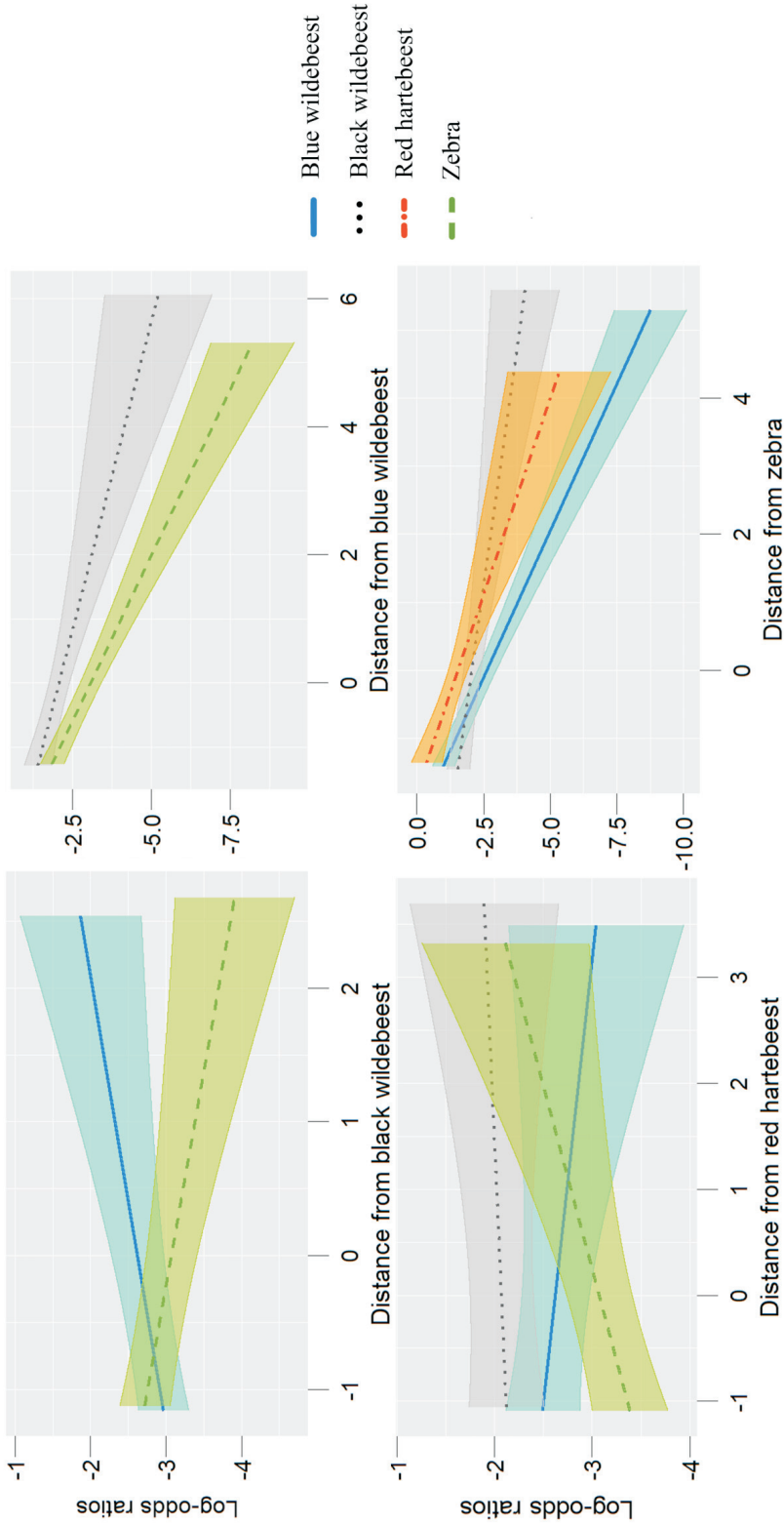


Fig. 7. Predicted estimates ($\pm 95\%$ confidence interval) for landscape selection by the four species for: distance from black wildebeest, distance from blue wildebeest, distance from red hartebeest and distance from zebra, at Telperion and Ezemvelo Nature Reserves, South Africa, 2018.

