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HIERARCHICAL FEEDING AND HABITAT SELECTION BY WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*) IN A MARGINAL HABITAT

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ABSTRACT

The spatiotemporal variations in the availability of food resources influence the movement of herbivores in a given area. In this study, variations in the selection of food resources by white rhinoceroses (*Ceratotherium simum simum*) was investigated in the Songimvelo Nature Reserve (South Africa) at three spatial scale levels (habitat, patch and grass species levels) during the two seasons (late wet and late dry season of a calendar year). White rhinoceros were tracked on foot, vehicle or horse, and individual groups were observed from a distance using binoculars to identify feeding habitats. At feeding habitat level, white rhinoceroses showed a preference for Low Open Woodlands and Old Lands during the late wet season but avoided Shrublands. No habitat preference was observed during the late dry season. At patch level, white rhinoceroses used patches with low rock cover and short leaf-table-height while remaining in the lower-lying areas of the Reserve. Rhinoceroses fed on grasses such as *Heteropogon contortus, Themeda triandra* and *Eragrostis spp.* during both seasons. The model selection at feeding patch level revealed that grass species presence, mean tuft diameter and species density were the most critical factors driving grass species selection in patches. This study provides evidence that white rhinoceroses' feeding behaviour changes at different spatial scales which result in different patterns of habitat use and movement in time and space within a given area.

Keywords: White rhinoceros, *Heteropogon contortus,* habitat selection, feeding patch selection, scale-dependent.

INTRODUCTION

Adequate quantities of food resources are essential to sustain animal populations in nature (Manly *et al.*, 2002). However, these food resources are unevenly distributed in time and space, vary in nutritional quality, and are found in patches (Owen-Smith, 1992a; Zhang *et al.*, 2009). This patchy distribution of resources has been recognised to influence herbivores' distribution and movement, as well as choice of specific foraging habitats and diet (Bao *et al.*, 2017; Bjørneraas *et al.*, 2012). As a result, many animals do not use all habitats available to them within an area and may respond differently to the environment, i.e. selection or no selection at given scales, yielding different payoffs (Losier *et al.*, 2015; Mårell and Edenius, 2006).

Ecological mechanisms, in general, are scale-dependent (Chalcraft *et al.*, 2008; Cohen *et al.*, 2016; Van Beest *et al.*, 2010). Foraging by grazers can be considered a hierarchical process where selection happens from the broader landscape and community levels, down to the smaller habitat, feeding area, patch, feeding station and bite levels (Owen-Smith *et al.*, 2010; Senft *et al.*, 1987; Van Der Merwe and Marshal, 2012). This selection process is affected by changing environmental conditions at given spatial and temporal scales (Burkepile *et al.*, 2013; Mládek *et al.*, 2013).

At habitat level, selection may be influenced by factors like topography, distance to water and predation (Bailey and Provenza, 2008), while at the feeding patch level, selection may be influenced by forage quality, forage abundance, plant species and social interaction (Van Der Merwe and Marshal, 2012). Although feeding and habitat selection by large herbivores have been extensively studied at different scales, it remains poorly understood for endangered species, like the white rhinoceros, that are reintroduced into areas (Emslie, 1999). Understanding the scale at which environmental factors influence feeding patterns of such species is paramount for their habitat management and conservation.

