

Seasonal diet preferences of black rhinoceros in three arid South African National Parks

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Abstract

Black rhinoceros diet and browse availability was investigated in Augrabies Falls (AFNP), Karoo (KRNP) and Vaalbos National Parks (VNP) in South Africa. Rhino tracks were followed and 18,804 standard bite volumes recorded. Browse availability of each plant species was recorded by measuring 14,800 plants and calculating reachable browse volume. The diet comprised 51, 53 and 41 plant species in AFNP, KRNP and VNP, respectively, but three species accounted for more than 65% of the diet in each park, making diet less diverse than available browse in AFNP and KRNP. Browse availability explained 14%, 15% and 52% of diet selection in AFNP, KRNP and VNP, with consumption of most plant species significantly different from availability. A few plant species were so highly preferred that browsing intensities were unsustainable, while some common species were totally rejected. Pressure on the eaten browse averaged 4.4%, 14.5% and 1.3% annually of the volume in AFNP, KRNP and VNP. In the dry season, there was a two to sevenfold increase in browsing pressure on species with actively photosynthesizing tissues. A few key species, including *Monechma* and *Zygophyllum* species, were identified as potential early warning indicators of black rhino browsing impact.

Key words: browse, *Diceros bicornis*, diet, diversity, preference, utilization

Résumé

Le régime et la disponibilité de brou pour les rhinocéros noirs furent étudiés dans les PN d'Augrabies Falls (AFNP), de Karoo (KRNP) et de Vaalbos (VNP), en Afrique du Sud.

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Nous avons suivi des traces de rhinos noirs et relevé 18,804 bouchées de volume standard. La disponibilité de chaque espèce végétale fut notée en mesurant 14,800 plantes et en calculant le volume de brou accessible. Le régime alimentaire comptait respectivement 51, 53, et 41 espèces végétales dans l'AFNP, le KRNP et le VNP, mais trois espèces représentaient plus de 65% de régime alimentaire, ce qui rendait ce dernier moins varié que le brou disponible dans l'AFNP et le KRNP. La disponibilité du brou expliquait 14, 15 et 52% du choix du régime dans l'AFNP, le KRNP et le VNP, et la consommation de la plupart des plantes était significativement différente de la disponibilité observée. Quelques plantes étaient si fortement préférées que l'intensité de leur consommation était non soutenable alors que certaines espèces fréquentes étaient totalement rejetées. La pression sur le brou consommé était en moyenne de 4.4, 14.5 et 1.3% du volume annuel dans l'AFNP, le KRNP et le VNP. En saison sèche, il y avait une multiplication de deux à sept fois de la pression sur des espèces dont les tissus sont activement photosynthétiques. Quelques espèces clés, dont des espèces de *Monechma* et de *Zygophyllum* furent identifiées comme indicateurs précoces potentiels de l'impact de la consommation par les rhinos noirs.

Introduction

The main aim of the current conservation strategy for the endangered black rhinoceros (*Diceros bicornis*) is to ensure a population growth above 5% per annum in Southern Africa to minimize the loss of genetic diversity and outpace outbreaks of poaching (Emslie, 2001a,b). However, population growth has been impeded by diet-related performance and overstocking of some reserves (Brooks, 2001; Du Toit, 2001). High population growth can only be maintained, if negative density-dependent feedback,

including food limitation, is avoided. This is therefore a management priority.

A detailed knowledge of black rhino diet has several uses: (i) estimating appropriate stocking rates for this critically endangered species (Adcock, 2001); (ii) determining key plant species as early warning indicators of food limitation and of threats to highly preferred plant species (Luske *et al.*, 2009); (iii) facilitate research on diet overlap with other herbivores (De Boer & Ijdema, 2007); (iv) facilitate research on nutritional requirements of black rhinos in the wild and in captivity (Atkinson, 1995); and (v) improve our understanding of diet selection by the species (Muya & Ogue, 2000).

Several studies have reported black rhino diet from single populations, and a few have investigated diet selection mechanisms with mixed results. Muya & Ogue (2000) found the utilization of twelve principle plants species to be negatively correlated with total plant phenol, alkaloid and ether extract, and positively correlated with availability and plant fibre, but not correlated with plant protein. Ganqa, Scogings & Raats (2005) found utilization of five plant species to be positively correlated with protein and negatively correlated with leaf:stem ratio, with no correlations with fibre and availability. Van Lieverloo *et al.* (2009) found no correlation between utilization of plant species and their digestibility, macro-elements, water content, fibre and twig/leaf ratios or availability.

As herbivores generally maximize energy intake subject to other constraints (Krebs & Davies, 1987), it is expected that plant utilization would positively correlate with plant availability, as it directly affects food search costs (Muya & Ogue, 2000). Other constraints that may affect diet selection include nutritional requirements and plant defence chemicals, and it has been proposed that herbivores deal with this by diversifying their diet to ensure nutritional balance and to minimize intake of each harmful chemical (Freeland & Janzen, 1978; Muya & Ogue, 2000; Owen-Smith, 2002). Seasonality in black rhino diet has been linked to leaf wilting (Goddard, 1968, 1970; Mukinya, 1977; Hall-Martin, Erasmus & Botha, 1982) and to succulents used as hot-season water sources (Joubert & Eloff, 1971; Hall-Martin, Erasmus & Botha, 1982; Ganqa, Scogings & Raats, 2005), but links are rarely substantiated.

