Journal of Mammalogy, 2024, **105**, 1336–1344
https://doi.org/10.1093/jmammal/gyae091
Advance access publication 8 September 2024
Research Article

Research Article

Resource selection at fine scale: what drives the decision of a generalist herbivore?

Melinda Boyers[1,2,*], Francesca Parrini[2]

[1]School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow G128QQ, United Kingdom
[2]Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa

[*]Corresponding author: School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow G128QQ, United Kingdom. Email: Boyers21@gmail.com
Associate Editor was Rafael Reyna

Abstract

Spatial patterns in topography and forage distribution significantly influence the movements and choices of large herbivores. However, understanding the foraging strategies of free-grazing herbivores at different temporal and spatial scales remains limited, as different behavioral decisions can apply at different hierarchical levels. This study investigates the fine-scale foraging strategies of the Plains Zebra (*Equus quagga*) in a South African savanna, with a specific focus on their selection of green vegetation at the plant and feeding patch levels. We used the Normalized Difference Vegetation Index as a proxy for vegetation productivity and quality. Our findings reveal that zebras adapted their foraging strategies according to scale and season. During the late-dry season and early-wet season, selection for greenness was at both the grass tuft and feeding site levels. In contrast, during the mid-dry season, selection was predominantly at the tuft level, focusing solely on greenness. These insights emphasize the importance of conducting multilevel studies when investigating factors influencing foraging decisions. Findings at 1 hierarchical level may not necessarily apply across other levels of investigation, highlighting the need for a nuanced and comprehensive approach to understanding the complex foraging behaviors of animals.

Key words: forage selection, greenness, Plains Zebra

Understanding how ecosystems are impacted by various factors remains a key challenge in animal ecology (Fryxell et al. 2004; Prins and Van Langevelde 2008; Balluffi-Fry et al. 2020). Studying mechanisms such as foraging strategies that free-grazing herbivores adopt at different spatial and temporal scales is becoming a focal point in animal ecology and ecosystem management (Senft et al. 1987; Bailey et al. 1996). Resource distribution plays a pivotal role in shaping the movement and distribution of herbivores (Muya and Oguge 2000). Predicting the distribution of large herbivore species, whether for conservation or management purposes, requires a clear understanding of how different species utilize available resources. Several factors come into play including grass height, grass species composition, woody canopy cover (Sinclair et al. 1985; Ben-Shahar 1991; Owen-Smith 2002), and grass greenness (Mcnaughton 1985; Sinclair et al. 1985)—all of which significantly affect the resources and overall habitat conditions for large grazers. The physical properties and structural characteristics of the grass also impact its acceptability (O'Reagain and Schwartz 1995). Notably, many animals exhibit a strong preference for green plant material over dry material, as observed in sheep and cattle (O'Reagain and Schwartz 1995). Furthermore, the greenness of vegetation is inversely correlated with its maturity (Van Soest 1994), meaning that younger vegetation tends to be greener and generally indicative of higher-quality forage (O'Reagain and Owen-Smith 2009). Spatial patterns in topography and forage distribution play a critical role in shaping the movements of large herbivores. However, our understanding of the relative importance of foraging decisions made across different spatial scales remains somewhat limited.

Different foraging response patterns are displayed at different scales, defining different hierarchies (Senft et al. 1987; Bailey et al. 1996; Wilmshurst et al. 1999; Rettie and Messier 2000; Bowers 2006) which may begin at the landscape scale and gradually refines down to finer scales, progressing through feeding patches, feeding stations, and finally, specific plant parts or bites (Bowers 2006). Decisions made at large temporal and spatial scales, e.g., where to begin grazing, can significantly influence behaviors at smaller scales, while decisions at smaller scales can be integrated and inform decisions at larger scales (Bailey et al. 1996). Thus, herbivores must integrate information from lower scales including bites, feeding stations, and patches, to assess spatial alternatives at higher scales encompassing foraging areas, camps, and home ranges (Bailey et al. 1996). Resource heterogeneity occurs at all spatial scales within the environment, making it challenging to determine in advance at which spatial-scale resource selection might predominate (Senft et al. 1987).

Different herbivore species exhibit different trade-offs between forage quality (measured by factors such as greenness and species) and quantity (forage mass). Plains Zebra (*Equus quagga*), a high-density nonruminant herbivore, possess a hind-gut digestive system that allows them to process food at a faster rate compared

Received: January 12, 2024; Editorial Decision: July 10, 2024; Accepted: July 26, 2024