White rhinoceros (*Ceratotherium simum simum;* henceforth white rhino) is a species of high conservation value (Ferreira *et al.*, 2012) mainly due to its role as an ecological engineer and threats to its survival through poaching (Ferreira *et al.*, 2015). White rhinos are essentially bulk grazers that feed on large volumes of low-quality grass species to maximise quantity (Skinner and Chimimba, 2005). Although white rhinos can tolerate large quantities of low-quality grasses, they require, in part, a high-quality diet (Waldram *et al.*, 2008). These animals feed in lower-lying areas, with a particular preference for certain grasslands and short grass species that grow 25 - 60 mm high (Kleynhans *et al.*, 2011). White rhinos have shown seasonal variations in species and habitat use, where they switch between grassy areas in the wet season and wooded areas in the dry season (Pedersen, 2009). For example, during the dry season, white rhinos in Hluhluwe iMfolozi Park graze in areas with low community diversity and consume grass species according to their availability, while avoiding unpalatable grasses (Perrin and Brereton-Stiles, 1999). Owen-Smith (1992b) observed that in the Sweetveld (i.e. area dominated by nutritious and palatable grasses), white rhinos occupy regions where soil nutrient-rainfall combination causes grasses to build up moderate levels of indigestible fibre in their leaves. However, in the Sourveld (i.e. area dominated by coarse and less palatable grasses), they feed mostly in areas of the landscape where soil nutrients accumulate (Owen-Smith, 1988).

Since the introduction of white rhinos in the Songimvelo Nature Reserve in 1984, their numbers have steadily increased past the proposed carrying capacity of one rhino per 49 ha. This increase led to a decrease in suitable habitats and an increase in competition for space between rhinos (Steyn and Stalmans, 2004), which resulted in the death of rhinos through fights. As a result, the management of the reserve began raising concerns about the availability of food for white rhinos during the critical dry season and habitat selection pattern. Since their introduction, white rhinos' distribution within the reserve was monitored consistently, but no scientific inference was conducted on their feeding and distribution. Food preference requirements are believed to be the primary factors responsible for successful re-introductions of species in a given area (Dutta *et al.*, 2016).

This study aimed to evaluate the seasonal dynamics (late wet and late dry seasons) in the feeding pattern of white rhinos at three spatial scales, i.e. habitat, food patch and grass species. This study therefore sought to answer (1) if white rhinos use different feeding habitats between the late wet and late dry season, (2) what are the characteristics of feeding patches used by white rhinos during the late wet and the late dry season, and (3) what factors drive the selection of grass species within feeding patches? Since the study area is not considered an ideal habitat for white rhinos because of its rugged and mountainous topography (Steyn, 2003), we predict that white rhinos will restrict their movements and feeding to the low lying areas of the study area.

MATERIALS AND METHODS

Study area: The study was conducted in the rugged and mountainous 31 000 ha game-fenced section of the Songimvelo Nature Reserve (49 000 ha; Fig. 1). The area contained 49 white rhinos during the study at a carrying capacity of one rhino per 133 ha. Elevations in the area range between 696 m and 1 884 m.a.s.l. The area is drained by two rivers (Komati and Mtsoli) and numerous streams, which have formed deep gorges and valleys in the area. The geology is very diverse, giving rise to (1) shallow and acid Mispah soil forms on the midslopes, (2) shallow to deep, neutral to acid loamy and clayey soils on the foot slopes (*i.e.* Mispah, Shortlands and Hutton soil forms), and (3) deep neutral loamy and sandy soils in the valley bottoms (*i.e.* Oakleaf and Dundee soil forms) (Steyn, 2003). Rainfall occurs mainly between November and March with an average rainfall of 575.7 mm recorded during the study and a long-term average rainfall of 645.7 mm recorded between 1988 and 2008. Temperature averages range from 4 °C minimum to 30.2 °C maximum (Weather Station 0481692 – Songimvelo).

Two biomes are found in the study area: the Grassland Biome in the higher-lying regions, and the Savanna Biome in the lower-lying Komati Valley (Mucina and Rutherford, 2006). In the lowland areas where rhinos are found, four plant communities were mapped by Stalmans *et al.* (1999): *Vachellia nilotica* - *Heteropogon contortus* low woodland/low grassland, *Cynodon dactylon* - *Melinis repens* low grassland, *Vachellia nilotica* - *Euclea crispa* low woodland/low grassland and *Loudetia simplex* - *Themeda triandra* short shrubland/low grassland. These plants communities were loosely grouped into Low Open Woodlands, Old Lands, and Shrublands, for this study.