This article compares the seasonal diet of black rhinos in three arid national parks with the available browse to identify the principal, preferred (*sensu* Petrides, 1975) and key food species during different seasons and to analyse

browsing pressure. We also test the following hypotheses that black rhino diet selection is (i) correlated with plant availability; (ii) has a higher Shannon diversity than both the available and eaten plant species; and (iii) exhibits seasonal differences linked to plant phenology.

Methods

Study areas

The study was conducted in the Waterval section of Augrabies Falls National Park (AFNP), the Doornhoek section of Karoo National Park (KRNP) and the Than-Droogeveld section of the now deproclaimed Vaalbos National Park (VNP), South Africa during 1997–2001 (Fig. 1, see Table 1 for study area details).

Browse availability

The study areas were stratified into preliminary vegetation communities, which were relatively homogenous in terms of species composition based on visual classification of 1:50,000 panchromatic aerial photographs and extensive ground-truthing. Sampling plots were placed randomly within each preliminary vegetation community and geo-referenced with a Global Positioning System (GPS)

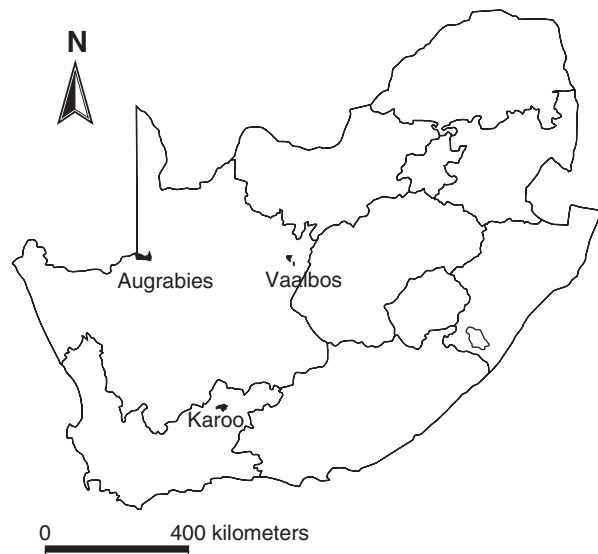


Fig 1 The location of Augrabies Falls, Karoo and Vaalbos National Parks in the Northern and Western Cape Provinces of South Africa.

Table 1 Overview of study areas

National Park	Augrabies Falls	Karoo	Vaalbos
Park section	Waterval	Doornhoek	Than-Droogeveld
Park location	28°25'–28°38'S19°53'–20°24'E	32°7'–32°23'S22°0'–22°35'E	28°27'–28°37'S24°11'–24°23'E
Section size	7,530 ha	7,092 ha	17,500 ha
Black rhinos (bull or cow + calf units)	6	3–4	8–12
Black rhino population growth 1994–1998 ³	3.5%	14.0%	17.2%
Black rhino density 1997–1998	0.08 km ⁻²	0.06 km ⁻²	0.06 km ⁻²
Altitude above sea level	420–750 m	915–1,900 m	1,001–1,175 m
Average annual rainfall ¹	123 mm	175–406 mm	417 mm
Monthly average max and min temp., January ¹	37.1 and 21.6°C	32.3 and 15.8°C	33.9 and 18.8°C
Monthly average max and min temp., July ¹	21.3 and 4.5°C	18.4 and 4.3°C	19.5 and 1.4°C
Annual frost nights ¹	0.9	19.5	31.6
Vegetation type ²	Lower Gariep Broken Veld, Bushmanland Arid Grassland, Lower Gariep Alluvial Vegetation	Gamka Karoo, Upper Karoo Hardeveld	Kimberley Thornveld
Average browse availability 0–2 m above ground	1,096 m ³ /ha	1,924 m ³ /ha	1,890 m ³ /ha
Potential competitors	Giraffe, springbok, klipspringer, rock hyrax	Eland, kudu, springbok, klipspringer, rock hyrax	Giraffe, eland, kudu, springbok, gemsbok

Sources: 1: SA Weather Service, 2002 Unpublished climate data; 2: Mucina & Rutherford, 2006; 3: Adcock, 2001.

receiver. The proportion of plots in each vegetation community was allocated according to the contribution of each vegetation community to total browse availability determined post priori.

