

Paper 2:

Megaherbivore snack attack or optimal foraging? – seasonal food selection by black rhino in Augrabies Falls National Park, South Africa.

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Abstract

Seasonal food selection by black rhino was studied in Augrabies Falls National Park. Free ranging black rhinos were tracked and their feeding on 3 049 plants along 83 feeding trails were recorded in Standard Bite Volumes (SBVs). Eleven species of trees comprised 4.8 % of the browsed SBVs, 17 species of forbs and dwarf shrubs comprised 42.2 %, while 23 species of shrubs comprised 53.1 %. *Zygophyllum cf. dregeana* and *Acacia mellifera* accounted for 56.7 % of the diet. The 10 most important (principal) food plants made up 88.4 % of the diet and included 2 species of *Acacia*, 2 of *Indigofera*, as well as *Zygophyllum*, *Euphorbia*, *Hermannia*, *Rhigozum*, *Monechma* and *Ziziphus*. Two preference indices compared SBVs to available numbers of plants along feeding trails and to the estimated available browse volume in the park. The indices concurred on 9 of the 12 most preferred species. Captive feeding was limited to separating preferred and avoided species. Diet preferences shifted from deciduous to evergreen plants from wet to dry season. Available browse volume and diet composition were significantly, but weakly correlated ($p=0.0072$, $r_s=0.37$). However, rhinos significantly preferred many plant species with low abundance. These can be used as early warning indicators for the condition of rhinos and vegetation. Ninetyseven % of browsing on large *Acacia mellifera* shrubs occurred below 200 cm above ground, with the preferred range being 101-150 cm. *A.mellifera* with high twig ($p=0.006$) and leaf densities ($p<0.0001$) were preferred. Browsing on some preferred species was heavy,

whereas on *A. mellifera* it was light but frequent. Results are used to test and discuss optimal foraging theory and conservation.

Keywords

Black rhino, seasonal diet, optimal foraging, preference indices, plant impact.

Introduction

The black rhino (*Diceros bicornis*) is listed as critically endangered (IUCN, 2003). The species was already declining due to habitat loss, when intensive poaching caused numbers to plummet from 65 000 in 1970 to 2 410 in 1995 (Emslie and Brooks, 1999). Increased safety surrounding the remaining populations and translocations to establish new populations has allowed recovery to 3100 animals (*Pers. comm.*: Richard Emslie, Rhino Management Group). This has facilitated live sales of this “Big 5” species to private game reserves at prices of about 60 000 USD each. However, prices are yet to be adequately reflected in allocations to research aimed at improving understanding of black rhino dietary and other habitat requirements. Thus, the rate of population recovery has been slowed by diet related poor performance, sickness and death both in captivity and in reserves where carrying capacity has been overestimated and/or overshoot by the population (Brooks, 2001; du Toit, 2001).

The main aim of current black rhino conservation is to ensure population growth above 5 % per annum in the remaining populations in order to minimize the loss of genetic diversity and significantly outpace any losses to poaching (Emslie, 2001a). High growth can only be maintained if negative density dependent feedback including food limitation is avoided, which means keeping populations around or below 75 % of the ecological carrying capacity.

This study compares the seasonal diet of black rhino in the Augrabies Falls National Park (AFNP) with the available browse to identify the principal, preferred and key food species during different seasons. To compare methods and strengthen the credibility of the results two measures of browse availability were employed for free ranging rhinos and supplemented with a captive rhino feeding study. The results facilitate plant monitoring and adjustment of browser stocking rates, and form part of a larger study on the feeding ecology and habitat suitability for black rhino in arid parts of Southern Africa.

The diet selection of black rhino in AFNP is of particular interest for two reasons. Firstly, the park has a low browse production and a high level of plant endemism (Zietsman and Bezuidenhout, 1999), which are potentially impacted by two mega-herbivores: black rhino and giraffe. Secondly, it has been suggested that arid habitats generally have more nutritious or digestible browse and thus can sustain high rates of black rhino reproduction despite low absolute black rhino ecological carrying capacity densities (Adcock, 2001). In this area, the two females have achieved excellent inter-calving intervals of 2 years on average, versus a combined South African / Namibian average of around three years.

This study also tests some current thoughts on browsing ecology. Optimal Foraging Theory (OFT) predicts that an animal, by virtue of genetic predisposition and learning, optimises its intake (Stephens & Krebs, 1986). Rate of energy intake is the most frequently applied “currency” of profitability and proxy for fitness in OFT modelling. The Marginal Value Theory of OFT predicts a browser should move to the next food plant when energy intake (E) divided by handling time (h) of feeding on the current plant drops to equal energy intake divided by searching time (s) plus handling time for the average food plant (h). This is expressed mathematically as $dE(h)/dh = E(h)/(s+h)$ (Stephens & Krebs, 1986). For food items that provide equal initial rates of energy intake ($dE(h)/dh$), the amount eaten is therefore a function of the rate of diminishing returns, which is determined by plant size. Within a species initial rate of energy intake is equal for all plant sizes, but diminishes faster in smaller

individuals, as full bite sizes are depleted. Smaller plants should therefore be browsed less intensely and frequently (hypothesis 1 in table 6). If initial profitability does not differ much between browse species, the correlation between plant sizes (available canopy volume) and browsing should also apply across species (hypothesis 2 in table 6). The consumption of each species cannot be explained by average plant size (available canopy volume) alone, but will be affected by rate of encounter or density. Density by itself can be tested as a predictor of consumption, but as a product of density *and* plant size the total available browse volume within feeding height seems a more appropriate parameter. Both measures shall be tested here (hypothesis 3 in table 6).

The equation $dE(h)/dh = E(h)/(s+h)$ predicts that plants with a higher rate of energy return, and thus plants with higher densities of leaves and twigs, should be browsed more intensively and/or frequently (hypothesis 4a in table 6). In the same vein, plants with seasonal loss of leaves, fresh shoots and fruits should be browsed less intensively (hypothesis 4b in table 6). Phenological changes in profitability differ in nature and strength between species and would be expected to affect the seasonal species preferences (hypothesis 5 in table 6).

OFT and rate of energy intake has proven a useful interpreter of systems comprised of food items with similar nutritional composition (Begon, Harper and Townsend, 1986). However, studies of browsing have shown that satisfying nutrient needs and/or avoiding detrimental levels of plant toxins often take precedence over energy needs (Owen-Smith, 2002). This led to the suggestion that browsers may be compelled to diversify their diet to avoid taking in too much of any one harmful chemical (hypothesis 6 in table 6)(Freeland & Janzen, 1978; Muya and Oguge, 2000; Owen-Smith, 2002).

“Ice cream species” are highly preferred food plant species, which may or may not be driven to near or actual local extinction by herbivory (Bureau of Land Management, 2003). Among

large herbivores ice cream species have been relatively well documented in elephants (Cowling and Kerley, 2002; Johnson *et al.*, 1999; Gadd, 2002; Holdo, 2003; Tanfangenyasha, 2001, Barnes *et al.*, 1994). The “snack attack” scenario of local extinction might be expected in a social animal, in which exploitation competition prevails, whereas in a territorial, solitary, long-lived animal, sustainable harvesting for long-term benefit should confer higher fitness. One can therefore hypothesise that all species and individual plants will be browsed sustainably by black rhino provided total energy requirements can be met (hypothesis 7 in table 6).