Table 2. The most parsimonious generalized linear models representing the coefficients that were used to determine the log-odd ratios for landscape selection by black wildebeest, blue wildebeest, red hartebeest and zebra at Telperion and Ezemvelo Nature Reserves, South Africa, 2018.

Black wildebeest <i>m1</i>					Blue wildebeest <i>m15</i>				
	Coefficients					Coefficients			
	Estimate	S.E.	Z-value	Pr(> z)		Estimate	S.E.	Z-value	Pr(> z)
(Intercept)	-2.724	0.366	-7.451	<0.001	(Intercept)	-2.625	0.176	-14.918	<0.001
Burnt	1.265	0.250	5.059	<0.001	Burnt	1.028	0.251	4.093	<0.001
NDVI	-0.259	0.176	-1.472	0.141	NDVI	-0.003	0.130	-0.026	0.979
Heterogeneity	-0.001	0.148	-0.009	0.992	Distance black	0.297	0.118	2.507	0.012
Distance blue	-0.481	0.136	-3.525	<0.001	Distance red	-0.119	0.111	-1.071	0.284
Distance red	-0.956	0.465	-2.054	0.040	Distance zebra	-1.158	0.118	-9.831	<0.001
Distance zebra	-0.304	0.112	-2.707	0.007	Heterogeneity	0.090	0.131	0.691	0.490
Elevation	-0.551	0.170	-3.251	0.001	WG	-0.403	0.262	-1.538	0.124
WG	-4.238	1.033	-4.101	<0.001	Heterogeneity:WG	-0.549	0.162	-3.40	<0.001

Red hartebeest <i>m14b</i>					Zebra <i>m13</i>				
	Coefficients					Coefficients			
	Estimate	S.E.	Z-value	Pr(> z)		Estimate	S.E.	Z-value	Pr(> z)
(Intercept)	-1.542	0.185	-8.319	<0.010	(Intercept)	-3.031	0.164	-18.455	<0.001
Burnt	-0.898	0.581	-1.546	0.122	NDVI	-0.331	0.116	-2.856	0.004
Heterogeneity	-0.089	0.237	-0.377	0.706	Heterogeneity	0.109	0.107	1.017	0.309
Distance zebra	-0.866	0.210	-4.132	<0.001	Distance blue	-0.955	0.113	-8.445	<0.001
NDVI	0.348	0.270	1.287	0.198	Distance red	0.320	0.109	2.947	0.003
WG	-3.244	0.731	-4.44	<0.001	Distance black	-0.313	0.114	-2.741	0.006
NDVI:WG	-1.563	0.811	-1.926	0.054	Burnt	0.008	0.293	0.029	0.977
					WG	0.725	0.220	3.302	<0.001

NDVI = Normalized difference vegetation index; WG: vegetation type wooded grassland.

areas close to where zebra were foraging (Fig. 7). In addition, red hartebeest slightly favoured areas being more homogeneous than what was available, but the effect of this factor was weak (Table 2).

Zebra

Zebra used the whole study area, having the widest distribution among the studied species (Fig. 3). In addition, zebra used both burnt and unburnt areas without showing a clear preference (log-odds = -0.01 ± 1.14) (Fig. 4). However, zebra strongly preferred the wooded grassland landscape compared to the open grassland (log-odds = 0.72 ± 0.23) (Fig. 5). They preferred areas with lower NDVI than what was available (Fig. 6), and they used areas close to both black and blue wildebeest, but far from red hartebeest (Fig. 7). Heterogeneous areas were slightly preferred, but this variable did not have a strong impact on zebra landscape use (Table 2).

DISCUSSION

Zebra had the widest distribution, being found across the entire study area, with a preference for the wooded grassland landscape, while the ruminants had a preference for the open grassland landscape, and exhibited less extensive distributions than zebra. Blue wildebeest had the widest distribution among ruminants, being found across both landscape types, red hartebeest had an intermediate distribution with a limited presence in the wooded grassland landscape and black wildebeest had the narrowest distribution, almost limited to the burnt areas in the open grassland landscape. Very similar distributions were observed by Helm (2007) and Deliberato (2017) in studies conducted between 2004 and 2005, and 2010 and 2016, respectively, in the same study area. Based on the fact that the former study took place during a normal rainfall year and the latter covered several years, the wettest being 2014 with 794 mm, followed by the driest being 2015 with

only 388 mm of rain (Deliberato, 2017), we can conclude that the below-average rainfall experienced during the study period did not influence the species distribution. In addition, the wide distribution of zebra agrees with Du Toit and Cumming (1999) in that non-ruminant species can use a wider set of resources than ruminants. Similarly, the ability of blue wildebeest to utilize a broader spectrum of vegetation types and to have a more flexible diet than both black wildebeest and red hartebeest (Codron & Brink, 2007), enabled them to exploit a wider part of the reserve.

