Termitaria as preferred browsing patches for black rhinoceros (*Diceros bicornis*) in Chipinge Safari Area, Zimbabwe

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Abstract: This study tested the hypothesis that the black rhinoceros browses more on termitaria than off termitaria vegetation due to elevated soil and foliar nutrient levels on termitaria. We investigated the role of termitaria in providing nutrient-rich forage for the black rhinoceros, by comparing the preference (selection ratio) for vegetation occurring on and off termitaria, and then testing its relationship with foliar nutrient concentrations. Soil nutrients, bite intensity, tree species diversity, vegetation density, canopy cover and basal area were also surveyed on and off termitaria. We sampled 25 termite mounds together with their corresponding control plots in Chipinge Safari Area, Zimbabwe. Soil and foliar N, P, K, Ca and Na concentrations were greater on termitaria than off termitaria, with approximately twice the concentration of these nutrients. Browse preference followed the between-site differences in soil and foliar nutrient concentrations, with higher selection ratios and bite intensities for vegetation on termitaria than off termitaria. *Diospyros quiloensis* was the most preferred browse species whilst *Combretum imberbe*, *Kigelia africana* and *Strychnos innocua* were the least. In conclusion, the black rhino preferred vegetation on termitaria to that in the surrounding matrix, and utilization of vegetation can be influenced by the soil substrate on which tree species grow.

Key Words: *Diceros bicornis*, preference, savanna, termitaria, vegetation, Zimbabwe

INTRODUCTION

Termites, through mound construction and soil particle redistribution, act as ecosystem engineers, altering soil physical properties, nutrient availability, hydrology and topography which can ultimately influence local plant richness, plant spatial distribution and vegetation dynamics (Dangerfield *et al.* 1998, Fleming & Loveridge 2003, Grant & Scholes 2006, Holdo & McDowell 2004, Joseph *et al.* 2012, 2013; Moe *et al.* 2009, Seymour *et al.* 2014). These changes have potential to influence browse selection by mammalian herbivores in savanna woodlands where termite mounds are an important feature of the landscape. For example, in the miombo woodlands of central Zimbabwe, Loveridge & Moe (2004) found that the black rhino browsed more on vegetation on termitaria than at distances from termitaria. In this study, however, preference was tested by comparing the cumulative browse scores on different trees with distance from the mound. However, the underlying causes for differences in browse preference were not tested. This limits our understanding of the factors driving the positive selection for vegetation on termitaria by the black rhino in the savanna.

The relatively nutrient-rich soils of termitaria reduce competition for limiting nutrients i.e. nitrogen (N) and phosphorus (P), which alters the competitive dominance of plants and may also enable the coexistence of nutrient-demanding plants. As a result, there is an increase in plant productivity and species richness on termitaria compared with the matrix (Fleming & Loveridge 2003, Joseph *et al.* 2012, Moe *et al.* 2009, Seymour *et al.* 2014, Sileshi *et al.* 2010). This potentially increases the quantity and variety of browse available for browsers, and at the same time reduces intraspecific competition between the animals. Woody plants on termitaria have also been found to have higher leaf N, P and palatability than those in the matrix (Grant & Scholes 2006, Holdo & McDowell 2004, Joseph *et al.* 2014). Additionally, termitaria act as fire refugia for woody plants which allow woody species to persist on mounds post fire (Joseph *et al.* 2013). Further, the

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soil moisture content is relatively higher on termitaria than the surrounding matrix (Dangerfield 1991), which maintains evergreen woody species on mounds. It is, therefore, expected that animals are likely to favour vegetation on termitaria over that in the matrix.

Our study site in south-eastern Zimbabwe, Chipinge Safari Area, is home to a black rhino population translocated in 1990 from the Zambezi Valley secondary to intensive poaching (Rachlow & Berger 1998). *Macrotermes* termitaria characterize much of the savanna vegetation on soils relatively poor in nitrogen (N), extractable phosphorus (P) and total exchangeable cations (Bloesch 2008, Brossard *et al.* 2007). Thus, if browse from termitaria has greater nutritional value than that found in the matrix, the possible significance of mounds as sources of nutrient-enriched forage for the black rhino is likely to be considerable.