Study area

The study was conducted in the Waterval section of Augrabies Falls National Park, South Africa during 1997-1999 (Figure 1). The park covers 55 365 ha along the Orange River at 28° 25'- 28° 38'S, 19° 53' – 20° 24' E, 120 Km west of Upington. The 7 530 ha Waterval section served as a fenced black rhino reserve at the time of the study. Waterval comprises narrow flood plains and steep gorges along the Orange River in the south, gravel plains in the centre and mountains in the north. Altitudes range from 420 to 750 metres above sea level. The climate is sub-tropical to tropical and arid with only 123 mm of annual, primarily summer rainfall (Weather Bureau, 2001). AFNP is located in the Orange River Nama Karoo vegetation type (Hoffmann, 1996) and in the Gariep Centre of Endemism, with 197 of a total of 364 species of flowering plants not having been recorded in other conservation areas (Zietsman & Bezuidenhout, 1999). Large herbivorous mammals have been reintroduced, including the megaherbivores giraffe (*Giraffa camelopardalis*) and black rhino. The black rhinos were introduced in 1986 and numbers averaged six until removal in 1999 pending a land claim. At the time of the field study there were 1 adult male, 2 adult females, 3 subadults and 2 calves. Reintroduction elsewhere within Augrabies Falls National Park is planned. Buk (Paper 1) described the study area in more detail.

Methods

Recording black rhino feeding in the field

At best the study-animals only allowed a short period of direct *in situ* observations, before either charging or fleeing. Therefore feeding data was collected by tracking. This method also has the advantage over direct observation that it samples feeding during dark hours as well. The main study on rhinos in the field was supplemented with a feeding study of some of the same animals in captivity.

For rhino tracking, park roads were frequented in proportion to the size of the habitat type through which they pass. The roads were driven slowly until a rhino track no more than 24 hours old was detected. The track was then followed on foot and Global Positioning System (GPS) receiver readings taken at regular intervals. Signs of feeding were meticulously sought after.

Feeding was recorded as the number of black rhino Standard Bite Volumes (SBVs) per plant. The concept of SBV applied here is a combination of two previously described methods. Firstly, the “bite”, which approximates the average amount of browse removed by a black rhino in one bite and defined as all severed twigs less than 5 mm in diameter within a circle of 5 cm in diameter or one thicker twig (Hall-Martin *et al.*, 1982), but without any reference to volume. Secondly, the “browse bottle” or “standardized browse volume” which refers to a standardised volume of browse defined by visual estimate by the users and a photograph of twig sizes, but otherwise unspecified and not directly related to observation of rhino feeding (Emslie & Adcock, 1994; Emslie, 1999; Kotze & Zacharias, 1993; Adcock, *pers.comm.*). The standard bite volume is equal to the approximate average volume of browse consumed in one bite as observed in the study area. Black rhinos were observed feeding in the field, the bites on a plant were counted and subsequently the browsed plant was examined. This was done on a diverse array of plants including trees, shrubs, dwarf shrubs, small succulents and large succulent *Euphorbias*. Feeding techniques vary, but typically the rhino uses its prehensile upper lip to grab several twigs up to 20 mm in diameter including any leaves,

flowers and fruits and chew them off. The volumes of simulated SBVs were measured on a later occasion and the mass of the removed browse weighed.

For each food plant the species was noted along with plant height and feeding height. For *Acacia mellifera* an additional record was made of the number of twigs bitten off on previous occasions. Twigs were used because SBVs were harder to estimate on old browsing. The twigs were recorded as either “recent” (dark severed surface) or “old” (light grey severed surface), and the densities of twigs as well as leaves were visually assessed on a four point scale from very low density to high density. Trails were aborted when no feeding had been detected for a distance of 500 metres.

Recording black rhino feeding in captivity

Captive feeding data was collected using a rhino bull and a cow with a young calf captured in Waterval and kept in holding pens at Waterval. The captive rhinos were fed nine plant species harvested within Waterval and presented twice a day in excess of consumption. In addition, each adult was given access to 22 kg of lucerne and 13 kg of game pellets per day. After the rhinos had adjusted to captivity for a week the food was weighed when presented and again when removed. Additional samples of the food plants were subjected to the same treatment, except for feeding, to establish evaporative losses.

Measuring availability and previous use of browse in the study area

The availability of browse for the reserve as a whole was obtained from Buk (Paper 1), who measured the dimensions of all plants except grasses in 58 belt transects located stratified random. From these measurements the canopy volumes from ground to 200 cm above ground were calculated using the method of Smit (1996). The leaf dry mass of *Acacia mellifera* was also calculated using the model of Smit (1996). As a second measure of availability, in this study the species, number and heights of all plants within 1 metre from either side of the rhino feeding trails were recorded.

For *Acacia mellifera* in the 58 belt transects an additional record was made of the number of twigs bitten off on previous occasions. The twigs were recorded as either “recent” (dark severed surface) or “old” (light grey severed surface), and the densities of twigs as well as leaves were visually assessed on a four point scale from very low density to high density.

Data analysis

Seasonal diet composition by SBVs and feeding trails

The percentage comprised by each plant species of the total SBVs consumed was calculated. The samples were divided into three distinct seasons based on plant phenology: Early dry season (March-May), late dry season (June-October) and rainy season (November-February)(Paper 1). Annual consumption was calculated as the average of the seasonal diets, to avoid bias from unequal sample sizes amongst seasons.

Food plant preference

Preference for each food plant species was calculated as consumption divided by availability (Petrides, 1975). This was done in three ways: a) % consumed SBVs divided by % of canopy volume 0-200 cm above ground in the entire reserve estimated from 58 belt transects; b) % consumed SBVs divided by % of plants along feeding trail and c) % mass consumed divided by % mass presented in holding pens.

The vertical distribution of black rhino feeding was determined on *Acacia mellifera*, as this shrub is a major food source and tends to offer leaves from close to ground level. Only specimens exceeding the maximum browsing height were included in the analysis of feeding height.

Statistical analysis followed Zar (1999) aided by the computer programme “Analyse-it version 1.67” (Analyse-it Software Ltd. 2003). Non-normal data necessitated use of non-parametric tests only. The original data, rather than percentages were analysed. For instance, observed

consumption in real terms (SBVs) was tested against the consumption expected from availability using chi-square or Fisher Exact Test to reveal significant preferences.

Results

Food selection at the species level

Fifty-one plant species were recorded in the diet sample from free ranging rhinos comprised of 5000.0 Standard Bite Volumes (SBVs) browsed from 3 049 plants on 83 feeding trails (Table 1). Eleven species of trees comprised 4.8 % of the browsed SBVs, 17 species of forbs and dwarf shrubs comprised 42.2 %, while 23 species of shrubs comprised 53.1 %. Just two species accounted for 56.7 % of the diet, while the 10 most important (principal) food plant species made up 88.4 % of the diet and 12 species were significantly preferred (Table 1, figure 1).

Seen across the whole range of eaten food plant species the numbers of SBVs consumed of each species by the tracked rhinos were significantly correlated with the total available canopy volumes of the plant species 0-200 cm above ground. This applies for the year as a whole (Spearman, $r_s=0.37$, $n=51$, $p=0.0072$), for the early dry season (March-May)(Spearman, $r_s=0.36$, $n=51$, $p=0.0091$) and for the late dry season (June-October)(Spearman, $r_s=0.40$, $n=51$, $p=0.0036$), but not for the wet season (November-February)(Spearman, $r_s=0.18$, $n=51$, $p=0.2174$). However, 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 0-200 cm above ground (Table 1). Preference values ranged from 0.00 (complete rejection) via 1.0 (neutral) to 445 (strong preference). The number of plants browsed upon of each species was not significantly correlated with their densities in the study area (Spearman, $r_s=0.48$, $n=10$, $p=0.1615$).

Three measures of diet preference were compared (Table 2). The first two are based on the number of SBVs consumed on the feeding trails of free ranging rhinos. In the first measure consumed SBVs were compared with the available canopy volume 0-200 cm above ground. In the second measure consumed SBVs were compared with the number of plants within 1 metre of feeding trails. These first two measures have 10 species in common among the 13 most preferred, while the ranking and especially preference values differ. The third measure of diet preference is based on percentage consumption of nine plant species presented to black rhinos in holding pens. This measure generally corresponded with observations of free ranging rhinos in classifying species as preferred or rejected, but ranking and preference values differed considerably (Table 2, Table 1).