White rhino feeding habitat use: White rhino groups, usually composed of adult females with young and/or subadults or both (Shrader and Owen-Smith, 2002), were located at least three days per week during the late wet (February to April) and the late dry season (June to August) of 2008. Tracking and observation of the rhinos were chance events and were conducted randomly within the area, as rhinos were not fitted with tracking devices. The same group of rhinos was not observed on consecutive days to maintain the independence of observations. All rhinos were identified using the unique ear-notches (Steyn and Stalmans, 2004). Observations commenced at daybreak until 11h00, depending on the weather condition between seasons. The animals were observed from a minimum distance of 200 m so as not to influence their feeding behaviour. Natural markers (rocks or trees) were used to visually mark the area where rhinoceros were observed feeding for further sampling.

As soon as the animals moved from the identified feeding area, a Garmin GPS was used to record the coordinates of the demarcated feeding area. Employing ArcMap 10.1 (ESRI, 2008), the recorded GPS coordinates were overlaid on a digital elevation model (DEM) with 90 m resolution to extract topographical data such as slope (in degrees) and elevation (in meters). Other habitat parameters that were recorded in the feeding area include rock cover (%), mean grass height (cm), leaf table height (cm), mean tuft diameter (cm) and woody density (plants/100 m^2).

Habitat availability is defined as the amount of habitat accessible to an animal (Beyer *et al.*, 2010). In this study, an area of 6 488 ha was identified as available habitat for the white rhinos by using digital elevation model (DEM) data, vegetation data, and a 10-year white rhino monitoring data from the management of the reserve (GPS observation points plotted on a map). For this study, the available area was broadly classified into three habitat types following the description of plant communities by Stalmans *et al.* (2001). Firstly, Low Open Woodlands (LOW) occurred on level or gentle slopes and were dominated by *Vachellia nilotica* (a medium to large leguminous tree), *Euclea crispa* (a single-stemmed small tree with many branches) and *Heteropogon contortus* (a rhizomatous perennial grass). Secondly, Old Lands (OL) were old settlement areas or cultivated lands, and were dominated by *Cynodon dactylon* and *Melinis repens.* Thirdly, Shrublands (SL) were characterised by shrubs and dominated by *Loudetia simplex* and *Themeda triandra* grasses.

White rhinos feeding patch and grass species use: A feeding patch was defined as any area where white rhinos spent 1 - 30 min feeding (Bailey *et al.*, 1996). Once a feeding patch was identified, and the rhinos had vacated the feeding area, the sampling of the patch was undertaken. A 10 x 10 m plot was demarcated in the centre of the feeding patch, and five 1 x 1 m subplots were placed within the plot (one in each corner and one in the centre of the grazed area). All rooted grass species within the subplots were identified and counted in order to determine densities. The tuft diameter of three randomly selected grasses of each species recorded within each subplot was measured using a calliper to determine basal diameters. Grass species heights were measured with a ruler, and leaf table height within each subplot was visually estimated. The grazing value of grass species as defined by Van Oudtshoorn (1999) was also recorded. Rock cover was visually estimated as a percentage of a 1 x 1 m quadrat. Within the identified feeding patches, grass species that showed signs of fresh grazing by white rhinos were identified and recorded by walking in random patterns within the 10 x 10 m plot.

Statistical analyses

Habitat level: The chi-square goodness of fit test was used to determine feeding habitat selection following the methodology described by Byers and Steinhorst (1984). Use and availability were defined as frequencies. When significant differences in the habitat use by rhinos were found, the Bonferroni Z-statistic was employed to construct Bonferroni confidence intervals.