In this study, we tested the hypothesis that the black rhino would browse more on vegetation located on termite mounds than that in the surrounding matrix (hereafter referred to as on termitaria and off termitaria, respectively) in Chipinge Safari Area, south-eastern Zimbabwe. We expected that the preference for vegetation on termitaria would be driven by the foliar nutrient status of the browse since browse preference by animals has been shown to be related to the nutritional quality of the browse (Cooper & Owen-Smith 1985, Cooper *et al.* 1988). Additionally, by determining preference for species occurring both on termitaria and off termitaria, we aimed to identify key browse species favoured by the black rhino in this system.

STUDY SITE

The study was conducted in Chipinge Safari Area (20°21′S, 32°43′E) covering 261 km² in south-eastern Zimbabwe. The area is relatively dry, and receives an average rainfall of 489 mm y^{-1} (Department of Meteorological Services unpubl. data). The mean daily temperature recorded over the last 20 y is 23.3 °C, with a minimum and maximum temperature of 9 °C and 41.7 °C, respectively (Department of Meteorological Services unpubl. data). The dominant tree species in the study site include *Colophospermum mopane* (J. Kirk ex Benth.) J. Léonard, *Diospyros quiloensis* (Hiern) F. White, *Combretum zeyheri* Sond., *Combretum mossambicense* Engl., *Combretum apiculatum* Sond. and *Combretum imberbe* Wawra. On rocky areas, *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin are found. The herbaceous layer is dominated by *Hyparrhenia filipendula* Stapf, *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., *Justicia anselliana* T. Anderson, *Clutia hirsuta* Eckl. & Zeyh. ex Sond., *Bromus catharticus* Vahl and *Hypoestes verticillaris* (L.f.) Roem. & Schult.

The mammalian fauna is represented by the black rhinoceros *Diceros bicornis* (Linnaeus, 1758), kudu *Tragelaphus strepsiceros* (Pallas, 1766), buffalo *Syncerus caffer* (Sparrman, 1779), warthog *Phacochoerus aethiopicus* (Pallas, 1766), bushbuck *Tragelaphus scriptus* (Pallas, 1766), grysbok *Rhacerus melanotis* (Thunberg, 1811), impala *Aepyceros melampus* (Lichtenstein, 1812) and bush pig *Potamochoerus larvatus* (F. Cuvier, 1822). The carnivores present in the study area include leopard *Panthera pardus* (Linnaeus 1758), spotted hyena *Crocuta crocuta* (Erxleben, 1777) and black-backed jackal *Canis mesomelas* (Schreber, 1775).

METHODS

Plot measurements

We surveyed vegetation on and off termite mounds in December 2013. The study area was divided into 10 blocks of *c.* 26 km² in area. Five blocks were randomly chosen for surveying. In each block, a belt transect (30 m wide; 5 km long) was constructed from the southern side running through the centre of the grid in a northerly direction. At each 1 km along each transect, excluding the starting point, a termite mound was selected for survey in the randomly chosen perpendicular to the transect. Five termite mounds were surveyed from each of the five transects for a total of 25 sites. Termitaria with surface area at least 100 m² and height ≥ 1 m were selected as they contained a variety of plant assemblages (Joseph *et al.* 2012). The long and short diameter of each termite mound was measured at right angles using a tape measure. The mean (±SE) termite mound height was 2.56 ± 0.5 m and average mound surface area was 334 ± 0.7 m². For each termite mound, a circular control plot was placed at least 30 m away from the centre of the target termite mound or from the centre of any other nearest mound in the area. The bearing of the control plot from the target mound was taken as the first value between zero and 360 generated from a scientific calculator. A new bearing was generated if the control plot was < 30 m from another termite mound in the vicinity. All mounds were assumed to be purely conical and the area of the control plots were calculated following procedures in Muvengwi *et al.* (2013).

Vegetation characteristics measured

Tree canopy cover (C) was calculated using the following equation.

$$c = \pi \left(\frac{d1}{2}\right)\left(\frac{d2}{2}\right)$$

where $d1$ is the longer diameter of the tree and $d2$ is the perpendicular short diameter measured using a tape measure. Tree basal diameter was measured using a forest calliper at just above the buttress swelling.