Two plot types were employed: belt transects (Mueller-Dombois & Ellenberg, 1974) for plants ≥ 100 cm and square plots within the belt transect for plants < 100 cm. Grasses were not sampled, as they were not recorded in the diet. Each belt transect was terminated when 30 plants regardless of species had been included, with the transect length determined as the centre between the 30th and 31st plant. Square plots were placed randomly inside the belt transect, and all plants < 100 cm tall were measured. The number of plots inside each belt transect was increased until they included a minimum of 50 shorter individual plants per belt transect. To accommodate different plant densities in different plant communities, the belt transects ranged from 5 to 50 m wide and 30 to 200 m long, while the nested square plots for plants < 100 cm were 1, 4, 9 or 16 m². The rationale for employing distance and fixed number sampling was to minimize confidence limits within the available

time, and sampling was also improved by sampling tree diversity with long plots, trees at low density with large plots and short vegetation with many, small plots (Newton, 2007). A total of 5550 plants ≥ 100 cm tall and 9250 shorter plants were measured in 186 belt transects (AFNP: N = 58; KRNP: N = 38; VNP: N = 90).

Each plant was identified *in situ*, to species level when possible. Alternatively, specimens were collected for later identification (SANParks, Kimberley; McGregor Museum Herbarium, Kimberley; National Museum Herbarium, Bloemfontein and National Botanical Institute (SANBI), Pretoria). Taxon names are in accordance with Arnold & De Wet (1993). We recorded the growth forms (trees, shrubs and forbs and dwarf shrubs) (Edwards, 1983) of all eaten plant species and visually determined the presence/absence of live leaves on the principal browse species with a propensity for leaf fall, both in plots and on random plants along feeding trails. Species in which more than 50% of plants were leafless in any month were regarded deciduous. A total of 3177 deciduous plants were sampled. Depending on plant shape, one to three plant canopy

heights (top, widest point and bottom of the canopy) and one or two sets of perpendicular canopy diameters were recorded with measuring tapes and used to calculate canopy volumes ≤ 200 cm above ground for all plant species for each vegetation community using the method developed by Smit (1996). Black rhinos normally browse from 0 to 200 cm above ground (Smithers, 1983; Du Toit, 1990; Buk, 2004). A TWINSPLAN analysis (McCune & Mefford, 1997), using plant canopy volumes ≤ 200 cm above ground, was refined by applying Braun-Blanquet procedures to form phyto-sociological tables (Whittaker, 1980). The ordination programme DECORANA (McCune & Mefford, 1997) was used to check whether the preliminary vegetation communities were distinct or could be amalgamated before forming the final vegetation communities. The browse availability methodology is described in more detail in Buk (2004). For logistical reasons in KRNP, the availability data could only be collected 1–2 years after the feeding data. Availability of heavily browsed, locally rare species could have changed in the short interim, but we assumed the data would still be representative for most species, given the moderate plant growth and herbivore stocking rates in KRNP.

Browse utilization

Feeding data were collected by tracking black rhinos. This method has the advantage of sampling feeding during dark hours too and causes a minimum of disturbance to the rhinos. One disadvantage compared to dung analysis is that it requires extra attention to detect feeding on forbs, grasses and fallen fruit (Van Lieverloo *et al.*, 2009). Direct feeding observations were only rarely possible. In search of fresh rhino tracks, and to reduce area biases, park roads were frequented in proportion to the size of the vegetation community through which they pass. Rhino tracks no older than approximately 24 h were detected by driving slowly along the roads and vehicle tracks. The rhino track was aged using recognised signs such as the time interval since the road was last driven along, disturbance to the prints from wind and animals, soil moisture in the prints, moisture in dung or in urine marks, freshness of browsing and locating the rhino. The rhino track was followed on foot and recorded on GPS. Signs of feeding by the tracked rhino were meticulously sought after and differentiated from other feeding by its freshness (desiccation), clustering of cuts, thickness of cuts, presence of rhino tracks and absence of other tracks.

Feeding was recorded as the number of black rhino standard bite volumes (SBVs), similar to previously described bite methods by Hall-Martin, Erasmus & Botha (1982), Emslie (1999) and Kotze & Zacharias (1993). The SBV is equal to the approximate average volume of browse consumed in one black rhino bite. SBVs were calibrated by observing black rhinos feeding in the field and counting the bites they took, and later estimating the volume and mass by clipping and weighing twigs from the same plant. Henceforth, a cylinder with the volume of the average SBVs was used to guide visual estimates. When signs of feeding were smaller than the average SBV they were recorded as a fraction ($\frac{1}{2}$ or $\frac{1}{4}$) of the SBV. The bite method is time-efficient and consistent allowing for higher data collection rate than highly time-consuming twig measurements, which have their own limitations (Brown, 2008). A total of 263 feeding trails were followed comprising 18,804 SBVs (Table 2).

Standard bite volumes were analysed by park, species and season, with the seasons based on climate and plant phenology as follows: Wet season (November–February) with fresh leaves and twigs; early dry season (March–May) with mature leaves; and late dry season (June–October) with leaf fall in deciduous plant species (SA Weather Service, 2002; Buk, 2004). The late dry season in VNP was further subdivided into preflush (June–August) and flush (September–October) when *Acacia mellifera* and *Grewia flava*, both main food plants, regained leaves. Diet selection for the full year was calculated as the average of the seasonal diets, to avoid bias from unequal sample sizes among seasons.