Contrary to our predictions, season did not have an effect on landscape selection by any species, meaning that all the species selected areas with the same characteristics, regardless of the season. Season affects ungulate selection through changes in grass quantity, quality and water content (Groom & Harris, 2009). The scarcity of grass and water during the dry season can force ungulates to move to areas that were less suitable before (Sinclair, 1985; Treydte *et al.*, 2009). However, rainfall was low during the entire study period, which minimized any seasonal variation in habitat use at the landscape scale. In fact, though the season did not affect herbivores selection at this spatial scale, it did at the feeding patch scale (Mariotti *et al.*, submitted). This highlights the importance of scale in ecological studies, as the same variable can affect herbivore behaviour in different ways at different spatial scales, as confirmed by many authors (Senft *et al.*, 1987; Skarpe, Jansson, Seljeli, Bergström & Røskaft, 2007).

Unexpectedly, greenness (as measured through NDVI) was an important factor in model selection for zebra and red hartebeest landscape use only. Zebra were found in areas with lower NDVI values than the average availability. This result was expected as zebra can forage on grass of low quality if quantity is not limiting (Owaga, 1975). Red hartebeest preferred areas with higher NDVI values than the average availability in the open grassland landscape, while preferring areas with lower NDVI values than the average in the wooded grassland landscape (Table 2). The selection for high greenness areas in the open grassland is in accordance with other studies (Demment & Van Soest, 1985; Duncan, Foote, Gordon, Gakahu & Lloyd, 1990). On the other hand, red hartebeest preference for lower NDVI values compared to what was available in the wooded grassland landscape does not mean that this species selected

grass of lower greenness in this area. Indeed, in a tree/grass mosaic landscape, areas with grass would have lower NDVI values compared to areas with trees (Pettorelli *et al.*, 2005; van Bommel *et al.*, 2006). Therefore, the preference for low NDVI areas in this landscape indicates the preference for open grassland patches within the wooded grassland. Though the use of NDVI has its limitations, it is the best available tool to analyse greenness at this spatial scale, and it is still able to give us indications about the grazers preference for grassland areas and for the greener areas within these areas.

Although the variable 'heterogeneity' was present in the best model of each species, it appeared to have an important influence only on blue wildebeest landscape use. The functional heterogeneity of a landscape depends on how animals perceive and respond to the landscape, which might not be accurately estimated by scientists (Owen-Smith, 2004). In this study, heterogeneity was based on differences in NDVI between neighbouring pixels at 250 m resolution. As the NDVI value is dependent on both greenness and vegetation biomass, with pixels with more tree cover having higher values than pixels with more grass cover (Pettorelli *et al.*, 2005; van Bommel *et al.*, 2006), the selection of more heterogeneous areas by blue wildebeest could be explained by their preference for edge areas. It is unclear why blue wildebeest preferred transitional areas, and, in this study we did not investigate more subtle preferences for grass layer heterogeneity. Future studies should investigate landscape heterogeneity in terms of variations in grass cover, as done by others (Watson, Odendaal, Barry & Pietersen, 2005; Gandiwa, 2014).