Chemical analysis of soil and foliar samples

Soil and foliar samples were tested for N, P, K, Ca, Mg and Na at the Department of Research and Specialist Services, Chemistry and Soil Research Institute in Harare, Zimbabwe. Soil samples were collected on and off termite mounds at a depth of 20 cm using a soil auger. In the laboratory, the soil samples were then air dried to drive out all the moisture before analysis. Total Ca, Mg, K and Na were extracted using the aqua regia digestion method (Anderson & Ingram 1993). Although the black rhino included twigs with diameter 1 cm and less in its diet, leaves were considered for chemical analysis since they were more likely to influence forage selection than other plant parts (Holdo 2003). General comparison of foliar nutrient concentration between termite mounds and control plots was done by pooling leaves from trees occurring at both sites for analysis. Also, foliar was collected from at least five individuals of the 15 tree species that were found both on and off termitaria. Foliar samples were first ashed, and then dissolved using aqua regia and the mixture dried under ultraviolet light. The resulting compound was then dissolved in concentrated HCl and filtered. The solution was diluted with distilled water. Using a spectrophotometer, total Ca and Mg were determined at 0.460 nm and 0.595 nm, respectively, and flame emission was used for K and Na. For both soil and foliar samples, determination of total N and P was based on a Kjeldahl method (Okalebo *et al.* 2002).

Calculations and statistical analysis

A preference or selection ratio (SR) was calculated for each common species i on and off termite mounds following Crawley (1983):

$$SR = \frac{d_i}{n_i}$$

where d_i is the proportion of damaged plants represented by species i, and n_i is the proportion of i in the plot. The overall selection ratio for a species was given by its median selection ratio across all plots in which it occurred. Only species with a minimum of two individuals per plot were included in the analysis because the inclusion of cases in which a single individual occurred could result in damage proportions of 0 or 100% (Holdo 2003). Black rhino browsing could be easily distinguished from that of any other browsers in the Chipinge Safari Area because

of the way they clip shoots and leaves to leave a scissor-like cut stump (Oloo *et al.* 1994, Ritchie 1963). In order to minimize errors, only fresh browse of less than 3 mo was considered in this study. Bite intensity was estimated by physical counting of twigs showing fresh signs of browsing by black rhino and was expressed both at tree species level and plot level (the termite mound and its control plot). Species diversity was calculated using the Shannon–Wiener index (Krebs 1999).

All data were tested for normality before analysis. Data on browsing height, basal area, bite intensity and canopy cover deviated from normality and was $\log_{10}$-transformed to meet assumptions of normality and homogeneity of variance. A paired *t*-test was used to compare vegetation attributes, bite intensity and soil and foliar nutrient concentrations between the two sampling sites (i.e. on and off termitaria). The relationships between vegetation utilization parameters (i.e. selection ratio and bite intensity) and the nutritional concentration of plant species occurring on and off termitaria was analysed using Pearson's correlation analysis. In all our tests $\alpha = 0.05$. We conducted statistical tests using SPSS 16 for Windows (SPSS Inc., 2007, Chicago, IL, USA).

RESULTS

Vegetation structural variables and diversity indices

A total of 1051 (on: 563, off: 488) individual woody plants were assessed during the study period. We identified a total of 47 woody species, and of these, 27 species occurred on termite mounds, 20 species occurred off termitaria and 15 species were common on and off termitaria. Vegetation on termitaria was more diverse and dense than that off termitaria (P < 0.05; Table 1). Woody canopy cover was also significantly greater on termitaria than off termitaria (Table 1). However, the basal area of trees and the browsing height of the black rhino did not differ between the sampling sites (P > 0.05).