Patch level: At the feeding patch level, elevation (m), slope (°), rock cover (%), mean grass height (cm), leaf table height (cm), mean tuft diameter (cm) and woody density (plants/100 m^2) were tested through independent t-tests to compare values between the late wet and the late dry season. The t-tests were performed when the data were normally distributed. Mann-Whitney U-tests were performed when distributional assumptions were not met. The density of species present in the patches and their contribution in the diet of white rhinos per season was also derived.

Grass species level: To determine which variables drive grass species selection in the feeding patches, candidate models were generated from a set of hypotheses at the species level using the multi-model inference (Anderson, 2008). These models were fitted using the logistic regression. For each model, a binary response variable (used or not used) was used and explanatory variables such as grass species (species), grass density (density), seasons, leaf table height (LTH), and mean tuft diameter (MTD) were tested. For the variable species, two *Bothriochloa* species were grouped as *Bothriochloa spp*., five *Eragrostis* species as *Eragrostis spp*. and three *Sporobolus* species as *Sporobolus spp*. Other species used in the model included *Heteropogon contortus*, *Cynodon dactylon*, *Setaria sphacelata* and *Themeda triandra*. The rarely utilised grass species were grouped in a single group called "other". Prior to fitting the models, an exploratory data analysis (EDA) was undertaken in order to test for co-linearity.

The package "AICcmodavg" (Mazerolle, 2013) was used to fit eight logistic regression models. The models were as follows: Species + MTD + Density, Season + Species + MTD + Density, Season + Species + MTD + Season x Density, Season + Species + Density + Season x MTD, Species + MTD, Season + Species + MTD, Species + Density, and Season + Species + Season x MTD + Season x Density. The models were compared using Akaike's Information Criterion for small samples (AIC_c) and calculated ΔAIC_c, Akaike weights (ω_i) and evidence ratios (Burnham and Anderson, 2002). The best model was judged the one with the lowest AIC_c value, and models with $\Delta AIC_c \leq 2$ were considered to have similar support for the data (Burnham and Anderson, 2002). The odds ratios and confidence intervals were also calculated for all explanatory variables of the best models. All statistical analyses were carried out in R version 3.0.0 (R Core Team, 2013).

RESULTS

White rhino habitat selection: In this study, there was a significant difference between the overall availability of habitats and their usage ($\chi^2 = 18.09$, $df = 2$, $P<0.001$; Table 1) during the late wet season, indicating selection of habitats by white rhinos. The Bonferroni intervals revealed that the Low Open Woodlands and Old Lands were utilised more than expected by white rhinos, whereas Shrublands were utilised less than expected. During the late dry season, there was no significant difference detected between overall habitats available and usage ($\chi^2 = 1.06$, $df = 1$, $P>0.05$), indicating that white rhinos were not selective of habitats.

Feeding patch use: Habitat variables of selected feeding patches were not significantly different between the late wet and the late dry seasons (Table 2), except for percentage rock cover and leaf table height. Rock cover was higher in the late dry season than the late wet season (late wet = 18%; late dry = 28%). Leaf table height was higher in the late wet season than the late dry (late wet = 4.36±1.20 cm; late dry = 3.57±1.23 cm). *Cynodon dactylon, Heteropogon contortus,* and *Eragrostis spp* were recorded as having the highest densities in both seasons (Table 3).

There was an association between the different grass species selected by white rhinos during the late wet season ($\chi^2 = 69.03$, df = 47, P = 0.02) but not during the late dry season ($\chi^2 = 47.12$, df = 47, P = 0.42). The grass species that were mainly used included: *Heteropogon contortus* (late wet = 23%; late dry = 25%), *Eragrostis spp.* (late wet = 14%, late dry = 15%) and *Themeda triandra* (late wet = 11%; late dry = 10%). *Bothriochloa insculpta* contributed 11% during the late wet season but was not used during the late dry season, while *Cynodon dactylon* was not used during the late wet season but contributed 4% usage during the late dry season.