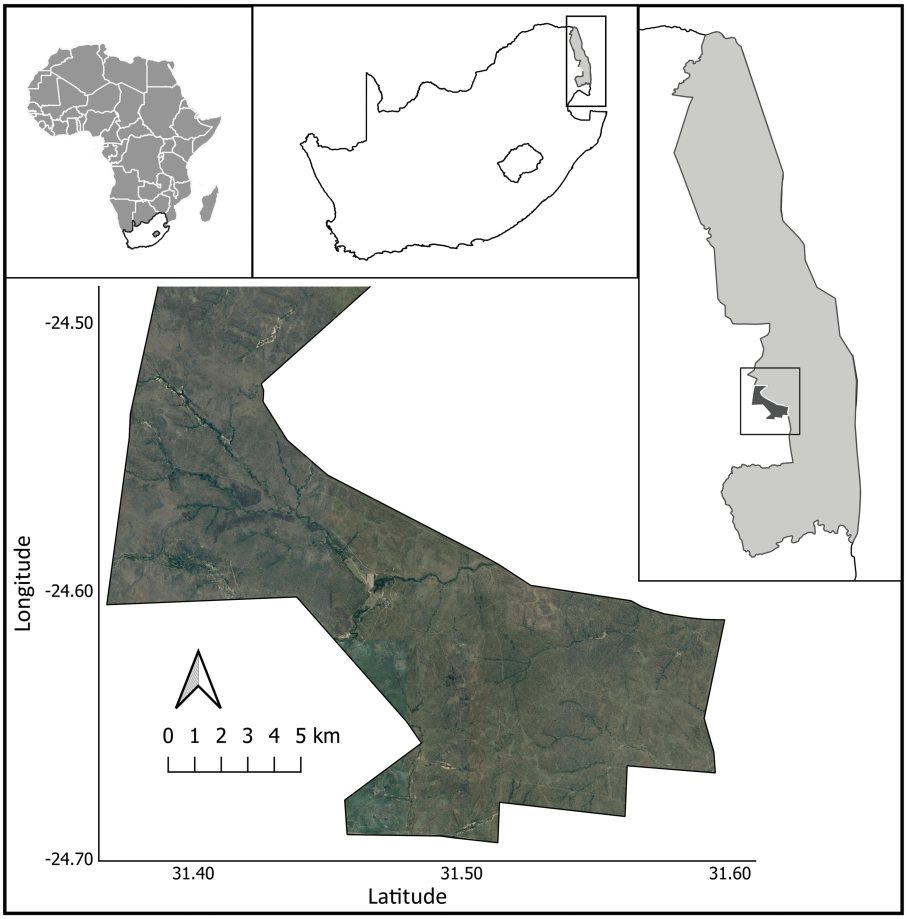

Fig. 1. Map of Manyeleti Game Reserve, including continental position (map inset top left), showing Kruger National Park situated on the border. There are no fences between Manyeleti Game Reserve and Kruger National Park. Maps were created in QGIS 3.14.16-Pi (http://qgis.osgeo.org) using Google Satellite Imagery (Map data @2020: Google, TerraMetrics).

to foregut ruminants, potentially allowing zebras to exploit a wider range of grass quality and quantity (Hack et al. 2002). Previous research in the southwestern region of the Greater Kruger National Park in South Africa (Sabi-Sands Game Reserve and Timbavati Game Reserve) found that grass height and greenness were positively associated with preference of zebras for specific grasses within their foraging areas (Ben-Shahar 1991; Bodenstein et al. 2000). In contrast, studies conducted in Punda Maria in Kruger National Park found that zebras accepted a broader range of grass greenness, including brown grass during both the early- and late-dry seasons (Macandza 2009). Grass biomass, rather than quality, was positively associated with presence of zebras in the 2 Maasai ranches in Kenya's Amboseli-Tsavo ecosystem (Groom and Harris 2009). At larger scales, zebras directed their movement toward patches rich in high-quality resources within the expansive natural landscape of Makgadikgadi Pans National Park in Botswana (Brooks and Harris 2008).

In this study, we investigated whether greenness, plant species, or a combination of both influenced feeding behavior of zebras across 2 distinct spatial scales: the grass tuft within feeding stations; and feeding stations within foraging areas. The aim is to elucidate how these selection criteria change with scale and across different seasons, contributing to a more comprehensive understanding of zebra feeding behavior. We expected that within a foraging area, zebra would select feeding stations based on species composition and greenness. Within a feeding station, we expected them to prioritize forage quality by selecting for greenness, while species composition may not be a significant factor in their decision-making process at this scale.

Material and methods.

Study area.

This study was conducted in Manyeleti Game Reserve (hereafter referred to as Manyeleti) located along the western boundary of Kruger National Park in the Mpumalanga Province, close to the border of the Limpopo province in South Africa (Fig. 1). Manyeleti is located within the savanna biome, characterized by a discontinuous overstory of woody plants and a herbaceous layer primarily dominated by C_4 grasses (Venter et al. 2003). The vegetation in this area is an open tree savanna, with the dominant tree species being *Senegalia nigrescens* and *Sclerocarya birrea*. The most dominant shrubs include *Grewia* spp., *Ziziphus mucronata*, *Flueggia virosa*, and *Ormocarpum trichocarpum*. Within the grass layer, *Heteropogon contortus*, *Themeda triandra*, *Digitaria eriantha*, *Urochloa mosambicensis*, *Panicum maximum*, and *Enneapogon* spp. are the dominant species. Various forbs are also present (Bodenstein et al. 2000). Manyeleti experiences high average summer temperatures, with a mean of 32.4 °C, while winters are generally mild, and free from frost, with an average temperature of 17.8 °C. Rainfall in this area is concentrated between October and April, with a long-term annual average of 572 mm over a 41-year period (Kingfisherspruit, KNP Scientific Services).

Field data collection.

We collected data at 2 spatial scales: the grass tuft within a feeding station; and the feeding station within a foraging area. The dry season is a critical period for African ungulates because limited rainfall leads to a decline in food quality during this period. To capture this crucial phase of the year, our data collection extended over 1 dry season from August to October 2010, and a transition period to the onset of the wet season in November 2010. Within the dry season, we further divided our observations into 2 distinct periods: the mid-dry season spanning from August to September; and the late-dry season in October, based on monthly rainfall and greenness values (Fig. 2).

In the early morning and late afternoon, which are the primary feeding times for ungulates, we drove throughout the reserve to locate grazing zebra individuals or groups within 100 m on either side of the road. The choice of this width is typically based on considerations of vegetation density and the visibility of animals. To avoid resampling the same herd, we did not return to the same area on the same day. Upon identifying a foraging individual or group, we observed their behavior, and once they had moved on, approached the foraging area on foot. The location of the foraging area was confirmed by presence of fresh bites, fresh zebra dung, and spoors. Fresh bites are identifiable by the white, undried appearance of the bitten leaf or stem, while older grazed grass quickly turns brown (Macandza 2009; Kleynhans et al. 2011). When we spotted the first signs of fresh feeding, we placed a 0.5 m × 0.5 m square to represent a feeding station (Novellie 1987). We defined a feeding station as the area accessible to the foraging zebra without requiring it to move its legs, consistent with definitions proposed by Bailey et al. (1996) and Novellie (1987). In cases where fresh footprints and/or signs of cropping revealed a foraging path, we placed 9 additional quadrats along the path. If a foraging path could not be identified, we placed 9 additional quadrats surrounding the central quadrat along the 4 cardinal directions. Grass tufts with fresh bites were classified as "used," and feeding stations with used grass tufts present were similarly classified as "used." For every used feeding station that we sampled, we also sampled 1 unused feeding station, which was identified by showing no signs of grazing. These unused feeding stations were randomly positioned, ensuring that they were at least 2 m apart from the feeding stations in use.

For both used and unused feeding stations, we recorded information regarding grass species composition, species basal cover, season, and average greenness using a handheld Normalized Difference Vegetation Index (NDVI) measuring tool (SpectroSense 2+, Skye Instruments, Netherlands). Within used feeding stations, we documented both used and unused grass tufts according to species, season, and tuft greenness using Walker's (1976) 8-point scale: 0%; 1% to 10%; 11% to 25%; 26% to 50%; 51% to 75%; 76% to 90%; 91% to 99%; and 100%.

Data analyses.