Soil and foliar characteristics

Soils on termitaria had approximately twice the levels of N, P, Ca and Na and much more K than off-termitaria soils (Figure 1a). Foliar nutrient concentrations were generally greater in vegetation on termitaria than off termitaria, also with approximately twice the concentration of tested nutrients (Figure 1b). However, the soil and foliar Mg concentrations did not differ between termitaria and off termitaria (P > 0.05; Figure 1a, b). Most of the tree species followed the between-sampling-site differences in soil nutrient concentrations, with greater foliar nutrient concentrations in trees on termitaria

Table 1. Mean (±SE) of some measured vegetation variables on and off termitaria in Chipinge Safari Area, Zimbabwe.

Variable	Treatment		*t*-value	P value
	On	Off		
Species diversity (H)	2.74 ± 0.2	2.14 ± 0.3	1.4	0.02
Canopy cover (m^2 ha^{-1})	7390 ± 1450	4880 ± 1020	− 1.3	0.03
Basal area (m^2 ha^{-1})	320 ± 20	312 ± 10	− 1.0	0.88
Shrub density (ha^{-1})	398 ± 32.9	301 ± 49.9	0.6	0.0001
Tree density (ha^{-1})	536 ± 93.6	379 ± 39.7	2.3	0.0001
Browsing height (m)	1.5 ± 0.3	1.5 ± 0.2	4.3	0.28
Bite intensity (ha^{-1})	2800 ± 170	1930 ± 160	5.4	0.0001

Table 2. Mean (± SE) leaf nutrient concentration (%) of trees browsed by the black rhino on and off termitaria in Chipinge Safari Area, Zimbabwe. Nutrient concentration is expressed on a dry matter basis. Different superscript letters (a, b) following means within a mineral element differ significantly (*t*-test, P < 0.05).