The Shannon species diversity index $H'(\ln)$ for the diet of free ranging rhinos was 2.30. This was significantly lower (Hutcheson, $t=6.72$, $df=59$, $p<0.001$) than $H'(\ln)=3.45$ for the available canopy volume at 0-200 cm above ground (Paper 1). If only plant species found in the diet were considered to be available browse the Shannon equitability of the diet J was 0.59 while the equitability of the browse was 0.77, which is significantly higher (Hutcheson, $t=3.96$, $df=188$, $p<0.001$).

Food selection at the plant level – feeding height on Acacia mellifera

Of 165 Standard Bite Volumes (SBVs) of browsing on *Acacia mellifera* plants exceeding 200 cm in height, 97 % were removed at 0 to 200 cm above ground. All records of foraging above 200 cm were due to one female black rhino breaking branches downward with her frontal horn, which made the browse available to her calf. Consumption on *Acacia mellifera* from 0 to 200 cm by 20 cm height intervals starting with 0-20 cm were 0.0 %, 3.0 %, 4.2 %, 10.3 %, 13.9 %, 25.5 %, 20.0 %, 13.9 %, 3.6 % and 2.4 %. When considering availability of canopy volume of *A. mellifera* at different height intervals, the preferred feeding height was 101-150 cm (Figure 2).

The number of SBVs eaten per plant differed (Kruskal-Wallis, $X^2=42.13$, $df=7$, $p<0.0001$) between the eight height classes of *Acacia mellifera* (Figure 3). Both the number of freshly eaten SBVs per plant and the number of twigs showing signs of being bitten off on previous occasions on each plant were correlated with available canopy volume (Spearman, $r_s=0.24$, $n=175$, $p<0.0015$ and Spearman, $r_s=0.17$, $n=202$, $p<0.0189$). The available volume of freshly eaten plants was derived from a highly significant regression with height ($n=322$, $r=0.92$, $p<0.0001$). The rhinos exhibited significant selection for certain of the eight height classes as measured by number of plants of each plant height class browsed versus plant density in each height class (Chi-square, $X^2=206.21$, $n=353$, $p<0.0001$), SBVs consumed per plant height class versus available canopy volume 0-200 cm above ground in each plant height class (Chi-square, $X^2=330.23$, $n=1161$, $p<0.0001$) and SBVs consumed per plant height class versus available leaf dry mass (LDM) in each plant height class (Chi-square, $X^2=157.42$, $n=1161$, $p<0.0001$). 1.8 to 2.6 times more was eaten from *A. mellifera* in the height classes from 81 to 200 cm than expected from the available LDM, while less than expected was eaten from smaller and higher height classes (Figure 3).

Food selection at the plant level – repeated browsing on Acacia mellifera

When corrected for the influence of plant height there was no significant correlation between amounts of fresh browsing by rhino on *Acacia mellifera* shrubs and the amounts of previous browsing on the same shrubs (Pearson, $n=165$, $p<0.20$). However, the amount of previous browsing was significantly greater among the freshly browsed *A. mellifera* shrubs on feeding trails than among the available *A. mellifera* shrubs in Waterval (measured in the belt transects) even after correcting for different height distributions (19.7 vs 10.1 bites per plant, Mann-Whitney, $U=25368.5$, $n=406$, $p<0.0001$). The difference was bigger for recent browsing (7.4 recent bites per freshly browsed *A. mellifera* vs. 0.04 recent bites on *A. mellifera* in general, Mann-Whitney, $U=27284$, $n=406$, $p<0.0001$) than for old browsing (12.3 vs. 10.1 old bites per plant, Mann-Whitney, $U=22053$, $n=406$, $p<0.0001$).

Food selection at the plant level – selection for twig and leaf density

The rhinos exhibited significant preferences for *A. mellifera* with certain leaf and twig densities (Table 3). The selection occurred at two levels. Firstly the rhinos avoided shrubs with very low densities and secondly browsed more from the shrubs with high densities.

Food selection in relation to season and phenology

The species composition of the black rhino diet was significantly different between the three seasons (chi-square, $X^2=709.89$, $n=5000$, $df=90$, $p<0.0001$) and between all three seasons tested pair wise (chi-square, all $p<0.0001$). Most of the principal food plant species exhibited significant seasonal variations in consumption (Table 1 and figure 1). The rhinos ate significantly more from *Acacia mellifera* shrubs that had leaves or had fresh shoots and ate significantly less from those with seedpods than expected from availability within 1 metre from feeding trails (Table 4).

Impact of browsing

A Standard Bite Volume (SBV) was estimated to encompass on average 8.0 litres or 0.008 m³ ($n=11$) of canopy volume collected with the prehensile lips of the black rhino into a bottle shape of about two litres before being bitten off. The wet weight of the SBV averaged 18.9 g (range 14.0 to 26.9 g)($n=11$). A bull rhino and a cow-calf combination held in pens after being captured in Waterval for translocation consumed 65.0 kg/day of wet weight ($n=9$). Other studies from holding pens found consumptions between 41.0 and 64.8 kg/day (Maddock, La Cock and Burger, 1995; Atkinson, 1995; Dreyer, 2001). If daily consumption is assumed to be a conservative 50 kg under natural conditions and a SBV equals 20 g and 0.008 m³ then annual consumption equals 7 300 m³ of canopy volume per bull or cow-calf combination. At peak stocking there were 4 such rhino units in Waterval equalling a consumption of 29 200 m³. The rare, but highly preferred *Tetragonia arbuscula*, occurred with only 82.5 m³ of total available canopy volume, while annual consumption was 0.33 % of 29 200 m³, which is 96.4 m³ or more than 117 % of the available volume. The top principal and highly preferred food,

Zygophyllum cf. dregeana, occurred with 109 979 m³ of canopy volume, while annual consumption was 30.55 % of 29 200 m³, which is 8 921 m³ or 8.1 % of the available volume. The second ranking principal food, *Acacia mellifera*, occurred with 1 143 242 m³ of available canopy volume, while annual consumption was 26.16 % of 29 200 m³, which is 7 639 m³ or just 0.7 % of the available volume.

When examining the impact of browsing on individual plants on the feeding trails the average number of SBVs consumed per plant was significantly correlated with the average available canopy volume 0-200 cm above ground of that species as measured in the belt transects (Spearman, n=9, rs=0.77, p=0.0159)(Table 5). However, the impact was heavier on smaller plant species as the proportion of the canopy volume consumed in the average browsing incidence was inversely correlated with plant size (Spearman, n=9, RS=-0.98, p<0.0001)(Table 5).

Discussion

Selection of food plant species

Just 11 food plant species each exceed 1.0 % of the annual diet, and these principal species total 89.5 % of the annual diet. These 11 principal food plant species include eight of the 12 significantly preferred species, but only 34.4 % of the browse volume available 0-200 cm above ground. This implies that only slightly more than 1/3 of the vegetation within reach effectively contributes to rhino carrying capacity. It also means that measuring and monitoring a few plant species is sufficient to assess and adjust black rhino stocking rate in AFNP.

Food diversity was lower in this study than in Laikipia, Kenya (Oloo *et al.*, 1994) (H' = 2.30 vs. 2.88), despite relatively high browse diversity (H' = 3.45) in Waterval (Paper 1). Three food plant species comprised 65 % of the annual diet in this study versus 66 % in Karoo N.P., South Africa, 66 % in Vaalbos N.P., South Africa (Buk, *in prep.*), 46 % in Nairobi N.P.,

Kenya (Muya and Ouge, 2000), 37 % in Masai Mara G.R., Kenya (Mukinya, 1977) and 30 % in Itala G.R., South Africa (Kotze and Zacharias, 1993).