Food plant preference and impact

Feeding preferences were calculated as the percentage of SBVs divided by percentage availability for each plant species (canopy volume ≤ 200 cm above ground) following Petrides (1975). The data were analysed using 'Analyse-it version 1.67' (Analyse-IT Software Ltd, 2003), and the methods documented in Zar (1999). Correlations between SBVs consumed of each plant species and their available canopy volumes were tested using Spearman correlation coefficient (Zar, 1999), while Fisher's Exact Test was used to test for significant differences between observed and expected values on the original data, rather than percentages. Seasonal difference in diet and patterns of diet change was tested for using a chi-square test of association (Zar, 1999). Diet and browse diversity and equitability

Table 2 Black rhino feeding by species (% of total diet volume), browse availability by species (% of total canopy volume ≤200 cm above ground) and diet preferences (feeding/availability) in the three study areas. Only the ten most eaten plants in each park are shown

Park/Browse species	Feeding			Browse			Preference			
	Jun-Oct			Full year			Jun-Oct			
	Mar-May	Jun-Aug	Sep-Oct	Nov-Feb	Full year	Mar-May	Jun-Aug	Sep-Oct	Nov-Feb	Full year
% Volume	% Volume	% Volume	% Volume	% Volume	% Volume	% Volume	Feeding/Availability	Feeding/Availability	Feeding/Availability	Feeding/Availability
Augrabies Falls National Park										
<i>Zygophyllum cf. dregeana</i>	21.90 ^{a3}	39.71 ^{b3}	25.57 ^{a3}	30.55 ³	1.63	13.4	24.4	15.7	18.7	
<i>Acacia mellifera</i>	41.47 ^{a3}	16.25 ^b L-	27.06 ^{c3} L+	26.16 ³	15.00	2.76	1.08	1.80	1.74	
<i>Euphorbia recitrana</i>	7.40 ^{a3}	9.19 ^{a3}	8.05 ^{a3}	8.36 ³	2.87	2.58	3.20	2.81	2.91	
<i>Indigofera pechuellii</i>	7.73 ^{ab3}	5.97 ^{a2}	9.51 ^{b3}	7.59 ³	2.58	2.99	2.31	3.69	2.94	
<i>Hermannia stricta</i>	2.73 ^{a3}	7.80 ^{b3}	2.47 ^{a3}	4.76 ³	0.47	5.82	16.6	5.26	10.1	
<i>Rhigozum trichotomum</i>	1.64 ^a	4.01 ^{b2}	3.72 ^{b3}	3.32 ²	1.07	1.53	3.75	3.47	3.10	
<i>Monechma spartioides</i>	1.49 ^{a3}	1.55 ^{a2}	5.41 ^b	2.83 ³	4.50	0.33	0.35	1.20	0.63	
<i>Indigofera heterotricha</i>	1.97 ^{a3}	1.57 ^{a1}	2.90 ^{a3}	2.11 ³	0.27	7.29	5.81	10.7	7.82	
<i>Acacia karroo</i>	0.22 ^{a3}	1.91 ^{b1}	1.58 ^{b3}	1.38 ³	4.15	0.05	0.46	0.38	0.33	
<i>Ziziphus mucronata</i>	1.53 ^a	0.37 ^b L-	2.36 ^{a2} L+	1.32	1.17	1.31	0.31	2.02	1.13	
Feeding trails/SBVs	25/1372	18/821	40/2807	83/5000						
Karoo National Park										
<i>Acacia karroo</i>	34.53 ^{a3}	13.18 ^{b3} L-	45.05 ^{c3} L+	29.14 ³	8.25	4.19	1.60	5.46	3.53	
<i>Zygophyllum</i> species	14.54 ^{a3}	38.12 ^{b3}	8.55 ^{c3}	22.37 ³	0.50	29.1	76.2	17.1	44.7	
<i>Lycium cinereum</i>	9.43 ^{a3}	17.96 ^{b3}	14.83 ^{c3}	14.79 ³	0.28	33.7	64.1	53.0	52.9	
<i>Salsola smithii</i>	20.35 ^{a3}	4.24 ^{b3} L-	10.15 ^{c3} L+	10.23 ³	0.02	950	198	474	477	
<i>Rhigozum obovatum</i>	11.02 ^{a3}	6.79 ^{b3} L-	9.07 ^{c3} L+	8.61 ³	4.00	2.76	1.70	2.27	2.15	
<i>Hermannia desertorum</i>	3.45 ^{a3}	4.62 ^{b3}	3.50 ^{a3}	3.95 ³	0.26	13.2	17.6	13.4	15.1	
<i>Delosperma</i> species	1.27 ^{a3}	1.98 ^{b3}	0.56 ^{c1}	1.33 ³	0.08	15.5	24.2	6.83	16.2	
<i>Eberlanzia ferox</i>	0.86 ^{a1}	2.50 ^{b1}	0.14 ^{c3}	1.30	1.56	0.55	1.60	0.09	0.83	
<i>Garuleum bipinnatum</i>	0.22 ^a	2.37 ^{b3}	0.41 ^a	1.18 ³	0.35	0.63	6.73	1.16	3.35	
<i>Grewia robusta</i>	0.26 ^{a3}	1.68 ^{b3}	0.60 ^{a3}	0.97 ³	5.68	0.05	0.30	0.11	0.17	
Feeding trails/SBVs	15/2668	31/3118	27/2914	73/8700						
Vaalbos National Park										
<i>Acacia mellifera</i>	43.43 ^{a3}	4.54 ^{b3} L-	21.82 ^c L+	29.00 ³	21.13	2.06	0.21	1.90	1.37	
<i>Grewia flava</i>	34.59 ^{a2}	0.55 ^{b3} L-	6.39 ^{c3} L+	22.08 ³	27.94	1.24	0.02	1.31	0.79	
<i>Acacia tortilis</i>	4.37 ^a	44.72 ^{b3}	0.57 ^{c3} L-	15.12 ³	5.84	0.75	7.66	1.41	2.59	
<i>Monechma incanum</i>	6.76 ^{a3}	18.84 ^{b3}	11.02 ^{c3}	9.64 ³	0.38	17.8	49.6	11.1	25.4	
<i>Rhigozum trichotomum</i>	2.18 ^{a2}	7.41 ^{b3}	18.41 ^{c3}	5.99 ³	0.40	5.45	18.5	3.95	15.0	
<i>Lycium hirsutum</i>	0.00 ^{a3}	8.14 ^{b1}	10.33 ^{b3}	3.89 ¹	5.16	0.00	1.58	2.00	0.75	
<i>Acacia erioloba</i>	2.72 ^a	4.64 ^b	7.23 ^{c3}	3.47	3.46	0.79	1.34	0.37	1.00	