The near-absence of red hartebeest and black wildebeest from the wooded grassland landscape suggests this area was not suitable for them. This could depend on a scarcity of grass leading to low intake rates, or grass species in the area being of too low quality or unpalatable for them. We reject the first possibility based on the fact that grass biomass in the wooded grassland landscape was higher than in the open grassland landscape (Mariotti *et al.*, submitted). We believe that our results suggest that grass quality in the wooded grassland landscape was too low to sustain our three ruminant species, which is also supported by the feeding patch scale results (Mariotti *et al.*, submitted). Indeed, zebra was the only species preferring this area and blue wildebeest was the only

ruminant species often found here. Zebra is a generalist non-ruminant which tolerates low-quality grass if available in large quantities (Owaga, 1975), while blue wildebeest appeared to behave as facultative specialist (Shiple, Forbey & Moore, 2009), able to tolerate lower grass quality if needed. On the other hand, both black wildebeest and red hartebeest acted as obligate specialist (Shiple *et al.*, 2009), consistently selecting for high-quality grass at this spatial scale as well as at the feeding patch scale (Mariotti *et al.*, submitted).

Black wildebeest always appeared closer to the other species than expected, and it is particularly interesting that despite differences in vegetation types preferences of black wildebeest and zebra, these two species were closer to each other than expected. This result is due to the abundance and distributions of the two species. Indeed, black wildebeest used their favourite habitat only, having a small and compact distribution, while zebra used every available habitat and were the most abundant of the study species. Thus, there was always a zebra closer to a black wildebeest than expected. Instead, zebra and red hartebeest were sighted further from each other than expected by chance and the same was true for blue wildebeest and black wildebeest. This might indicate interspecific competition between the species (Sinclair, 1985; Arsenault & Owen-Smith, 2002). When two species that select similar resources coexist, a differentiation in realized niche is necessary, with the result of one species using a different resource than the other one (Day & Young, 2004). Such differentiation in resource use is applied by both zebra and blue wildebeest in their consistent use of the lower-quality wooded grassland. If this behaviour is expected for zebra, only few studies have focused on the behaviour of coexisting black and blue wildebeest (Du Toit & Cumming, 1999; Helm, 2007). These studies support our results showing that blue wildebeest's lower reliance on pure grasslands probably allowed them to exploit a larger proportion of the study area compared to black wildebeest, also allowing them to utilize the high-quality grass growing under trees and in wetlands (Treydte, Heitkönig & Ludwig, 2009; Fynn, Murray-Hudson, Dhliwayo, Scholte, 2015, Mariotti *et al.*, submitted).

High levels of competition and an overuse of resources can lead to a species decline and eventually disappearance from an area (Sinclair & Norton-Griffiths, 1982). In this case, it would most


probably be the endemic black wildebeest, being the species with the most restricted range and having a limited genetic pool caused by two bottleneck events (Codron & Brink, 2007; Grobler *et al.*, 2011). The same distribution of black and blue wildebeest observed in this study has been reported by Helm (2007) and Deliberato (2017) for the same study area, and it has therefore been unvaried for a decade. Though the persistence of black wildebeest in the reserve is comforting, this study shows that the presence of large burnt areas in flat grasslands are potentially important for sustaining the endemic black wildebeest and that grass quality in the wooded grassland landscape might be of too low quality to sustain ruminants year-round. This implies that regular burning in the wooded grassland landscape would increase the overall grass quality of the area, making it more suitable for ruminants, and for black wildebeest in particular. However, more long-term studies would be needed to confirm this as on the other hand, the creation of large burnt areas in the wooded grassland landscape would attract black wildebeest to this area, increasing the chances of inbreeding. Indeed, sympatric black and blue wildebeest can interbreed and give birth to fertile hybrids (Fabricius, 1988; Grobler *et al.*, 2011). This study captures space utilization over limited space and time, and long-term monitoring programmes would be required in order to assess whether our findings apply across broader temporal scales. In addition, more studies are needed on coexisting black and blue wildebeest, to better understand their interrelationships. In conclusion, our study highlights the importance of biotic factors in driving herbivore landscape use and distribution, with particular attention at differences in black and blue wildebeest landscape use, and gives management suggestions which could be applied to other grassland protected areas.



ACKNOWLEDGEMENTS

We thank the Oppenheimer family for giving us permission to work in their reserve. We thank the managers Elsabé Bosch, Maroti Tau and John De Jager for their kind collaboration. This work is based on the research supported by the National Research Foundation of South Africa (Grant Numbers: 105729, 113474).