The choice of food plant genera in Waterval showed similarities with other study sites. *Acacia*, *Zygophyllum*, *Hermannia* and *Rhigozum* species were principal and/or preferred food plants in Karoo and Vaalbos N.P. as well (Buk, *in prep.a*). *Acacia* species were also important in Itala, South Africa, Masai Mara, Kenya and Nairobi, Kenya (Kotze and Zacharias, 1993; Mukinya, 1977; Muya and Ouge, 2000), *Indigofera* species were important in Tsavo, Kenya (Goddard, 1970) and *Euphorbia* species were important in Olduvai Gorge, Tanzania, Liwonde, Malawi and in Kunene, Namibia (Goddard, 1968; Bhima and Dudley, 1996; Hearn, 2000). Forbs and dwarf shrubs comprised a smaller proportion of the diet in Waterval (42 %) than in Karoo N.P. (48 %)(Buk, *in prep.a*) and Addo Elephant N.P. (54 %)(Hall-Martin, 1982), but a larger proportion than in Vaalbos N.P. (18 %)(Buk, *in prep. a*). The proportion of forbs and dwarf shrubs in the available browse was 23 % in Waterval, 47 % in Karoo and 5 % in Vaalbos (Paper 1; Buk, *in prep. b*; Buk, *in prep. c*). This confirms that forbs and dwarf shrubs are important in black rhino diet where they are available, and that they tend to become preferred where they are rare.

The preference for plants with leaves and fresh shoots essentially caused wet and early dry season preferences for *A. mellifera* and *Ziziphus mucronata* as well as wet season preference for *Monechma spartioides*. During the dry season the foliage of these three species dry out and *A. mellifera* and *Ziziphus mucronata* shed their leaves (Paper 1). During the late dry season preferences therefore shifted towards “green bite” (Tainton, 1981) in the form of the evergreen *Zygophyllum cf. dregeana* and *Hermannia stricta* (Figure 1).

The black rhinos did not diversify their diet as compared to browse availability to avoid high concentrations of detrimental plant chemicals or to satisfy nutrient needs, thus rejecting hypothesis 6 (Table 6). As hindgut fermenters rhinos do *not* benefit from bacterial

detoxification of ingested material early in the digestion, yet prefer some plants which are toxic to other browsers, such as *Euphorbia* species (Table 1, Goddard, 1968; Bhima and Dudley, 1996; Hearn, 2000). However, black rhinos probably do limit their intake of some chemically defended plant species (Muya and Oguge, 2000). Nevertheless, species which are not toxic to rhinos are eaten in such large quantities that the net result is that the diet is less diverse than the available browse.

Food value is ambiguous and specific to one species of herbivore. For instance, *Boscia albitrunca*, is heavily browsed by other mammalian browsers, but almost uneaten by black rhino. *Euphorbia gregaria* looks similar to the preferred *Euphorbia rectirama*, but is strongly avoided by black rhino (Table 1), while it is browsed by klipspringer. Only research into plant nutrients and defence chemicals, as well as dietary needs of black rhino, can provide satisfactory explanations for black rhino food preferences. Two studies analysed black rhino plant food nutrient contents (Ghebremeskel *et al.*, 1991; Dierenfeld *et al.*, 1995), and one study further analysed for plant defence chemicals and compared this to an indirect measurement of diet preferences (Muya and Oguge, 2000). However, a more comprehensive approach spanning seasons and different study sites is required to make general conclusions.

Measures of diet and preference

The differences between the three indices of food plant preference are due to several factors. Captive feeding may obviously not reflect natural foraging, and the advantages of controlled manipulation are usually outweighed by the logistical limitations on providing and weighing large amounts of fresh browse of different species. Applying findings from captive feeding to field conditions should therefore be limited to qualitative statements such as rejected, neutral and preferred food plants. Matipano (2003) also found significant differences in diet between black rhinos in bomas and in the wild. The preference index based on SBVs divided by plant numbers along feeding trails suffers from three main

limitations: 1) the plant composition along the feeding trail already reflects habitat and micro-habitat selection by the foraging rhino (Paper 3) rendering this frequently used method inherently flawed; 2) density is a poor measure of availability (Paper 1). Thirdly, measures are essentially mismatched in this method as browse availability is measured in plant numbers and feeding is measured in plant volume. However, only recording the number of plants eaten, rather than SBVs, gives an inaccurate measure of both feeding and availability. Nevertheless, it is a widely employed method due to its speed and ease of use. Measuring available browse volume along feeding trails is impractical and does not resolve the problem of habitat and micro-habitat selection.

The preference index based on SBVs divided by canopy volume in the whole reserve provides much better information, but it requires highly time-consuming vegetation analysis.

Food resource types

Owen-Smith (2002) suggested that food plants can be grouped into “resource types” based on their properties and function for browsers. “Staple resources” provide adequate-quality food for most of the year and include palatable, deciduous woody plants. The data presented here in conjunction with unpublished, preliminary plant nutrient data suggest that *Acacia mellifera*, *Ziziphus mucronata*, *Indigofera pechuellii* and *Indigofera heterotricha* be labelled staple resources. “Reserve resources” should sustain browsers through a mild-average dry (or cold) season and include the more palatable evergreen woody plants. In Waterval they include *Euphorbia rectirama*, *Hermannia stricta*, *Rhigozum trichotomum* and *Acacia karroo*. If reserve resources become scarce, browsers are forced to switch to “buffer resources” which are abundant plants of low palatability such as chemically defended evergreens. Candidates include *Schotia afra* and *Boscia* species. “Quality resources” are highly nutritional and digestible food plants, which may only be seasonally available. Being high in protein and only seasonally green *Monechma spartioides* can be categorised a quality resource. *Zygophyllum cf. dregeana* is also high in protein and highly utilized in the late dry season as well as during

the other seasons. This makes it a quality, reserve and staple resource in one, and probably the most critical food plant species for black rhinos in Waterval.

While staple resources maintain browsers through much of the year, in a seasonal system it is the production of and competition for the limited reserve resources that determines how many animals of a browser population can survive through the critical dry or cold season. Access to quality resources determines how much a female can allocate for reproduction (Owen-Smith, 2002). Estimating reserve resources and quality resources are therefore shortcuts to assessing ecological carrying capacity and capacity for reproduction of a population. Observing a switch from reserve resources to buffer resources is an indication of extraordinary nutritional stress. The concept of resource types was developed for kudu, and is believed to be applicable to black rhino, although resources appear less clear-cut (Adcock *et al.*, 2001).

Optimal foraging

As predicted by Optimal Foraging Theory (OFT) more Standard Bite Volumes were eaten from larger plants within a species and from species with larger growth forms, apparently supporting hypotheses 1 and 2 (Table 6). However, the correlations were relatively weak and as discussed below it appears large plants especially were left long before diminishing rates of energy intake could have taken effect. Hypothesis 3a was not supported, as density of plant species and their proportion in the diet were not correlated. Hypothesis 3b was only partly supported. The correlation between canopy volumes of browse species and their contribution to rhino diet was significant, but “only” explained 14 % ($rs^2=0.14$) of the variation in contribution of each species to the diet, and many species contributed significantly more or less than expected. As predicted in hypothesis 4 individual plants with higher densities of leaves and twigs were indeed preferred, and *Acacia mellifera* plants seasonally without leaves or without fresh shoots were highly rejected. Curiously, *A. mellifera* plants with pods were rejected. Perhaps *A. mellifera* twigs carrying pods or the pods themselves are

chemically defended. The preference for leaves and fresh shoots led to significant seasonal differences in species preferences, as predicted in hypothesis 5. In summary there is partial support for optimal foraging and maximisation of the rate of energy intake as a factor in black rhino diet selection.