Table 2 (Continued)

Park/Browse species	Feeding			Browse			Preference				
	Jun-Oct			Jun-Oct			Jun-Oct				
	Mar-May	Jun-Aug	Sep-Oct	Nov-Feb	Full year	Full year	Mar-May	Sep-Oct	Nov-Feb	Full year	
% Volume	% Volume	% Volume	% Volume	% Volume	% Volume	% Volume	Feeding/Availability	Feeding/Availability	Feeding/Availability	Feeding/Availability	
<i>Salsola</i> sp.	0.21 ^a	3.26 ^{bc3}	5.15 ^{c3}	2.76 ^{b3}	2.64 ³	2.64 ³	0.91	14.2	22.4	12.0	11.5
<i>Ziziphus mucronata</i>	1.27 ^a	3.19 ^b	0.99 ^{al}	1.64 ^a	1.83	1.83	0.63	1.57	0.49	0.81	0.90
<i>Lycium cinereum</i>	0.41 ^a	0.48 ^a	2.67 ^{b3}	0.96 ^a	0.99 ³	0.99 ³	1.14	1.33	7.42	2.67	2.75
Feeding trails/SBVs	29/1217	17/722	23/1760	38/1406	107/5104	107/5104					

Significant seasonal differences ($P < 0.05$) in feeding are indicated by different letters, while significant difference between observed and expected feeding based on availability is indicated by ¹($P < 0.05$), ²($P < 0.001$) or ³($P < 0.0001$). Preference significantly different from neutral is shown in bold. L- and L+ indicate decrease and increases in % of deciduous plants with leaves.

were calculated using Shannon's indices (Begon, Harper & Townsend, 1986). Differences in Shannon diversity and equitability between the diet and available browse were tested using the Hutcheson test (Hutcheson, 1970; Zar, 1999). Note that in this method, degrees of freedom are not derived directly from sample size, but are subject to a calculation.

The impact of the black rhinos on food plants was calculated with the knowledge that a rhino unit (bull rhino or a cow-calf combination) eats about 50 kg per day (Atkinson, 1995; Maddock, La Cock & Burger, 1995; Buk, 2004). Using the average weight and volume for SBVs, the average browsing pressure was then calculated as the percent of volume removed annually from (i) the total browse, (ii) the eaten browse species (species recorded in the diet) and (iii) the eaten browse weighted according to the contribution of each species to the diet. The black rhinos concentrated their feeding on a few species, and the two latter calculations of browsing pressure give a much better indication of the level of impact on the plant species of significance to the rhinos.

Results

Selection of food plant species

A total of 18,804 standard bite volumes (SBVs) were recorded, on 127 plant species with 51 plant species in AFNP, 53 in KRNP and 41 in VNP (Table S1). The ten most eaten (principal) food plant species made up 88.4%, 93.9% and 94.7% of black rhino diet in AFNP, KRNP and VNP, respectively, but only 33.7%, 21.0% and 67.0% of the available browse ≤ 200 cm above ground in each park, respectively (Table 2). Just two plant species accounted for 51.1–56.7% of the diet in each of the three parks, while three species accounted for 65.1–66.3% (Table 2). The three most eaten species in each park were *Zygophyllum cf. dregeana*, *Acacia mellifera* and *Euphorbia rectirama* (AFNP); *A. karroo*, *Zygophyllum sp.* and *Lycium cinereum* (KRNP); and *A. mellifera*, *Grewia flava* and *A. tortilis* (VNP) (Table 2). In each park, twelve plant species were significantly preferred (Table S1).