We investigated use versus nonuse at 2 distinct spatial levels of selection: feeding stations within a foraging area; and grass tufts within a feeding station. We considered a feeding station as "used" when any species present within it displayed clear indications of having been eaten, while a grass tuft was scored as "used" if it had fresh bite marks. We categorized our seasons based on rainfall patterns and mean NDVI greenness of the grass. These defined seasons included the mid-dry season (August–September 2010), the late-dry season (October 2010), and the early-wet season (November 2010). For data analyses, we only included the 4 most abundant grass species that were present in a minimum of 10 foraging areas used by zebras per season. This selection was made to ensure a large enough sample size and enable a reliable comparison of acceptability of these particular grass species. The remainder of the species were collectively categorized as "other."

We analyzed our data using generalized linear mixed-effects models (GLMMs). In our models for feeding station selection, the explanatory variables were presence or absence of individual species, season (mid-dry, late-dry, and early-wet), cover, and NDVI values of each feeding station as fixed effects, with foraging area as the random effect. We found collinearity between the basal cover of species and the NDVI measurement—consequently, species basal cover was excluded from the analysis. In the models addressing grass tuft selection, explanatory variables included grass species, season (mid-dry, late-dry, and early-wet), and grass tuft greenness as fixed effects, with foraging area and feeding station as nested random effects. Because of false convergence errors during analysis, when the model fitting functions fail to converge on a maximum likelihood estimate, often due to insufficient data points within a

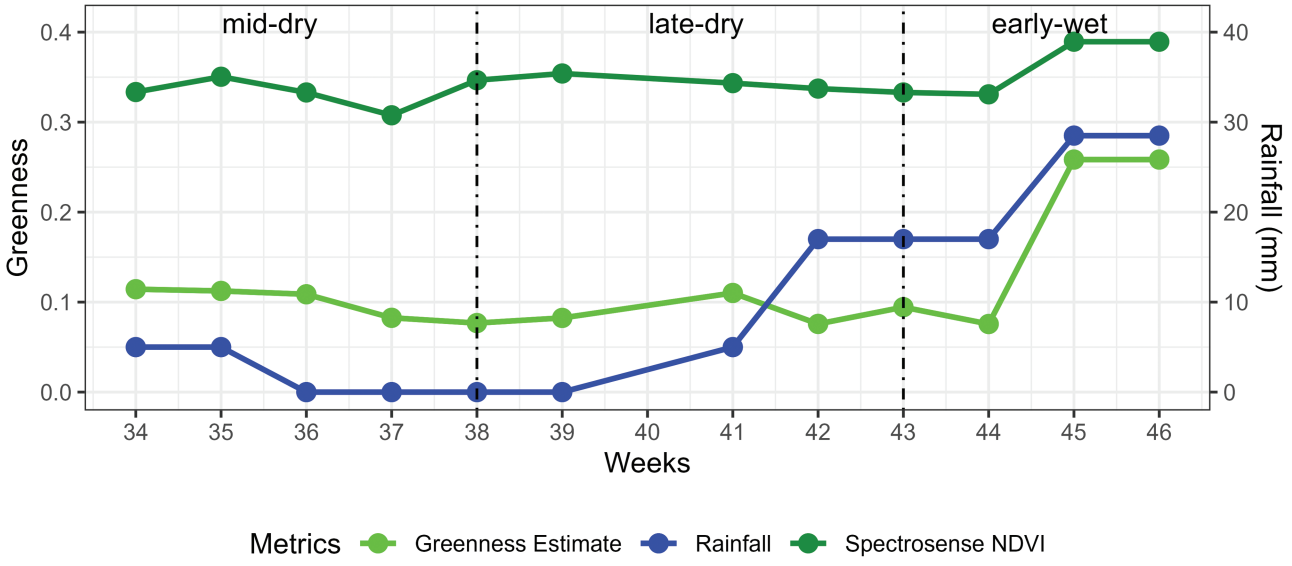

Fig. 2. The relationship between estimated greenness values and Spectrosense NDVI as well as rainfall over the study period (August to November 2010).