Snack attack and plant impact

Several of the food plant species were so highly preferred they could be labelled “ice cream species”. A few species, especially *Tetragonia arbuscula* and *Plexipus garipensis*, even appeared to be under “snack attack” – unsustainable browsing driving them towards local extinction. Hypothesis 7a (Table 6) was thus rejected. Other plant species may have been over-utilized by black rhino locally within Waterval or/and in combination with other browsers. This could apply to *Zygophyllum cf. dregeana*, which would have serious implications, as this species comprises almost a third of the rhino diet. Preliminary nutrient data suggest the reasons for the high preference for *Zygophyllum cf. dregeana* include high contents of moisture, protein, calcium and sodium as well as low fibre contents. One reason why black rhinos do not conserve their food resources as well as might have been anticipated may be that the assumption of a solitary, territorial animal is not fully met. The home ranges of adult female black rhinos are occupied by her sub-adults too and overlap with home ranges of other females and males (Tatman *et al.*, 2000; Paper 3), so conserving food plants may not benefit the individual in a communal setting.

With regards to hypothesis 7b, the picture is a mixed one. On the one hand, it does seem as if each browsing incidence is generally of a sustainable nature. Uprooting of plants and breaking of branches were relatively rare, although the aridity made *A.mellifera* branches prone to die-back upon browsing (Joubert and Eloff, 1971). Even the species with the smallest growth form was browsed only by 15 % of its canopy volume during an average incident of browsing, while larger species seem to be left long before feeding returns would be expected to diminish. For instance, only 1.4 % of an *Acacia mellifera* would be consumed

in an average browsing incidence. The reason for this conservative browsing could be 1) an evolved behaviour to allow for food plant recovery and re-growth; 2) to avoid a rapid, induced chemical defensive response by the plant after prolonged feeding (Furstenburg & Van Hoven, 1994; Bryant *et al.*, 1992) or 3) the rhinos could be limited by the rate at which they can digest the food rather than the rate of food intake (Owen-Smith, 2002).

On the other hand, freshly browsed *Acacia mellifera* plants had been browsed far more frequently in the past than other *A. mellifera*, and this may not be sustainable in the long-term. Repeated incidences of relatively light browsing do not support the notion of a long-term induced chemical defensive response in *A. mellifera*. Instead, this feeding pattern could be a profitable browsing strategy. *Acacia drepanolobium* and *Acacia nigrescens* both react to relatively heavy browsing by strong growth, which fully compensates for the browsing and is higher in nutrients as well as either is equal or lower in physical (spines) and chemical (tannins) defences (Gadd *et al.*, 2001; du Toit *et al.*, 1990). If *A. mellifera* reacts the same way the black rhinos can benefit from browsing selected shrubs lightly but frequently, because the shrubs become denser, more nutritious and less toxic. The process results in a positive feedback loop, similar to that known from grazing lawns. However, in the long term either a reduction in plant growth or competition from other plant species appears to put an end to the loop (Gadd *et al.*, 2001; du Toit *et al.*, 1990). Further data analysis suggests that the repeated browsing is the consequence of preferred feeding areas rather than preferred feeding plants (Paper 3).

The highest impact on *Acacia mellifera* occurred on plants in the 81-120 cm height class and the preferred feeding height range on *A. mellifera* was 101-150 cm. By comparing feeding height on plants exceeding 200 cm in height of only species with the vertical browse availability the actual feeding height preference was revealed - uninfluenced by species preferences and total vertical browse distribution in the study area. Species with smaller growth forms were more frequent among the highly preferred food plant species and a larger percentage of each individual was consumed in a feeding incident. The implication is that

smaller plant species, especially nutritious and/or evergreen ones, are more vulnerable and prone to over-utilization by black rhino, despite being below the preferred feeding height. This is exacerbated by smaller plants being browsed by all sizes of browsers (du Toit, 1990). Illustrating these points, in a Kenyan study on the impact of black rhinos and elephants on *Acacia drepanolobium* the highest rates of plant mortality occurred in the 0-0.5 m height class with 15 % mortality/year by rhinos and 16 % by elephants, although the damage to top shoots by rhino peaked in the 0.5-1 m class and in the >6m class for elephant (Birkett, 2002).

To improve our understanding of what levels of plant impact are sustainable we need data on growth rates of browse species under a range of different conditions. To begin to grasp the complexity of a multi-browser system we also need to study diet overlaps and niche displacement.

Conservation and monitoring

None of the food plant species in the black rhino diet have a threatened conservation status (Hilton-Taylor, 1996; Golding, 2002). Some of the food plants are absent from the species lists of three closest major conservation areas (Zietsman and Bezuidenhout, 1999) and may be endemics. However, none of the food plants are believed to be rare or endangered (*Pers.comm.*: Dr. Bezuidenhout).

To increase the number of black it is desirable to keep rhino populations at or below the density of maximum population increase and to translocate excess animals to new rhino reserves. In black rhinos this Maximum Yield Density (MYD) is at 85 to 90 % of the Ecological Carrying Capacity (ECC) due to low maximum annual rate of production of the species (Cromsigt *et al.*, 2002), while the onset of density dependence may only occur at 75 % of ECC. In fact, slowing of population growth may occur even later because a growing herbivore population may eat into a standing capital of forage and because in a large, slowly reproducing species density dependence takes a long time to translate into reproduction and

mortality (Emslie, 2001b). Population growth is therefore a late and poor indicator of MYD. Body condition and faecal nutrient contents is an earlier indicator of density dependence, while food resources are the earliest warning indicators. Adcock *et al.* (2001) therefore recommended use of selected plants as early warning indicators of rhino population growth. Monitoring of plants also allows monitoring of plant conservation targets.

It is therefore recommended that the canopy volume of the six most principal food plant species, which are all preferred as well, be monitored annually, preferably with exclusion plots as controls. In addition, the highly preferred *Hermannia spinosa*, *Tetragonia arbuscula*, *Barleria rigida* and *Indigofera heterotricha* should be monitored with exclusion plots to gauge impacts of rhinos and other browsers on the vegetation.

Conclusions

The black rhinos did exhibit some behaviour consistent with maximising rate of energy intake, but concurrently had strong specific food plant preferences to the degree of unsustainable “snack attack”. This dichotomy is not necessarily inconsistent with optimal foraging. It could rather be an indication that the rhinos are processing several currencies of optimisation simultaneously, such as energy and nutrient acquisition as well as chemical plant defence avoidance. For a better understanding of the underlying determinants of food selection analysis for a wide range of plant nutrients and defence chemicals in the available browse is therefore recommended in a variety of rhino areas.

This study revealed black rhinos select their food at many levels: species, feeding height, density of leaves and twigs, season/phenology and previous feeding. Buk (Paper 3) further documents that black rhinos indirectly select food by preference for habitats and microhabitats. Therefore, feeding preferences based on canopy volume in the park and on plant numbers along feeding trails gave different results. Feeding trials in holding pens (boma) gave results that only shared qualitative trends with studies in the wild.

While the rhinos did not seriously impact any rare and endemic plant species, they did impact other plant species significantly, including their own most important food resource. This stresses the need for monitoring key resources as early warning indicators of health of the rhinos and the vegetation.

To further our understanding and management of plant-browser interactions there is a need to not only collect data on browse availability, browse growth rates and browser competition in different settings, but also to develop rapid, yet accurate methods of doing so.