Preference index values for different growth forms were significant for all parks. AFNP: 0.19 (trees), 2.10 (shrubs) and 0.85 (dwarf shrubs (< 0.5 m) and herbs) ($\chi^2 = 1212.7$, $n = 5000$, $df = 2$, $P = 0$); KRNP: 22.7, 0.24 and 1.31 ($\chi^2 = 4628.7$, $n = 8701$, $df = 2$, $P = 0$); VNP: 1.67, 0.76 and 2.71 ($\chi^2 = 497.7$, $n = 5104$, $df = 2$, $P = 0$). No grass was recorded in the diet.

The number of SBVs of each species in each park correlated significantly with the available canopy volumes ≤ 200 cm above ground of the plant species. This applied to the lumped annual data for AFNP (Spearman, $r_s = 0.37$, $n = 51$, $P = 0.0072$), KRNP (Spearman, $r_s = 0.39$, $n = 53$, $P = 0.0035$) and VNP (Spearman, $r_s = 0.72$, $n = 41$, $P < 0.0001$), and for all the seasons across the parks. Browse availability thus explained 14%, 15% and 52% ($r_s^2 = 0.14$ – 0.52) of the variation in contribution of each species to the diet in AFNP, KRNP & VNP, respectively. When each plant species was tested using Fisher's Exact Test, the consumption of most plant species differed significantly from that expected from their available canopy volumes (Table 2 and Table S1). Preference values ranged from 0.00 (complete rejection) through 1.0 (neutral) to 2852 (strong preference). Common species completely rejected included *Pentzia incana* (18.8% of available canopy volume), *Elytropappus rhinocerotis* (11.0%) and *Eriocephalus ericoides* (6.8%) in KRNP and *Tarchonanthus camphorathus* (24.2%) in VNP.

Diet diversity

The Shannon species diversity index $H'(\ln)$ for the diet of rhinos was 2.30 in AFNP, 2.10 in KRNP and 2.12 in VNP. In comparison, the Shannon diversity $H'(\ln)$ of the available canopy volume ≤ 200 cm above ground was significantly higher in AFNP with 3.45 (Hutcheson, $t = 5.19$, $df = 179$, $P < 0.001$) and 3.08 in KRNP (Hutcheson, $t = 5.52$, $df = 199$, $P < 0.001$), but not significantly different in VNP with 2.09 (Hutcheson, $t = 0.22$, $df = 193$, $P > 0.5$). If only plant species found in the diet are

considered to be available browse, Shannon diversity in the strict sense can no longer be computed for the browse, but it is possible to compare Shannon equitability 'J' (Begon, Harper & Townsend, 1986) of the diet (J_d) with the equitability of the eaten browse species (J_b). Again, diet is less diverse (less equitable) than the composition of eaten plant species in both AFNP (AFNP $J_d = 0.58$ versus AFNP $J_b = 0.77$ (Hutcheson, $t = 5.19$, $df = 179$, $P < 0.001$)) and KRNP (KRNP $J_d = 0.53$ versus KRNP $J_b = 0.65$ (Hutcheson, $t = 2.49$, $df = 94$, $P < 0.05$)), but not significantly different in VNP (VNP $J_d = 0.57$ versus VNP $J_b = 0.50$ (Hutcheson, $t = 1.62$, $df = 197$, $P < 0.20$)).

Seasonal food selection

Among the ten principal browse species in each park, the numbers of deciduous species were 2, 3 and 4 in AFNP, KRNP and VNP, respectively, and comprised 27.5%, 48.0% and 68.0% of the diet (Table 2). The period with more than 50% leafless *Acacia mellifera* was 4 months in VNP compared to 2 months in AFNP. The species composition of the black rhino diet was significantly different between seasons in all three parks (AFNP: $\chi^2 = 709.89$, $n = 5000$, $df = 100$, $P < 0.0001$; KRNP: $\chi^2 = 2231.57$, $n = 8701$, $df = 104$, $P < 0.0001$; and VNP: $\chi^2 = 3397.39$, $n = 5104$, $df = 120$, $P < 0.0001$). Pair-wise tests for all seasons were also significantly different (chi-square, all $P < 0.0001$). The intake of deciduous species was largely dependent upon the presence of leaves (Fisher's Exact Test, $P = 0$) (Table 3, left side). The rhinos compensated by eating more of a variety of evergreen species during the dry season (Fisher's Exact Test, $P = 0$) (Table 3, right side).