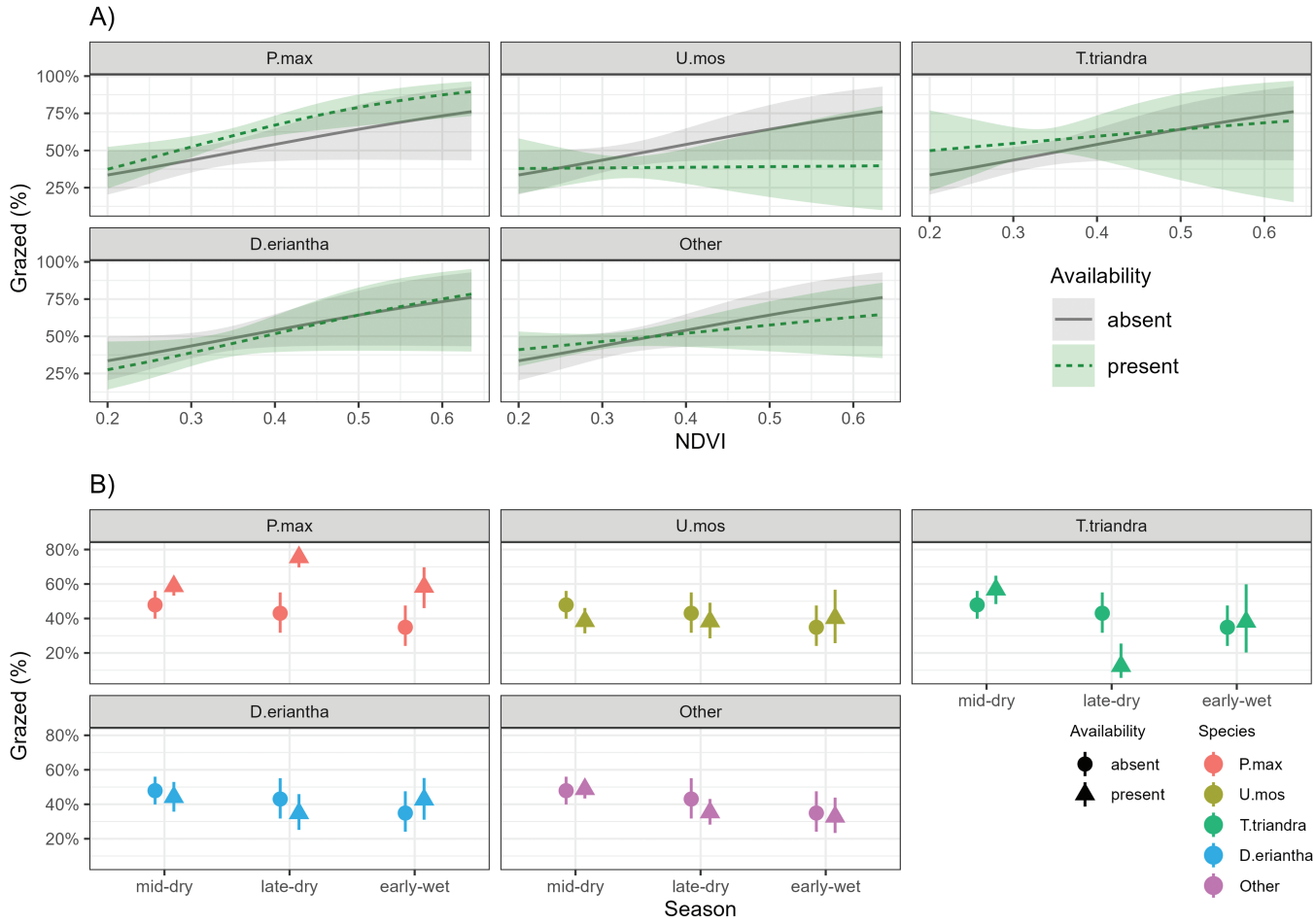

Fig. 3. (A) Feeding station selection estimates for 5 species categories within NDVI categories (± 95% confidence interval) for Manyeleti: P.max = *Panicum maximum*; U.mos = *Urochloa mosambicensis*; Other = all other grasses; T.triandra = *Themeda triandra*; and D.eriantha = *Digitaria eriantha*. The dotted regression line indicates present and solid regression line represents absent from feeding station. (B) Feeding station selection estimates per species per season (± 95% confidence interval) for Manyeleti. From data collected over a 3-month period between August and November 2010.

categorical variable level, we combined the greenness ranks 50% to 75% and 76% to 90% into a single rank of 50% to 90% green.

All models were compared using Akaike's Information Criterion (AIC). Further model comparison was conducted by calculating the relative likelihoods of all candidate models (w_i) and evidence ratios derived from these relative likelihoods ($E_{i,j} = w_i/w_j$). Evidence ratios are used to compare strength of evidence between models within the same set, where a higher evidence ratio signifies stronger support for model i over model j (Anderson 2008). We also calculated the conditional R^2 for our mixed-effect models. This metric describes the proportion of variance explained by both fixed and random factors (Nakagawa and Schielzeth 2013). For the best model(s), we calculated the log-odd ratios from model coefficients and the 95% confidence intervals from variances and covariances of the estimated parameters. We used the R statistical software environment (R Core Team 2018) with R packages "lme4" (Bates et al. 2015) to perform the GLMM analysis, "AICcmodavg" (Mazerolle 2019) to perform the model selection, and "emmeans" (Lenth 2024) to estimate marginal means from models.

Results

We sampled a total of 94 foraging areas, 1,120 used and unused feeding stations (in equal numbers), and 4,861 grass tufts (2,223 grazed and 2,638 non-grazed) within the used feeding stations. Throughout or study, we documented a total of 28 different grass species, 9 of which were never eaten by zebras (Supplementary Data SD1). Of the 19 species consumed, the 4 most abundant species were *P. maximum*, *U. mosambicensis*, *T. triandra*, and *D. eriantha*. The remaining species were grouped under "other" for data analyses. Our focus in both feeding station selection and grass tuft selection analyses was to determine whether either the presence of specific species or their greenness influenced selection. Moreover, we investigated how selection at these spatial scales varied across seasons—specifically the mid-dry, late-dry, and early-wet seasons.

The best model explaining feeding station selection included interactions between feeding station greenness and presence of species, as well as between seasons and presence of species (Model 8, AICc weight = 0.72; Supplementary Data SD2). Specifically, feeding stations with *P. maximum* showed an increased probability of being selected as mean greenness increased, up to a greenness to 60%. Beyond this point, the presence of *P. maximum* presence did not further explain selection (Fig. 3A). Conversely, feeding stations with *U. mosambicensis* displayed a declining probability of selection as mean greenness increased (Table 1). The remaining species categories (*T. triandra*, *D. eriantha*, and "other") did not increase selection by being present but did increase selection with an increase of mean greenness within the feeding station. In addition, during the late-dry season there was an increased probability of a feeding station being selected with an increase in *P. maximum* and an avoidance of

Table 1. Generalized linear mixed model results of the 2 best models representing the coefficients that are used to determine the log-odd ratios for feeding station selection.