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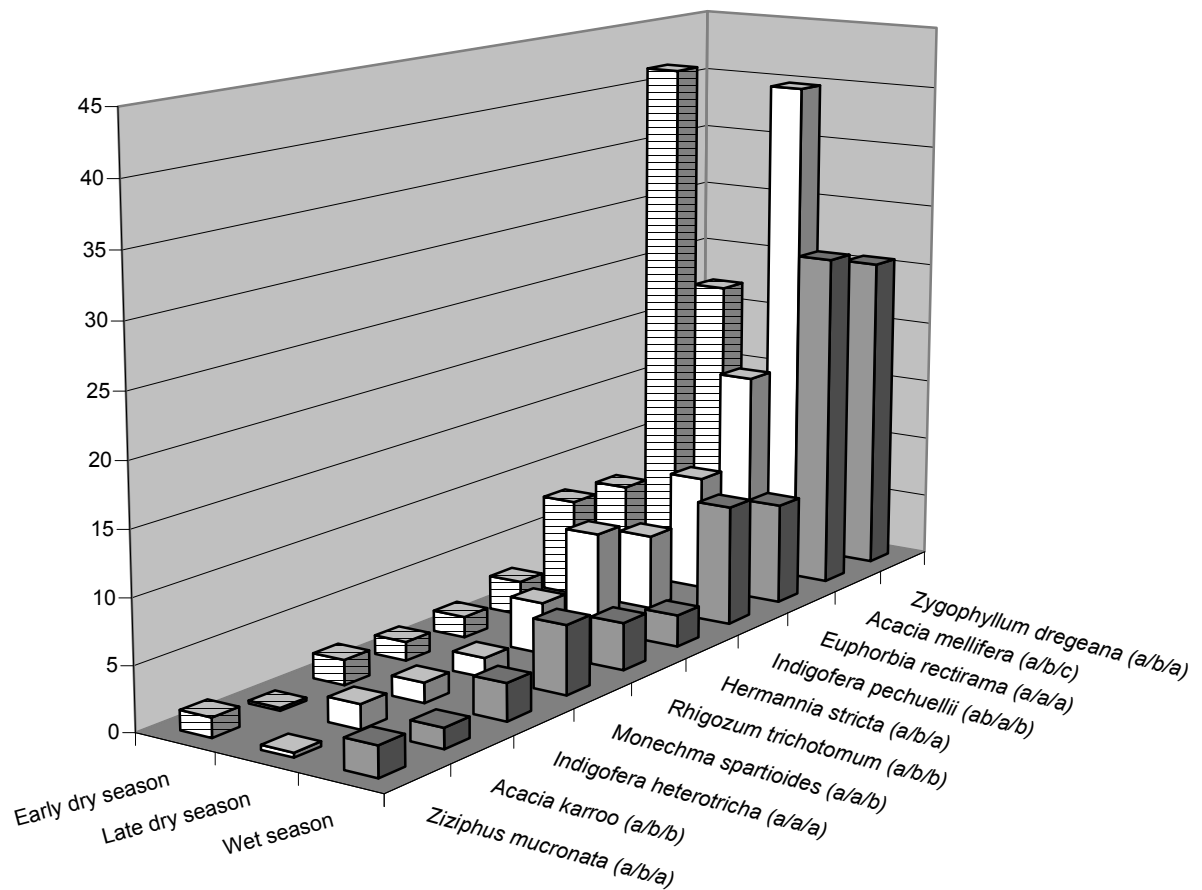


Figure 1.

The seasonal variation of the ten most important (principal) food plant species as a percentage of the total black rhino diet. Differing letters in brackets indicate significant differences between seasons ($P<0.05$, chi-square).

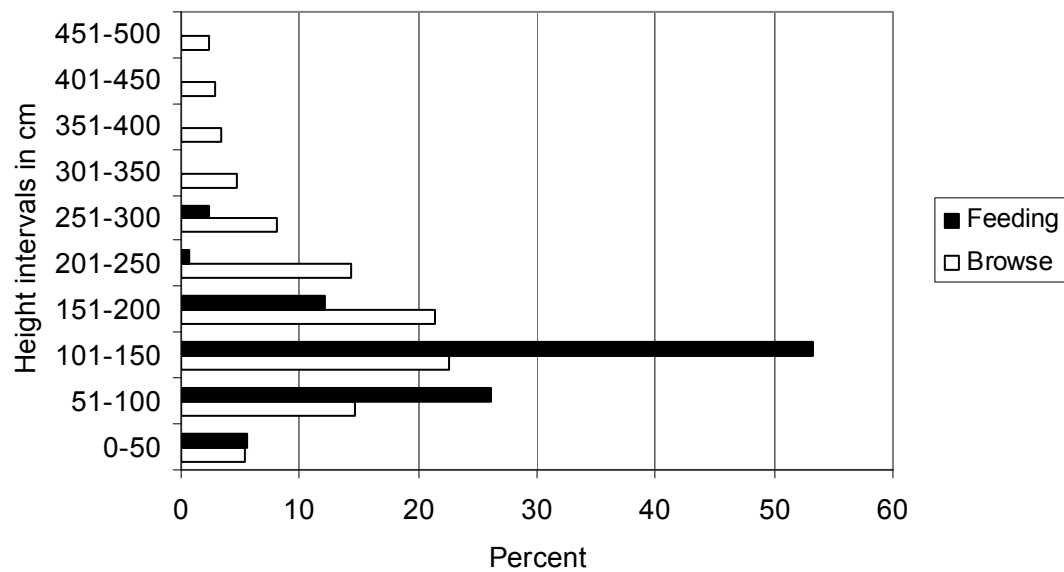


Figure 2.

Vertical distribution of feeding (n=165 bites) and canopy volume on *Acacia mellifera* in Waterval, AFNP.

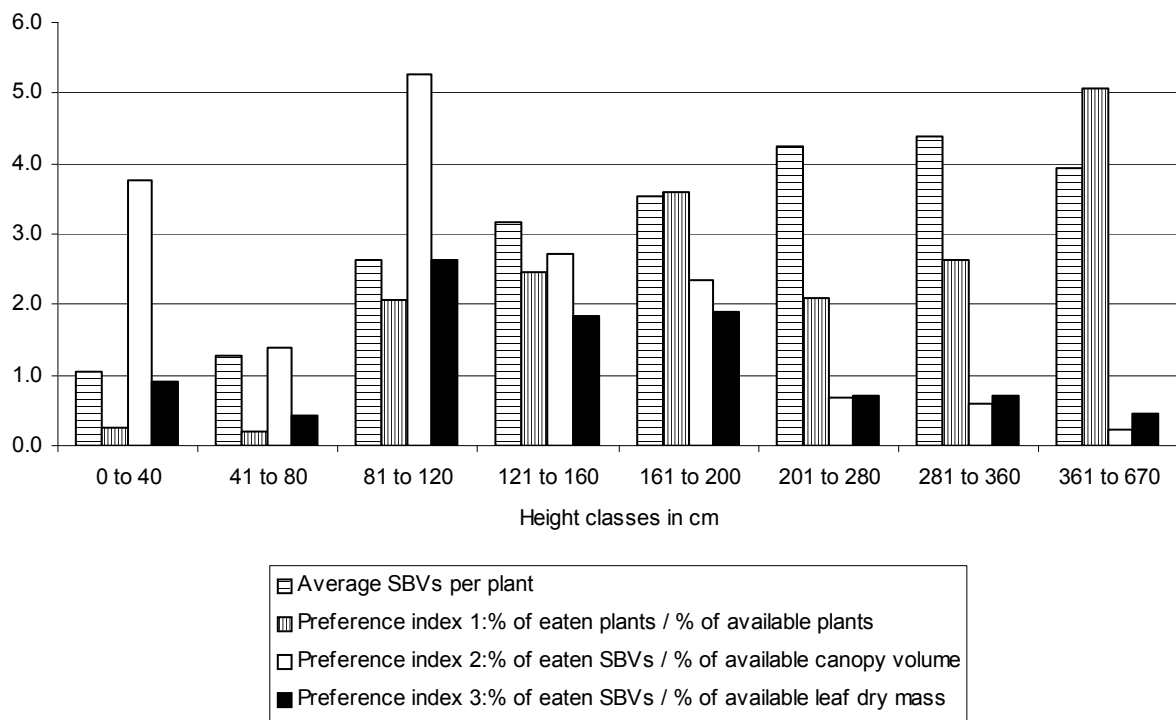


Figure 3.