Grass species scale: At the grass species scale, grass species presence, grass species density, mean tuft diameter and season were important drivers for grass species selection within feeding patches. The highest ranked model (Table 4: $\Delta AIC_c = 0.00$; $\omega_I = 0.51$) included grass species, the density of grass species and mean tuft diameter, as variables (Table 4). This model also showed that in a feeding patch, white rhinos are more likely to select *Themeda triandra*, *Heteropogon contortus* and *Setaria sphacelata* and avoid *Cynodon dactylon* and *Eragrostis spp* (Table 5). The second best model (Table 4) included season, grass species, mean tuft density and grass density as variables ($AIC_c = 275.59$; $\Delta AIC_c = 1.93$; $\omega_I = 0.20$) indicating that season also played a role in the selection of grass species by white rhinos.

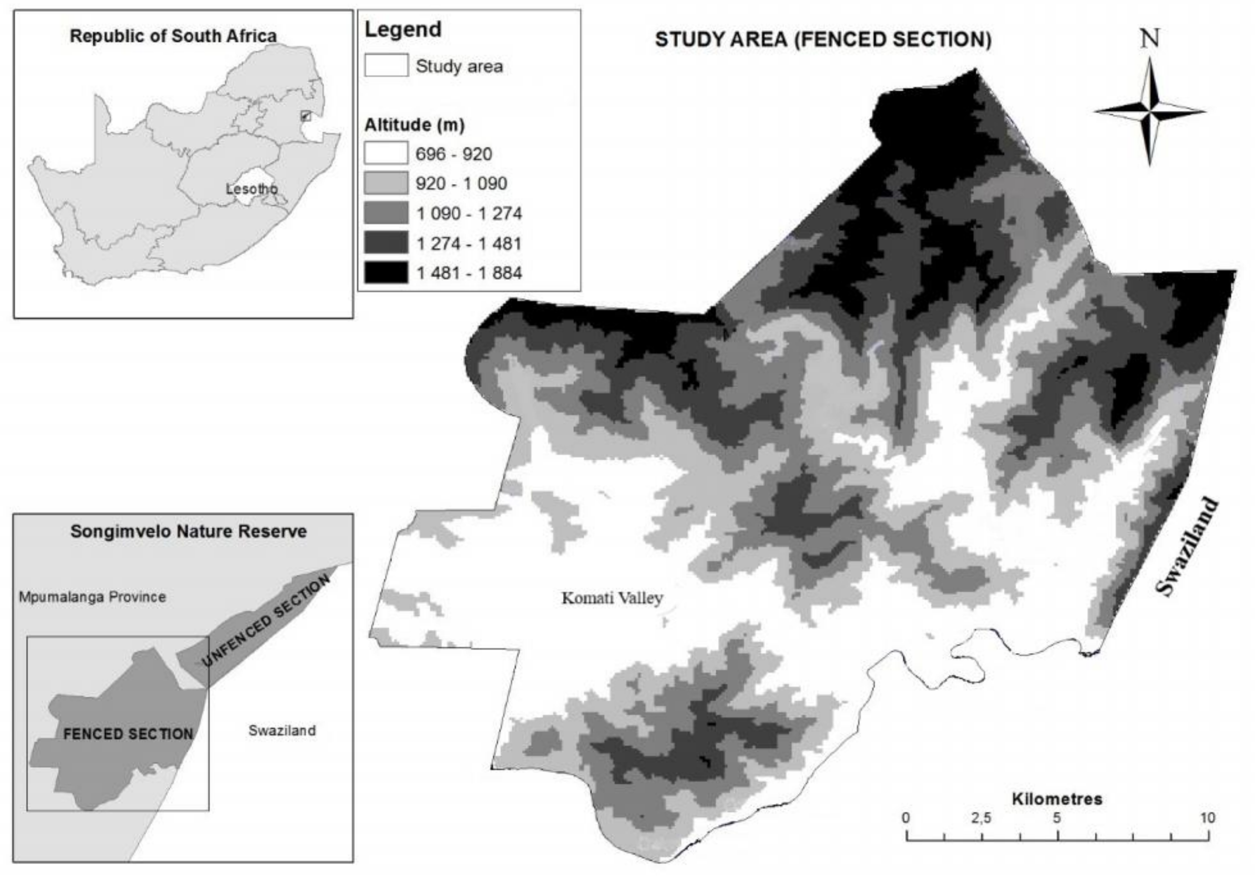

Figure 1. The location of the study area comprising the fenced section of Songimvelo Nature Reserve (habitat use analyses were performed in the lower lying Komati Valley only) and elevation ranges.

Table 1. Feeding habitat selection by white rhinos in the Songimvelo Nature Reserve during the late wet season.

HT	Total area (ha)	Relative area	Usage		Proportion of usage		Bonferroni intervals for *P*
			Obs	Exp	Exp	Actual	
LOW	4 542	0.70	64	57	0.70	0.79	0.68≤P≤0.88
OL	452	0.07	12	5	0.06	0.15	0.05≤P≤0.24
SL	1 494	0.23	5	19	0.23	0.06	-0.00≤P≤0.12*
Total	6 488	1	81	81			

* *P≤0.05*; HT = Habitat types; LOW = Low Open Woodlands; OL = Old Lands; SL = Shrublands. Obs = observed; Exp = expected.

Table 2. Comparison of habitat variables on feeding patches selected during the late wet and the late dry season.

	Mean ± SD		t or U	*P*
	Late wet	Late dry		