	Best model			Second model		
	Log-odds	Std. error	*P*	Log-odds	Std. error	*P*
Predictors						
(Intercept)	−1.53 (−3.07 to 0.01)	0.79	0.051	−0.12 (−0.44 to 0.19)	0.16	0.442
NDVI	4.23 (−0.32 to 8.79)	2.32	0.068			
T.triandra [present]	1.13 (−1.61 to 3.88)	1.40	0.419	0.38 (0.08 to 0.69)	0.16	0.014
U.mos [present]	1.00 (−0.74 to 2.74)	0.89	0.260	−0.33 (−0.59 to −0.07)	0.13	0.011
D.eriantha [present]	−0.47 (−2.19 to 1.24)	0.88	0.589	−0.15 (−0.43 to 0.13)	0.14	0.303
P.max [present]	−0.21 (−1.86 to 1.44)	0.84	0.803	0.50 (0.21 to 0.79)	0.15	0.001
Other [present]	0.72 (−0.85 to 2.29)	0.80	0.367	0.02 (−0.25 to 0.29)	0.14	0.886
Season [late-dry]	−0.20 (−0.77 to 0.38)	0.30	0.509	−0.17 (−0.75 to 0.40)	0.29	0.554
Season [early-wet]	−0.54 (−1.18 to 0.10)	0.33	0.099	−0.19 (−0.71 to 0.33)	0.27	0.480
NDVI × T.triandra [present]	−2.27 (−10.39 to 5.85)	4.14	0.584			
NDVI × U.mos [present]	−4.06 (−9.22 to 1.11)	2.64	0.124			
NDVI × D.eriantha [present]	0.95 (−4.13 to 6.03)	2.59	0.715			
NDVI × P.max [present]	1.89 (−2.93 to 6.72)	2.46	0.442			
NDVI × Other [present]	−2.01 (−6.62 to 2.61)	2.35	0.394			
T.triandra [present] × season [late-dry]	−2.03 (−2.93 to −1.13)	0.46	<0.001	−2.06 (−2.96 to −1.16)	0.46	<0.001
T.triandra [present] × season [early-wet]	−0.22 (−1.14 to 0.70)	0.47	0.638	−0.46 (−1.31 to 0.39)	0.43	0.293
U.mos [present] × season [late-dry]	0.19 (−0.26 to 0.63)	0.23	0.409	0.16 (−0.28 to 0.61)	0.23	0.474
U.mos [present] × season [early-wet]	0.61 (−0.08 to 1.31)	0.35	0.084	0.32 (−0.31 to 0.95)	0.32	0.323
D.eriantha [present] × season [late-dry]	−0.20 (−0.68 to 0.28)	0.25	0.422	−0.21 (−0.69 to 0.27)	0.24	0.387
D.eriantha [present] × season [early-wet]	0.48 (−0.13 to 1.09)	0.31	0.126	0.42 (−0.12 to 0.95)	0.27	0.129
P.max [present] × season [late-dry]	0.97 (0.47 to 1.47)	0.25	<0.001	0.91 (0.42 to 1.40)	0.25	<0.001
P.max [present] × season [early-wet]	0.52 (−0.12 to 1.17)	0.33	0.111	0.49 (−0.08 to 1.07)	0.29	0.090
Other [present] × season [late-dry]	−0.36 (−0.83 to 0.11)	0.24	0.130	−0.35 (−0.82 to 0.12)	0.24	0.143
Other [present] × season [early-wet]	−0.13 (−0.74 to 0.48)	0.31	0.675	−0.25 (−0.78 to 0.28)	0.27	0.349
Random effects						
N	94_{FA}			94_{FA}		
Observations	2,348			2,348		
Marginal R^2/conditional R^2	0.114/NA			0.106/NA		

T. triandra within the feeding station compared to the other seasons (Fig. 3B).

The best model explaining within grass tuft selection included the interaction between species and greenness, as well as between species and season (weight and evidence ratio = 1; Supplementary Data SD3). In both the mid- and late-dry seasons, the majority of grass tufts fell below the 10% greenness threshold (Table 2). The few grass tufts in higher greenness categories were grazed almost 100% when available (Fig. 4A). Overall, the 11% to 25%, 26% to 50%, and 51% to 90% greenness categories were more selected in comparison to those within the 1% to 10% greenness category (Fig. 4B). During the early-wet season, there was an increase in the number of grass tufts within the 11% to 25% and 26% to 50% greenness categories, which resulted in zebras grazing more on the greener tufts (Fig. 4A). Thus, across all periods, an increase in grass tuft greenness correlated with an increased probability of selection. Within each greenness class, when season was held constant, zebras consistently showed a preference for *P. maximum* over other species, except in the over 51% greenness category (Fig. 4D). Notably, during the late-dry season, *P. maximum* was the preferred grass species while there was no difference in species selection in the other 2 seasons (Fig. 4C).

Discussion

In this study, we analyzed zebra selection for feeding stations within foraging areas and for grass tufts within these feeding stations. Contrary to our initial expectations, selection for specific species occurred predominantly at the level of individual tufts. Selection for greenness was observed at both levels—feeding stations and grass tufts—during the late-dry season and early-wet season and only at the tuft level during the mid-dry season.

We had hypothesized that zebras would base their selection for feeding stations within foraging areas on both greenness and species composition. Notably, we found that greenness played a significant role in explaining the use of feeding stations only during the late-dry and early-wet seasons, while it did not show a significant effect during the mid-dry season. In contrast, a separate study investigating the foraging area selection of zebras and other grazers in another savanna area of South Africa (Ezemvelo Nature Reserve)

Table 2. Generalized linear mixed model results representing the coefficients that are used to determine the log-odd ratios for grass tuft selection.

	Eaten		
	Log-odds	**Std. error**	***P***
Predictors			
(Intercept)	−0.01 (−0.30 to 0.28)	0.15	0.926
Species [U.mos]	−1.87 (−2.33 to −1.40)	0.24	<0.001
Species [Oth]	−0.79 (−1.10 to −0.48)	0.16	<0.001
Species [T.triandra]	−0.65 (−1.11 to −0.19)	0.23	0.005
Species [D.eriantha]	−2.46 (−2.99 to −1.92)	0.27	<0.001
Greeness 11% to 25%	2.29 (1.92 to 2.66)	0.19	<0.001
Greeness 26% to 50%	3.86 (3.09 to 4.64)	0.40	<0.001
Greeness 51% to 90%	3.73 (2.44 to 5.01)	0.66	<0.001
Season [late-dry]	0.29 (−0.14 to 0.71)	0.22	0.188
Season [early-wet]	−2.45 (−3.18 to −1.72)	0.37	<0.001
Species U.mos: Greeness 11% to 25%	1.69 (1.01 to 2.36)	0.34	<0.001
Species Oth: Greeness 11% to 25%	0.94 (0.43 to 1.46)	0.26	<0.001
Species T.triandra: Greeness 11% to 25%	0.17 (−0.55 to 0.88)	0.36	0.649
Species D.eriantha: Greeness 11% to 25%	2.11 (1.17 to 3.06)	0.48	<0.001
Species U.mos: Greeness 26% to 50%	0.62 (−1.12 to 2.36)	0.89	0.486
Species Oth: Greeness 26% to 50%	0.23 (−0.81 to 1.26)	0.53	0.667
Species T.triandra: Greeness 26% to 50%	0.28 (−1.26 to 1.82)	0.79	0.720
Species D.eriantha: Greeness 26% to 50%	1.89 (0.51 to 3.27)	0.70	0.007
Species U.mos: Greeness 51% to 90%	16.82 (−1,215.18 to 1,248.82)	628.58	0.979
Species Oth: Greeness 51% to 90%	1.57 (−1.32 to 4.46)	1.47	0.288
Species T.triandra: Greeness 51% to 90%	−1.90 (−2,907.89 to 2,904.09)	1,482.68	0.999
Species D.eriantha: Greeness 51% to 90%	3.64 (0.74 to 6.53)	1.47	0.014
Species [U.mos] × season [late-dry]	0.42 (−0.19 to 1.03)	0.31	0.181
Species [Oth] × season [late-dry]	−1.29 (−1.74 to −0.84)	0.23	<0.001
Species [T.triandra] × season [late-dry]	−0.85 (−2.32 to 0.61)	0.75	0.253
Species [D.eriantha] × season [late-dry]	−0.26 (−0.98 to 0.46)	0.37	0.477
Species [U.mos] × season [early-wet]	−0.64 (−1.98 to 0.71)	0.69	0.353
Species [Oth] × season [early-wet]	−0.68 (−1.59 to 0.22)	0.46	0.139
Species [T.triandra] × season [early-wet]	−14.33 (−569.19 to 540.53)	283.10	0.960
Species [D.eriantha] × season [early-wet]	−0.58 (−1.73 to 0.56)	0.58	0.317
Random effects			
$N_{Feeding.site}$	1,120		
$N_{Foraging.Area}$	93		
Observations	4,861		
Marginal R^2/conditional R^2	0.510/0.594		