Table 3 Significant seasonal changes in black rhino diet as a function of leaf phenology. The numbers represent significant changes between seasons (Table 2) in the contribution to diet of the 10 most eaten plant species in each of the three parks

	Change in leaf phenology					
	Deciduous plant species			Evergreen plant species		
	Increase in % plants with leaves	No change	Decrease in % plants with leaves	Season of increase in % deciduous plants with leaves (Nov–Feb)	Season of no change (Mar–May)	Season(s) of decrease in % deciduous plants with leaves (Jun–Aug–Sep–Oct)
Diet change						
Increased diet contribution	10	3	0	2	5	21
No change	1	4	0	4	11	7
Decreased diet contribution	0	2	9	15	5	1

Browsing intensity

With SBVs averaging $8.0 \pm 2.6 \text{ dm}^3$ and $18.7 \pm 7.2 \text{ g}$ ($n = 25$), it was estimated that the average rhino unit would consume 7807 m^3 of browse per year. The average browsing pressure by the black rhinos was 0.57% of the total standing browse volume per year in AFNP, 0.35% in KRNP and 0.24% in VNP (Table 4). However, average browsing pressure was much higher on the eaten plant species (1.58–4.21%), while the average browsing pressure tended to be higher still on the eaten browse when weighted according to diet composition (1.30–14.5%) (Table 4). The average browsing pressure on the eaten browse varied considerably between seasons, ranging from 2.0 to 6.8 times higher in the dry season, with the KRNP having a notably high

43.5% pressure in the dry season (Table 4). Principal browse species with relatively high browsing pressure included *Z. cf. dregeana* (10.7%) in AFNP, *L. cinereum* (10.6%) and *S. smithii* (10.2%) in KRNP and *M. incanum* (6.0%) and *R. trichotomum* (3.5%) in VNP (Table 4). Browsing pressures on other highly preferred species were 32.7% on *S. verbenaca* and 18.4% on *Z. pubescens* in VNP and 489% on *S. calluna* in KRNP (Table 4).

Discussion

Selection of food plant species

Browse availability explained 14%, 15% and 52% of the variation in contribution of each species to the diet of

Table 4 Browsing pressure from black rhino on selected plant species in the three study areas

	Browsing pressure (% of volume/year) in the three study areas		
	AFNP	KRNP	VNP
Average browsing pressure	0.57	0.35	0.24
Average browsing pressure on the eaten browse species	1.67	4.21	1.58
Average browsing pressure on the browse weighted by contribution to the diet of each species (seasonal min–max)	4.41 (3.51–6.90)	14.5 (10.4–43.5)	1.30 (0.59–4.02)
Principal browse species			
<i>Acacia mellifera</i>	0.99		0.32
<i>Acacia karroo</i>	0.19	0.71	0.12
<i>Acacia tortilis</i>			0.61
<i>Delosperma</i> sp.		3.33	
<i>Euphorbia rectirama</i>	1.66		
<i>Grewia flava</i>			0.19
<i>Indigofera heterotricha</i>	4.47		
<i>Indigofera pechuellii</i>	1.68		
<i>Hermannia desertorum</i>		3.04	
<i>Hermannia stricta</i>	5.77		
<i>Lycium cinereum</i>		10.6	0.65
<i>Monechma incanum</i>			5.99
<i>Rhigozum trichotomum</i>	1.77	0.43	3.54
<i>Salsola smithii</i>		10.2	
<i>Salsola</i> sp.			2.71
<i>Zygophyllum cf. dregeana</i>	10.7		
<i>Zygophyllum</i> sp.		8.96	
Other preferred species			
<i>Hermannia spinosa</i>	7.41		
<i>Indigofera heterotricha</i>	4.45		
<i>Salsola calluna</i>		489	
<i>Salvia verbenaca</i>			32.7
<i>Zygophyllum pubescens</i>			18.4

rhinos in AFNP, KRNP & VNP, respectively. This indicates availability was an important diet selection criteria in VNP, but less so in AFNP and KRNP.

Contrary to the diet diversification hypothesis (Muya & Ouge, 2000), in AFNP and KRNP, the black rhino diet was less diverse than both available and eaten browse, while in VNP a trend towards a more diverse diet was not statistically significant. In Laikipia, Kenya Shannon species diversity index $H'(\ln)$ for the diet of black rhinos was 2.88 (Oloo, Brett & Young, 1994) compared to 2.30 in AFNP, 2.10 in KRNP and 2.12 in VNP. Instead of diversifying their diet to deal with dietary and possible chemical defence constraints, the rhinos concentrated their feeding on a few species. Three plant species contributed more than 65% of the diet in each of the three study areas. This compares to other South African studies, where three plant species accounted for 81% (summer) and 50% (winter) of black rhino diet in the Great Fish River Reserve (Ganqa, Scogings & Raats, 2005), and 30% in Itala Game Reserve (Kotze & Zacharias, 1993). In Kenya, three species contributed 46% of rhino diet in Nairobi N.P., 37% in Masai Mara Game Reserve and 36%/56% (wet/dry season) in Laikipia (Mukinya, 1977; Oloo, Brett & Young, 1994; Muya & Ouge, 2000). The dependence of black rhinos on a few plant species strongly limits their food resources. It is thus important to monitor these few key species to gauge rhino food availability.