[§]ORCID iDs

E. Mariotti:  orcid.org/0000-0002-9938-8249

F. Parrini:  orcid.org/0000-0002-5517-3123

C.J. Louw:  orcid.org/0000-0003-2986-8340
 J.P. Marshal:  orcid.org/0000-0003-2490-4584

REFERENCES

- Anderson, D.R. (2008). *Model based inference in the life sciences: a primer on evidence*. New York, London: Springer.
- Archibald, S. & Bond, W.J. (2004). Grazer movements: Spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13(3), 377–385.
- Arsenault, R. & Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos*, 97, 313–318.
- Arsenault, R. & Owen-Smith, N. (2008). Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, 117(11), 1711–1717.
- 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.
- Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. *Scientific American*, 225, 86–93.
- Ben-Shahar, R. (1991). Selectivity in large generalist herbivores: feeding patterns of African ungulates in a semi-arid habitat. *African Journal of Ecology*, 29, 302–315.
- Bergman, C.M., Fryxell, J.M., Gates, C.C. & Fortin, D. (2001). Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology*, 70, 289–300.
- Bothma, J. du P., Van Rooyen, N. & Du Toit, J.G. (2002). Antelope and other smaller herbivores. In J. Du P. Bothma (Ed.), *Game ranch management*, 4th edn (pp. 149–175). Pretoria, South Africa, Country: Van Schaik.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd edn). New York: Springer.
- Casebeer, R.L. & Koss, G.G. (1970). Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *African Journal of Ecology*, 8, 25–36.
- Codron, D. & Brink, J.S. (2007). Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. *European Journal of Wildlife Research*, 53, 90–99.
- Coetzee, C. (2012). *The effect of vegetation on the behaviour and movements of Burchell's zebra, Equus burchelli (Gray 1824) in the Telperion Nature Reserve, Mpumalanga, South Africa* (Ph.D. thesis). Pretoria, South Africa: University of Pretoria.
- Cromsigt, J.P.G.M., Prins, H.H.T. & Olff, H. (2009). Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions*, 15, 513–522.
- Cromsigt, J.P.G.M., van Rensburg, S.J., Etienne, R.S. & Olff, H. (2009). Monitoring large herbivore diversity at different scales: comparing direct and indirect methods. *Biodiversity and Conservation*, 18, 1219–1231.
- Day, T. & Young, K.A. (2004). Competitive and facilitative evolutionary diversification. *BioScience*, 54, 101.
- Deliberato, H.G. (2017). *Resources overlap and the distribution of grazer assemblages at Telperion and Ezemvelo nature reserves* (Ph.D. thesis). Johannesburg, South Africa: University of the Witwatersrand.
- 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. & Cumming, D.H. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity & Conservation*, 8(12), 1643–1661.
- Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G. & Lloyd, M. (1990). Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia*, 84, 411–418.
- Fabricius, P. (1988). Fecund black wildebeest × blue wildebeest hybrids. *South African Journal of Wildlife Research*, 18(1), 35–37.
- Fynn, RWS., Murray-Hudson, M., Dhliwayo, M., Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, 23, 559–581.
- Gandiwa, E. (2014). Vegetation factors influencing density and distribution of wild large herbivores in a southern African savannah. *African Journal of Ecology*, 52, 274–283.
- Grobler, J.P., Rushworth, I., Brink, J.S., Bloomer, P., Kotze, A., Reilly, B. & Vrahimis, S. (2011). Management of hybridization in an endemic species: decision making in the face of imperfect information in the case of the black wildebeest—*Connochaetes gnou*. *European Journal of Wildlife Research*, 57(5), 997–1006.
- 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.
- Gureja, N. & Owen-Smith, N. (2002). Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. *South African Journal of Wildlife Research*, 32(1), 31–38.
- Hamunyela, N. (2017). *Foraging behaviour of ruminant and non-ruminant grazers as a function of habitat heterogeneity in Telperion and Ezemvelo Nature Reserves (Ezemvelo section)* (Ph.D. thesis). Johannesburg, South Africa: University of the Witwatersrand.
- Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R. & Funston, P. (1999). Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, 90, 69–78.
- 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.
- Helm, C.V. (2007). *Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa*. (Ph.D. thesis). Pretoria, South Africa: University of Pretoria.
- Illius, A.W., Gordon, I.J., 1987. The allometry of food