Species	Location	N	P	K	Ca	Mg	Na
Combretum apiculatum	On	0.7 ± 0.06[a]	2.0 ± 0.13[a]	7.0 ± 0.12	0.08 ± 0.001[a]	0.4 ± 0.01[a]	0.09 ± 0.001[a]
	Off	0.4 ± 0.12[b]	0.9 ± 0.02[b]	5.1 ± 0.15	0.03 ± 0.001[b]	0.1 ± 0.01[b]	0.03 ± 0.001[b]
Combretum imberbe	On	0.8 ± 0.05[a]	3.0 ± 0.27[a]	5.2 ± 0.21[a]	0.9 ± 0.06[a]	0.7 ± 0.03	0.7 ± 0.02
	Off	0.5 ± 0.04[b]	0.9 ± 0.01[b]	3.4 ± 0.04[b]	0.3 ± 0.01[b]	0.5 ± 0.02	0.4 ± 0.01
Combretum molle	On	0.5 ± 0.06	5.0 ± 0.35	7.5 ± 0.06[a]	1.0 ± 0.06[a]	0.4 ± 0.01[a]	1.0 ± 0.07
	Off	0.5 ± 0.04	3.0 ± 0.06	2.3 ± 0.09[b]	0.06 ± 0.001[b]	0.2 ± 0.001[b]	0.8 ± 0.02
Combretum mossambicense	On	1.0 ± 0.01[a]	3.0 ± 0.07[a]	3.3 ± 0.01[a]	0.3 ± 0.01[a]	0.2 ± 0.01	0.1 ± 0.01
	Off	0.3 ± 0.02[b]	0.6 ± 0.02[b]	0.9 ± 0.01[b]	0.09 ± 0.001[b]	0.1 ± 0.01	0.1 ± 0.01
Combretum zeyheri	On	6.0 ± 0.06[a]	7.0 ± 0.21[a]	4.1 ± 0.10	0.6 ± 0.02[a]	0.4 ± 0.11	0.09 ± 0.001
	Off	3.0 ± 0.06[b]	3.0 ± 0.12[b]	4.2 ± 0.03	0.2 ± 0.01[b]	0.4 ± 0.002	0.05 ± 0.001
Dichrostachys cinerea	On	6.0 ± 0.15[a]	0.6 ± 0.01[a]	8.2 ± 0.21[a]	3.0 ± 0.05[a]	0.4 ± 0.02[a]	0.5 ± 0.02
	Off	0.9 ± 0.03[b]	0.4 ± 0.01[b]	4.0 ± 0.12[b]	0.9 ± 0.03[b]	0.2 ± 0.01[b]	0.3 ± 0.02
Diospyros quiloensis	On	7.0 ± 0.16[a]	8.0 ± 0.17[a]	9.2 ± 0.06[a]	0.9 ± 0.03[a]	0.5 ± 0.01[a]	0.7 ± 0.02[a]
	Off	3.0 ± 0.04[b]	4.0 ± 0.02[b]	4.5 ± 0.06[b]	0.3 ± 0.02[b]	0.2 ± 0.01[b]	0.3 ± 0.01[b]
Grewia bicolor	On	5.0 ± 0.13	3.5 ± 0.06	3.3 ± 0.02[a]	0.5 ± 0.10[a]	0.4 ± 0.15	0.3 ± 0.01[a]
	Off	3.0 ± 0.06	2.0 ± 0.11	0.9 ± 0.02[b]	0.2 ± 0.08[b]	0.5 ± 0.02	0.1 ± 0.01[b]
Grewia monticola	On	0.4 ± 0.02	0.6 ± 0.02[a]	5.3 ± 0.08[a]	0.6 ± 0.09[a]	0.8 ± 0.01	0.5 ± 0.02
	Off	0.3 ± 0.02	0.2 ± 0.01[b]	3.2 ± 0.10[b]	0.3 ± 0.01[b]	0.5 ± 0.01	0.4 ± 0.03
Kigelia africana	On	6.0 ± 0.16[a]	7.5 ± 0.10	9.2 ± 0.07[a]	0.7 ± 0.02[a]	0.4 ± 0.13	0.5 ± 0.01[a]
	Off	3.0 ± 0.06[b]	4.5 ± 0.05	5.1 ± 0.01[b]	0.2 ± 0.02[b]	0.4 ± 0.10	0.2 ± 0.001[b]
Lantana camara	On	0.7 ± 0.06[a]	4.0 ± 0.02[a]	6.1 ± 0.06[a]	0.7 ± 0.11[a]	0.5 ± 0.03[a]	0.3 ± 0.02[a]
	Off	0.2 ± 0.01[b]	2.0 ± 0.09[b]	3.0 ± 0.07[b]	0.3 ± 0.01[b]	0.07 ± 0.001[b]	0.04 ± 0.001[b]
Sclerocarya birrea	On	0.09 ± 0.002	5.0 ± 0.04	5.3 ± 0.12	0.5 ± 0.03[a]	0.7 ± 0.02[a]	0.06 ± 0.002
	Off	0.06 ± 0.002	3.0 ± 0.15	4.7 ± 0.01	0.1 ± 0.001[b]	0.05 ± 0.001[b]	0.05 ± 0.001
Strychnos innocua	On	0.6 ± 0.04[a]	0.8 ± 0.06	3.4 ± 0.03	0.6 ± 0.01[a]	0.07 ± 0.002	0.09 ± 0.001
	Off	0.2 ± 0.01[b]	0.8 ± 0.02	2.2 ± 0.02	0.02 ± 0.001[b]	0.02 ± 0.001	0.03 ± 0.001
Ximenia caffra	On	5.0 ± 0.08[a]	7.0 ± 0.09	8.3 ± 0.09[a]	1.0 ± 0.02[a]	0.7 ± 0.02[a]	0.9 ± 0.01
	Off	2.0 ± 0.15[b]	5.0 ± 0.14	5.4 ± 0.13[b]	0.5 ± 0.01[b]	0.07 ± 0.001[b]	0.5 ± 0.07
Ziziphus mucronata	On	0.8 ± 0.06	7.0 ± 0.02	5.4 ± 0.03	0.5 ± 0.02	0.3 ± 0.01	0.5 ± 0.01
	Off	0.5 ± 0.06	4.0 ± 0.02	4.4 ± 0.01	0.3 ± 0.02	0.4 ± 0.01	0.3 ± 0.01

than those off termitaria (P < 0.05; Table 2). However, *Combretum molle*, *Grewia bicolor*, *Sclerocarya birrea* and *Ziziphus mucronata* seemed not to respond much to soil differences between sampling sites (Table 2).