found no preference for greenness during the late-dry season and wet season, but only during the early- and mid-dry season (Mariotti et al. 2020). These discrepancies raise questions about the potential factors contributing to such differences. It is indeed difficult to determine whether these variations are due to differences in the scale under investigation (within foraging area in our study vs. foraging areas within patches; Mariotti et al. 2020) or if they are attributable to different environmental conditions present in the 2 study areas. Our results showed that although species explained selection for feeding stations in our area, it was mostly related to greenness. Indeed, feeding stations with *P. maximum* were more likely to be selected, but this preference was only observed when greenness of the feeding station was above 30%. In instances where greenness was lower, species composition did not explain selection for feeding stations. Therefore, selection for feeding stations was not driven by species composition as much as we expected, but rather by greenness. A similar preference was observed for zebra dietary selection in Maputo Special Reserve, southern Mozambique, whereby fibrous grass with low grazing value was selected because it remained very green throughout the dry season (Mandlate et al. 2019). The contrasting findings highlight the complexity of factors influencing zebra behavior and emphasize the importance of considering

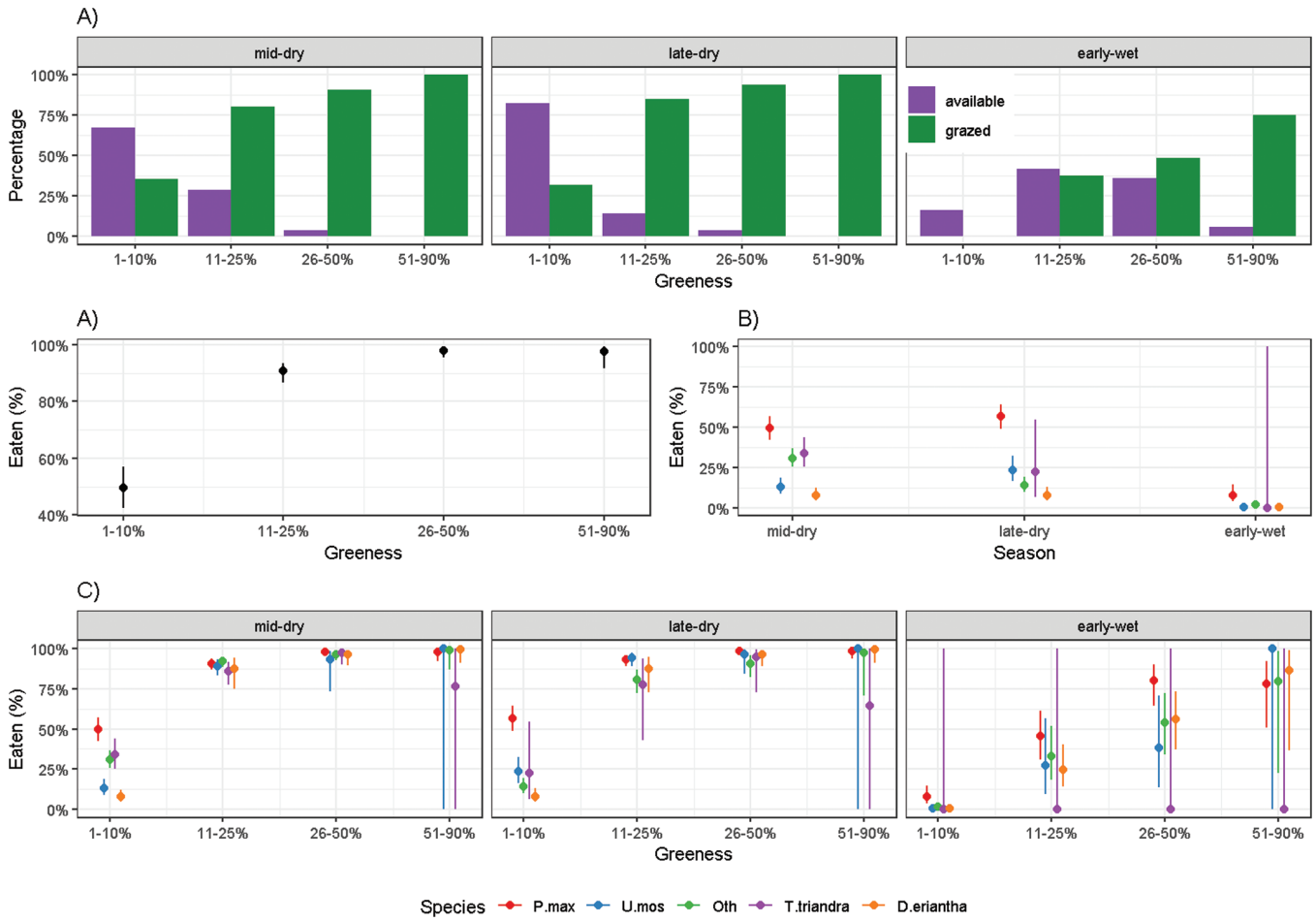

Fig. 4. (A) Percentage of available grass tufts compared to percentage of grass tufts that are grazed within each greenness category in the 3 different seasons: mid-dry season; late-dry season; and early-wet season. (B) Grass tuft greenness selection estimates (± 95% confidence interval) for Manyeleti. (C) Grass species selection estimates per greenness category (± 95% confidence interval) for Manyeleti. (D) Grass species selection estimates per season (± 95% confidence interval) for Manyeleti. P.max = *Panicum maximum*; U.mos = *Urochloa mosambicensis*; Other = all other grasses; T.triandra = *Themeda triandra*; and D.eriantha = *Digitaria eriantha*. Data collected over a 3-month period between August and November 2010.

various factors when interpreting animal foraging decisions in different environments.