Elevation (m)	854±28	861±24	-1.01	0.32^{ns}
Slope (°)	3.8±2.3	4.9±3.3	-1.46	0.15^{ns}
Rock cover (%)	17.8±16.9	28.2±18	245.5	0.04*
Mean grass height (cm)	40.2±22.1	30.58±21.32	265.5	0.08^{ns}
Woody density	17±17	6±5	260.0	0.07^{ns}
Mean tuft diameter (cm)	13.8±5.7	15.4±13.1	332.5	0.59^{ns}
Leaf table height (cm)	4.4±1.2	3.6±1.2	2.41	0.02*

* *P≤0.05* ; ns = not significant

Table 3. Density of selected grass species in feeding patches, their grazing value and their utilisation by white rhinos between the late wet and the late dry season. Other grass species were excluded from the analysis.

Grass species	Grazing value	Density (Mean ± SD)		Utilisation (%)	
		Late wet	Late dry	Late wet	Late dry
Aristida spp.	L	9.63±12.86	5.83±0.58	1.75	4.17
Bewsia biflora	L	5.88±7.83	3.51±5.63	3.51	2.08
Bothriochloa bladhii	L	3.50±6.67	-	1.75	-
Bothiochloa insculpta	A	14.38±36.28	14.80±1.97	10.53	-
Brachiaria brizantha	A	4.80±8.02	2.25±14.05	1.75	2.08
Brachiaria serrata	A	2.71±4.24	2.46±1.53	1.75	2.08
Cynodon dactylon	H	39.38±15.21	119.85±131.09	-	4.17
Digitaria spp.	H	8.83±6.04	4.67±8.45	1.75	-
Eragrostis spp.	A/H	35.00±28.08	35.23±28.79	12.27	14.59
Heteropogon contortus	A	34.20±4.41	26.58±7.27	22.81	25.00
Hyperthelia dissoluta	A	5.72±6.24	6.75±9.36	3.51	2.08
Hyparrhenia hirta	A	7.66±4.90	10.52±3.78	3.51	6.25
Loudetia simplex	A	5.62±2.49	7.32±18.50	5.26	-
Panicum maximum	H	2.00±1.15	6.67±8.07	1.75	-
Setaria sphacelata	H	-	17.91±0.58	-	8.33
Sporobolus spp.	L	21.55±12.13	16.50±12.15	5.26	4.16
Themeda triandra	H	8.67±2.14	4.33±0.58	10.53	10.42
Tragus berteronianus	L	8.77±4.29	-	3.51	-
Trachypogon spicatus	L	1.00±0.55	6.27±1.26	-	4.17
Tristachya leucothrix	A	-	9.88±2.12	-	2.08
Urochloa mossabiscensis	H	9.35±12.80	-	1.75	-

Grazing values: H = high, A = average and L = low.