Selection ratio and bite intensity

Generally, browse selection ratios were higher on termitaria than off termitaria (P < 0.05; Table 3), indicating positive selection for browse on termitaria by the black rhino. The highest selection ratio was in *Diospyros quiloensis* whilst *Combretum imberbe*, *Kigelia africana* and *Strychnos innocua* were the least selected (Table 3). *Combretum molle*, *Combretum zeyheri*, *Grewia monticola*, *Ximenia caffra*, *Lantana camara* and *Ziziphus mucronata* also had higher selection ratios than other species (Table 3). Although *S. birrea* and *C. mossambicense* occurred on and off termitaria (Table 2), the two species were avoided by the black rhinos at both sites. Bite

Table 3. Mean (±SE) bite intensity and selection ratio of common species browsed by the black rhino (*Diceros bicornis*) on and off termitaria in Chiping Safari Area, Zimbabwe. Different superscript letters (a, b) following means within selection ratio and bite intensity differ significantly (*t*-test, P < 0.05).

Common species	Selection ratio			Bite intensity		
	On	Off	P	On	Off	P
Combretum apiculatum	2.4 ± 0.2[a]	1.3 ± 0.1[b]	< 0.001	2.7 ± 0.3[a]	1.5 ± 0.6[b]	< 0.05
Combretum imberbe	0.4 ± 0.2[a]	0.2 ± 0.02[b]	< 0.05	1.3 ± 0.5[a]	0.3 ± 0.3[b]	< 0.05
Combretum molle	3.9 ± 0.6[a]	2.2 ± 0.3[b]	< 0.05	3.6 ± 0.5[a]	0.8 ± 0.4[b]	< 0.05
Combretum zeyheri	4.5 ± 0.1[a]	2.3 ± 0.1[b]	< 0.001	3.4 ± 0.5[a]	0.8 ± 0.4[b]	< 0.05
Dichrostachys cinerea	1.7 ± 0.1[a]	1.1 ± 0.04[b]	< 0.001	2.8 ± 0.4[a]	1.8 ± 0.4[b]	< 0.05
Diospyros quiloensis	5.9 ± 0.8[a]	2.5 ± 0.2[b]	< 0.05	3.1 ± 0.5	3.1 ± 0.2	> 0.05
Grewia bicolor	1.3 ± 0.3[a]	0.6 ± 0.2[b]	< 0.05	2.0 ± 0.6[a]	1.1 ± 0.3[b]	< 0.05
Grewia monticola	2.0 ± 0.1[a]	1.0 ± 0.1[b]	< 0.001	3.0 ± 0.6[a]	0.8 ± 0.5[b]	< 0.05
Kigelia africana	0.6 ± 0.2	0.5 ± 0.2	> 0.05	2.2 ± 0.7	2.3 ± 0.4	> 0.05
Lantana camara	2.2 ± 0.2[a]	1.9 ± 0.03[b]	> 0.05	2.9 ± 0.5[a]	1.8 ± 0.4[b]	< 0.05
Strychnos innocua	0.5 ± 0.2	0.5 ± 0.2	> 0.05	2.6 ± 0.5[a]	0.8 ± 0.4[b]	< 0.05
Ximenia caffra	3.0 ± 0.1	2.0 ± 0.04	< 0.05	3.0 ± 0.6[a]	1.2 ± 0.3[b]	< 0.05
Ziziphus mucronata	3.7 ± 0.5[a]	2.0 ± 0.1[b]	< 0.05	2.4 ± 0.5[a]	1.5 ± 0.6[b]	< 0.05
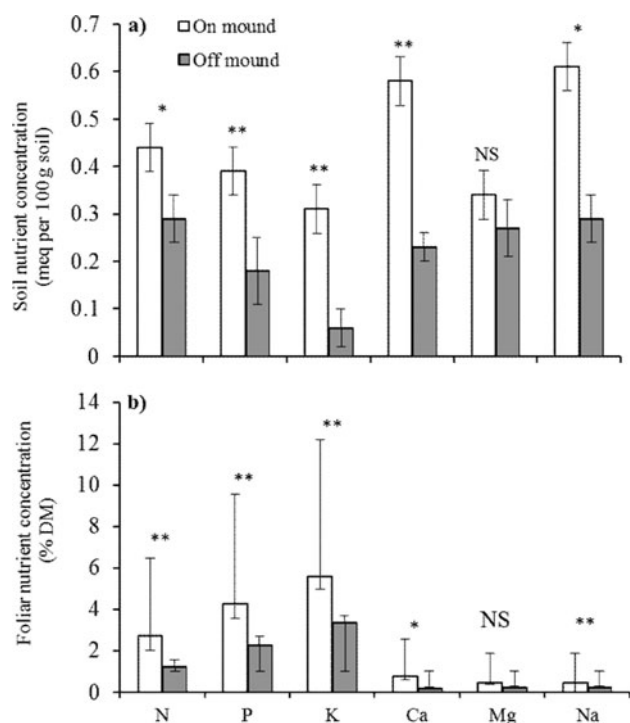
Figure 1. Mean (±SE) soil (a) and foliar (b) nutrient concentration on and off termite mounds in Chiping Safari Area, Zimbabwe. For each sampling site, *n* = 25. Tests of significance are based on a paired *t*-test. *, P < 0.05; **, P < 0.001. NS, not significant.