Within each feeding station, we expected that zebras would primarily select grass tufts based on their greenness rather than species. Indeed, zebras did select grass tufts with the highest greenness, but the influence of species was also important. During the late-dry season, characterized by most species displaying low greenness, tufts of *P. maximum* were the most selected among all species. However, an interesting pattern emerged from our results: if zebras had to choose between a tuft of *E. rigidior* with greenness above 51% versus *P. maximum* with greenness less than 10%, they would choose *E. rigidior*. Interestingly, zebras in the Timbavati Nature Reserve preferred *U. mosambicensis* over other species including *P. maximum* throughout the year (Bodenstein et al. 2000). In contrast, our study showed a general avoidance of *U. mosambicensis* except when greenness levels were high. *Urochloa mosambicensis* grows in disturbed and overgrazed areas, which may result in an "accidental" reason for not selecting feeding stations presenting this species during the mid-dry season.

At a broader scale than that investigated in this study, Ben-Shahar and Coe (1992) found that zebras exhibited seasonal movement between grass communities characterized by a high proportion of nutritious species, rather than distinct selection for particularly nutritious species within communities. Our study did not look at the grass community level, but we focused on within foraging area selection, a hierarchical level between grass tuft and plant community (Senft et al. 1987).

Our findings revealed an interesting trend: as the feeding stations became greener, the probability that species composition could explain selection decreased. It does indeed make sense that when the overall palatability of the general grass sward increases, selection for specific plant species becomes less pronounced. This suggests that while zebras do exhibit selectivity for certain species, it appears more prominent during the drier months. Studies conducted in other regions such as Timbavati Nature Reserve (Bodenstein et al. 2000) and Hluhluwe iMfolozi Park (Kleynhans et al. 2011) noted that *P. maximum* made up a significant proportion of the diet of zebra in Timbavati Nature Reserve, similar to our observations in the current study area. *Panicum maximum* is known for its nutritional value and longer greenness retention compared to other species, especially during the dry season (van Oudtshoorn 2009) when it is preferred by many grazers (Mutanga et al. 2004). Although zebras in our study area favored *P. maximum* throughout the study period, during the early-wet season when most grasses were green, the greenest tufts were selected regardless of species. Our results are consistent with previous studies that have identified vegetation greenness as the primary driver of herbivore selection (Merkle et al. 2016; Mariotti et al. 2020). This consistent pattern emphasizes the significant influence of greenness on herbivore foraging behaviors.

Studies that have examined how selection criteria of an animal are influenced by the scale at which the selection occurs have yielded contrasting results. Some studies (Fortin et al. 2005) have demonstrated that different criteria might be used across varying scales, while others (Ward & Saltz, 2006) suggest that animals might employ the same selection criteria across different spatial scales. For instance, research on migratory Elk (*Cervus elaphus*) revealed distinct forage quality selection patterns at different spatial scales compared to residential Elk (Hebblewhite et al. 2008). Migratory Elk exhibited different selection patterns at the larger scales compared to finer scales, while residential Elk displayed consistent forage quality selection across all spatial scales. The contrasting selection criteria between migratory and residential Elk resulted in improved quality forage for the former but also increased predation risk (Hebblewhite et al. 2008). Similarly, our study findings suggest that zebras used similar selection criteria across the 2 spatial scales examined. The primary driving force behind their selection was predominantly attributed to changes in vegetation greenness due to seasonal variations. Although we observed some selection for species composition, the prevalence of *P. maximum*, which maintains its greenness for a longer period during the dry season, suggests that greenness remains a principal driver of selection. This pattern is consistent with findings that greenness plays a pivotal role in influencing animal foraging decisions across different spatial scales.

The relationship between small-scale foraging decisions and the broader distribution patterns of herbivores is well-documented (Pretorius 2009). At smaller scales, animals face spatial variability among the grass canopy due to inherent variations in the nutrient content among different plant species. Our observations of free-grazing zebra at Manyeleti show that zebras adapt their foraging strategies based on greenness and specific species, particularly at finer scales. This was notably pronounced during the late-dry season, and somewhat less prevalent in the early-wet season. To deepen our understanding of foraging strategies of large herbivores, future research should focus on comparing selection dynamics across various hierarchical levels and variations, integrating small-scale patterns with broader scales encompassing foraging areas and beyond, and utilizing tools such as satellite remote sensing imagery. This integration could provide a comprehensive perspective, enriching our understanding of how animals navigate and make foraging decisions across multiple scales and changing environmental conditions.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. List of species sampled within the study area.

Supplementary Data SD2. Some candidate high-ranking and low-ranking mixed-effect models and their coefficients, describing feeding station selection in Manyeleti Game Reserve, showing various explanatory variables and interactions (×) included in models.

Supplementary Data SD3. Candidate mixed-effect models and their coefficients, describing grass tuft selection in Manyeleti Game Reserve, showing various explanatory variables and interactions (×) included in models listed from higher to lower ranked.

Acknowledgments

We express gratitude to Mpumalanga Parks and Tourism for accommodating us during this study. A special thanks to Jimmy Thanyani from Manyeleti Game Reserve for access to areas which made this project a success.

Author contributions

MB and FP conceived the ideas and designed the methodology. MB and FP conducted the investigation process and curated data, while MB performed the formal analysis. All authors contributed critically to the drafts and gave final approval for publication.

Funding

This research was funded by the Centre for African Ecology, University of Witwatersrand.

Conflict of interest

None declared.

Data availability

Contact the corresponding author.

References

Anderson DR. 2008. Model-based inference in the life sciences: a primer on evidence. New York (NY, USA): Springer-Verlag New York.

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49(5):386–400. https://doi.org/10.2307/4002919

Balluffi-Fry J, Leroux SJ, Wiersma YF, Heckford TR, Rizzuto M, Richmond IC, Vander Wal E. 2020. Quantity-quality trade-offs revealed using a multiscale test of herbivore resource selection on elemental landscapes. Ecology and Evolution 10(24):13847–13859. https://doi.org/10.1002/ece3.6975

Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Ben-Shahar R. 1991. Selectivity in large generalist herbivores: feeding patterns of African ungulates in a semi-arid habitat. African Journal of Ecology 29(4):302–315. https://doi.org/10.1111/j.1365-2028.1991.tb00468.x

Ben-Shahar R, Coe MJ. 1992. The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. Oecologia 90(3):422–428. https://doi.org/10.1007/BF00317701

Bodenstein V, Meissner HH, van Hoven W. 2000. Food selection by Burchell's zebra and blue wildebeest in the Timbavati area of the Northern Province Lowveld. South African Journal of Wildlife Research 30(2):63–72. https://hdl.handle.net/10520/EJC117098.