- intake in grazing ruminants. *Journal of Animal Ecology*, 56(3), 989–999.
- Illius, A.W. & O'Connor, T.G. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, 283–294.
- Janis, C.M. & Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, 92, 267–284.
- Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B. & Loft, E.R. (2002). Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology*, 83, 530–544.
- Kröger, R. & Rogers, K.H. (2005). Roan (*Hippotragus equinus*) population decline in Kruger National Park, South Africa: influence of a wetland boundary. *European Journal of Wildlife Research*, 51, 25–30.
- Mazerolle, M.J. & Mazerolle, M.M.J. (2017). Package 'AICcmodavg'. <https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf>
- McNaughton, S.J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science*, 191(4222), 92–94.
- McNaughton, S.J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, 55, 260–294.
- Moe, S.R., Wegge, P. & Kapela, E.B. (1990). The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. *African Journal of Ecology*, 28, 35–43.
- Odadi, W.O., Jain, M., Van Wieren, S.E., Prins, H.H. & Rubenstein, D.I. (2011). Facilitation between bovids and equids on an African savanna. *Evolutionary Ecology Research*, 13(3), 237–252.
- Owaga, M.L. (1975). The feeding ecology of wildebeest and zebra in Athi-Kaputei plains. *African Journal of Ecology*, 13, 375–383.
- Owen-Smith, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, 75, 1050–1062.
- Owen-Smith, N. (1996). Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, 26(4), 107–112.
- Owen-Smith, N. (2002). *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge, U.K.: Cambridge University Press.
- Owen-Smith, N. (2004). Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, 19, 761–771.
- Parrini, F. & Owen-Smith, N. (2010). The importance of post-fire regrowth for sable antelope in a southern African savanna: importance of post-fire regrowth for sable. *African Journal of Ecology*, 48, 526–534.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N. Chr. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20, 503–510.
- QGIS Development Team (2016). QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Development Core Team. (2018). R: a language and environment for statistical computing. R Foundation for Statistical Computing.
- 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.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987). Large herbivore foraging and ecological hierarchies. *BioScience*, 37, 789–799.
- Shipley, L.A., Forbey, J.S. & Moore, B.D. (2009). Revisiting the dietary niche: when is a mammalian herbivore a specialist? *Integrative and Comparative Biology*, 49, 274–290.
- Sinclair, A.R.E. (1985). Does interspecific competition or predation shape the African ungulate community? *The Journal of Animal Ecology*, 54, 899.
- Sinclair, A.R.E. & Norton-Griffiths, M. (1982). Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia*, 53, 364–369.
- Skarpe, C., Jansson, I., Seljeli, L., Bergström, R. & Røskaft, E. (2007). Browsing by goats on three spatial scales in a semi-arid savanna. *Journal of Arid Environments*, 68, 480–491.
- Stommel, C., Hofer, H. & East, M.L. (2016). The effect of reduced water availability in the Great Ruaha River on the vulnerable common hippopotamus in the Ruaha National Park, Tanzania. *PLOS ONE*, 11(6): e0157145.
- Swanepoel, B.A. & Bredenkamp, G.J. (2007). The vegetation ecology of Ezemvelo Nature Reserve, Bronkhorstspuit, South Africa. *South African Journal of Botany*, 73, 315–316.
- Tack, J.D. & Fedy, B.C. (2015). Landscapes for energy and wildlife: conservation prioritization for golden eagles across large spatial scales. *PLOS ONE*, 10(8).
- Treydte, A.C., Heitkönig, I.M.A. & Ludwig, F. (2009). Modelling ungulate dependence on higher quality forage under large trees in African savannahs. *Basic and Applied Ecology*, 10, 161–169.
- van Bommel, F.P., Heitkönig, I.M., Epema, G.F., Ringrose, S., Bonyongo, C. & Veenendaal, E.M. (2006). Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana. *Journal of Tropical Ecology*, 22(1), 101–110.
- Watson, L.H., Odendaal, H.E., Barry, T.J. & Pietersen, J. (2005). Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation*, 122, 173–180.
- Wilmschurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, 77(8), 1223–1232.
- Winnie, J.A., Cross, P. & Getz, W. (2008). Habitat quality and heterogeneity influence distribution and behavior in African Buffalo (*Syncerus caffer*). *Ecology*, 89, 1457–1468.