Average amount of feeding and preference ratio for height classes of *Acacia mellifera* (n=179 SBVs) in Waterval, Augrabies Falls National Park.

Table 1

Diet, browse availability and diet preferences of black rhino in Waterval, Augrabies Falls National Park.

Browse species	Diet				Available browse	Diet preference			
	Mar-May	Jun-Oct	Nov-Feb	Full year	Waterval	Mar-May	Jun-Oct	Nov-Feb	Full year
	% of volume consumed				% vol	Diet / browse availability			
<i>Zygophyllum cf. dregeana</i>	21.90 ^{a3}	39.71 ^{b3}	25.57 ^{a3}	30.55 ³	1.63	13.44	24.36	15.69	18.74
<i>Acacia mellifera</i>	41.47 ^{a3}	16.25 ^b	27.06 ^{c3}	26.16 ³	15.00	2.76	1.08	1.80	1.74
<i>Euphorbia rectirama</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	16.59	5.26	10.12
<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	10.73	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	2.36 ^{a2}	1.32	1.17	1.31	0.31	2.02	1.13
<i>Lycium bosciifolium</i>	0.77 ^a	1.83 ^a	0.53 ^a	1.13 ¹	0.73	1.05	2.50	0.73	1.55
<i>Phaeoptilum spinosum</i>	0.58 ^a	1.75 ^{b1}	0.15 ^a	0.93 ¹	0.42	1.39	4.16	0.37	2.20
<i>Petalidium lucens</i>	2.33 ^{a2}	0.24 ^b	0.60 ^b	0.88	0.66	3.53	0.37	0.91	1.34
<i>Indigofera pungens</i>	1.49 ^a	0.00 ^{b2}	1.07 ^{a1}	0.73 ³	1.90	0.79	0.00	0.56	0.38
<i>Schotia afra</i>	0.69 ^{a3}	0.00 ^{b3}	1.60 ^{a3}	0.71 ³	12.70	0.05	0.00	0.13	0.06
<i>Hermannia spinosa</i>	0.73 ^{a1}	0.63 ^a	0.61 ^{a2}	0.65 ³	0.05	13.50	11.60	11.26	11.96
<i>Maytenus linearis</i>	0.07 ^{a3}	1.46 ^b	0.04 ^{a3}	0.64 ³	1.98	0.04	0.74	0.02	0.32
<i>Dyerophytum africanum</i>	0.66 ^{ab}	0.94 ^a	0.07 ^{b3}	0.58	0.83	0.79	1.13	0.09	0.70
<i>Monechma genistifolium</i>	1.49 ^{a1}	0.12 ^b	0.18 ^b	0.48	0.42	3.53	0.29	0.42	1.14
<i>Polygala cf. seminuda</i>	0.22 ^a	0.24 ^a	0.96 ^{b1}	0.48	0.34	0.64	0.72	2.83	1.40
<i>Zygophyllum microcarpum</i>	0.33	0.85	0.07 ¹	0.46	0.44	0.75	1.94	0.16	1.05
<i>Sericocoma avolans</i>	0.51	0.37	0.33	0.39	0.34	1.49	1.07	0.96	1.13
<i>Rhus pendulina</i>	0.00 ^{a3}	0.73 ^b	0.21 ^{a3}	0.38 ³	1.41	0.00	0.52	0.15	0.27
<i>Euclea psedobenus</i>	0.15 ¹	0.65	0.12 ²	0.35 ²	0.78	0.19	0.83	0.15	0.44
<i>Tetragonia arbuscula</i>	0.69 ¹	0.12	0.32 ¹	0.33 ²	0.01	98.92	17.41	45.80	47.25
<i>Grewia flava</i>	0.00	0.00	0.89 ³	0.30 ²	0.00	NA	NA	NA	NA
<i>Blepharis furcata</i>	0.00 ^a	0.49 ^b	0.11 ^{ab}	0.24	0.24	0.00	2.03	0.45	0.99
<i>Barleria rigida</i>	0.22	0.00	0.53 ¹	0.23 ¹	0.02	12.86	0.00	31.43	13.69
<i>Acacia erioloba</i>	0.29	0.00	0.43	0.22	0.32	0.91	0.00	1.34	0.67
<i>Boscia foetida</i>	0.00 ^{a2}	0.49 ^b	0.00 ^{3a}	0.20 ³	1.18	0.00	0.41	0.00	0.17
<i>Tamarix usneoides</i>	0.04 ¹	0.27	0.14 ¹	0.17 ¹	0.55	0.07	0.50	0.26	0.31
<i>Asparagus sp.</i>	0.07 ³	0.12 ³	0.18 ³	0.13 ³	3.65	0.02	0.03	0.05	0.04
<i>Aptosimum spinescens</i>	0.07	0.00	0.32 ¹	0.13	0.04	2.08	0.00	9.16	3.57
<i>Euphorbia gregaria</i>	0.22 ³	0.00 ³	0.20 ³	0.12 ³	5.15	0.04	0.00	0.04	0.02
<i>Nicotiana glauca</i>	0.00	0.00	0.36 ¹	0.12	0.00	0.00	0.00	445.28	148.43
<i>Psilocalaun absimile</i>	0.00	0.12	0.11	0.09	0.15	0.00	0.81	0.71	0.58
<i>Cleome foliosa</i>	0.07 ²	0.00 ¹	0.18 ³	0.08 ³	1.13	0.06	0.00	0.16	0.07
<i>Plexipus garipensis</i>	0.00	0.00	0.18	0.06	0.00	NA	NA	NA	NA
<i>Ceraria namaquensis</i>	0.00 ³	0.12 ¹	0.00 ³	0.05 ³	1.32	0.00	0.09	0.00	0.04
<i>Ehretia rigida</i>	0.00	0.12	0.00	0.05	0.00	NA	NA	NA	NA
<i>Suaeda fruticosa</i>	0.00 ²	0.00 ¹	0.14 ³	0.05 ³	1.02	0.00	0.00	0.14	0.05
<i>Hermannia minutiflora</i>	0.00	0.00	0.14	0.05	0.00	0.00	0.00	142.49	47.50
<i>Adenolobus garipensis</i>	0.00 ³	0.00 ³	0.14 ³	0.05 ³	4.42	0.00	0.00	0.03	0.01
<i>Thesium lineatum</i>	0.07	0.00	0.07	0.04	0.14	0.52	0.00	0.51	0.30
Unidentified	0.07	0.00	0.07	0.04	0.00	NA	NA	NA	NA
<i>Salsola sp.</i>	0.00	0.00	0.11	0.04	0.00	0.00	0.00	53.43	17.81
<i>Commiphora erythrophyllum</i>	0.00	0.00	0.11	0.04 ¹	0.21	0.00	0.00	0.51	0.17
<i>Osteospermum microcarpum</i>	0.07 ³	0.00 ¹	0.00 ³	0.02 ³	1.44	0.05	0.00	0.00	0.01
<i>Sisymbrium sparteae</i>	0.00 ³	0.00 ²	0.04 ³	0.01 ³	1.58	0.00	0.00	0.02	0.01
<i>Boscia albitrunca</i>	0.00 ³	0.00 ³	0.04 ³	0.01 ³	2.70	0.00	0.00	0.01	0.00
<i>Euclea undulata</i>	0.00	0.00	0.04	0.01	0.00	0.00	0.00	8.91	2.97
<i>Forsskaolea candida</i>	0.00 ³	0.00 ³	0.00 ³	0.00 ³	4.30	0.00	0.00	0.00	0.00
Standard Browse Volumes	1372.00	820.75	2807.25	5000.00					
Trails or Plots	25	18	40	83	58				
Plants				3049	>4640				

Significant seasonal differences ($P < 0.05$) in feeding are indicated by different letters, while significant differences between observed and expected feeding based on availability are indicated by ¹ ($P < 0.05$), ² ($P < 0.001$) or ³ ($P < 0.0001$).