Table 4. Candidate models (models with $\Delta AIC_c<7$) to test the importance of grass species and other variables in the feeding patches selected by white rhinos in the Songimvelo Nature Reserve.

Rank	Explanatory variables	AIC_c	ΔAIC_c	k	ω_i	LL
1	Species + MTD + Density	273.66	0.00	11	0.51	-125.27
2	Season + Species + MTD + Density	275.59	1.93	12	0.20	-125.13
3	Season + Species + MTD + Season x Density	277.67	4.00	13	0.07	-125.06
4	Season + Species + Density + Season x MTD	277.75	4.09	13	0.07	-125.10
5	Species + MTD	277.80	4.14	10	0.06	-128.44
6	Season + Species + MTD	279.73	6.06	11	0.02	-128.30
7	Species + Density	279.81	6.15	10	0.02	-129.44
8	Season + Species + Season x MTD + Season x Density	279.85	6.19	14	0.02	-125.02

MTD = mean tuft diameter; AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = differences in Akaike's information criterion; k = number of parameters; ω_I = AIC_c weights; LL = log likelihood.

Table 5. Odds ratios, log (odds ratios) and confidence intervals of selected grass species in the best model.

Grass species	Odds ratio	Log (odds ratios)	Confidence intervals	
			2.5%	97.5%
Cynodon dactylon	0.13	-0.89	0.00	1.94
Eragrostis spp.	0.55	-0.26	0.10	2.63
Heteropogon contortus	3.81	0.58	0.48	36.51
Other Grasses	0.28	-0.55	0.05	1.25
Setaria sphacelata	1.99	0.30	0.16	51.34
Sporobolus spp	1.09	0.04	0.13	9.24
Themeda triandra	5.96	0.78	0.57	141.51

DISCUSSION

This study suggests that the feeding habitat selection of white rhino differs between seasons. During the late wet season, the observed selection of Low Open Woodlands by white rhinos can be attributed to the size of the habitat type, which represents 70% of the total available area, and the fact that it is predominantly found in the lower-lying Komati valley. Selection can also be attributed to grass species composition as *Heteropogon contortus* was the most dominant species in the Low Open Woodlands. *Heteropogon contortus* is of average grazing value (Soromessa, 2011) and may remain palatable to white rhinos throughout the year if kept short through grazing (Hempson *et al.*, 2015).

Old lands, on the other hand, representing only 7% of the total available area, were selected during the wet season possibly because of high grass cover and the nutritional value of grass species present (*e.g. Heteropogon contortus*). In other studies, white rhinos were observed feeding on short grasslands to take advantage of the most nutritious grasses available (Pedersen, 2009; Shrader and Perrin, 2006). The Old lands in this study are made up of old cultivated areas and settlement areas and have a low tree density (Stalmans *et al.*, 2001). The grass species found in the old lands were kept short through grazing (MW *pers. obs.*), thus making these turfs more attractive to white rhinos. The avoidance of Shrublands (representing 23% of the total available area), although more substantial in size than Old Lands, is probably because of an increase in the woody density and the abundance of grass species such as *Hyparrhenia hirta* and *Hyperthelia dissoluta* which are less palatable and not preferred by white rhinos (Shrader, 2003).

By contrast, during the late dry season, white rhinos used all available habitats in proportion to their availability, possibly to maximise intake of grasses as resources will have depleted at the time. As forage quality is low in the study area during the dry season (Steyn and Stalmans, 2001), white rhinos, as bulk grazers, would become less selective and feed on less nutritious grass species in order to maximise food intake (Shrader and Perrin, 2006).