Table 4. Pearson correlation coefficient (*r*) matrix of selection ratio, bite intensity, and foliar nutrient concentration of browse species browsed by the black rhino (*Diceros bicornis*) on and off termitaria in Chiping Safari Area, Zimbabwe.*, P < 0.05; **, P <0.01.

Variable	Selection		Bite intensity	
	On	Off	On	Off
N	0.57*	0.21*	0.48*	0.21
P	0.55*	0.24	0.55	0.43
K	0.27*	0.34*	0.43*	0.55*
Ca	0.44*	− 0.16	0.27*	0.13
Mg	0.09	0.03	0.36	0.10
Na	0.45**	0.35*	0.52**	0.42*

Relationships between nutrient concentrations and selectivity parameters

Selection ratio was positively correlated to foliar N, K and Na concentrations on and off termitaria but only correlated to P and Ca on termitaria (Table 4). Bite intensity was related to Na and K concentrations in all sampling sites but N and Ca were only related to bite intensity on termitaria (Table 4). There was no relationship between the selection ratio and bite intensity and foliar Mg on and off termitaria (P > 0.05).

DISCUSSION

Our study confirmed that the black rhino prefers vegetation on termitaria to that off termitaria which is consistent with previous other studies (Holdo & McDowell 2004, Loveridge & Moe 2004, Mobæk *et al.* 2005). We recorded higher selection ratios and bite intensities on vegetation on termitaria than that off termitaria,

intensity per plot was significantly higher on termitaria than off termitaria (P < 0.05; Table 1), being greater by a factor ranging from 1.6 for *Z. mucronata* up to 4.5 for *C. molle*, and by a factor of 3.3 for *S. innocua* (Table 3). The most selected species *D. quiloensis* had similar bite intensity on and off termitaria (P > 0.05).

indicating positive selection for vegetation on termitaria. This difference in preference followed the between-site differences in soil and foliar nutrient concentrations, woody species diversity and vegetation density.

Termitaria offer good, almost year-round browsing due to increased soil nutrients (Holdo & McDowell 2004, Seymour *et al.* 2014) and increased vegetation nutrient status (e.g. N and P) and leaf palatability (Ruggiero & Fay 1994, Holdo 2003, Joseph *et al.* 2014). Thus, the preference for foliage on termitaria by the black rhino is due to the nutrient-rich soil and vegetation on termitaria relative to that off termitaria. Studies on plant response to resource availability (Bryant *et al.* 1989, Watson 1977) also suggest that plants growing on termitaria may be less defended than plants growing in the nutrient-poor surrounding inter-mound matrices (Loveridge & Moe 2004, Van der Plas *et al.* 2013). Plants growing on nutrient-poor soils often have high concentrations of secondary compounds such as tannins that deter herbivory (Bryant *et al.* 1989, Coley *et al.* 1985). Thus, termitaria act as nutrient hotspots that produce nutrient-rich palatable browse which enables the black rhino to maximize dietary nutrient as well as mineral intake (Ruggerio & Fay 1994). Additionally, due to improved nutrient absorption by plants resulting from the high cation exchange capacity of the clay-rich termitaria soils, plant growth on termitaria is enhanced relative to the surrounding matrix (Arshad 1982). The elevated plant productivity, in conjunction with the aforementioned factors likely increases the quantity of browse available for browsers, and at the same time reduces intraspecific competition between the animals.