Table 2.

Comparison of three different measures of diet preferences by black rhino. *P* signifies whether the preference differs significantly from neutral (1.0).

Measure of species preference based on									
Free ranging rhinos and canopy volume in the park			Free ranging rhinos and plant numbers on feeding trails			Rhinos in holding pens and weight of eaten food			Rank
% consumed browse volumes/ % canopy volume in reserve			% browse volumes/ % of plants along feeding trail			% mass eaten / % mass presented			
Species		<i>p</i>	Species		<i>p</i>	Species		<i>p</i>	
<i>Tetragonia arbuscula</i>	47.25	<0.001	<i>Acacia karroo</i>	3.86	0.3991	<i>Zygophyllum dregeana</i>	2.57	<0.0001	1
<i>Zygophyllum dregeana</i>	18.74	<0.0001	<i>Tetragonia arbuscula</i>	3.31	0.7018	<i>Ziziphus mucronata</i>	1.71	0.0304	2
<i>Barleria rigida</i>	13.69	<0.05	<i>Lycium bosciifolium</i>	3.31	0.6201	<i>Euphorbia rectirama</i>	1.70	<0.0001	3
<i>Hermannia spinosa</i>	11.96	<0.0001	<i>Barleria rigida</i>	2.48	0.8360	<i>Monechma spartioides</i>	1.69	0.1350	4
<i>Hermannia stricta</i>	10.12	<0.0001	<i>Euphorbia rectirama.</i>	2.21	0.0002	<i>Acacia mellifera</i>	1.13	0.2499	5
<i>Indigofera heterotricha</i>	7.82	<0.0001	<i>Acacia mellifera</i>	2.02	<0.0001	<i>Rhus pendulina</i>	1.07	0.0942	6
<i>Aptosimum spinescens</i>	3.57	>0.05	<i>Indigofera pechuellii</i>	1.89	0.0046	<i>Diospyros lycioides</i>	0.75	0.0968	7
<i>Rhigozum trichotomum</i>	3.10	<0.001	<i>Hermannia stricta</i>	1.79	0.0196	<i>Acacia karroo</i>	0.58	<0.0001	8
<i>Indigofera pechuellii</i>	2.94	<0.0001	<i>Petalidium lucens</i>	1.71	0.4077	<i>Schotia afra</i>	0.33	<0.0001	9
<i>Euphorbia rectirama</i>	2.91	<0.0001	<i>Plexipus garipensis</i>	1.65	0.8529				10
<i>Phaeoptilum spinosum</i>	2.20	<0.05	<i>Phaeoptilum spinosum</i>	1.24	0.9287				11
<i>Acacia mellifera</i>	1.74	<0.0001	<i>Rhigozum trichotomum</i>	1.17	0.7997				12
<i>Lycium bosciifolium</i>	1.55	<0.05	<i>Zygophyllum dregeana</i>	1.13	0.0005				13

Table 3.

Fresh feeding on *Acacia mellifera* shrubs in relation to their leaf and twig densities compared to availability in 58 belt transect plots.

Twig density	% of eaten plants / % of plants in plots	SBVs / eaten plants	% of SBVs / % of plants in plots	Plants in plots	Eaten plants	SBVs
High	1.09	4.47	1.32	39	38	170
Medium	0.98	3.85	1.01	145	127	489
Low	1.10	3.13	0.92	75	74	232
Very low	0.29	2.33	0.20	11	3	7
Total				270	242	898
P (chi ²)	0.2344	0.3389	0.0006			
Leaf density	% of eaten plants / % of plants in plots	SBVs / eaten plants	% of SBVs / % of plants in plots	Plants in plots	Eaten plants	SBVs
High	0.53	4.14	0.58	30	14	58
Medium	1.33	3.84	1.37	172	203	780
Low	0.41	2.48	0.27	61	22	55
Very low	0.00	-	0.00	6	0	0
Total				269	239	893
P (chi ²)	<0.0001	0.2427	<0.0001			

Table 4.

The average number of standard bite volumes (SBVs) per *Acacia mellifera* freshly eaten by black rhinos along their feeding trails in relation to the seasonal presence or absence of leaves, fresh shoots and seedpods in Waterval, AFNP.

Presence	Leaves		Fresh shoots		Seedpods	
	Available plants	SBVs / plant	Available plants	SBVs / plant	Available plants	SBVs / plant
Present	134	0.80	5	5.00	31	0.39
Absent	21	0.05	123	0.03	96	1.00
P (chi ²)		0.0006		<0.0001		0.0140

Table 5.

The impact of browsing on individual plants of a range of species of differing sizes.

Plant species	Density Plants/ha	Average canopy volume Cubic metres/plant	Feeding rate SBVs/plant	Average browse impact % of available volume eaten
<i>Indigofera pungens</i>	354.0	0.06	1.12	14.9
<i>Zygophyllum dregeana</i>	219.5	0.07	1.13	12.9
<i>Indigofera pechuellii</i>	257.2	0.19	1.34	5.6
<i>Monechma spartioides</i>	295.1	0.21	1.40	5.3
<i>Euphorbia rectirama</i>	27.0	1.40	2.05	1.2
<i>Acacia mellifera</i>	80.7	1.88	3.31	1.4
<i>Maytenus linearis</i>	5.4	3.33	1.14	0.27
<i>Schotia afra</i>	8.4	14.56	4.54	0.25
<i>Acacia karroo</i>	1.8	21.89	2.42	0.09

Table 6. Overview of the hypotheses and the outcome of their testing.

Hypothesis			Result	Significance	Comment	
1	Within a plant species individual plants are browsed in proportion to their available browse volume in terms of	a) intensity	Yes	$p<0.0015$	Rs=0.24	
		b) frequency	Yes	$p<0.0189$	Rs=0.17	
2	The amount of browsing on individual plants of a range of species is proportional with their average available browse volume		Yes	$p=0.0159$	Rs=0.77	
3	Browse species occur in black rhino diet in proportion to their	a) density	No	$p=0.1615$	Rs=0.48	
		b) canopy volume within feeding height	Yes	$p=0.0072$	Rs=0.37	
4	Within a species individual plants with high density of	a) twigs are browsed more in terms of	1) intensity	No	$p=0.3389$	
			2) frequency	No	$p=0.2344$	
			3) combined	Yes	$p=0.0006$	
		b) leaves are browsed more in terms of	1) intensity	No	$p=0.2427$	
			2) frequency	Yes	$p<0.0001$	
			3) combined	Yes	$p<0.0001$	
5	There are significant seasonal differences in the diet of black rhino		Yes	$p=0.0159$		
6	a) The diversity of the black rhino diet is higher than that of the available browse		No	$p<0.001$	The diet is significantly <u>less</u> diverse than the available browse	
	b) The equitability of black rhino diet is higher than that of the availability of the eaten plant species		No	$p<0.001$	The diet is significantly <u>less</u> equitable than the eaten browse	
7	Black rhino browsing is sustainable on	a) all species	No		A few species are browsed heavily	
		b) individual	(Yes)		Feeding is low intensity, but high frequency – see discussion	

Photos on the following page:

Top left: A black rhino nibbling on *Acacia karroo*

Top right: *Euphorbia rectirama*

Second row, left: *Acacia mellifera*

Second row, right: Loading a black rhino into the holding pens (boma) where the captive feeding data was collected

Third row, left: One bite freshly removed by a black rhino from *Ziziphus mucronata*

Third row, center: *Zygophyllum cf. dregeana*

Third row, right: A twig of *Acacia mellifera* with fresh leaves and a beetle

Bottom row, left: An exceptionally clear black rhino trail

Bottom row, center: *Indigofera pechuellii*

Bottom row, right: Measuring plant dimensions for estimates of available canopy volume