The habitat selection pattern observed in Songimvelo Nature Reserve in the late dry season could also have been influenced by other factors, e.g., the number of rhinos in the study area and the relatively low annual rainfall during the study period, as observed in another study (Shrader and Perrin, 2006). The 49 rhinos (1 rhino/133 ha) present in Songimvelo Nature Reserve during the study was above the recommended stocking rate of 1 rhino/160 ha, *i.e.* 40 individuals (Steyn, 2004). The annual rainfall of 518 mm recorded during the study period was also lower than the long-term average annual rainfall of 665 mm (20-year data from Weather Station [0481692 X] – Songimvelo). These results, coupled with the fact that the study area consisted of the Sourveld, would make food scarce during the late dry season, probably increase dispersal and make white rhinos less selective.

At the feeding patch scale, there was no temporal change in the variables measured during this study. Although there was a significant difference in percentage rock cover and leaf table height of the selected feeding patches between seasons, this result is attributed to structural changes between wet and dry seasons. The reduced leaf table height in the late dry season would consequently make rocks in the used areas more prominent. It is, therefore, possible that other variables that were not measured in this study, could better explain the use of the feeding patches by white rhinos.

All feeding patches were located in the low-lying areas, and use by white rhinos at this scale was probably constrained by topography and accessibility. White rhinos prefer patches in low-lying areas (Shrader *et al.*, 2006), although Owen-Smith (1988) reported these animals using *Themeda* grasslands growing on hillslopes during the late dry season in iMfolozi. In this study, no rhinos were observed utilising the grassland areas on the mountain tops despite the presence of palatable species such as *Themeda triandra* and *Cynodon dactylon* on them. The avoidance of mountain tops in Songimvelo Nature Reserve can be attributed to the difference in elevations and the steeper slopes which excludes the 2 000 kg white rhinos (average adult rhino size) from reaching these elevations.

At the grass species level, this study found that the presence of certain grass species, i.e. *Heteropogon contortus*, the mean tuft diameter, the grass density and season drive the selection of feeding patches. *Heteropogon contortus* was previously found to have a high acceptance by white rhinos throughout the year if it is maintained short through grazing (Shrader, 2003). The catenal position also influences soil moisture availability in bottomlands, containing more clay than uplands, which sustain green grass and produce a higher grass biomass and in turn drive the selection of certain grass species (Scholes, 1990; Scoones, 1995). The high grass biomass, as well as high tuft diameter (bunch-forming grasses) observed in this study, can be very attractive to white rhinos (Veldhuis *et al.*, 2016). Although the "greenness" of grass was not measured in this study, this variable could also have played a role in the selection of the feeding patches and grass species (e.g., *Setaria sphacelata* and *Heteropogon contortus*), as green grasses are likely to have higher nutrient concentrations (Ramoelo *et al.*, 2015).

Conclusions: This study showed that at feeding habitat level, white rhinos were selective during the late wet season and not selective during the late dry season. At patch level, white rhino consistently used patches in low lying areas whilst remaining selective of grass species. The selection of grass species within feeding patches was driven by seasonal changes in grass species quality and quantity (i.e. composition, density and grazing value) as well as the basal diameter of grass. These results were in line with the hypothesis that herbivores are selective during periods of abundant food resources, but less selective during the crunch periods when resources are at their lowest (Owen-Smith, 2008). This study demonstrates that the feeding behaviour of white rhinos is scale-dependent and is a consequence of environmental and seasonal variations. We suggest therefore that the spatio-temporal availability of food resources is taken into consideration by management in marginal areas like the Songimvelo Nature Reserve, situated in the Sourveld region and highly mountainous. The importance of maintaining adequate numbers of white rhinos in such marginal areas, as well as sound ecosystem management, are paramount to the successful conservation of this species.

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