Bowers J. 2006. Feeding patch selection of African buffalo (*Syncerus caffer caffer*) in the central region of the Kruger National Park [master's thesis]. [Gauteng (Republic of South Africa)]: Tshwane University of Technology.

Brooks CJ, Harris S. 2008. Directed movement and orientation across a large natural landscape by zebras, *Equus burchelli antiquorum*. Animal Behaviour 76(2):277–285. https://doi.org/10.1016/j.anbehav.2008.02.005

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86(5):1320–1330. https://doi.org/10.1890/04-0953

Fryxell JM, Wilmshurst JF, Sinclair ARE. 2004. Predictive models of movement by Serengeti grazers. Ecology 85(9):2429–2435. https://doi.org/10.1890/04-0147

Groom R, Harris S. 2009. Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment. African Journal of Ecology 48(1):159–168. https://doi.org/10.1111/j.1365-2028.2009.01097.x

Hack MA, East R, Rubenstein DI. 2002. Status and action plan for the plains zebra (*Equus burchellii*). In: Moehlman PD, editor. Equids: zebras, asses and horses status survey and conservation action plan. Gland (Switzerland); Cambridge (UK): IUCN/SSC Equid Specialist Group, p. 43.

Hebblewhite M, Merrill E, McDermid G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78(2):141–166. https://doi.org/10.1890/06-1708.1

Kleynhans EJ, Jolles AE, Bos MRE, Olff H. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. Oikos 120(4):591–600. https://doi.org/10.1111/j.1600-0706.2010.18712.x

Lenth R. 2024. emmeans: estimated marginal means, aka least-squares means. R package version 1.10.3. https://doi.org/10.32614/CRAN.package.emmeans

Macandza VA. 2009. Resource partitioning between low-density and high-density grazers: sable antelope, zebra, and buffalo [dissertation]. [Johannesburg (Republic of South Africa)]: University of Witwatersrand.

Mandlate LC, Arsenault R, Rodrigues FHG. 2019. Grass greenness and grass height promote the resource partitioning among reintroduced Burchell's zebra and blue wildebeest in southern Mozambique. Austral Ecology 44(4):648–657. https://doi.org/10.1111/aec.12708

Mariotti E, Parrini F, Louw CJ, Marshal JP. 2020. What grass characteristics drive large herbivore feeding patch selection? A case study from a South African grassland protected area. African Journal of Range & Forage Science 37(4):286–294. https://doi.org/10.2989/10220119.2020.1768146

Mazerolle MJ. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). https://doi.org/10.32614/CRAN.package.AICcmodavg

Mcnaughton SJ. 1985. Ecology of a grazing ecosystem—the Serengeti. Ecological Monographs 55(3):259–294. https://doi.org/10.2307/1942578

Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society of London, B: Biological Sciences 283(1833):20160456. https://doi.org/10.1098/rspb.2016.0456

Mutanga O, Prins HHT, Skidmore AK, Wieren S, Huizing H, Grant R, Peel M, Biggs H. 2004. Explaining grass-nutrient patterns in a savanna rangeland of Southern Africa. Journal of Biogeography 31(5):819–829. https://doi.org/10.1111/j.1365-2699.2004.01072.x

Muya SM, Oguge NO. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. African Journal of Ecology 38(1):62–71. https://doi.org/10.1046/j.1365-2028.2000.00213.x

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4(2):133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Novellie PA. 1987. Comparison of the foraging strategies of Blesbok and Springbok on the Transvaal Highveld. South African Journal of Wildlife Research 8(4):137–144. https://hdl.handle.net/10520/AJA03794369_3261

O'Reagain PJ, Owen-Smith RN. 2009. Effect of species composition and sward structure on dietary quality in cattle and sheep grazing South African sourveld. The Journal of Agricultural Science 127(2):261–270. https://doi.org/10.1017/S0021859600078047

O'Reagain PJ, Schwartz HJ. 1995. Dietary selection and foraging strategies of animals on rangeland - coping with spatial and temporal variability. In: Journet M, Grenet E, Farce M-H, Thériez M, Demarquilly C, editors. Recent developments in the nutrition of herbivores. Paris (France): INRA Editions, p. 407–423.

Owen-Smith N. 2002. Adaptive herbivore ecology: from resources to populations in variable environments. Student edition. Gauteng (Republic of South Africa): Wits University Press.

Pretorius Y. 2009. Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores [dissertation]. [Wageningen (Netherlands)]: Wageningen University.

Prins H, Van Langevelde F. 2008. Resource ecology: spatial and temporal dynamics of foraging. Netherlands: Springer Science. https://doi.org/10.1007/978-1-4020-6850-8

R Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Rettie WJ, Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23(4):466–478. https://doi.org/10.1034/j.1600-0587.2000.230409.x

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37(11):789–799. https://doi.org/10.2307/1310545

Sinclair ARE, Dublin H, Borner M. 1985. Population regulation of Serengeti wildebeest—a test of the food hypothesis. Oecologia 65(2):266–268. https://doi.org/10.1007/BF00379227

van Oudtshoorn F. 2009. Guide to grasses of Southern Africa. Pretoria (Republic of South Africa): Briza Publications.

Van Soest PJ. 1994. Nutritional ecology of the ruminant. London (UK): Cornell University Press.

Venter F, Scholes R, Eckhardt H. 2003. The abiotic template and its associated vegetation pattern. In: Du Toit JT, Rogers K, Biggs HC, editors. The Kruger experience: ecology and management of savanna heterogeneity. Washington (DC, USA): Island Press; p. 83–128.

Walker BH. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. South African Journal of Wildlife Research 6(1):1–32. https://hdl.handle.net/10520/AJA03794369_3332

Ward D, Saltz D. 2006. Forging at different spatial scales: Dorcas gazelles foraging for lilies in the negev desert. Ecology 75(1):48–58. https://doi.org/10.2307/1939381

Wilmshurst JF, Fryxell JM, Farm BP, Sinclair ARE, Henschel CP. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology 77(8):1223–1232. https://doi.org/10.1139/z99-088