In all three parks, *Acacia*, *Zygophyllum*, *Hermannia*, *Rhigozum* and *Salsola* species were principal and/or preferred food plants, while *Indigofera* and *Euphorbia* were important in AFNP and *Grewia* in VNP. Other parks show similar trends, with *Acacia* species being important in Itala, Masai Mara and Nairobi National Park, *Indigofera* species in Tsavo National Park, *Grewia* in Great Fish River Reserve (GFRR) and *Euphorbia* in Olduvai Gorge, Liwonde National Park, GFRR and in Kunene (Goddard, 1968, 1970; Mukinya, 1977; Kotze & Zacharias, 1993; Bhima & Dudley, 1996; Hearn, 2000; Muya & Ouge, 2000; Ganqa, Scogings & Raats, 2005). These studies also show that not all species in these plant families are preferred and/or principal food plants. Only an analysis at the species level can reveal what determines preference. Four common, but completely rejected, species (mentioned in the results) are all known to be high in aromatic oils containing terpenes or phenols with antimicrobial properties (Proksch *et al.*, 1982; Zdero & Bohlmann, 1990; Vries, Klaasen & Johnson, 2005; Matasyoh *et al.*, 2007) and this could play an important role in diet selection.

The preferences for different growth forms showed no pattern across parks, and merely reflected selection for species. The complete absence of grass in the recorded diet could be an artefact of the tracking method, which ideally should be performed in conjunction with faecal analyses (Van Lieverloo *et al.*, 2009). However, we did manage to record many thin-stemmed plants, uprooted forbs and fallen fruits in the diet in these parks as well as grasses in more mesic parks. We also noted that grass bitten off with browse was discarded. Finally, feeding on grass was quite noticeable in these arid parks. We therefore believe the consumption of grass by black rhinos was very small.

There were significant seasonal changes in the diet in all three parks. These changes in diet showed a pattern of avoiding leafless deciduous plants (Table 3).

Browsing intensity

This study confirms that rhinos have a significantly restricted diet with a preference for a few key plant species and a tendency to select leafy species in the dry season. Diet overlap with other browsers (such as kudu (*Tragelaphus strepsiceros*); De Boer & Ijdema, 2007) could further reduce the capacity of the vegetation to sustain the browsers through the dry (or frosty) seasons. In this study, the browsing intensity of black rhinos on the vegetation as a whole was relatively low, but reached much higher levels on the eaten browse species, and increased two to sevenfold in the critical dry season. VNP had the lowest average browsing intensity, because of the abundance of preferred *Acacia* and *Grewia* species, but showed the highest seasonal increase in browsing pressure, because VNP had the biggest proportion of deciduous diet (68%) and a long leafless period. AFNP had less browse and a higher browsing intensity, but less seasonal fluctuation because of the least deciduous diet (28%) with a short period without leaves. KRNP had high browsing intensity. This was due partly to a deciduous diet (48%) and partly to unfavourable browse composition, including a high proportion of rejected aromatic, karoo shrubs. The low abundance of three of the four most eaten species in KRNP resulted in extreme browsing intensity of 43.5%/year in the dry season. Rhino population growths during 1994–1998 and densities during 1997–1998 are listed in Table 1. During 1998–2001, population growth was 11.9% in VNP (Adcock, 2001), whereas all rhinos were temporarily removed from the other parks.

If highly preferred food plant species contribute a significant part of the rhino diet, they should be monitored as critical species for black rhinos, especially if they provide dry-season browse. Examples are *Zygophyllum* species in AFNP and KRNP, and *Monechma incanum* and *Rhigozum trichotomum* in VNP. Little is known about sustainable browse rates and diet overlap between black rhino and other browsers, but there are indications that some species very heavily browsed in KRNP, possibly to unsustainable levels, similar to black rhino impact on *Euphorbia* species in GFRR (Heilmann *et al.*, 2006; Luske *et al.*, 2009). Results suggest that *Salsola smithii* and *S. calluna* in KRNP had 102% and 489%, respectively, of their volumes eaten by black rhino per year. These particular figures are most likely inflated, because in KRNP measurement of consumption preceded availability by 1–2 years, by which time feeding had reduced availability of these two scarce species. Regardless of this methodological shortcoming, of any possible influence of other browsers and of the lack of data on plant growth rates, these results indicate a severe impact. Since this field study, stocking rate of black rhinos has been drastically reduced in KRNP, and both *Salsola* species have accomplished striking increases in availability (KG Buk, personal observations).

Conclusions

We have shown that diet selection was correlated with plant availability and that diet exhibited seasonal differences, linked to rejection of deciduous species when leafless. Pressure on eaten browse increased two to sevenfold in the dry season in these arid parks. We rejected the hypothesis that black rhino diet is more diverse than available or eaten browse species, with the opposite true in two parks. Finally, we identified key wet- and dry-season plant species for black rhino, and a few species severely affected by browsing. The abundance of key plant species should be monitored (i) to act as an earlier warning of food limitation than either rhino body condition or population performance can provide and (ii) to protect preferred plant species against local extinction.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Diet and diet preferences of black rhino in Augrabies Falls National Park (Waterval Section), Karoo National Park (Doornhoek Section) and Vaalbos National Park (Than-Droogeveld Section). Significant ($P < 0.05$) preferences (eaten % SBV/available % volume) are in bold.

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