We found higher woody species diversity on termitaria compared with inter-mound control plots, an observation which is consistent with other studies (Fleming & Loveridge 2003, Joseph *et al.* 2012, 2013; Moe *et al.* 2009). In addition, the elevated clay content of termitaria soils increases water retention enabling the establishment and growth of evergreen woody species (Joseph *et al.* 2012, Van der Plas *et al.* 2013) and maintenance of green foliage (Jouquet *et al.* 2006) on mounds. Joseph *et al.* (2013) also found that termitaria through mechanisms such as higher soil moisture content, reduced grass cover, and a higher elevation relative to the matrix reduce the effect of fire on mound vegetation which allows the persistence of woody species on termitaria post fire. Therefore, the black rhino prefers vegetation on termitaria than that in the matrix because of the all year-round availability of diverse evergreen woody species and green foliage on termitaria. Another hypothesis, which is supported by our data, is that the black rhino prefers termitaria vegetation because it resembles the dense woodland habitat which it favours (Tatman *et al.* 2000). We found that the tree and shrub density and canopy cover were greater on termitaria than off termitaria. Thus,

the densely vegetated mounds provide such habitat where the black rhino may find both shade and cover while feeding (Loveridge & Moe 2004, Mobæk *et al.* 2005).

There was a marked difference in selection among the tree species, which supports the suggestion that the black rhino is a selective bulk feeder (Ritchie 1963). *Diospyros quiloensis* was the most-preferred species both on and off termitaria. In a similar study, in the Chewore Safari Area, Zimbabwe, elephants were found to select the same plant species as the black rhino in this study (Muvengwi *et al.* 2013). We also found higher selection ratios for *C. molle*, *C. zeyheri*, *G. monticola*, *X. caffra*, *L. camara* and *Z. mucronata* than other species. These woody species with high selection ratios should be considered critical browse species requiring close monitoring as they could be a key factor in the successful conservation of the black rhino in its current range or in future re-introductions in its former range. Of all the measured elements, only foliar P and Ca and N and Ca were positively correlated to selection ratio and bite intensity on termitaria, respectively. Termitaria soils and plants are endowed with ample P and Ca providing essential minerals for the black rhino, hence the preference for foliage on termitaria. High levels of N in termitaria foliage imply a high amount of crude protein, which allows greater intake (Cooper *et al.* 1988) and may account for the high bite intensity exhibited by the black rhino on termitaria foliage. However, some common species that often occurred on termitaria which were enriched in these elements (*C. mossambicense*: N, P, Ca; *S. birrea*: Ca) were not consumed by the black rhino. This suggests that other chemical and physical factors acting alone or in combination may have hindered browsing on these species.

We remain conservative in the interpretation of our data because we did not take into consideration phenological patterns and foliage colour differences between vegetation from termitaria and inter-mound control plots, which have a potential to influence plant species selection ratio (Holdo 2003, Parrini & Owen-Smith 2010). Also, data from this research are short-term, with a high probability of asynchrony in leaf development due to differences in soil nutrients, water availability and effect of fire between termitaria and inter-mound control plots. Additionally, soil cores are point samples that miss nutrient dynamics over time. Thus, we recommend long-term studies which can capture the temporal dynamics of soil and foliar nutrient dynamics on and off termitaria over time.

In closing, the applied value of this study is twofold: given the current plight of black rhino in the miombo system, not only do our findings confirm the importance of termitaria as a source of browse; they also identify key browse species, factors that will prove pertinent to management if future re-introductions are to take place over the former range of the black rhino.

ACKNOWLEDGEMENTS

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